University of Groningen

A historical ecology of two closely related gull species (Laridae)

Camphuijsen, Cornelis Jan

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2013

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Camphuijsen, C. J. (2013). *A historical ecology of two closely related gull species (Laridae): Multiple adaptations to a man-made environment*. [s.n.].

Copyright
Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the “Taverne” license. More information can be found on the University of Groningen website: https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment.

Take-down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): http://www.rug.nl/research/portal. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Download date: 04-06-2022

Colofon

Cover illustration © Bas Teunis 2012 - displaying Lesser Black-backed Gulls *Larus fuscus*

Cover design printed version Dick Visser, RUG, Groningen, **pdf version** Kees Camphuysen

Printed by Grafische Industrie De Marne, Leens

Preferred citation: Camphuysen C.J. 2013. A historical ecology of two closely related gull species (Laridae): multiple adaptations to a man-made environment. Ph.D.-thesis, Univ. Groningen, Groningen.

Full colour PDF version: A full colour PDF version of the entire thesis (separate files for each chapter and appendices as well as a complete PDF) is available by the author:

kees.camphuysen@nioz.nl

or via the website

http://home.planet.nl/~camphuys/home.html

ISBN/EAN: 978-90-9027538-3

RIJKSUNIVERSITEIT GRONINGEN

A HISTORICAL ECOLOGY OF TWO CLOSELY RELATED GULL SPECIES (LARIDAE)

MULTIPLE ADAPTATIONS TO A MAN-MADE ENVIRONMENT

Proefschrift

ter verkrijging van het doctoraat in de
Wiskunde en Natuurwetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de
Rector Magnificus, dr. E. Sterken,
in het openbaar te verdedigen op
vrijdag 21 juni 2013
om 12:45 uur

door
Cornelis Jan Camphuijsen

geboren op 25 mei 1959
te Amsterdam

Promotor : Prof. dr. T. Piersma

Copromotor : Dr. H.W. van der Veer

Beoordelingscommissie : Prof. dr. C. Both
Regius Prof. dr. P. Monaghan
Prof. dr. C. Perrins

Contents

Boxed information and summarized papers

Summarised papers

Boxed information

English summary

- In this thesis, results are presented of a comparative study of the foraging ecology, breeding biology, foraging distribution, and population dynamics of two sympatric large gulls, the European Herring Gull *Larus argentatus* (**HG**) and the Lesser Black-backed Gull *Larus fuscus* (**LBBG**), breeding at Texel in the western Wadden Sea. The work aimed at understanding recent, contrasting population trends: a decline in HGs and a continuing increase in LBBGs. This was evaluated using three hypotheses: (1) HGs being outcompeted by a newcomer, the LBBG, (2) LBBGs profiting from an empty niche; population trends unrelated, or (3) overwinter survival is responsible for differences in demographic trends (Chapter 1).
- The relaxation of the Victorian exploitation with its ruthless destruction of wildlife is one of the main factors explaining the rapid growth of many populations of (sea-)birds in the 20th century, large gulls included. Only two species of gulls nested in The Netherlands around 1900, while 10 species occur as breeding birds today. Gull breeding populations reached unprecedented levels in the late 20th/early 21st century: HGs peaked in the 1980s, LBBGs around 2005. Multiple causal factors have been at work simultaneously to effectuate these population changes. Four episodes of major change were identified: (1) early measures of conservation in the early 20th century, (2) a resumption of persecution in the 1930s to 1960s, (3) a relaxation of persecution coinciding with a general recognition of the effects of chemical pollution in a period when anthropogenic (unnatural) resources became very large, and (4) population declines or reduced growth in the late 20th century when landfills were closed and when fisheries discards started to decline (App. 2).
- Contrary to expectations, the reproductive success of LBBGs was very low, particularly as a result of high levels of chick predation (cannibalism). The breeding success of HGs was consistently higher than that of LBBGs and levels of chick predation were much lower (App. 3). Productivity indices for both species were poor-moderate (<50% of the eggs laid produced fledglings). LBBGs were clearly more marine orientated than HGs and the diet of the former was dominated by discarded fish species. HGs utilised intertidal resources extensively and added fish prey to their diet during chick care (Chapter 2).
- Cyclic fluctuations in chick growth were found in both species: similar drops and gains in body mass, indicating alternating periods of low and more favourable provisioning. Body mass increments of chicks were significantly reduced in weekends and enhanced during the week. A weekly rhythm in commercial fishing effort matched these patterns exactly (Chapter 3).
- With a supplementary feeding experiment, it was investigated if parents would increase the time devoted to chick defence when the needs for chicks to feed were lowered artificially. To measure nest attendance, adults were instrumented with radio-transmitters. The results were ambiguous: nest attendance of supplemented pairs was enhanced in one study plot, but reduced in another. Although supplemented birds fledged more young than controls, the difference was not significant. Chick predation and fledging success were significantly different between study plots. Autocatalytic interactions and collective, site-specific differences in the ability to defend chicks from attacking adults may explain the results (Chapter 4).
- The timing of first returns, prospecting, egg-laying, hatching, chick care, when the breeding areas were abandoned in autumn, and changes therein over the years was examined in LBBGs. The birds were geographically segregated by age throughout their annual cycle and southward movements after the breeding season had a different start in immatures (early), adults (intermediate) and juveniles (late). Juveniles wintered furthest to the south. The timing of spring migration was early in adults, intermediate in immatures, and late in juveniles. There was no evidence that one of the sexes returned earlier and prospecting breeders in the colony were synchronised with Herring Gulls. The seasonality in fisheries effort could not explain the onset of breeding, but an annual rise in effort in June coincided with the earliest phase of chick care. A comparison between older (<2000) and more recent data (≥2000) indicated an overall shortening of the time spent at breeding latitudes by one month (Chapter 5).
- HGs colour-ringed as chicks (n= 3124) in 12 colonies in 1986-88 yielded 86,247 ring-readings on 1358 locations by 868 observers. One-fifth of all sightings originated areas within a radius of 5km from the ringing site. Only 0.8% were reported at over 300km from the natal colony (10.7% at 6-10km, 8.9% at 11-25km, 17.7% at 26-50km, 22.9% at 51-100km, 14.4% at 101-200km, and 4.1% at 201- 300km). Colony-specific differences in travelling distance, dispersal rate, and direction of movements suggested a grouping of colonies in three: (1) eastern Wadden Sea islands (Rottumeroog-Vlieland), with higher dispersal rates and winter movements mostly south-west to south-east, (2) Texel and 4 mainland coast colonies (Callantsoog-Wassenaar), with a shorter mean range and movements mostly to the south, and (3) colonies in the Delta area (Europoort- Saeftinghe) with short range movements and winter dispersal in many directions. Adults reached their greatest mean distances on average one month earlier than

immatures, which in turn arrived one month earlier than juveniles. In spring, adults moved on two months ahead of immatures, which in turn moved earlier and closer to the natal home-range than juveniles. Herring Gulls breeding in The Netherlands occupied a mid-position between dispersive and sedentary tendencies (Chapter 6).

- In HGs, a mean apparent annual adult survival was calculated of 79% in females and 86% in males. Additive year effects provided highest model support in LBBGs, in which apparent survival for both sexes combined varied between 81% and 100% (mean ≈91%) (Chapter 7). These findings, in combination with estimated return rates of recruits replacing adults that died (App. 6), led to estimated of a balance per annum (BPA) of -0.08 [i.e. population growth rate lambda = 0.92) in LBBGs and -0.23 (lambda = 0.77)in HGs (Chapter 2).
- Tracking studies revealed exceptionally long or distant foraging trips in actively breeding LBBGs. The characteristics, frequency, and triggers of unusual trips were evaluated. Exceptionally long and distant trips occurred irregularly but annually, in many individual birds and in all phases of breeding. Additional time for individual maintenance rather than extra effort in chick provisioning was suggested as an explanation. Exceptional trips were relatively rare when the chicks were still young and highly vulnerable (<10d of age). The reproductive success in birds that performed exceptional trips was not compromised (Chapter 8).
- Inter-pair dietary specialisations were studied in HGs and related to fecundity parameters. The overall dietary spectrum and levels and incidence of dietary specialisations changed when energetic demands increased during chick care. Prior to hatching, most pairs focussed on bivalve prey, but 25% of the pairs had distinct dietary biases. During chick care, both chick growth and fledging rates were positively correlated with the amount of fish prey provided. Prey spectra diversified overall during chick care and fewer specialists were detected. Particularly low chick growth rates were found in pairs that had a dietary bias towards crustacean prey (Chapter 9).
- The GPS tracking data from 34 LBBGs encompassing 2199 foraging trips combined with dietary information and reproductive status showed that there are sexually distinct foraging strategies, that are maintained throughout incubation and chick-care. The marginally larger males travelled farther from the colony than females, spent more time in the North Sea. Males fed mostly on fisheries discards at offshore trawlers with few alternative resources nearby. Females foraged predominantly on land or in the Wadden Sea, where they had multiple foraging options including nearshore shrimpers. Foraging range, trip duration and the proportion of time at sea increased with wing length. Our findings did not support the usual inference that sexual segregation is mediated primarily by differences in competitive strength (i.e. differences in size) as both sexes foraged in competitive environments around fishing vessels. Females, accessed a wider variety of resources and a broad prey spectrum, by exploring a whole suite of foraging opportunities and habitats nearer the colony (Chapter 10).
- The distribution and feeding range of HGs and LBBGs were assessed, using ship-based surveys in the southern North Sea. Both species occurred in association with commercial fishing vessels and their distribution is described in relation to distance to the coast and distance to the colonies. The feeding range of LBBGs (95% of all birds within 135 km of the colony) was considerably larger than that of HGs (95% within 54 km), a difference that could not be explained by differences in flight capacities. Neither the vulnerability to robbery indices, nor the feeding success indices of both species supported earlier suggestions that LBBGs have outcompeted HGs at fishing vessels. The feeding range of LBBGs could not solely be explained by a general avoidance of HGs near the coast, nor by fisheries further offshore in comparison with the coastal zone (Chapter 11).
- Adult LBBGs were tracked during the breeding season using a high resolution GPS. The study revealed intriguing yet infrequent behavioural patterns indicating birds sat on the sea surface, drifting passively with the tidal current, for several hours: resting at sea rather than in the breeding colony. It is assumed that the drifting birds were resting (asleep), and possibly, a good rest, away from the colony, is essential for individual birds (Chapter 12).
- Because the designation of marine protected areas (MPAs) for seabirds should bear relevance to the ecological importance of these regions, simple presence/absence information of the occurrence at sea is not sufficiently accurate and could even be misleading. Large amounts of data have been collected to assess distribution patterns of seabirds around the world. Ship-based surveys and sensor data (tracking studies) from instruments attached to individual birds were used to evaluate recently developed protocols to facilitate spatio-temporal quantification of space use and identification of behaviour in the context of MPA designations. Limitations of traditional techniques and exciting possibilities of new protocols and the latest generations of electronic devices attached to seabirds are presented. The advanced approaches in

data collection and spatial analysis is expected to enhance our understanding of offshore seabird distribution *and* their activities, which can guide the designation of marine protected areas (Chapter 13).

- The occurrence of mammalian prey in the diet of both gulls was investigated to quantify the predation on mammals, comparing gulls breeding in coastal and inland colonies. Coastal nesting specialised birds and a majority of individuals in an inland colony were found to commonly feed on mammalian prey. Most prey were obtained on inland fields, perhaps during ploughing or similar activities of farmers, some may have been captured within the colonies, and some will have been the result of scavenging at roadsides. Since gulls breeding along the coast increasingly suffer from shortages of discarded marine fish during chick-rearing, inland breeding may become more frequent and gulls are expected to increasingly focus on alternative foraging habitats and prey species, mammals included (Chapter 14).
- All relevant parameters describing the breeding success are summarised in App 3. Assuming that fluctuations in resources during breeding would affect fecundity, the fact that reproductive success varied independently between the two species is interpreted as an indication that key resources were different. In fact none of the key parameters expressing breeding success, perhaps with the exception of chick depredation, were somehow correlated between the two gulls (Chapter 15).
- Evidence is provided for resource partitioning between and within the two species: LBBGs were numerically dominating in continental mainland foraging sites, within the colony, inland at Texel, and offshore on the North Sea. Male LBBGs utilised offshore resources, females foraged closer to the colony. HGs numerically dominated over LBBGs in all intertidal areas, including the deeper gullies (subtidal areas) of the Wadden Sea. At sea, with increasing distance to the North Sea shoreline HGs were increasingly outnumbered by LBBGs. If the key habitats are seen as resources, the numerical abundance of each species could seen as a proxy for resource use. The species' exploitation strategies are apparently discretely segregated rather than opportunistic. Each of the key habitats (or resources), are shared with different assemblages of competitors targeting the same or similar prey (guilds). Within these guilds dominance hierarchies become established and in most of the scenarios, HGs and LBBGs are among the largest (most powerful) species. The enormous variety of prey items require highly different skills and in each of these resources more specialised and efficient competitors are encountered (Chapter 15).
- The at-sea studies gave an important insight in the abundance and distribution at sea. Foraging behaviour and prey choices were studied in a competitive setting: both species were confronted with the same prey in experiments with different numbers of competitors, around the North Sea and through the year. HGs were the more successful foragers at trawlers (competitive strength). The abundant HGs at sea in winter are probably wintering birds from Nordic colonies rather than local residents. In summer, LBBGs become numerically dominant at some distance away from the coast. It is doubtful of HGs ever foraged at distant trawlers, and fish prey delivered to the chicks today originated from different fishing vessels than that of most LBBGs (App 7, Chapter 15).
- It is obvious that the breeding populations of both species are currently not flourishing. Even in HGs, where the reproductive success is often reasonably high, the low survival of adults, immatures and fledglings and the low recruitment rates lead to a negative BPA. The near-absence of even only prospecting "recruits" and nesting birds in immature plumage at Texel suggests that these colonies are currently "ageing" (Chapter 15).
- The recent population trends of HGs and LBBGs breeding in the Western Wadden Sea fluctuate more or less independently, even though the birds do compete for certain resources (no support for hypothesis #1). HGs currently have more favourable breeding results, but relatively poorer winter survival and recruitment rates. It is concluded that winter mortality may have increased as a result from reduced access to open landfill areas and intensified intra-specific competition within their wintering range (supporting hypothesis #3) (Chapter 15).
- LBBGs have profited from a fishing fleet modernisation in the 1960s: a type of fisheries that has generates vast amounts of discards, but that peaked in the late 1980s and early 1990s. This must have been "vacant niche" (supporting hypothesis #2). The problems that LBBGs currently face at Texel (low breeding success, high levels of cannibalism), are signs of regular food shortages during breeding. Recent reductions in fishing effort will have led to reductions in the amount of discards produced at sea; a key resource for this species. Further declines in discards as a resource can be foreseen because the European Commission proposed a complete ban on discarding, to be effectuated sometime between now and 2019 (Chapter 15).

Nederlandse samenvatting

- Dit proefschrift is het resultaat van een vergelijkend onderzoek naar de broedbiologie, voedselecologie, foerageergebieden en populatiedynamica van twee grote meeuwen, de Zilvermeeuw (**ZM**) en de Kleine Mantelmeeuw (**KLM**), in de westelijke Waddenzee. Het onderzoek werd uitgevoerd in een grote, gemengde broedkolonie op Texel. Het werk is opgezet zodat recente, per soort verschillende populatietrends kunnen worden begrepen: een afname in het aantal nestelende ZM, terwijl het aantal broedende KLM verder toenam. Uitgangspunt waren drie hypothesen: (1) ZM werd verdreven van de beste voedselbronnen door de nieuwkomer, de KLM; (2) KLM profiteerde van een "lege niche"; de populatietrends van beide soorten zijn onafhankelijk van elkaar; (3) de oorzaak van verschillende demografische trends moet in overwinteringsgebieden gezocht worden en gezien de gescheiden overwintering is er geen verband tussen de populatietrends (Hfdst. 1).
- Beschermende maatregelen, na een lange periode van exploitatie en verstoring van kolonies in de Victoriaanse tijd (en daarvoor), veroorzaakten een sterke groei van zeevogelpopulaties in de 20^{e} eeuw in Europa. Ook meeuwen hebben van deze bescherming geprofiteerd. Rond 1900 broedden er slechts twee meeuwensoorten in Nederland, tegenwoordig zijn dat er tien. Veel populaties kenden een periode van snelle groei na een aarzelend begin, maar dat werd gevolgd door een stabilisering of een afname van het aantal broedparen. ZM piekten in de jaren tachtig, KLM rond 2005. Vier perioden van verandering worden beschreven: (1) de eerste beschermende maatregelen in het begin van de 20^{e} eeuw, (2) een herziening van de plannen gevolgd door een intensieve bestrijding van broedende meeuwen tussen 1930 and 1960, (3) het stopzetten van de bestrijding, samenvallend met een toegenomen milieubewustzijn, in een periode waarin meeuwen profiteerden van een verruimd onnatuurlijk voedselaanbod (met name visafval en vuilstorts), en (4) een stagnatie van de groei van populaties in een periode waarin veel vuilstortplaatsen gesloten werden en de vissersvloot kromp (App 2).
- Tegen de verwachting in bleek het broedsucces van KLM lager dan dat van ZM, vooral als gevolg van kuikenpredatie (kannibalisme). Het broedsucces van ZM was vrijwel elk jaar duidelijk hoger en de kuikenpredatie was minder (App. 3). De productiviteitsindices voor beide soorten varieerden van "slecht" tot "matig" (<50% van de gelegde eieren leverde een uitgevlogen jong op). KLM waren duidelijk meer de open zee georiënteerd dan ZM en hun voedsel bestond hoofdzakelijk uit overboord gezette, ondermaatse vis. ZM foerageerden vooral in de getijzone op schelpdieren, maar de succesvolste paren voerden vis aan in de kuikenfase (Hfdst. 2).
- Bij beide soorten werd een duidelijke ritmiek gevonden in de ontwikkeling van opgroeiende jongen: collectieve toe- en afname in lichaamsgewicht, als gevolg van een wisselende aanvoer van voedsel. De groei van kuikens liep terug in weekends, maar nam snel toe in het midden van de week. Het wekelijkse patroon past precies op de wekelijkse ritmiek in aanwezigheid van vissersvloten op zee rond de kolonies (Hfdst. 3).
- Om te zien of oudervogels meer tijd aan de verdediging van hun jongen zouden besteden wanneer die kunstmatig zouden worden bijgevoerd, werd een bijvoerexperiment opgezet. De aanwezigheid van volwassen vogels werd gemeten met behulp van radiozenders. De resultaten waren niet eenduidig en opvallend verschillend tussen de beide studiegebieden. Nesten die werden bijgevoerd leverden wel meer uitvliegende jongen op, maar het verschil met controleparen was niet significant. Kuikenpredatie en uitvliegsucces verschilde vooral sterk tussen de beide studiegebieden, maar minder sterk tussen bijgevoerde of niet-bijgevoerde paren. In beide gebieden werden collectief verschillende reacties van adulte vogels waargenomen in perioden van voedselschaarste, waardoor de kuikens in het ene gebied op grote schaal doodgepikt werden, terwijl zij elders vrijwel allemaal gespaard bleven (Hfdst. 4).
- Veranderingen in de terugkeer op de broedplaats, het tijdstip van leggen en de uitkomst van eieren, kuikenzorg en het vertrek uit de broedgebieden werd onderzocht bij KLM. Vogels van verschillende leeftijd leefden geografisch gescheiden. De trek naar het zuiden begon met onvolwassen vogels, gevolgd door adulten en tenslotte juvenielen. De jongste vogels overwinterden ook het verst weg. In het voorjaar trokken adulte vogels eerst, daarna onvolwassen en tenslotte ook juveniele dieren naar het noorden. Er werd geen verschil tussen de geslachten gevonden en KLM kwam min of meer tegelijk met ZM aan in de broedgebieden. Er was geen verband tussen het begin van de eileg en seizoensvariaties in visserijinspanning (als proxy van voedselaanbod) rond de kolonie. Een vergelijking van historische (<2000) en meer recente aflezingen (≥2000) liet zien dat de totale tijd die KLM doorbrengen in de broedgebieden is verkort (Hfdst. 5).
- Nederlandse ZM zijn standvogels of trekvogels over een korte afstand, met overwinteringsgebieden in Zuid Nederland, België en Noord-Frankrijk. In totaal 3124 in 12 kolonies als kuiken gekleurringde ZM (1986-88)

leverden 86.247 aflezingen op van 868 waarnemers op 1358 verschillende locaties. Eén vijfde van alle aflezingen was binnen 5km van de ringplaats. Slechts 1% werd gemeld op meer dan 300km van de geboortekolonie (11% op 6-10km, 9% op 11-25km, 18% op 26-50km, 23% op 51-100km, 14% op 101-200km, en 4% op 201-300km). Koloniespecifieke verschillen in afstand, mate van dispersie en de richting van trekbewegingen leidden tot een groepering van kolonies: (1) oostelijke Waddeneilanden (Rottumeroog-Vlieland), hoge dispersie, verplaatsingen vooral in ZW-ZO richting, (2) Texel en 4 kolonies op het vasteland (Callantsoog-Wassenaar), kortere trekwegen vooral naar het zuiden, en (3) kolonies in het Deltagebied (Europoort-Saeftinghe), met een korte afstandstrek alle kanten op. Adulten bereikten de grootste afstand tot de kolonie gemiddeld een maand eerder dan onvolwassen vogels, die op hun beurt een maand eerder arriveerden dan juvenielen. In het voorjaar vertrokken adulte vogels twee maanden eerder dan onvolwassen exemplaren, die weer eerder vertrokken en verder naar het noorden doordrongen dan de jongste categorie (Hfdst. 6).

- Bij ZM werd een schijnbare adulte overleving berekend van gemiddeld 79% bij wijfjes en 86% bij mannetjes. Niet het geslacht maar verschillen tussen jaren gaven de sterkste ondersteuning voor overlevingsmodellen van KLM, waarbij de overleving wisselde van 81%-100% (gemiddeld ≈91%) (Hfdst. 7). Deze resultaten, gecombineerd met geschatte terugkeerpercentages van rekruten, die gestorven adulte vogels moeten compenseren (App. 6), leidden tot een geschatte jaarbalans (*BPA*) van -0.08 bij KLM en -0.23 bij ZM [populatietoename lambda = 0.92 bij KLM, 0.77 bij ZM] (Hfdst. 2).
- GPS loggers op de rug van KLM lieten zien dat actieve broedvogels soms enorm lange of verre voedselvluchten ondernamen. Uitzonderlijk lange of verre voedselvluchten kwamen elk jaar, maar onregelmatig voor bij veel verschillende vogels, in verschillende fasen van de broedcyclus. Vermoedelijk ging het hierbij om aansterking of verzorging van adulte vogels zelf en niet om een bijzondere voedselaanvoer voor de jongen. Uitzonderlijk lange trips kwamen zelden voor als de jongen nog klein waren (<10d oud). Het broedsucces van vogels die hun jongen soms lang in de steek lieten was niet minder dan dat van andere paren (Hfdst. 8).
- Bij ZM werd bekeken hoe de prooikeuze van afzonderlijke paren onderling verschilde en wat dat voor effect had op het broedsucces. Zowel de breedte van het voedselspectrum als het voorkomen van voedselspecialisten veranderde wanneer de energiebehoefte toenam in de kuikenfase. Voordat de eieren uitkwamen voerden de meeste ZM vrijwel alleen schelpdieren aan, maar 25% van de paren was min of meer gespecialiseerd op een bijzondere voedselbron. Kuikengroei en uitvliegpercentages waren positief gecorreleerd aan de hoeveelheid afgeleverde vis in de kuikenfase. Het prooienspectrum verbreedde zich dan en er waren minder voedselspecialisaties herkenbaar. Bij ZM die bijzonder veel krabben aanvoerden voor de jongen werden relatief lage groeisnelheden bij de kuikens gemeten (Hfdst. 9).
- Uit een analyse van 2199 voedselvluchten van 34 KLM die met GPS loggers waren uitgerust bleek dat de beide geslachten verschillende foerageergebieden bezochten. De maar nauwelijks grotere mannetjes foerageerden voornamelijk op de Noordzee, terwijl wijfjes de meeste tijd in de onmiddellijke omgeving van de kolonie doorbrachten. Mannetjes foerageerden hoofdzakelijk bij treilers op grote afstand tot de kust, met weinig alternatieve foerageermogelijkheden in de directe omgeving. Wijfjes foerageerden veel op het land, in de kustzone en in de Waddenzee, waar zij veel verschillende mogelijkheden in een klein zoekgebied ter beschikking hadden, waaronder ook vissersschepen. Er werd een positief verband gevonden tussen de grootte van de dieren (vleugellengte) en de tijdsduur die op open zee werd doorgebracht. Het is onwaarschijnlijk dat alleen competitief vermogen (lichaamsgrootte) tot dit verschil tussen de geslachten aanleiding gaf. Beide geslachten foerageerden bij vissersschepen en de kleinere wijfjes hadden te maken met competitief sterkere Zilvermeeuwen rond garnalenvissers (Hfdst. 10).
- De foerageergebieden op de Noordzee werden in kaart gebracht door tellingen vanaf schepen. Het bereik van KLM (95% binnen 135 km vanaf de kolonies) was aanzienlijk groter dan dat van ZM (95% binnen 54 km), een verschil dat niet kon worden verklaard door verschillen in vliegvermogen. Beide soorten werden in grote aantallen rond commerciële vissersschepen aangetroffen. Noch soortspecifieke verschillen in gevoeligheid voor kleptoparasitisme, noch verschillen in foerageersucces ondersteunden vermoedens dat ZM door KLM van vissersschepen verdreven zouden zijn. Omgekeerd kon het bereik van de KLM niet alleen worden verklaard door de afwezigheid van ZM of de aanwezigheid van visserij op zee (Hfdst. 11).
- Volwassen KLM, gevolgd met GPS loggers, bleken vaak urenlang op zee te drijven, langzaam verdriftend in de richting van de overheersende stroming en wind. Deze vogels leken te rusten op zee in plaats van in de kolonie, waar tenminste de jongen nog verdedigd konden worden. Vermoed wordt dat de drijvende vogels in rust waren (sliepen) en gespeculeerd wordt dat de vogels beter uitrusten op zee, buiten de voortdurende drukte van een grote kolonie Hfdst. 12.
- Beschermde gebieden op zee zouden op zijn minst een ecologische betekenis moeten hebben voor de diersoorten waarvoor zo'n gebied wordt aangewezen. Om deze plaatsen te ontdekken en af te bakenen is

meer nodig dan alleen tellingen op zee of simpele plaatsbepalingen door loggers en andere op de vogels aangebrachte instrumenten. Wanneer dit soort gegevens kan worden aangevuld met gedragswaarnemingen, komen voor verspreidingsmodellen beter toegesneden gegevens ter beschikking. De beperkingen en mogelijkheden van de nieuwe protocollen in vergelijking met traditionelere technieken worden toegelicht, met als conclusie dat de nieuwe methode tot een beter begrip van verspreidingpatronen leidt (Hfdst. 13).

- Het voorkomen van zoogdieren in prooiresten van beide meeuwen werd onderzocht met een vergelijking tussen kolonies in het binnenland en aan de kust. Gespecialiseerde kustbroeders en een meerderheid van broedvogels in het binnenland bleken veel zoogdieren te eten. Prooien werden in het binnenland bemachtigd, misschien vooral tijdens het ploegen door boeren, andere moeten in de kolonie gevangen zijn of langs wegen, doodgereden, gevonden. Omdat kustbroedende meeuwen met voedselgebrek kampen zouden zoogdieren in de toekomst wel eens veel vaker op het menu kunnen komen staan (Hfdst. 14).
- Gegevens die het broedsucces beschrijven zijn samengevat in App 3. Aannemend dat het broedsucces samenhangt met fluctuaties in de voedselbeschikbaarheid, dan is het onafhankelijk van elkaar variëren van broedparameters een aanwijzing dat verschillende voedselbronnen van belang zijn voor de twee soorten (Hfdst. 15).
- Aangetoond wordt dat de belangrijkste gebieden van beide soorten maar gedeeltelijk overlappen: KLM waren het talrijkst in het binnenland, in de kolonie, op het Texelse boerenland en ver op zee. ZM waren veel talrijker in de getijzone. Langs de kust, met toenemende afstand tot het strand, zijn naar verhouding steeds meer KLM te zien. Als de kerngebieden worden beschouwd als potentiële voedselgebieden, dan kan de numerieke verdeling van de vogels gezien worden als een indicatie van het belang als foerageergebieden. In elk van deze gebieden komen de vogels weer andere soorten tegen die in meer of mindere mate op bepaalde prooisoorten zijn gespecialiseerd (*guilds*). In elk van deze gebieden komen pikordes tot stand, waar ZM en KLM naar verwachting in veel gevallen als sterke (dominante) soorten zullen functioneren (Hfdst. 15).
- Op zee werden de verspreiding en de talrijkheid van meeuwen onderzocht, terwijl het foerageergedrag en de prooikeuze werden bestudeerd in achter vissersschepen: dezelfde prooien in experimenten met verschillende constellaties van concurrerende vogels door het jaar heen en in de gehele Noordzee. ZM waren gemiddeld meer succesvol dan KLM bij het net. De talrijke ZM in de winter broeden vermoedelijk in noordelijk gelegen kolonies en zij vertrekken in de zomer. KLM zijn daardoor 's zomers, althans op enige afstand tot de kust, de talrijkste en daarmee competitief sterkere soort. Het is de vraag of ZM ooit (voor KLM arriveerden) bij treilers op grote afstand tot de kust hebben gefoerageerd, maar tegenwoordig brengen zij in elk geval visa an die van andere schepen afkomstig moet zijn dan die van KLM (App 7, Hfdst. 15).
- Het is duidelijk dat beide populaties momenteel niet floreren. Zelfs bij ZM, met een redelijk broedsucces in de meeste jaren, zorgt de lage overleving van broedvogels en jonge dieren tot een klein aantal rekruten en een afnemende populatie. Ondanks de hoge jaarlijkse overleving bij KLM zorgt het teleurstellende broedresultaat ook hier voor een stabilisatie of een afname. Het kleine aantal rekruten maakt de gemiddelde leeftijd van de broedvogels vermoedelijk toeneemt (Hfdst. 15).
- De meest recente populatieontwikkelingen van ZM en KLM in de westelijke Waddenzee lijken niet met elkaar in verband te staan, althans niet als gevolg van directe competitie tussen de beide soorten (geen ondersteuning van hypothese #1). ZM hebben tegenwoordig een wat hoger broedsucces dan KLM, maar kennen een veel lagere overleving in de winterperiode. Verondersteld wordt dat het verdwijnen van open vuilnisbelten en een toegenomen competitie met "lokale" Zilvermeeuwen aan de verminderde overleving ten grondslag ligt (ondersteuning voor hypothese #3) (Hfdst. 15).
- KLM hebben geprofiteerd van een modernisering van de vissersvloot in de jaren zestig: een visserijtype waarbij enorme hoeveelheden visserijafval werden geproduceerd, de boomkorvisserij. De vlootomvang bereikte een hoogtepunt aan het einde van de jaren tachtig, begin jaren negentig, waarna de vloot weer kromp. Deze moderne boomkorvisserij moet de "vakante niche" zijn geweest (hypothese #2) waarvan ZM niet hebben weten de profiteren. De problemen de KLM tegenwoordig doormaken (laag broedsucces, kannibalisme op een grote schaal) zijn de uitvloeisels van structurele voedselschaarste in de broedtijd. De vermindering van de vlootomvang, vooral de afname van grote boomkorvissers, zal gezorgd hebben voor een flinke vermindering in de voedselbeschikbaarheid. De plannen van de Europese Commissie om het overboord gooien van ondermaatse vis verder te reduceren zal de populatie verder onder druk zetten (Hfdst. 15).

1. Introduction

This thesis concentrates on the population dynamics, marine distribution, breeding biology, demography and foraging ecology of two sympatric and closely related seabird species, the

European Herring Gull *Larus argentatus* Pontoppidan, 1763,

and the

Lesser Black-backed Gull *Larus fuscus* Linnaeus, 1758.

These large gulls (Charadriiformes, Laridae) often breed in mixed, usually coastal colonies in NW Europe. Within The Netherlands, protective measures in the early 20th century, followed by a whole suite of other factors, have facilitated a rapid growth and expansion of established breeding populations of gulls and new colonisations (see Appendices 1-2). Herring Gulls peaked with 90,000 breeding pairs in the mid-1980s, but subsequently declined to 52,000 pairs in 2009; a 42.5% reduction in just about two decades. Lesser Black-backed Gulls colonised The Netherlands in the late 1920s. The population remained small for decades, but increased spectacularly after the mid-1960s (Spaans 1998abc). They continued to increase to *c.* 90,000 pairs in the early 21st century, when the numbers of Herring Gull declined (Fig. 1.1). This thesis is not about bird conservation or desired population levels, even though an interest in these contrasting population trends triggered the colony studies at Texel (western Wadden Sea, The Netherlands). The work aims at understanding current population dynamics rather than to make proposals to alter them in any direction.

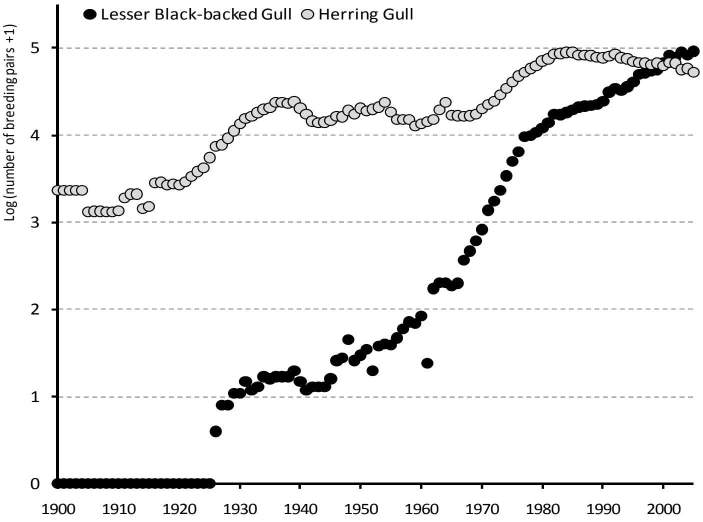


Figure 1.1. Trends in numbers of breeding pairs of Herring Gulls and Lesser Black-backed Gulls (log $n+1$) in The Netherlands in the 20th century.

This thesis

Most of the material presented in this thesis was based on field studies of the foraging ecology and breeding biology in a mixed colony at the Dutch Wadden Sea island Texel in 2006-2012, but this is only part of the story. In an earlier life, I studied seabirds offshore, working on the same (and other) bird species from a different perspective. These studies evolved from simply recording nearshore migratory movements (Camphuysen & Van Dijk 1983) and seabird strandings (Camphuysen 1989a, 1998, 2010) to offshore studies of the distribution, behaviour, multi-species foraging assemblages, feeding success and prey preferences of seabirds at sea (Camphuysen *et al.* 1995, Camphuysen & Webb 1999, Camphuysen 2005, Camphuysen *et al.* 2006). The writing of this thesis provided an opportunity to bring these different data together: the breeding biology of two species of seabirds within a mixed colony versus their offshore distribution, foraging ecology and feeding interactions as directly observed within marine environment, with all its constraints and opportunities. Different perspectives on the same animals.

The underlying research questions required an analysis of a substantial variety of aspects, ranging from reproductive success and chick growth via intra- and interspecific competition for resources to aspects of timing, migratory movements and at-sea distribution. Demographic studies in long-lived seabirds require more than just a few years of data. It should not come as a surprise that a study that started from scratch only in 2006 cannot possibly provide all the necessary data to confidently parameterise population models. For example, even though a reasonable insight in the current reproductive success of both species has been obtained, reliable estimates of annual survival and recruitment simply need more time (Bijlsma *et al.* 2012). An early estimate of (apparent) survival has been provided in this thesis, but given the sample size obtained, such estimates have to be considered preliminary results. Only highly preliminary estimates of recruitment rates and levels of immi- and/or emigration could be made. The study was broad, and some results have further matured than others. The so far published or drafted papers (Chapters 3-14 in this thesis) tell only part of the story that is currently emerging. To unfold that emerging story, and as a base fundament for future work, the thus far collected data and the literature reviews that have been completed are presented in appendices (Appendix 1-10). All this material is not required reading, but may be consulted. A comprehensive overview of the studies underlying this work (base material) is presented in Appendix 0. The results of the field studies, the basis for the topical papers (Chapters 3-14), most of which are presented in considerably more detail in the Appendices (1-10), have been summarised in Chapter 2. A synthesis can be found in Chapter 15.

The human attitude

Gulls are not very popular with most of us. Many people, confronted with gulls or with gull studies, respond in a highly stereotypic way: “*Gulls? There are enough of them and they eat everything*”. In fact, most people have no idea about the population size of gulls, their foraging ecology, or any other aspects of their biology. Firm is the almost universal belief, however, that there are so many “of them” that they should be considered a problem or a pest rather than a pleasure or a conservation issue. Gulls are bad news, is the general opinion. When reading historical essays and even scientific publications, it is important to remember that gulls were probably disliked and thus on the black list in the mind of the author. Numbers and inflicted “damage” may have been exaggerated or may simply have been assumed to be true.

Large gulls have been identified, rightly or not, as significant agents of change in the alteration of bird communities (Appendix 1). Large gulls bred historically with other bird species and these have developed defensive mechanisms against these predators (Stienen 2006, Oro & Martínez-Abraín 2007). Many wildfowl species nest in fact deliberately in the vicinity of gull colonies, because gulls are alert to, for example, ground predators, leading to greater hatching success (Bergman 1957, Anderson 1965, Bourget 1973, Van Dijk 1986, Götmark & Åhlund 1988). Oro & Martínez-Abraín (2007) reviewed the interactions recorded between Yellow-legged Gull *Larus michahellis* and 10 sympatric waterbirds in the Mediterranean and showed that while the gulls negatively affected survival, fecundity, foraging ecology and nesting habitat availability for many species, the annual population growth rates of most sympatric waterbirds showed positive values. These and other findings put the depredation by gulls into an ecological perspective. It calms critics only temporarily, however and even today, and worldwide, we read similar stories of gulls as menacing predators over and over again (e.g. Fuellhaas *et al.* 1997, Soanes *et al.* 2010).

Tinbergen (1953) described the colonies of Herring Gulls on the Frisian Islands and in Holland and Germany as “overcrowded”. There were 20,000 breeding pairs at the time. Mörzer Bruijns (1958) considered a national population of 10,000 breeding pairs of Herring Gulls quite enough and saw this as the upper limit. A prolonged campaign of destruction to reach this goal had only limited success (Spaans 2007, details in Appendix 2). As indicated above, following a marked decline in breeding numbers since the 1980s, the population of Herring Gulls has currently arrived at *c.* 52,000 pairs. A similar decline in the UK led to the inclusion of Herring Gulls on the Red List (Eaton *et al.* 2009), a signal of serious conservation concern.

Historical population trends

The study started with an analysis of historical trends: how did this all came about? The present situation, and recent population trends, cannot be properly evaluated without at least some understanding of what happened over the past 100 years or so. The way we ourselves, humans, have influenced the trends in numbers of breeding gulls, or rather how we failed at times to get what we wanted, is an important and returning issue. The adaptations of gulls to a man-made environment had to be considered from the perspectives of an established breeding species facing new challenges (the Herring Gull) and of a newcomer invading ecological niches (the Lesser Black-backed Gull). Appendix 2 provides an overview of historical aspects and trends, but also of the drivers that may have been important in shaping them.

In Appendix 2 it is shown that ground-nesting birds were ruthlessly exploited throughout the 19th century. Around 1900, only two species of gulls were breeding in The Netherlands (Snouckaert van Schauburg 1908): *ca.* 20,000 pairs of Black-headed Gulls *Chroicocephalus ridibundus* and nearly 2500 pairs of Herring Gulls. The onset of bird conservation in the early 20th century fundamentally changed the fortunes of many breeding (sea-)birds within The Netherlands (Anon. 1880, 1892, 1893, Thijsse 1909, Saris 2007) and elsewhere in western Europe (Cramp *et al.* 1974). Throughout the 20th century, numerous changes in the natural environment occurred, many of which with an anthropogenic background, to which gulls responded or adapted. Key issues have been fisheries (Garthe *et al.* 1996, Camphuysen & Garthe 2000, Tasker *et al.* 2000), and human waste disposal (Spaans 1971, Verbeek 1977, Coulson *et al.* 1987, Belant *et al.* 1993). Other factors have been the eutrophication of coastal waters (Postma 1985, Beukema & Cadée 1986, Van der Veer *et al.* 1989, Klein & Van Buuren 1992, Valiela 2006), discharges of chlorinated hydrocarbons into the marine environment (Koeman *et al.* 1968, 1969, 1972, Koeman & Van Genderen 1972), and oil pollution (Hartung 1976, Dunnet 1982, Etkin 1999). The list could be extended to include for example agricultural innovations, the introduction of predators (mammals), and the substantially increased use of beaches and dune areas by tourists.

Main episodes of population change - Four different episodes could be recognised. First and foremost, the onset of bird conservation in the early 20th century: for the first time colonial seabirds could breed more or less undisturbed. With shooting and unlimited egging halted, breeding populations promptly increased.

Second, in the 1930s, concerns were expressed about the rapidly increasing numbers of gulls and what followed was an unprecedented campaign of destruction to keep these populations within limits. Herring Gulls were kept at or below 20,000 breeding pairs, where an upper limit of 10,000 pairs was aimed for. Lesser Black-backed Gulls (first breeding in the late 1920s) failed to substantially increase in numbers and it is likely that many breeding attempts failed as a result of the campaign against Herring Gulls (nests, eggs, and chicks of the two species are difficult to separate).

The third episode started somewhere in the late 1960s, when the unwanted side-effects of chemical pollution became apparent. Environmental awareness gradually crept into the human mind, at least in modern western societies (Lytle 2007). The ruthless persecution of gulls was halted. At the same time, however, the fishing fleet modernised and massive quantities of undersized fish became spilled overboard on a routine basis (Jennings & Kaiser 1998, Tasker *et al.* 2000). Ever larger open landfill areas provided additional anthropogenic food, and the effects of eutrophication became apparent in our coastal waters and in the Wadden Sea. Many of these factors were beneficial for large gulls and the populations exploded.

Finally, the fourth episode started somewhere in the late 1980s. Populations increased rapidly, but on the Continental mainland, breeding opportunities rapidly declined as a result of the (re-) introduction of mammalian predators (Red Fox *Vulpes vulpes*). This led to the demise of ground-nesting colonies in dune areas and gulls had to give up these areas and commenced breeding in industrial estates or in cities (Woutersen & Roobeek 1992). Gulls breeding in Zuid-Holland apparently moved south and joined colonies in Europoort/Maasvlakte, whereas those nesting in Noord-Holland moved to Texel and to industrial areas in IJmuiden (Spaans *et al.* 1996). This is a period in which fisheries peaked but then started to decline, our coastal waters became cleaner, and many landfill areas were decommissioned and covered up. Population growth came to a halt and numbers declined in Herring Gulls in the late 1980s and early 1990s. Lesser Black-backed Gulls continued to increase, but the growth slowed down in the early 21st century.

Table 1.1 Factors affecting the distribution, fecundity, annual survival or resource size of large gulls breeding in The Netherlands, 1900-2010.

					First episode			Second episode				Third episode		Fourth episode	
Subject	Form	Effect on	Effect	Mechanism	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s
Mammalian predation	Breeding dispersal	Colony	**Negative**	Dispersal, emigration									░	░	░
Persecution and control	Disturbances	Colony	**Negative**	Dispersal, emigration	▓			▓	▓	▓	▓	░			░
Subject	Form	Effect on	Effect	Mechanism	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s
Chemical pollution	Bioaccumulation	Fecundity	**Negative**	Egg/chick mortality						▓	▓	▓	▓	░	░
Climate	Floodings, extreme weather	Fecundity	**Negative**	Egg/chick mortality	░	░	░	░	░	░	░	░	░	░	░
Climate	Timing, adaptation	Fecundity	**Negative**	Mismatches									░	░	░
Early exploitation	Egging	Fecundity	**Negative**	Egg mortality	▓	░			▓						
Mammalian predation	Red Fox introductions	Fecundity	**Negative**	Egg/chick mortality									░	░	░
Oil pollution	Smothering eggs	Fecundity	**Negative**	Egg mortality											
Persecution and control	Culling	Fecundity	**Negative**	Egg mortality		░	░	░	░	▓	▓	▓	▓	░	░
Weather	Wet summers	Fecundity	**Negative**	Egg/chick mortality	░	░	░	░	░	░	░	░	░	░	░
Controlled egging	First eggs	Fecundity	**Negative**	Clutch size	░	░	░								
Controlled egging	Colony protection	Fecundity	Positive	Egg/chick survival	░	░	░								
Early conservation	Colony protection	Fecundity	Positive	Egg/chick survival		▓	▓	░				▓	▓	▓	▓
Subject	Form	Effect on	Effect	Mechanism	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s
Bivalve fisheries	Stock depletion	Resources	**Negative**	Food shortages								░	▓	▓	░
Eutrophication	Habitat deterioration	Resources	**Negative**	Loss foraging habitat							░	░	░	░	
Fisheries	Stock depletion	Resources	**Negative**	Food shortages						░	░	░	░	░	░
Invasive species	Species extinctions, reductions	Resources	**Negative**	Food shortages									░	░	░
Invasive species	Species replacements	Resources	Neutral	Dietary shifts									░	░	▓
Agriculture	Intensification	Resources	Positive	Extra feeding opportunities							░	░	░	░	░
Eutrophication	Nutrients, increase productivity	Resources	Positive	Higher prey energetic values							░	░	░	░	
Fisheries	Discarding	Resources	Positive	Accessibility (dem.) fish prey							░	▓	▓	▓	░
Fisheries	Overfishing predatory fish	Resources	Positive	Increase fish suitable size							░	░	░	░	░
Waste management	Domestic refuse dumps	Resources	Positive	Extra feeding opportunities		░	░	░	░	░	▓	▓	▓	▓	░
Bivalve fisheries	Harvest and transport	Resources	Positive	Enhanced accessibility							░	░	▓	▓	░
Invasive species	Added species	Resources	Positive	Dietary shifts									░	▓	▓
Climate	Warming	Resources	Variable	Shifts in resources	░	░	░	░	░	░	░	▓	▓	▓	▓
Subject	Form	Effect on	Effect	Mechanism	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s
Chemical pollution	Bioaccumulation	Survival	**Negative**	Adult mortality						▓	▓	▓	▓	░	░
Early exploitation	Shooting	Survival	**Negative**	Adult mortality	▓	▓	░								
Oil pollution	Mobility oiled birds	Survival	**Negative**	Adult mortality		░	░	░	░	▓	▓	▓	▓	░	░
Persecution and control	Poisoning	Survival	**Negative**	Adult mortality				▓	▓	▓	▓				
Weather	Severe winters	Survival	**Negative**	Adult mortality	░	░	░	░	▓	░	▓	░	░	░	░
Early conservation	Ban on shooting	Survival	Positive	Adult mortality	▓	▓	▓								
	not, unimportant				1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s
░	some or localised			**Important negative factors:**	3	1	0	2	4	6	7	4	5	1	0
▓	important, widespread			**Important positive factors:**	1	2	2	0	0	0	1	3	4	5	2

A qualitative assessment of positive (beneficial) and negative factors, possibly influencing population trends of Laridae breeding in The Netherlands, is provided in Table 1.1. Some factors affected the possibilities to breed in certain areas, others affected fecundity, resources or annual survival. The effects were categorised as either positive, neutral or negative. Considering strongly negative or positive effects (dark grey in Table 1.1), the balance was negative in the 1900s (more important negative than positive factors), positive in the 1910s and 1920s, strongly negative in the 1930s to early 1970s, and largely positive in the late 1970s-early 21st century.

Direct and indirect impacts - Factors affecting seabird populations can be split into food-related aspects (affecting resources), and circumstances that affect fecundity and survival more directly (direct kills, conservation measures, marine pollution). Confusingly, food-related factors usually affect populations also via changes in fecundity and annual survival. There is this extra step and the phenotypic plasticity of an organism that will make population-level effects more difficult to demonstrate. Proving the consequences of any issue in isolation is particularly difficult, due to confounding and interacting combinations with other factors. Effects of a given factor may be masked in populations that are subject to major shifts due to other changes. Field experiments are difficult to design.

Hypotheses

The recent, contrasting population trends of Herring Gulls and Lesser Black-backed Gulls have been addressed before, leading to several different hypotheses:

(1) Herring Gulls have changed their resource exploitation patterns as a consequence of inter-specific competition with Lesser Black-backed Gulls. Herring Gulls have been forced to focus on less profitable prey (Noordhuis & Spaans 1992).
(2) Lesser Black-backed Gulls have filled an empty niche rather than outcompeted Herring Gulls. The population trends are unrelated (Camphuysen 1995a, Garthe *et al.* 1999).
(3) Differences in foraging behaviour and food availability outside breeding season are responsible for the marked differences in demographic trends in the two species (Kim & Monaghan 2006).

These three scenario’s were kept in mind when the studies started and the third hypothesis provided arguments to not only collect data over the breeding season. **Hypothesis (1)** assumes that the recent population trends are somehow related: Herring Gulls being pushed away from a favourite and apparently crucial resource by a newcomer, the Lesser Black-backed Gull. To support this claim, evidence should be provided that both species concentrate on a shared, particularly important resource during chick care. Lesser Black-backed Gulls should be dominant or superior (higher feeding success) in a competitive setting; hence, the feeding success rates of Herring Gulls must be compromised in mixed feeding flocks.

Hypothesis (2) assumes that the demographic trends are not (directly) related. It requires a careful study of phenotypic characteristics of the two species and the identification of that vacant niche(s) that could be occupied solely or predominantly by Lesser Black-backed Gulls. Which resource, novel, previously untapped or underexploited, could have facilitated this spectacular and sudden population growth of Lesser Black-backed Gulls in the Southern North Sea that commenced only in the late 1960s? Herring Gulls must have been unable to profit.

Hypothesis (3) implies that the species may (or may not) interact and compete over resources during breeding, but that the demographic trends are not affected by these interactions. It proposes that differences in fecundity are of lesser importance than differences in winter survival and recruitment rates. The comparative study from which the hypothesis was taken suggested that the two species may show different (winter) survival rates, because of their different wintering environments. Because the locations to which young birds disperse in winter play part in their subsequent recruitment to the colonies, these differences may have affected recruitment rates to the colony (Kim & Monaghan 2006). This hypothesis does not exclude the possibility of inter-specific competition outside the breeding season, but this is unlikely given differences in migration strategies and wintering areas (Speek & Speek 1984, Wernham *et al.* 2002). Hypothesis (3) suggests in fact that the observed population trends may be unrelated to most factors summarised in Appendix 2 (summarised in Table 1.1).

Herring Gull club with resting Lesser Black-backed Gulls in foreground, 20 April 2013 (CJ Camphuysen)

Territorial dispute in Lesser Black-backed Gulls, 13 May 2008 (CJ Camphuysen)

2. Study results summarised

This chapter, a comprehensive summary of the study results, provides an overview of the underlying research questions, the lines of thought, and the most relevant results of field studies and field experiments conducted. This summary provides a context for each of the topical papers, currently published, under review or drafted, that are included in this thesis (Chapters 3-14). In this summary, some data are provided, but most of the base material is presented in Appendices (Appendix 1-10) and in the papers (Chapters). Each of the Appendices is written in a chapter format, but all this material is not required reading. Appendices contain data that are useful for comparative studies, for colleagues studying colonial seabirds, notably gulls. Conclusions are drawn following a final discussion of the main findings of this study in Chapter 15 (Synthesis).

The Appendices may be consulted and will be referred to where needed in the course of this thesis. In most of the Appendices there are aspects that are highlighted or summarised in a Box format. Boxes are numbers in order of appearance, with the Appendix number as a first value (e.g. ^{App}Box 5.1 is the first box in Appendix 5). References to Tables and Figures that can only be found in the Appendices have superscript 'App' as a prefix (e.g. ^{App}Fig. 5.6 as the sixth figure in Appendix 5). Figures and Tables within each of the Chapters are numbered in order of appearance, with the Chapter number as a start value (e.g. Fig. 1.1 for the first figure in Chapter 1).

Species comparisons

Birds so closely related that interbreeding and hybridisation occurs (Appendix 1) may also compete for resources such as breeding sites or food (Burger & Shisler 1978, Bergman 1982, Mierauskas & Buzun 1991, Hario 1994, Gonzalez-Solis *et al.* 1997, Garthe *et al.* 1999b, Arcos *et al.* 2001). Comparisons between the two species of gulls are a returning issue in this thesis. A resumption of ecological and demographical studies of large gulls in The Netherlands in the early 21st century was partly inspired by the idea of inter-specific competition, or by the "*competitive exclusion principle*" (Gause's law), to be exact, raised by earlier researchers (Noordhuis 1987, Spaans & Noordhuis 1989, Noordhuis & Spaans 1992). Gause's law is a proposition stating that two resource-limited species having identical patterns of resource use cannot coexist in a stable environment (Gause 1934). One species will be better adapted and will outcompete or eliminate the other (Allaby 1994). To address this issue and to control for variable environmental conditions (between-season variation), it was important that both species were studied simultaneously. So far, comprehensive studies of the breeding biology of either species in The Netherlands were conducted in different seasons. Moreover, the Lesser Black-backed Gull is still such a recent addition to the Dutch coastal ecosystem, that many underlying ecological facts and features in the region have not even been quantified yet. The gaps in knowledge needed to be filled: base line data had to be collected. At Texel, the two species were studied simultaneously in a large mixed colony from 2006 to 2012.

Two species with identical ecologies cannot live together in the same place at the same time, but since any two species are infinitely unlikely to be exactly identical, a search for ecological differences does not constitute verification of this hypothesis (Pianka 1994). Interesting is an evaluation of the ecological overlap, and how much overlap two species can tolerate and still coexist (Pianka 1994). The two large gulls studied at Texel form mixed feeding flocks, their dietary preferences overlap and at least some foraging areas are shared. Inter-specific competition between the two species for particular resources is thus likely to occur. When one species ultimately eliminates the other when the two compete (and the system is allowed to go to saturation), competitive exclusion has occurred, even if the elimination took place only for part of the dietary spectrum (Pianka 1994). A basic question addressed in the thesis was: do these two gulls outcompete one another at all at particular resources, and does this have effects on their reproductive success (short-term), or on the breeding population as a whole (long-term) ?

An important line of thought in the preparation of this thesis was the representativity of the work for the biogeographic population. What about (factors influencing) population trends in neighbouring colonies, in neighbouring regions, or in other countries around the North Sea? How representative are data collected in one (large) colony for larger parts of the breeding population? While the foraging ecology (or dietary 'preferences'; a risky word) or even the reproductive success of the same species in two neighbouring colonies can be quite different, there are more or less similar population trends spanning much of the (NW) European population simultaneously (Lloyd *et al.* 1991, Spaans 1998abc, Seys *et al.* 1998, Garthe *et al.* 2000, Mitchell *et al.* 2004). A meta-population analysis, at least for the moment, was considered an overambitious and potentially confusing sidetrack. Such an analysis is required, however, to clarify why on a pan-European scale many populations have changed more or less in concert. In this thesis, I refrained from spending much time on this issue.

The ecological facts of life

The project started with an explorative investment. In order to be able to understand current population trends (n_{now}) or to predict future trends (n_{future}), information on current birth rates (fecundity, B), death rates (D), and levels of emigration (E) and immigration (I) had to be collected (Begon *et al.* 1990) :

$$N_{\mathrm{now}} = N_{\mathrm{then}} + B - D + I - E \quad \text{or} \quad N_{\mathrm{future}} = N_{\mathrm{now}} + B - D + I - E$$

In stable populations, breeding birds produce enough recruits to replace adults that die (Perrins 1991). Fundamental data to be obtained in the present study were thus: breeding success, estimates of annual survival and recruitment rates. Most studies of the breeding biology of large gulls in the Netherlands had been discontinued sometime in the 1990s and recent data were simply not available. Earlier more comprehensive studies had been conducted at Schiermonnikoog (Drent 1967, Baerends & Drent 1970, 1982, Veen *et al.* 2003), Terschelling (Spaans 1971, Spaans & Spaans 1975, Bukacińska *et al.* 1996, Bukaciński *et al.* 1998), IJmuiden (Cottaar & Verbeek *unpubl. data*), Wassenaar (Tinbergen 1936c, 1953, Bouman *et al.* 1991), and Schouwen (Vercruijsse 1999). But picking vital rates of any of these studies was no option, if current trends required an explanation.

In order to assess the current reproductive performance (B) of both species, a new study was designed from scratch in a nearby, large and always accessible (weather conditions) mixed colony at the Wadden Sea island Texel. Assessing reproductive success (fecundity) alone was not sufficient. Any differences found between the two species, or between seasons (later between colonies and regions), would require an explanation. Therefore, factors influencing reproductive rates had to be assessed simultaneously. In order to understand inter-specific and seasonal differences in fledgling rates, data on the timing of nest initiation, on clutch size, clutch volumes, egg losses, chick losses, chick provisioning, growth rates, and fledgling mass were collected.

A colour-ring programme was started simultaneously to be able to evaluate levels of mortality and site-fidelity (D, I, and E). Colour-rings could not just be deployed at Texel, but also at relatively well studied colonies on the neighbouring island (Vlieland) and at the nearest substantial colony on the Continental mainland (IJmuiden). Colour-rings also provided information on the wintering movements of the two species, more or less as bycatch. Technological innovations in the course of this project allowed even more detailed investigations, independent of observer effort (Appendix 5, $^{\mathrm{App}}$Box 5.1-2). Radio tags and GPS loggers were deployed to measure nest attendance, foraging range and time budgets during breeding.

Density dependence - Even though Herring Gulls had declined in numbers within The Netherlands in recent years (Fig. 1.1, Appendix 2), populations of both species were at or close to an all-time high when the studies commenced. Spaans *et al.* (1987) examined the effects of a markedly increased population size on Herring Gull reproductive success at Terschelling. Between 1968 and 1984, the increase in breeding numbers was more than 5-fold. In actual study plots, the increase was 3-fold with "a corresponding decrease" in the reproductive success. Higher levels of cannibalism (associated with higher nesting densities) were thought to have caused decline in breeding success (in 1983-1984 0.34-0.44 young fledged pair^{-1}, compared to 1.25-1.50 fledglings pair^{-1} in 1967-1969).

Numerous publications contain descriptions of density-dependent changes of vital rates based on empirical observations (Lack 1954, Fowler 1981). Notable issues raised in this and other studies on (presumed) effects of changes in nest densities are changes in synchronisation and timing of laying, egg size, levels of chick depredation, drops in fecundity, and shifts in the age of recruitment (Darling 1938, MacRoberts & MacRoberts 1972, Burger 1974, Parsons 1976, Coulson *et al.* 1982, Becker & Erdelen 1986, Watanuki 1988, Velarde 1992, Bukacińska & Bukaciński 1993, Jahl 1994, Wilkens & Exo 1998, Velando & Alonso-Alvarez 2001). Fowler (1981) suggested that for species with low reproductive rates, long life-spans and populations that are limited by resources, most changes in vital rates occur at high population levels close to the carrying capacity. Species with high reproductive rates, short life-spans, and populations held below the limits of environmental resources exhibit most density-dependent changes at low population levels. The two study species are seabirds with rather long life-spans and low reproductive rates (Schreiber & Burger 2002). If indeed current (high) population levels were close to carrying capacity, we were told to expect reductions in both fecundity and survival. For Herring Gulls breeding in The Netherlands, vital rates were evidently compromised in the late 1980s and early 1990s, a time when the population stabilised at peak levels (Spaans *et al.* 1987b, Noordhuis & Spaans 1992, Bukacińska *et al.* 1996).

Measures of fecundity: breeding in high densities

The comprehensive study of the breeding biology of the two species of gulls at Texel commenced in 2006. Aspects of the breeding biology based on these new studies have been published in 2010 (Camphuysen & Gronert 2010a), but an update is presented in Appendix 3 (laying dates, clutch size, egg volumes, hatching rates, chick growth, depredation and fledging rates).

A first research question was: is the current reproductive success in line with expectations based on recent population trends? It appeared that the reproductive success of Lesser Black-backed Gulls was almost always substantially lower than that of Herring Gulls (summarised in Table 2.1). The fledging rates in Herring Gulls averaged (mean ± SD) 0.88 ± 0.29 chicks pair^{-1} (range 0.48-1.33) between 2006 and 2012, fledging rates in Lesser Black-backed Gulls amounted to only 0.49 ± 0.17 chicks pair^{-1} (0.26-0.71). Only in 2011, when Herring Gulls suffered from relatively high levels of egg and chick mortality, did the reproductive success of Lesser Black-backed Gulls (0.69 chicks pair^{-1}) exceed that of Herring Gulls (0.48 chicks pair^{-1}).

A major problem for the Lesser Black-backed Gull, less so for the Herring Gull, appeared to be the high level of chick depredation (cannibalism). Chick depredation from cannibalism was particularly high in Lesser Black-backed Gulls in 2006-2009 and again in 2012 (>60%) and fairly high in 2011 (49%) (Table 2.1). Chick depredation in Herring Gulls tended to remain well below 40% in all years except in 2009 (51%). The studies were comprehensive enough to set out and investigate the underlying problem of high levels of cannibalism, and most vital rates are summarised in Appendix 3. Some more important aspects are highlighted below.

Clutch size - Many authors have demonstrated or suggested an adaptive relationship between food supply or territory quality and clutch size, but the proximate mechanism by which clutch size is still only partly understood (Perrins 1970, Bolton *et al.* 1993, Winkler & Allen 1996, Monaghan & Nager 1997, Korpimäki & Wiehn 1998, Monaghan *et al.* 1998). Experienced adults tend to occupy better territories and produce larger clutches than recruits. Spaans *et al.* (1987) provided data just before and after a dramatic increase in the numbers of breeding pairs on the island Terschelling. In 1983-84 (mean clutch size 2.54 ± 0.68, n= 723), at peak densities, clutches were significantly smaller than in 1967-69 (2.74 ± 0.52, n= 599; t_{1320}= 5.9, P< 0.001), just before the population increase. In the 1960s, however, birds breeding at Terschelling produced significantly smaller clutches than Herring Gulls breeding at the nearby island Schiermonnikoog (2.88 ± 0.39, n= 160; t_{757}= 3.17, P< 0.01; Drent 1967, Spaans & Spaans 1975). Recent data on clutch size collected at Texel (2.73 ± 0.55, n= 427) are similar to those found at Terschelling in the 1960s. At Schouwen (Delta area) in the early 1990s, where the participation of colour-ringed recruits into the breeding population was monitored over 1991-94 (young and inexperienced birds; Vercruijsse 1999), a mean clutch size of 2.67 ± 0.57 (n= 105) was found, similar to the clutch size reported for (more experienced?) birds at Terschelling in the 1980s. The clutch size at Schouwen in the 1990s was not significantly different from that at Texel in recent years (t_{530}= 0.99, n.s.).

For Lesser Black-backed Gulls, fewer data are available to document any possible change. Bukaciński *et al.* (1998) found a mean clutch size 2.92 ± 0.32 eggs (n= 26) at Terschelling in 1992, a value that is not significantly different from the clutch size found at Texel today (2.76 ± 0.53, n= 654, but note that the sample size was very different. Further details on clutch size are provided in Camphuysen & Gronert 2010a, information that was further updated in Appendix 3.

Table 2.1. Summarised data on laying, clutch size, clutch volume, chick growth, chick depredation, and fledging success, Kelderhuispolder 2006-2012 (from ^{App}Table 3.3-4, ^{App}Box 3.4 and Camphuysen & Gronert 2010a).

Herring Gull	Mean	clutch	clutch	chick growth (mass)			chick	fledging
Year	laying	size	vol	*a*	*b*	*k*	pred%	chicks pr^{-1}
2006	10-May	2.71	247.0	839.0	17.1	6.6	33.3	0.62
2007	08-May	2.58	244.9	844.9	16.0	6.3	39.1	0.80
2008	07-May	2.86	249.1	780.6	16.4	6.9	25.0	1.10
2009	06-May	2.69	239.8	775.1	15.5	6.6	51.2	0.81
2010	05-May	2.81	247.6	764.9	15.4	6.2	20.0	1.33
2011	04-May	2.77	244.6	805.3	18.0	7.0	16.7	0.48
2012	07-May	2.64	246.3	804.5	16.6	6.8	31.3	1.04
Totals	06-May±2.0	2.72±0.1	245.6±3.0	802.0±31.0	16.4±0.9	6.6±0.3	30.4±11.8	0.88±0.3
Min	04-May	2.58	239.8	764.9	15.4	6.2	16.7	0.48
Max	10-May	2.86	249.1	844.9	18.0	7.0	51.2	1.33

Lesser Bl-b Gull	Mean	clutch	clutch	chick growth (mass)			chick	fledging
Year	laying	size	vol	*a*	*b*	*k*	pred%	chicks pr^{-1}
2006	15-May	2.75	226.4	662.7	14.7	5.9	60.3	0.26
2007	10-May	2.73	224.9	671.8	13.9	5.3	66.7	0.46
2008	10-May	2.84	224.1	693.4	15.2	6.0	63.4	0.35
2009	12-May	2.80	221.4	635.6	15.2	6.3	62.3	0.37
2010	14-May	2.80	226.2	778.5	19.5	7.8	35.4	0.71
2011	13-May	2.82	224.2	627.5	14.4	5.7	49.3	0.69
2012	18-May	2.59	217.4	635.9	14.7	5.6	60.7	0.57
Mean ± SD	13-May±2.9	2.76±0.1	223.5±3.2	672.2±52.4	15.4±1.9	6.3±0.8	56.9±10.9	0.49±0.2
Min	10-May	2.59	217.4	627.5	13.9	5.3	35.4	0.26
Max	18-May	2.84	226.4	778.5	19.5	7.8	66.7	0.71

Clutch volumes – Egg size is commonly held to be an important index of egg 'quality' because it reflects the quantity of yolk, reserves available to the chick during embryonic development and on hatching (Bolton 1991). The ability to produce large eggs and to rear chicks successfully may be positively related to parental quality. Overall clutch volume in Herring Gulls breeding at the nearby island Terschelling was found to have declined between the late 1960s (steep population increase) and the mid-1980s (stabilising numbers, higher densities; Spaans *et al.* 1997b). We were therefore interested in the mean clutch volumes in Herring Gulls at Texel, after some more decades of population declines. The maximum length and breadth of each egg was measured to the nearest 0.1mm and volume (V) was calculated using the formula $V = K_v * L * B^2$ (Stonehouse 1966), where L is maximum length, B is maximum breadth and K_v is a constant (^{App}Box 3.1). K_v was calculated as 0.5035 by Spaans & Spaans (1975). The mean volume off Herring Gull eggs at Terschelling in the 1980s (253.4 cc, n= 188 in 1983, 260.3cc, n= 190 in 1984) was below that found in the 1960s (261.8 cc, n= 73 clutches; Spaans *et al.* 1987). These values are well above the clutch volumes found at Texel today (245.6 ± 3.0 cc, Table 2.1, Appendix 3). The smaller clutch volumes could be indicative for a relatively poorer condition of nesting females at Texel today in comparison with that of females in the earlier studies.

Spaans *et al.* (1994) compared egg volumes from 3-egg clutches in eight colonies of Lesser Black-backed Gulls along the Dutch coast (Schouwen to Schiermonnikoog). Clutch volumes found at Texel today (223.5 ± 3.2 cc, n= 7; Table 2.1, Appendix 3) are slightly larger in comparison to the overall mean over all these colonies in 1992-93 (mean 211.9 ± 5.8 cc). Birds nesting at Europoort (1992 and 1993), Maasvlakte (1993) and Schiermonnikoog (1993) produced the smallest clutch volumes (207.7 ± 4.6 cc).

Hatching rates – In Lesser Black-backed Gulls breeding at Texel (2006-2012), hatching rates were negatively correlated with the proportion of predated eggs (r^2= 0.92, n= 7). In Herring Gulls, the fraction of addled eggs, (which was not related to egg predation) and the percentage of stolen eggs, both contributed equally to the variability in hatching success (Appendix 3). There was no correlation in annual egg losses through depredation between the two study species.

Variations in chick growth - Annual variations in chick growth rates (k) were small (6.3 ± 0.8 in Lesser Black-backed Gulls, 6.6 ± 0.3 in Herring Gulls, Table 2.1, ^{App}Box 3.4). Variations in body mass gained at 40d of age in Lesser Black-backed Gulls varied *c.* 150g between the year with the most favourable chick growth (2010, 778 ± 15g) and the season with rather modest growth (2011, 627 ± 12g). In Herring Gulls the modelled differences between years were smaller: an 80g difference between the most favourable season (2007, 845 ± 13g) and the worst (2010, 765 ± 13g).

Cannibalism – Levels of chick depredation were particularly high in Lesser Black-backed Gulls. Specialised cannibals were only a minor part of the issue. In years with exceptionally high levels of chick depredation (>50-60%), many adults were involved and territories were raided (all chicks present instantly killed) one after the other. Enclosures would normally have prevented hungry chicks to venture into other territories to put themselves at risk (Hunt & McLoon 1975, Hunt & Hunt 1976), but entire patches were cleared from chicks in a few days time, irrespective of the presence of fences. Part of the failure of experiments conducted in 2008 (see below) must have been caused by such collective, spreading attacks, that were more violent in some study plots than in others (^{App}Fig. 3.15). Enclosures (in the experiments both controls and treatments) that happened to be in the main affected area were simply cleared from chicks by raiding adult birds (depredated corpses were found outside as well as inside the enclosure). Enclosures that happened to be at the periphery of such an affected region were largely spared. Chick depredation in Lesser Black-backed Gulls peaked markedly later than in Herring Gulls, with larger, energetically more demanding chicks involved (^{App}Fig. 3.13).

Cyclic fluctuations in chick growth - A particularly interesting finding were cyclic fluctuations in Lesser Black-backed Gull chick growth, particularly in chicks of at least two weeks old (>15d; Chapter 3). Similar drops and gains in chick body mass occurred in many inspected nests during subsequent visits, indicating alternating periods of low and more favourable provisioning. The observed cycles matched the weekly rhythm in commercial fishing effort around Texel (and in most areas of the Southern North Sea). When fishing effort peaked (Tue-Thu), chick growth was favourable, but when fishing effort was low (Fri-Sun) chicks tended to lose mass. Chick cannibalism rates were a mirror image of the rhythmic cycle in growth increments and peaked in weekends ("*Killing the kids on Sundays*"; Camphuysen & Gronert 2010b).

Herring Gulls experienced similar cyclic ups and downs in chick growth as Lesser Black-backed Gulls (Chapter 3), but chick depredation was more modest (except in 2009). Herring Gulls bred in considerably lower densities than Lesser Black-backed Gulls (^{App}Table 3.9), and violent interactions between neighbouring territories were probably less frequent. Exactly how important fisheries discards from beamtrawlers are for both species had thus to be investigated in depth.

A supplementary feeding experiment - In 2008, a supplementary feeding experiment conducted by Janne Ouwehand at Texel aimed at *reducing* chick depredation levels, by supplementing chicks under the expectation that supplemented pairs would spend more time at the nest site to guard the chicks (Chapter 4). The experiment was inspired by a study of Bukaciński *et al.* (1998) who provided Lesser Black-backed Gulls at Terschelling with additional food until 7 days after hatching or until fledging and compared the effect with control nests. The hypothesis tested by Bukaciński *et al.* was that food was in short supply during the chick stage and that the behaviour of adults and young would be responsible for the low success under such circumstances. Pairs whose chicks were fed showed a higher fledging success than control pairs. In experimental pairs, the length of feeding trips by females was shorter than in control pairs, and rates of chick feeding were higher in experimental broods. Chicks fed until fledging developed more rapidly and reached higher a fledging mass at an earlier age than controls. Starvation occurred only in control chicks. It was concluded that when food was in short supply, fledging success was adversely affected as a result of starvation and higher depredation rates arising from changes in behaviour of both adults and chicks.

At Texel, the results were ambiguous (Chapter 4). Nest attendance of supplemented pairs was enhanced in one study plot, but reduced in another. The hypothesis that food provisioning would increase the time available for nest attendance was not supported. Chick depredation levels were on average higher in control nests than in food supplemented nests, but the difference was not significant. Although supplemented birds fledged more young than controls, the difference was not significant. Many of the results obtained were tendencies in the expected direction, but with non-significant outcomes. While the sample size may have been too low during the experiments (leading to low power), this was not different from similar studies elsewhere with more clear-cut results (see discussion in Chapter 4). Chick depredation and fledging success were significantly different between the two study plots at Texel. The results were possibly ruined by the fact that the reproductive success of the population as a whole was virtually nil in one of the study plots (where both experimental pairs and controls were monitored), and quite substantial in the other (leading to a higher success in experimental pairs *and* controls).

Breeding densities – Colony censuses, initially, were not part of the research protocols at Texel. This was under the assumption that a colony census would be conducted annually and independently by reserve wardens and/or SOVON, as part of the annual monitoring of colonial breeding birds and under Natura 2000 regulations. The Kelderhuispolder study plots were part of a much larger colony, and a small scale census did not seem to contribute much. Struck by the high levels of cannibalism in the first years of study, however, and inspired by Spaans *et al.* (1987), Brouwer *et al.* (1995) and other publications on density dependent effects on behaviour and reproductive success in gull breeding populations, it was decided to at least assess breeding densities in the Kelderhuispolder. In 2009, 2010, and 2011 the breeding population of Herring Gulls within the study area was estimated at 1288 (160 ha^{-1}), 1023 (120 ha^{-1}), and 890 (110 ha^{-1}) breeding pairs respectively (^{App}Table 3.8). Lesser Black-backed Gulls were estimated to number 1816 (220 ha^{-1}), 1986 (240 ha^{-1}), and 2026 (250 ha^{-1}) pairs respectively. Territories with empty nests were included in these censuses. Spaans *et al.* (1987) reported an increase from 35 nests ha^{-2} in the late 1960s to 97 nests ha^{-2} in the early 1980s. It is difficult to compare nesting densities between colonies directly (see issues raised in Appendix 3), but the Kelderhuispolder censuses suggest that nesting densities of Herring Gulls alone were higher than the densities for the two species combined in the 1980s at Terschelling.

Non-breeding issues – Striking was the incidence of empty nests during nest counts (strip-transect surveys to assess breeding densities). Some 20-30%, or occasionally as many as 60% of the well-constructed nests were empty. The territory-holders involved apparently never produced eggs and this points to considerable levels of 'non-breeding' in birds that were in fact actively engaged in the prospecting phase. Roughly between one-fifth and a third of the territory holding large gulls returned to the colony but did not breed in a given season. The issue of non-breeding is again addressed below and in Appendix 6

Productivity indices – The World Seabird Union and the Circumpolar Seabird Group present population trends and seabird breeding productivity indices (PI) according to standardised protocols. Seabird productivity indices range from poor to moderate and good based on the number of fledglings per nest over mean the clutch size (CSG 2010). The adoption of a common protocol facilitates comparisons between colonies over larger geographical scales. Good productivity is characterised by ≥50%, poor productivity by ≤10%, and moderate productivity as >10% to <50% of mean clutch size (Table 2.2). At Texel, productivity was moderate to poor throughout, with Lesser Black-backed Gull producing consistently less than Herring Gulls.

Table 2.2. Productivity indices (PI= F/CS*100) for Herring Gulls and Lesser Black-backed Gulls breeding at Texel, 2006-2012. Qualifications (poor <10%, moderate 10-50%, good >50%) according to World Seabird Union and Circumpolar Seabird Group protocols (CSG 2010).

Herring Gull	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**
Clutch size (CS)	2.71	2.58	2.86	2.69	2.81	2.77	2.64
Fledglings (F)	0.62	0.80	1.10	0.81	1.33	0.48	1.04
PI (%)	23	31	38	30	47	17	39
Qualification	moderate	moderate	moderate	moderate	moderate	moderate	moderate
Lesser Black-backed Gull	2006	2007	2008	2009	2010	2011	2012
Clutch size (CS)	2.75	2.73	2.84	2.80	2.80	2.82	2.59
Fledglings (F)	0.26	0.46	0.35	0.37	0.71	0.69	0.57
PI (%)	9	17	12	13	25	24	22
Qualification	poor	moderate	moderate	moderate	moderate	moderate	moderate

The annual cycle

The annual cycle of birds is made up of a sequence of life-history stages: breeding, moult and migration. Relationships between events in one period of the annual cycle and behaviour in subsequent seasons are important determinants of individual life histories and population dynamics (Bogdanova *et al.* 2011). Each stage is thought to have evolved to occur at the optimum time (Dawson 2008). Climate change has advanced the phenology of many organisms (Both *et al.* 2005, Møller *et al.* 2009). Migratory animals face particular problems because climate change in the breeding and the wintering range may be asynchronous, preventing rapid response to changing conditions. However, studying such associations is challenging, given the difficulties in following individuals across seasons, particularly in migratory species (Bogdanova *et al.* 2011).

Nearly all seabirds are colonial and have synchronously timed breeding cycles within colonies (Hamer *et al.* 2002). The timing of breeding has often been proposed as a vital aspect of breeding success. Some studies have indicated that, although breeding early generally leads to greater overall survival of chicks, several important interactions among egg 'quality', parental quality as well as early laying may affect breeding success (Arnold *et al.* 2006, Drent 2006, Drent *et al.* 2006). Although the timing and duration of the period of full gonadal maturation is principally controlled by photoperiod (Gwinner 1975), non-photoperiodic cues could modulate the exact time of laying (Perrins 1970, Dawson 2008). Ambient temperatures could influence laying dates by affecting the availability and quality of food (Perrins 1979). Lesser Black-backed Gulls and the Herring Gulls experience similar photoperiodic cues and weather conditions in the prospecting phase. If the onset of laying would vary independently between the two species, other factors, such as food availability around the colony or the condition of the birds following a wintering period, could be more important.

The annual cycles of Herring Gulls and Lesser Black-backed Gulls breeding at Texel are characterised by returns from wintering areas to the breeding grounds in late March, *c.* five-month breeding periods that last until August, a complete post-nuptial moult and a retreat to the wintering areas in the course of September and October (Appendix 4, $^{\mathrm{App}}$Figs. 4.1-2).

Laying dates - At Texel (2006-2012), Herring Gulls commenced laying in late April, on average one week before Lesser Black-backed Gulls (Table 2.1). Herring Gulls breeding in the Wadden Sea at Terschelling were found to have advanced their laying dates between the late 1960s and the late 1980s (Spaans *et al.* 1987, 1997b). Clutch initiation in Herring Gulls at Terschelling was studied just before and after a dramatic increase in the numbers of breeding pairs (1966-1969: 6000-8000 pairs, 1983-1984: 21,000-21,500 pairs). In 1983-1984, Herring Gulls bred, on average, 5-9 days earlier than in 1967-1969 (1967-1969: 18-19 May, 1983-1984: 10-14 May). The studies at Texel showed that the onset of breeding in Herring Gulls has advanced even further (7 May ± 2.2 d, n= 7), and seemed breed earlier every year (Appendices 3-4).

For Lesser Black-backed Gulls, comparative information on laying dates is sparse. Bukaciński *et al.* (1998) reported a median laying date of 10-12 May for birds nesting at Terschelling in 1992, which is similar to the current mean laying date at Texel (Table 2.1). From 2006 to 2012, with the ever earlier laying Herring Gulls, the actual laying dates of Herring Gulls and Lesser Black-backed Gulls at Texel were increasingly out of sync ($^{\mathrm{App}}$Figs 4.4-5). A comparison of earlier (<2000) and later (>2000) re-sightings of colour-ringed Lesser Black-backed Gulls suggest that, in recent years, movements towards the colony in spring are delayed by *c.* on month (Chapter 5). A late spring return leaves little time to restore the body condition that is needed to breed successfully. Colony visits in the prospecting phase are a gradual process (prospecting birds are extremely shy at first and do not stay overnight within the colony). At Texel, in both species, colony visits occurred in favourable (still) weather after late February, but increased in frequency and duration only after late March. Colour-ring re-sightings in Lesser Black-backed Gulls showed that cumulative return rates within the colony, in the prospecting phase, were similar between years and for males and females (Chapter 5).

Colony departures - the onset of autumn migration or the dispersal away from the breeding grounds commenced in July and August, again in both species. GPS tracking data collected for Lesser Black-backed Gulls indicated that successful breeders abandoned the colony when the chicks were *c.* 50d of age and capable of flight ($^{\mathrm{App}}$Table 4.3). The autumn movement to the south had a different start in immatures (early), adults (intermediate) and juveniles (late). Juveniles remained near the breeding colony to a later date than adults ($^{\mathrm{App}}$Fig. 4.3), and post-fledging chick care (Holley 1986) must therefore have been minimal. A similar difference in timing was found in Herring Gulls, but this time based on colour-ring readings (Chapter 6). In Lesser Black-backed Gulls, it could be established that immature (non-territorial) birds travelled earlier southward than failed breeders (the timing of which was similar to successful breeders). This could point at the importance of a prolonged presence at established territories: post-breeding territorial defence. Future possibilities to breed may be enhanced in failed breeders, if territories are continued to be occupied and defended throughout the breeding season. A comparison of earlier (<2000) and later (>2000) resightings of colour-ringed Lesser Black-backed Gulls indicated that in recent years movements away from the colony were more advanced earlier in autumn. Adult birds did not linger around for much longer after the breeding season, but left immediately (Chapter 5).

Wing moult - Investment in one activity usually occurs at the expense of another (Bridge 2006). In seabirds, the moult of flight feathers and breeding are generally thought to be mutually exclusive, because adults need to be at their most efficient when feeding young (Harris 1971). Wing moult introduces gaps in a wing, resulting in reduced flight efficiency and manoeuvrability (Swaddle & Witter 1997, Hedenström & Sunada 1999, Bridge 2003). These effects may be especially detrimental to seabirds that rely heavily on flight for capturing prey.

The post-nuptial moult starts within the colonies, but is completed either in wintering areas or at autumn stopovers. Gulls, that sequentially replace their primaries, temporarily have gaps in their wings that will vary in size and position(s) during the course of the moult. Hedenström & Sunada (1999) investigated the aerodynamic effects of moult gaps, and modelled the effect gap size and position. Both had a detrimental effect on aerodynamic performance as measured by lift curve slope, effective aspect ratio and the aerodynamic efficiency of the wing. The effect was largest when the moult gap was well inside the wing (i.e. the earliest stages of wing moult in gulls), because the circulation declines close to the wing tip.

The onset of primary moult at Texel was different between the two species, with a start in Herring Gulls *c.* 1.5–2 month earlier than Lesser Black-backed Gulls (during laying and incubation rather than during chick care; Appendix 4). Half way incubation (late May), two-thirds of the Herring Gulls had developed a moult gap inside the wing. The earliest Lesser Black-backed Gulls to shed inner primaries were seen in late June to mid-July ($^{\mathrm{App}}$Figs. 4.9-10), which is the second half of chick care. Hence, the "most detrimental effects" of wing moult (the onset, the inner wing gap) were timed differently in both species: around hatching in Herring Gulls and during chick care in Lesser Black-backed Gulls. A study of the foraging ecology was required to evaluate how the onset of primary moult coincided with (changes in) the exploitation of particular resources and foraging activities in either species.

In August, clubs within the colony and nearby roosts and bathing places were littered with loose feathers. Contour feathers as well as 'flight feathers' (primaries, secondaries and tail feathers) were dropped during preening. With a 6 month period to complete the primary moult (Ginn & Melville 1983), a start mid-July as in Lesser Black-backed Gulls would mean that the last primary is renewed in December, *i.e.* in the wintering areas ($^{\mathrm{App}}$Fig. 4.3). Active primary moult occurs during long-distance migration in other words, but birds may interrupt the moult so as to migrate without gaps in the wings (Harris 1971, Muusse *et al.* 2011). Herring Gulls would have completed primary moult about on average one month earlier, but would still be in active moult during their dispersive movements to wintering areas.

Seawatching results- An analysis of seawatching data revealed a relatively high abundance of Herring Gulls in coastal waters during chick-care. Herring Gulls are recorded year-round by seawatchers, but a large proportion of the wintering birds are "foreign birds" breeding further north and east (see also Coulson *et al.* 1984, Speek & Speek 1984). As will be shown in Chapter 6, most of the Herring Gulls breeding in the Wadden Sea spend their winter further to the south in The Netherlands, in Belgium and in northern France. Most adults move away from their breeding grounds, move south in August and return in February/March; a passage that goes undetected by seawatchers. The numbers of Herring Gulls at sea in May are relatively low and numbers of Herring Gulls increased to peak in late June/early July, when seawatchers recorded high numbers of Herring Gulls following trawlers (Platteeuw *et al.* 1994). In August, numbers of Herring Gulls observed at sea declined markedly, indicating a contraction away from the North Sea coastal waters when the breeding colonies are abandoned (Appendix 4, ^{App}Box 4.2).

Winter dispersal and migratory movements

Migration has evolved in many organisms (Alerstam 1990). The basic driving forces for migration are ecological and biogeographic factors like seasonality, spatiotemporal distributions of resources, habitats, predation and competition (Alerstam *et al.* 2003). The benefit of increased resource availability will be balanced by costs associated with the migratory process in terms of time, energy and mortality (Alerstam *et al.* 2003). Bird migration has been studied by means of ringing for over 100 years (Jenni & Camphuysen 2001). The use of colour-rings was a major and more recent breakthrough, allowing individuals to be observed and recognised from a distance (Shedden *et al.* 1985, Raevel & Duponcheel 1993, Meininger 1999, Rock 1999). New technological advances, especially tracking with satellite PTTs and GPS-loggers, have further revolutionised the studies of bird migration (Georges *et al.* 1997, Birdlife International 2004, Gill *et al.* 2008, Hebblewhite & Haydon 2010, Shamoun-Baranes *et al.* 2012). The two study species, large gulls of more or less similar size, represent different migration strategies. These alternative migratory strategies were not key parts of the Kelderhuispolder research project, but the differences between the two species are highly distinct an require at least some understanding and evaluation (Appendix 5) :

Herring Gulls breeding in northern Norway, in Russia and in the Gulfs of Bothnia and Finland are mainly migratory, but those breeding in The Netherlands and in many other parts of temperate Europe are generally considered dispersive or semi-residents (Landsborough Thomson 1924, Parsons & Duncan 1978, Glutz von Blotzheim & Bauer 1982, Cramp & Simmons 1983, Kilpi & Saurola 1984, Olsson 1988, Calladine 2002, Bosman *et al.* 2012). In the early days of the gull studies at Texel, an important and so far underexplored dataset was kindly provided by Arie Spaans: ringing details and 86,247 subsequent sightings of 3124 colour-ringed Herring Gulls marked as chicks in 12-14 colonies in The Netherlands between 1986 and 1988 (100 per annum per colony; Camphuysen 2008c). One-fifth (20.5%) of all sightings originated from the home-ranges (areas within a radius of 5km around the ringing place). Only 0.8% of all sightings were at over 300km from the natal colony. The maximum distance travelled did not vary much between adults, immatures, and juveniles, but the timing of outward and return movements was different for each of the age categories. With reference to studies in other European countries, it was concluded that Herring Gulls breeding in The Netherlands occupied a mid-position between dispersive and sedentary tendencies (Chapter 6).

Lesser Black-backed Gulls are essentially migratory throughout their range (Landsborough Thomson 1924, Schüz 1933, Baker 1980, Glutz von Blotzheim & Bauer 1982, Cramp & Simmons 1983, Kilpi & Saurola 1984, Alerstam 1990, Rock 2002, Bosman *et al.* 2012, Hallgrimsson *et al.* 2012). For Lesser Black-backed Gulls, migratory movements could be evaluated based on a combination of colour-ring sightings (mainly ringed 1986-1995), modern colour-ring data (ringed 2006-present), satellite tracking (SOVON/IfV Vogelwarte Helgoland; 2007-2011; Klaassen *et al.* 2011) and GPS loggers (UvA/NIOZ; 2008-2012; Appendix 5). Sightings of Lesser Black-backed Gulls ringed in The Netherlands were reported from The Netherlands, Belgium, France, Federal Republic of Germany, the United Kingdom, Italy, the Iberian Peninsula, and NW Africa (Algeria-The Gambia). The representation of adult Lesser Black-backed Gull colour-ring sightings in France, Portugal and Spain is overwhelming, indicating that these are probably the main wintering areas for birds breeding in The Netherlands (details in Appendix 5). Note, however, that ring-reading effort in NW Africa is comparatively low. Winter sightings were typically southwest of the breeding grounds (95% of all winter sightings south of 51°N in a narrow band to the SW of the ringing grounds (median direction of migration 207°, range 95% 188°-219°; Camphuysen *et al.* 2009). Recoveries in Italy, Algeria, and even those along the Spanish east coast can be considered extra-limital (^{App}Fig. 5.5). Of birds carrying Argos satellite PTTs ringed at Vlieland that wintered in Portugal, Spain or Morocco, the date of crossing of the Bay of Biscay was used as an indicator of the timing of their major legs of autumn and spring migration towards and from their final destinations in winter. Autumn migration (25 autumn crossings logger) was considerably more variable in timing (mean 12 October ± SD 44.1d) than spring migration (29 crossings documented; 25 March ± 16.6d; ^{App}Table 5.2, ^{App}Fig. 5.7).

Juvenile long-distance migration - Juvenile Lesser Black-backed Gulls colour-ringed at Texel left their breeding grounds later than older birds and wintered on average on further away than subadults and adults (^{App}Fig. 4.3). Individuals may have an innate predisposition to explore wintering areas primarily in a particular compass direction (external orienting cues, probably of the earth's magnetic field; Gwinner & Wiltschko 1978). Baker (1980) termed the initial movements of juveniles "exploration" rather than the more often used "post-fledging dispersal". Baker suggested that this phase of exploration aims at establishing a familiar area within, or beyond, the normal breeding range of the species in order to identify suitable places at which breeding can be attempted later in life. He considered the first autumn migration of a young bird as a continuation of that exploration process. "*Young birds in particular alternate migration units in the standard autumn direction with movements back along, and sideways from, the standard track or direction. Spring migration is a repeat of the autumn process.*" (Baker 1980). Southward movements in autumn by colour-ringed juvenile Lesser Black-backed Gulls were indeed a seemingly gradual, more time consuming process than in adults and immatures (2-5cy birds). We did not find many deviations from the standard directions of autumn movements, however.

Colour-rings versus modern instrumentation - As stressed in Chapter 6, enthusiast ring-readers (volunteers, amateur bird-watchers mostly) tend to collect data in areas where the reward (*i.e.* the frequency of colour-ring sightings) is high (e.g. refuse tips, harbours, breakwaters, beaches, and other areas where gulls occur in large flocks and can be read rather easily). Hence, the results show primarily where the ring-readers go. Nevertheless, the migratory flyways have been documented with great success with colour-ring sightings. The sample size that is possible with colour-rings and the fact that all age-categories can be ringed and monitored together compensate for the most obvious shortcomings. If the question is which *habitats* the birds use, satellite PTTs, GPS loggers and 'similar' devices are invaluable because the results are independent of the activities of observers. The birds are continuously tracked; some even for many years.

The logger data have demonstrated that Lesser Black-backed Gulls forage while underway to and from their breeding areas. Klaassen *et al.* (2011) observed that numerous stopovers are used and that their overall progress is relatively slow in comparison with most other migrants. The data suggest, however, that most birds return in time to be able to participate in the prospecting phase (*i.e.* during late March), although some birds do not arrive earlier than late April (Appendix 4). The interpretation of logger data is not always that straightforward, and it is an ongoing project to try and disentangle logger data into useful components of presumed or apparent [foraging] behaviour (Shamoun-Baranes *et al.* 2010, 2012ab, Bakker *et al.* 2012).

Most Herring Gulls winter so close to the breeding colony that a single day's flight would be enough to return. Some colour-ringed gulls with well known winter-"territories" near the breeding grounds were seen to travel to and forth the breeding colony on subsequent days prior to territory establishment. A single GPS-tagged Lesser Black-backed Gull utilising important stop-overs in winter in the UK returned briefly to England after a first return to the colony in spring. The results suggest that birds that have returned in spring still use a wide range of foraging opportunities, prior to the actual prospecting and laying phase within the colony. Unfortunately, there is no direct information on the arrival condition of potential breeding birds and if there would a need for females to enhance their physical condition by replenishing stores (fattening up) prior to egg-laying. Given the variations in the onset of laying discussed earlier (details in Appendices 3-4), this could be highly relevant information that will for now remain as a pending question.

Annual survival and Balance per Annum

The rate at which a population fluctuates depends not only on the fecundity (*B*) but also on the survivorship (or mortality rates, *D*) of individuals that belong to that population (Tinbergen 1953, Harris 1970, Davis 1975, Newton 1989, Aebischer & Coulson 1990, Perrins *et al.* 1991, Newton 1998, Siriwardena *et al.* 1999, Weimerskirch 2002, Skalski *et al.* 2005).

Lesser Black-backed Gulls and Herring Gulls are long-lived seabirds. Based on ringing recoveries, the maximum recorded life-span of Herring Gulls is 32 years and 1 month (Helsinki 71386) and of Lesser Black-backed Gulls 32 years and 9 months (London GM.02212; Perdeck & Speek 1963, Staav & Fransson 2006, Staav 2008, ^{App}Box 6.1). Wild birds usually live only a small fraction of their potential life-span and differ in this respect markedly from (modern western) man and from animals in captivity (Lack 1954). Annual survival rates in large gulls, as in many seabirds, vary around 85-95% (Coulson & Butterfield 1986, Pons & Migot 1995, Schreiber & Burger 2002), while those of young (juvenile) birds are normally considerably lower. The minimum age of first breeding in large gulls is usually between 4 and 5yrs (Glutz von Blotzheim & Bauer 1982, Cramp & Simmons 1983) and gulls can therefore often breed several times in their lives. Given a life-expectancy of somewhere between 10 and 20 yrs, anything between 5 and 15 breeding attempts would be realistic.

Actual survival rates are technically difficult to estimate (Clobert & Lebreton 1991). An important research question was, however, is the annual survival in line with expectations based on recent population trends? In Chapter 7 the apparent survival (*i.e.* survival confounded by permanent emigration; White & Burnham 1999, Allard *et al.* 2010) was estimated on the basis of re-sightings of colour-ringed birds within the colony. Apparent survival was assessed for adults of both species using re-sightings of colour rings deployed at Texel (details in Appendix 6 and Chapter 7). It appeared that the annual survival of Lesser Black-backed Gulls was substantially higher than that of Herring Gulls. In Herring Gulls, a mean apparent annual adult survival of only 79% was found in females and 86% in males. Apparent survival for both sexes combined varied between 81% and 100% (mean ≈91%) in Lesser Black-backed Gulls. Contrary to the earlier measurements of fecundity were the differences in annual survival between the two species more in line with expectations based on recent population trends.

Staying alive: the need for self-maintenance - The GPS tacking studies in Lesser Black-backed Gulls breeding at Texel revealed the occasional occurrence of exceptionally long or distant foraging trips that were difficult to explain in a context of optimal foraging. The characteristics, the frequency, and the possible triggers of these exceptional trips were examined in comparison with thousands more regular, shorter trips, in the context of reproductive performance and chick growth (Chapter 8). Exceptionally long and distant trips occurred irregularly, but every breeding season, and in most tracked individual birds. The hypothesis that exceptional trips were conducted only by failed breeders, but not by active breeders during incubation or chick care, had to be rejected. Exceptional trips in active breeders were relatively rare when the chicks were still young and highly vulnerable (<10d of age), however, and occurred mostly when chicks were large enough to be no longer in immediate need of adult company at the colony. Tracking data had revealed earlier that not all time spent at sea is used to forage and feed, but also to rest for hours on end (Shamoun-Baranes *et al.* 2010). Allocating time to rest on such trips could be an important aspect in the process of individual recovery from stressful periods, enhancing the individual survival probabilities and thereby future reproductive opportunities. Evidence is provided that these extraordinary trips provided additional time for individual birds (self-maintenance or self-provisioning, replenishing exhausted resources) rather than extra provisioning for the chicks. The reproductive success in birds that performed exceptional trips was not compromised, pointing at compensatory behaviour by partners. The results, a by-product of GPS tracking studies, are interpreted as evidence that time needed for individual maintenance by the parents themselves was important during breeding.

During breeding, the environmental conditions may deteriorate, or individual birds may be unable to meet the energetic demands of their offspring for other reasons. Several breeding attempts by gulls nesting at Texel have been given up and the chicks were left to starve to death (^{App}Fig. 3.11). It is tempting to believe, as Chapter 8 will show, that individual birds sometimes *temporarily* give up (leaving the burden of chick care to the partner), just to restore condition, and resume chick care after such a break. It would provide that third possibility between giving up a breeding attempt to enhance the likelihood of individual survival and to continue an attempt while risking an earlier death.

Intermittent breeding and floaters - As potentially long-lived seabirds, a current breeding attempt will have to be evaluated by both parents against the likelihood of individual survival and a future reproductive success (Weimerskirch 2002). Under poor conditions (low resources, poor individual condition), birds may forego breeding altogether. While both gulls have been described as 'annual breeders' (Cramp & Simmons 1983), it appeared that in anyone season at Texel a considerable number of adults did not breed, even though territories had been occupied and defended and nest bowls had been constructed in the prospecting phase (see also Calladine & Harris 1997). On average less than half the colour-ringed Lesser Black-backed Gulls (46.8 ± 15.8%) and two-thirds of the Herring Gulls (66.3 ± 11.4%, ^{App}Table 6.3) that returned to the breeding colony in any given year was subsequently demonstrated to breed. The results suggest that Lesser Black-backed Gulls at Texel breed on average once every 2.1 years. For Herring Gulls, a breeding frequency of once every 1.5 years can be estimated.

The nest counts at Texel in 2009-2011 resulted in high numbers of well-constructed nests in which no eggs had been laid. These sites were often occupied by territorial non-breeding pairs (ringed and unringed), were initially defended, but abandoned (or rarely visited) later in the season. Prospecting seabirds explore their future breeding place and obtain information about the colony. Decisions to forego breeding may relate to individual condition, or to foraging conditions in the prospecting phase (or *expected* conditions during chick care).

New (unringed and therefore anonymous) birds that bred, apparently filled sites that were at or near territories previously taken by other adults. A pool of non-breeding adult birds ("floaters") can buffer density fluctuations within a breeding population (Calladine & Harris 1997). If the availability of resources (food or nest sites) increases, members of that pool may attempt to breed. Floaters may comprise a large fraction of any bird population, and can be quick to fill breeding vacancies (Zack & Stutchbury 1992). Floaters regularly visit breeding territories which presumably allows them to assess the availability and quality of nesting territories. In many colonial seabirds, non-breeders remain in flocks separate from the breeding colonies (Hudson 1985), while older age classes of floaters are more likely to visit the breeding sites (Birkhead & Hudson 1977). It is unclear how this behaviour may influence their subsequent success in gaining a territory and a mate (Zack & Stutchbury 1992). The issues of recruitment, (adult) non-breeding, and intermittent breeding, are topics of current investigations. These issues require a long-term data set with colour-ringed birds that can be individually monitored over time.

Adults that had skipped one or more breeding season typically re-established territories close to or exactly at the initial breeding location. Intermittent breeding has been recorded or suspected for both species of gulls (Drost *et aL* 1961, Kadlec & Drury 1968, Migot 1992, Pons & Migot 1995, Calladine & Harris 1997). Drost *et al.* (1961) estimated 25% non-breeding in Herring Gulls (male 21%, n= 122, female 28%, n= 150) breeding in Wilhelmshaven (FRG). In 11% of the cases, both partners skipped a season simultaneously. Kadlec & Drury (1968) estimated that that

15-30% of the adult Herring Gulls in New England (Canada) did not breed in any given year. [Chabrzyk & Coulson (1976) and Coulson *et al.* (1982) commented that this last figure may have been inflated because it included 5-7 year old birds that have not yet bred]. Data obtained by a Leslie matrix model on demographic changes in French Herring Gulls suggested that a large proportion (c. 50%) of potentially mature birds did not breed (Migot 1992). In a later paper, Migot compared breeding parameters before and after the closing of a large refuse tip where breeders used to find most of their food (Pons & Migot 1995) and found only c. 2% non-breeders. Calladine & Harris (1997) found that 33-37% of adult Herring Gulls and 34-40% of adult Lesser Black-backed Gulls with previous breeding experience failed to breed in 1993-1994 respectively. About half of these birds failed to breed in both years.

Immature mortality – While adult Herring Gulls from Texel were characterised by their relatively low annual survival (Chapter 7), preliminary results suggest that young birds faced similar problems (Appendix 6, ^{App}Fig. 6.5). Vercruijsse (1999) found that at least 22% of all fledglings from his study colony at Schouwen in the 1990s reached the age of potential first-breeding (5 yr). Only 6% of the Herring Gulls that fledged from the Kelderhuispolder at Texel reached that age. In Lesser Black-backed Gulls at Texel the number of fledglings that reached sexual maturity (14%) was more than twice that of Herring Gulls; a difference that is reflected in the number of confirmed recruits of either species in the Kelderhuispolder in 2010-2012.

Recruitment and the Balance Per Annum - For a breeding population to remain stable, the breeding birds have to produce enough young that survive to breed themselves, to replace adults that die (Perrins 1991). With the adult annual survival rate roughly known (Chapter 7), it is possible to deduce the proportion of young that must survive to breed in a stable population (at equilibrium, the number of young surviving per pair to breed must equal twice the annual adult mortality). Birkhead and Sears (quoted in Perrins 1991) calculated the *Balance Per Annum* (BPA; the difference between the number of chicks per pair surviving to breeding age and the number of adults dying per pair per year).

Using preliminary results of colour-ring data (details in Appendix 6), it was estimated that from the first three cohorts (2006-2008), only 20% of the chicks (51 out of 254) of Lesser Black-backed Gulls and 13% of Herring Gulls (15 out of 114) had survived to potential breeding age (^{App}Table 6.1). Based on a mean fledging rate of 0.49 fledglings pair^{-1} (Table 2.1), the 20% juveniles of Lesser Black-backed Gulls that reached sexual maturity would result into 0.10 chicks pair^{-1} as potential recruits. Considering an annual adult mortality of 0.18 adults pair^{-1} (annual survival 91%; Chapter 7), the BPA would be -0.08 in Lesser Black-backed Gulls. With a mean fledging rate of 0.88 fledglings pair^{-1} in Herring Gulls, but with a higher juvenile mortality (87%), a marginally higher 0.12 chicks pair^{-1} would reach the age of sexual maturity. The higher adult mortality of *c.* 0.35 adults pair^{-1} (mean annual survival 82.5%) would lead to a BPA of -0.23 in Herring Gulls:

Individuals pair^{-1} annum^{-1}	fledglings	adults dead	juv. breeding age	BPA
Lesser Black-backed Gull	0.49	0.18	0.10	-0.08
Herring Gull	0.88	0.35	0.12	-0.23

In the absence of significant numbers of immigrants (*I*), both populations may thus be considered unstable or declining, but the former mainly as a result of low reproductive success, the latter mainly as a result of lower annual survival. Rather few genuine "recruits" (prospecting birds and confirmed breeders) have been demonstrated to have returned to the Kelderhuispolder colonies (Appendix 6). If the BPA assessments were based on only these birds, it would be considerably lower. The evidence for low levels of immigrants (*I*) and emigrants (*E*) is provided in Appendix 6.

Foraging ecology

Animals feed selectively. Food selection poses questions about decision rules to behavioural ecologists, about species diversity to the community ecologist and about niche segregation to evolutionary ecologists (Hughes 1993). Foragers should specialise on energetically high-value food that can be easily handled and consumed (profitable prey). If such prey items are scarce, absolutely or as a result of interspecific competition, lower valued prey items must be included in the diet. Competition for food reduces the availability and quality of food because it reduces forager encounter rates with preferred prey items (Sih 1993). Optimal Diet Theory (ODT) predicts that food depletion or reduced access to resources as a result of intense competition should result in broader diets (Sih 1993). Competition could also lead to spatial segregation of competing predators, whether or not associated with dietary shifts.

The catholic foraging habits of large gulls, certainly Herring Gulls, are legendary (Glutz von Blotzheim & Bauer 1982, Cramp & Simmons 1983, Pierotti & Good 1994), but how flexible these birds actually are is not that clear. Starvation events are not uncommon in large gulls, suggesting that when a given resource is in short supply, it may be difficult to quickly shift to another untapped or underexplored opportunity. What is clear, however, is that at the species level, Herring Gulls and Lesser Black-backed Gulls in most North Sea colonies are generalists, not specialists (Bergman 1960, Ehlert 1961, Harris 1965, Andersson 1970, Spaans 1971, Dernedde 1994, Nogales *et al.* 1995, Garthe *et al.* 1999b, Bellebaum *et al.* 2000, Dierschke & Hüppop 2003, Kubetzki & Garthe 2003, Coulson & Coulson 2008, Bustnes *et al.* 2010, Calvino-Cancela 2011). Currently, both Herring Gulls and Lesser Black-backed Gulls species are abundant, widespread and therefore significant components of the North Sea and Wadden Sea coastal ecosystems. In the historical overview in this thesis (Appendix 2), a variety of factors is listed, many of which (may) have affected adult survival, reproductive success and population dynamics at least to some extent. Large gulls, just as many other large bird species, have no serious predators as adults, and the availability of food is thus probably an important limiting factor (Lack 1954). A better insight in the foraging ecology of both species was therefore considered an important aspect of the studies, assuming that the carrying capacity of not just the intertidal, but also marine and terrestrial ecosystems had been shaping the most recent population trends (Spaans 1992). Underlying the studies of the foraging ecology of both species was the ambition to quantify food consumption in the context of the carrying capacity of coastal and nearshore ecosystems. To be able to do so, species-specific prey preferences, differences in prey profitability, and patterns and trends in prey availability have to be quantified. One of the first questions to be answered was considerably more basic: what exactly do the two gulls eat and when? The aim of this work was to assess the "mainstream" foraging activities of the population at large, the occurrence of individual specialisations in foraging behaviour and prey choice, and the demographic consequences of these aspects.

There is a rooted belief that '*gulls eat just anything*', which basically implies that an investigation of the foraging habits would be of little interest. But even if the feeding habits for the population at large may best be described in terms of "*taking almost anything available of suitable size, texture, etc.*" (Snow & Perrins 1998), a simple literature review shows that this is an over-simplification. Neighbouring colonies often differ in the composition of the utilised prey. Individual birds tend to specialise and rarely explore the complete spectrum of dietary possibilities that would characterise the species. It was the aim to combine information of foraging behaviour collected at sea (much of which collected prior to 2006) with dietary data collected during colony studies (since 2006). The use of electronic instruments and colour-rings provided a more direct link between foraging habitats, dietary biases, reproductive success and other vital rates.

Prey types – From the extensive dietary information presented in Appendix 7 it is obvious that while both species are generalists, there are clear preferences for certain prey types. In the egg phase, 246 different prey species or types were encountered, 48% of which were found in the diet of both gulls (overlapping resources). The 55 "unique" prey of Lesser Black-backed Gulls and 74 of Herring Gulls were all rarely encountered (frequency of occurrence <1%). Three commoner prey species were characteristic for Herring Gulls (absent in the prey spectrum of Lesser Black-backed Gulls) : Mussels *Mytilus edulis* (70%), Common Shore Crab *Carcinus maenas* (7%), and Cockles *Cerastoderma edule* (4%). During chick care, 280 different species or types of prey were found, 51% of which in the diet of both species. In total 47 rare prey species occurred only in Lesser Black-backed Gulls, 88 only in Herring Gulls. Rather many prey types were frequent (frequency of occurrence 1-25%), common (26-50%) or staple food (>50%) in one species, but rare in the other. Mussels (54% in Herring Gulls) were again non-overlapping commoner prey.

Of particular interest for the comparative study was the *overlap* in frequently or commonly occurring prey types (Table 2.3). Marine fish was the most important prey for Lesser Black-backed Gulls throughout the breeding season, but it was an important component of the diet of Herring Gulls during chick care in particular (cf. Spaans 1971, Chapter 9, Appendix 7). The fish list of both species is dominated by likely discarded species (demersal roundfish and flatfish; Appendix 7, ^{App}Box 7.6) and points at a potential area of competitive interactions between the two gulls: foraging opportunities behind commercial trawlers (Camphuysen *et al.* 1995; Appendix 7, ^{App}Box 7.7-7.9). The more fatty, energy rich fish species (sandeels Ammodytidae, clupeids Clupeidae, mackerels *Scomber scombrus*, *Trachurus trachurus*) are more frequently encountered in the prey samples of Lesser Black-backed Gulls than in those of Herring Gulls, even during chick care (details in Appendix 7). In the list in Table 2.3, "unidentified insects" and even "Coleoptera" (beetles) are rather diffuse groups in which the exact prey choice could in fact have been completely non-overlapping. All the other prey types are identified to species or genus level and these include terrestrial resources (earthworms *Lumbricus terrestris*, maize *Zea mays*, and eggs and chicks of other gulls in the colony), and various species of crustaceans.

Table 2.3. Overlapping prey spectra. Listed are prey species of which the frequency of occurrence was >1% (frequent or common) in both Lesser Black-backed Gulls and Herring Gulls during the eggphase and during chick care. Source: n= 10,234 prey samples, Kelderhuispolder 2006-2011. Details in Appendix 7.

Group	**Eggphase**	**Post-hatching**
Insecta	unident insect	unident insect
	Coleoptera spp	Coleoptera spp
Oligochaetes		*Lumbricus terrestris*
Crustacea		*Crangon crangon*
	Liocarcinus holsatus	*Liocarcinus holsatus*
Pisces		*Sprattus sprattus*
	Merlangius merlangus	*Merlangius merlangus*
	Trachurus trachurus	*Trachurus trachurus*
		Ammodytes
	Pleuronectes platessa	*Pleuronectes platessa*
	Limanda limanda	*Limanda limanda*
		Solea solea
Aves	large gull egg	large gull egg
		large gull pullus
Plantae	*Zea mays*	*Zea mays*

An overlap in frequently taken prey species is still no sure sign of resource competition. Peaks in egg consumption (a form of cannibalism) within the colony were different between the two predator species and actually mirrored species-specific differences in the timing of laying rather than just the availability of eggs in the colony (^{App}Fig. 7.1). Under the same conditions, the slightly larger Herring Gull would be expected to select and consume slightly larger sized prey than Lesser Black-backed Gulls, for as far as these prey would fall within the swallowing capacities of these birds (Swennen & Duiven 1977, Camphuysen 1994b, ^{App}Box 7.8-9). In fact, Whiting *Merlangius merlangus* and flatfish Pleuronectiidae transported into the colony by Herring Gulls breeding at Texel were substantially smaller than those captured by Lesser Black-backed Gulls (Appendix 7). Only the mean size of Swimming Crabs *Liocarcinus holsatus* fitted the expectation based on size-differences of the two predators. A direct comparison of size classes consumed by gulls is tricky if the *purpose* of the prey is left out of consideration (e.g. brought in to provision the chick, or taken by the adults themselves). However, all the available evidence, including data corrected for size-adjustments during chick care, suggests that Herring Gulls explored fish resources with different prey size characteristics than Lesser Black-backed Gulls.

Competition for prey – An important question that could not be answered during studies within a breeding colony was: what happens if the two species compete for similar prey. At-sea studies of discards consumption (prey preferences, size selection, competitive quality) of both species were analysed, using data that had been collected years earlier, in the same general area, onboard commercial trawlers and onboard fisheries research vessels. During sessions of experimental discarding, the success rates of the two species as scavengers could be compared directly (Appendix 7, ^{App}Box 7.7-9, Chapter 11, Camphuysen 1994b).

In seabird feeding frenzies at the trawl of fishing vessels, with both species present in substantial numbers, Herring Gulls were on average more successful than Lesser Black-backed Gulls. Herring Gulls were capable of swallowing a wider range of size categories and tended to select on average slightly larger prey than Lesser Black-backed Gulls, as could be expected from the differences in body size. The differences were small, but consistent in all sessions of experimental discarding where both species were represented, in spring and in summer, near breeding colonies and further offshore. The results of the discard experiments on board a commercial beamtrawler in summer in the North Sea just to the north off the Frisian islands (details in ^{App}Box 7.8) were indicative for a dominance hierarchy among scavengers with Great Black-backed Gulls at the top, Herring Gulls second, and Lesser Black-backed Gulls third in rank. The differences between Herring Gulls and Lesser Black-backed Gulls in foraging success were small, but consistent (see also results of discard experiments on board research vessels; ^{App}Box 7.9). Herring Gulls took relatively many morsels of offal (success indices 1.33 versus 0.73) and gadoid roundfish (SI 1.34 versus 0.87) in comparison with Lesser Black-backed Gulls, suggesting that the former was most successful in getting easy (smooth) prey with a higher calorific value than the latter. Lesser Black-backed Gulls took significantly more (spiny) gurnards than Herring Gulls (SI 1.27 versus 0.35; ^{App}Box 7.7). There was no evidence that Lesser Black-backed Gulls outmanoeuvred Herring Gulls as scavengers behind fishing vessels. The results of discard experiments behind trawlers in summer in the Southern North Sea indicated that, within the dominance hierarchy established behind the boat during hauling and catch sorting, Great Black-backed Gulls were at the top, Herring Gulls ranked second and Lesser Black-backed Gulls ranked third (from a combination of success indices and vulnerability to kleptoparasitism; ^{App}Box 7.7-9).

Changes in resources- Feeding opportunities and other environmental factors have changed over decadal scales, and gulls must have adapted in order to survive and breed successfully. Seabirds respond mostly with variations in diet, foraging behaviour and reproductive success rather than with adult survival rate to changing environmental conditions (Cairns 1987, Montevecchi 1993, Jones *et al.* 2002). Cairns (1987) suggested that seabird survival rates are low only when their prey is extremely scarce, rise quickly with slightly improved feeding conditions, and are constant in moderate to good feeding conditions (Jones *et al.* 2002). Penniman *et al.* (1990) referred to the element of plasticity exhibited by Western Gulls *Larus occidentalis*, and their ability to fall back on a predictable food supply of offal and garbage when marine food was not readily available. Their expectation implied that there always is that apparently untapped resource available in case of a shortage of more natural or preferred prey. One could wonder if such an underexploited resource indeed exists.

Seasonal changes in prey availability are just another challenge these birds have to cope with. The gull studies at Texel would need to identify the exact location of the foraging areas and the actual resources, to assess the energetic constraints involved in successful foraging and feeding for breeding birds. The first years of study were important to identify prey items and to get a feel for intra-specific variability, intra-season variability and the variability between seasons. The next step was to gather information on the whereabouts of foraging gulls. Once we have collected firm data on both these aspects, the next step will be to try and quantify the most important resources, followed by assessing resources of alternative prey.

The dietary studies of Herring Gulls breeding in the Kelderhuispolder were sufficiently detailed to assess intra-pair variations in prey choice throughout the breeding season (Appendix 7). Differences in reproductive success between pairs with different prey spectra could be examined. Inter-pair dietary specialisations (within and between the different phases of breeding) were studied empirically and related to fecundity parameters in Herring Gulls (Chapter 9). It appeared that the overall dietary spectrum and the level and incidence of dietary specialisation changed when the energetic demands increased during chick care. Prior to hatching, most pairs focussed entirely on bivalve prey, but 25% of the pairs had distinct dietary biases. During chick care, chick growth and fledging rates were strongly correlated with the amount of fish prey provided, prey spectra diversified overall and fewer specialists were detected. Particularly low chick growth rates were found in pairs that had a dietary bias towards crustacean prey. Intra-population niche variation meant that individuals within the same population were subject to different selective pressures, which can be beneficial in periods of major environmental change.

Lesser Black-backed Gulls generally produced rather fewer prey remains around the nest, and intra-pair differences were therefore more difficult to quantify. The results summarised in Appendix 7 suggest, however, that marine fish prevailed throughout the breeding season and the differences between pairs were seemingly smaller (or less obvious).

Sexual differences in provisioning - Combining GPS tracking data with dietary information and reproductive status we found sexually distinct foraging strategies in Lesser Black-backed Gulls, that were maintained throughout incubation and chick-care (summarised in Chapter 10). Individuals differed in foraging behaviour and foraging range, trip duration and the proportion of time at sea increased with structural size of the birds. During foraging trips, the marginally larger males travelled farther from the colony than females, spent more time in the North Sea. The differences between the sexes might be considered ends along a continuum of individual variation in foraging behaviour (Bolnick *et al.* 2003). Even with only 34 tracked individuals, the habitat use varied from almost completely terrestrial to completely marine habitat use, suggesting a tendency of individuals to specialize on particular foraging areas, at least during the breeding season.

Males were apparently feeding mostly for fish (discards at offshore trawlers) in a competitive setting with other scavengers, but with few alternative resources nearby. Females foraged predominantly on land, accessed a wider variety of resources and must have had a broader prey spectrum. In the Wadden Sea, however, they utilised shrimp fishing vessels in deep gullies near the colony. The foraging distribution of female Lesser Black-backed Gull overlapped more with that of the more powerful Herring Gulls, which would involve inter-specific competition for discards at shrimpers.

The utilisation of marine habitats

The offshore distribution of seabirds has been one of the prime subjects of long-term studies in the North Sea (Reid & Camphuysen 1998). In summer, Herring Gulls and Lesser Black-backed Gulls are largely confined to nearshore waters (Camphuysen & Leopold 1994, Stone *et al.* 1995). In winter, Lesser Black-backed Gulls have more or less abandoned these latitudes, while Herring Gulls are much more widespread throughout the North Sea. In Appendices 7-8 the offshore distribution of large gulls is characterised. Topics include (1) the offshore distribution from ship-based surveys (from Camphuysen & Leopold 1994, updated), (2) a comparison of the two gulls feeding at fishing vessels throughout the North Sea and year-round, and (3) the consumption of discards throughout the North Sea (from Camphuysen *et al.* 1995), (4) natural, offshore, multi-species feeding associations for fish prey (from Camphuysen & Webb 1999), and (5) novel findings based on recent tracking studies, including (6) sex-specific foraging strategies (Camphuysen *et al.* under review), and (7) observations of gulls resting at sea (Shamoun-Baranes *et al.* 2010).

The data presented in Appendix 8 have further emphasised the status as summer visitor (and passage migrant) of Lesser Black-backed Gulls in the North Sea. Their abundance between October and March is low, also in recent years, despite an apparently increased tendency to winter in the UK and in the French Channel area (according to Alerstam 1990). In spring and summer, Lesser Black-backed Gulls occur further offshore than Herring Gulls (notably in the NW North Sea). Herring Gulls occur year-round, but are widespread in the North Sea only in winter when they are distributed throughout the North Sea, in inshore as well as in offshore waters and even including the central North Sea. The SOVON Satellite PTTs failed to show extensive use of marine resources by Herring Gulls, apart from frequent visits to coastal breakwaters (coastal shellfish on hard substrate). This was true in winter as well as during the breeding seasons and it casts doubt over the reproductive status of birds that do scavenge at offshore trawlers in summer and on the breeding origin of the birds occur within the North Sea in winter.

The southern North Sea as a foraging area- The southeastern North Sea is currently one of the most important areas for Lesser Black-backed Gulls in western Europe (Skov *et al.* 1995, Stone *et al.* 1995; Appendix 8). It is this area where beamtrawlers are operating most intensively and are the dominant fishery (Rijnsdorp *et al.* 1998, Jennings *et al.* 2001, Hutton *et al.* 2004). The establishment of a so-called "Plaice-box" (a partially closed area in the North Sea, established in 1989 to reduce the discarding of undersized Plaice *Pleuronectes platessa* in the main nursery areas) has banned larger beamtrawlers from nearshore areas off the Frisian Islands (Pastoors *et al.* 2000), but smaller vessels occur throughout coastal waters of the southern and southeastern North Sea, the Western Wadden Sea included (see also Appendix 9). The smaller beamtrawlers are allowed to fish within 12 nm of the coast and within the plaice box (a closed area used to reduce fishing mortality) but large beamtrawlers of (>300 HP) are allowed to fish only outside the 12 nm limit and outside the plaice box. The seabirds at sea surveys confirmed that Lesser Black-backed Gulls in summer are by far the most numerous scavengers at distant beamtrawlers (Chapter 11, Appendix 8). GPS logger data confirmed that Lesser Black-backed Gulls visit both the nearshore fishing grounds as well as those several dozens of miles from the coast. For breeding Herring Gulls, the more distant large beamtrawlers are too far offshore to be of interest. The observations on board a commercial beamtrawler in the 1990s in the German Bight, however, showed that rather large flocks of fully mature Herring Gulls join these fleets at distances away from the colony. Their status of these birds is unclear, but it is possible that non-breeding adults (parts of the floater population) utilise these offshore foraging opportunities.

The marine habitats of Lesser Black-backed Gulls breeding at Texel include the shallow and turbid nearshore coastal waters (0-10m depth contours) immediately bordering the beaches and the island Noordhaaks, the still shallow, but gradually deeper waters to the west towards the Brown Ridge (Bruine Bank; 10-30m deep). In summer, under calm conditions, the most turbid nearshore waters are separated from the deeper waters by a distinct front (the coastal front). Foraging gulls (Lesser Black-backed Gulls included) often tend to concentrate their attention at the front and foraging conditions are often different within and beyond that zone. To fully appreciate the behavioural differences in these respective areas, the GPS logger data will need to be analysed in considerable detail (currently ongoing project with the Bouten group of the IBED/University of Amsterdam in which accelerometers will be used to "assess" the behaviour of tagged individuals with high resolution settings). A third area is the boundary between the mixed waters of the Southern Bight and the thermally stratified waters of the Central North Sea: the Frisian Front area

(Pingree & Griffiths 1978, 1980, Creutzberg 1989,Markones *et al.* 2008). Lesser Black-backed Gulls are common in the Frisian Front area (Chapter 11), but birds from Texel are probably poorly represented (GPS tagging results, ^{App}Fig. 8.9). How exactly important areas for seabirds should be separated from less important ones is the topic of Chapter 13. Ship-based survey and tracking data provided two complementary perspectives of marine habitats. Data loggers are normally fully independent of observer effort (recording data also at night), but for example species interactions cannot (yet) be derived from the data obtained. Instrumented individual birds from one or more breeding colonies give no information about the whereabouts of the rest of the population: other breeding birds from nearby or distant colonies, non-breeding adult birds as well as immatures. A combination of tracking data with ship-based surveys (and special attention for behaviour patterns) is therefore recommended.

The utilisation of intertidal and terrestrial habitats

The international Wadden Sea (Denmark, Germany and The Netherlands), with a surface area of *c.* 10,000 km², represents the largest marine wetland in Europe. Wetlands of comparable size are rare elsewhere in the world (Wolff 1976). The characteristic hydrographical properties of the area, combining a high primary production with additional import of organic matter create the primary food source on which high densities of crustaceans, fish, birds, and marine mammals are dependent. Benthic macrofauna are an integral component of the Wadden Sea ecosystem and they provide food sources to humans and many animal species (Compton *et al.* 2012). Many of the birds are shorebirds and waterbirds that use the Wadden Sea either as a wintering area, or as a stop-over between wintering and breeding grounds. It was an ambition to set up studies on waterbirds utilising the Wadden Sea also during the breeding season, in order to evaluate effects of fluctuations in prey stocks on demographic parameters more directly.

The Herring Gull is, or was, the second most important molluscivorous bird species in the Dutch Wadden Sea in terms of annual flesh consumption (Smit & Wolff 1981, Cadée 1995). The Lesser Black-backed Gull is a newcomer in Dutch nearshore waters. Both species breed in high numbers on the Wadden Sea islands must be considered important (apex) predators/scavengers in the coastal zone and within the Wadden Sea. The results of the study presented Appendix 9 indicate that the intertidal resources are the principal domain of Herring Gulls. Intertidal areas around Texel were almost exclusively exploited by Herring Gulls (Appendix 7 and 9). Shore crabs and bivalves typically exposed during low tide at intertidal mudflats, are common prey for Herring Gulls, rarely taken by Lesser Black-backed Gulls. This is nothing new, except that the recent tracking studies revealed that Lesser Black-backed Gulls from Texel do forage in the Wadden Sea in considerable numbers, but almost exclusively in the deeper gullies where fishing vessels operate. There was no evidence for Lesser Black-backed Gulls searching for prey on Wadden Sea mudflats or that they were commonly foraging in any of the other intertidal areas. On the North Sea beach, however, moribund Atlantic jackknife clams *Ensis directus* were commonly utilised by Lesser Black-backed Gulls, but during these ephemeral mass strandings the birds were clearly outnumbered by Herring Gulls.

Breakwater mussels - Herring Gulls nesting at Texel appeared to utilise the resources on breakwaters along the mainland coast of Noord-Holland (mainly mussels *Mytilus edulis*, exposed during low tide) in great numbers. These hard substrate mussels attracted Herring Gulls from Texel particularly in summer and must be seen as the most important intertidal foraging area for them. It is a predictable and large resource (low tide) with few competing species (low numbers of Oystercatchers and some other waders). There was a distinct seasonal pattern in numerical abundance of foraging gulls from Texel on the mainland coast breakwaters (details in Appendix 9). Based on year-round ring-reading effort, numbers of birds from Texel were lowest in winter (Dec-Mar), while a marked increase occurred in Apr-May, followed by a slight dip in Jun-Jul, and a peak period from late July through September. In fact, Herring Gulls from around the country were attracted to this area, numbers were particularly high in August-September.

From recent observations in the Marsdiep area, a seasonal pattern in body mass index (BMI, gAFDM mm^{-3} 10^6) could be deduced with a peak in 'mussel quality' in May-July and a distinct dip in January-March (Appendix 9). A rapid increase in mussel BMI in spring coincided with increasing exploitation rates of the Noord-Holland breakwater mussels by adult Herring Gulls from the Texel colonies. When the mussel BMI gradually declined in late summer, however, the numbers of foraging Herring Gulls continued to increase, until they fell in line with a continuing decline in mussel BMI in autumn and early winter. The peak in numerical abundance of adult Herring Gulls occurred just *after* the peak in mussel condition. An explanation for this "mis-match" is that this sector of mainland coast is attractive for Herring Gulls for more reasons than just the availability or quality of mussels. Large roosts are formed in the area on beaches, on the dikes, and in the hinterland (arable land and grasslands with limited human disturbance). Aug-Sep is a phase during which large gulls undergo a complete (post-nuptial) moult and the easy and nearby access to mussels (of still rather high quality) probably is an attractive bonus for these birds.

Inland resources - Terrestrial resources are shared by both species, but the exact overlap (or differences) in prey choice needs further attention. Sewage plants, cities, rubbish dumps, meadows, and agricultural fields offer resources that are commonly shared between the two species. There is a poorly documented but widespread belief that large gulls increase in numbers on inland foraging areas, backed up by an increase in inland breeding attempts (Vegelin 1989, Van der Helm 1992, Cottaar 1994, 2002, Poot 2008). From mammalian prey found in diet studies at Texel, Vlieland and elsewhere in The Netherlands, it could be demonstrated that both gull species do indeed utilise resources on the mainland (Chapter 14, Appendix 9). Specialised coastal nesting birds and a majority of individuals in an inland colony were found to feed on mammals frequently. Most mammalian prey may have been obtained on inland fields, during farming activities, some may have been captured within the colonies, and some were scavenged at roadsides.

The importance of landfill areas for Herring Gulls is (or was) beyond doubt (Spaans 1971, Burger 1981, Coulson *et al.* 1987, Belant *et al.* 1993, Duhem *et al.* 2005). This anthropogenic source of food has often been assumed to have facilitated the marked increase of populations of scavenging seabirds and as such have been responsible for the success of gulls in Western Europe (Spaans 1971, Kihlman & Larsson 1974, Horton *et al.* 1983, Blokpoel & Spaans 1991, Pons 1992, Vermeer 1992, Pons 1994, Kilpi & Oest 1998, Bellebaum *et al.* 2000, Ratcliffe 2004). As shown in Appendix 2 and 9, the availability of domestic refuse from landfill areas within The Netherlands has declined markedly in recent decades as a result of changes in waste management (Werkgroep Afvalregistratie 2007). In countries like Portugal and Spain but also within the UK large and accessible open landfill remains the predominant method of waste disposal (Anon. 2001, Price 2001). Target waste management percentages for individual countries within the European Union vary greatly: *i.e.* France and the Netherlands dispose only *c.* 10% of their waste via landfill, whereas the United Kingdom has set the limit at 60% (Anon. 2001). Hence, as an overwinter resource, landfill areas may still be important for (migratory) Lesser Black-backed Gulls, but much less so for the largely resident or dispersive Herring Gulls.

A bias in foraging distribution - One striking result of the recent colour-ring projects and tracking studies of birds breeding at Texel was the relatively large number of sightings of both species of gulls to the south and southeast of the study colony (^{App}Figs. 8.8, 9.2). The northern half of the Island Texel was apparently visited by a small number of birds from the Kelderhuispolder and Geul colonies. The high number of foraging gulls on the northern half of Texel and off the NW and NE coasts were apparently birds breeding on other colonies on the island or, as also found in the satellite PTT tracking data, were birds from Vlieland (IfV & SOVON unpubl. data; ^{App}Box 5.1). An explanation for the S-orientation of the gulls breeding at the southern tip of the island (also an explanation for the large number of breeding pairs in these colonies) could be the recent history Red Foxes in the dune areas of Zuid- and Noord-Holland (Appendix 2). Ground-nesting is now virtually impossible, but the feeding opportunities are likely similar as before. Gulls from the dunes in Zuid-Holland have probably moved to the industrial areas of Maasvlakte and Europoort, while those from Schoorl and Callantsoog have moved to safe havens in IJmuiden and at Texel. Their feeding areas off the mainland coast (in case of the birds from Texel between IJmuiden and the island itself) are still important.

Pulling the strings together

The next 12 chapters are topical papers, most of which have touched upon in this introduction. Considerably more material is included in the Appendices 1-10. The conclusions are drawn in a synthesis (Chapter 15), which is a final chapter just preceding the appendices and the list of references, where the research questions formulated at the beginning of the studies are addressed. It is clear that not all questions could be answered at this stage and new issues have emerged in the course of the project. The synthesis therefore also addresses new research needs: overseeing the data that were collected over the past field seasons, considering the results and patterns found, what type of data should be given priority in future studies of the same population.

3. Cyclic, synchronised chick starvation events in generalist seabirds caused by periodicity in fisheries discards availability

Reviewed **Marine Ecology Progress Series** [in revision]

Kees (C.J.) Camphuysen

Royal Netherlands Institute for Sea Research, NIOZ, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands
E-mail: kees.camphuysen@nioz.nl

Abstract Cyclic fluctuations in chick growth were found in two species of seabirds, large gulls Laridae, breeding sympatrically in the southern North Sea. Similar drops and gains in body mass in many inspected nests during subsequent visits, indicating alternating periods of low and more favourable provisioning. Body mass increments of chicks were significantly reduced in weekends, especially at higher age when energetic demands are high. A weekly rhythm in commercial fishing effort matched these patterns exactly. Both seabirds are ecological generalists, but a single prey resource, fish prey provided as discards from trawlers, appeared crucial during the final phase of chick-rearing. Population-level consequences are foreseen for both species if the European Common Fishery Policy will succeed in the otherwise much needed instigation of sustainable fisheries.

Key words: fisheries discards – scavenging seabirds – fitness consequences – population dynamics – European CFP

Introduction

Many studies have shown that seabirds are sensitive to changes in food supply, and therefore have potential as monitors of fish stocks (Furness & Camphuysen 1997). However, responses vary among species and care must be taken when interpreting seabird data as proxies for fish abundance or vice versa. Most large gulls Laridae, for example, have opportunistic foraging strategies and a broad prey spectrum (ecological generalists). As a result, factors influencing foraging success and chick provisioning rates are usually not easy to identify and population dynamics may be difficult to interpret.

In the Netherlands, as in most countries around the North Sea, recent population trends of two such ecological generalists, Lesser Black-backed Gulls *Larus fuscus* and Herring Gulls *Larus argentatus*, can be characterised by prolonged periods of exponential increase followed by a stabilisation or even a decline in breeding numbers (Spaans 1998a). The timing was different, however, with Herring Gulls peaking in the late 1980s and Lesser Black-backed Gulls in the early 21st century (Van Dijk *et al.* 2010). Herring Gulls have declined since the early 1990s, while numbers of Lesser Black-backed gulls are now stabilising or in decline. In counts of breeding birds in the same area, examined year by year, almost any pattern of fluctuation can be found (Newton 1998). Populations of long-lived seabirds such as large gulls, however, normally remain fairly stable through time. Life history theory predicts that long-lived (‘K-selected’) species mature late, have small clutches, few large offspring, make smaller reproductive efforts and have a high adult annual survival probability (MacArthur & Wilson 1967, Pianka 1970, Stearns 1992). Population declines may therefore become apparent only after many years of breeding failures. Population status may be assessed more directly by measuring vital rates, such as reproductive success or annual survival (Eberhardt 2002, Gaston *et al.* 2009). In an attempt to understand recent population dynamics of Lesser Black-backed Gulls and Herring Gulls in the southern North Sea, the foraging ecology, breeding success and demography were investigated in a comparative study in one of the largest mixed colonies of the western Wadden Sea, At Texel (The Netherlands) in seven consecutive breeding seasons (2006-2012).

In most colonies in the North Sea, Lesser Black-backed Gulls appear to be more marine orientated and travel further offshore on foraging trips than Herring Gulls (Camphuysen 1995a, Garthe *et al.* 1999a). While at sea, both species are primarily scavengers for discards behind fishing vessels (Garthe *et al.* 1996), although more natural prey (including swimming crabs, nereid worms, pelagic fish) may also be important (Schwemmer & Garthe 2005, Luczak *et al.* 2012). Herring Gulls also rely heavily on resources in the intertidal zone, preying upon bivalves and intertidal crustaceans. The intertidal zone is rarely exploited by Lesser Black-backed Gulls. Both species forage also on inland sites (mainly insects, fruits, mammals, and domestic refuse; Camphuysen *et al.* 2006, 2010). In the present study, in line with earlier reports (Harris 1965, Götmark 1984, Garthe *et al.* 1999b, Dierschke & Hüppop 2003), there was no shortage of evidence of ecological differences between the two taxa. Despite these differences, however, developing chicks of both species experienced cyclic, and often synchronised episodes of starvation (a collective and substantial loss of mass in chicks), pointing at some single, perhaps shared, key resource. In this contribution the characteristics, likely cause(s), and population-level implications of these episodes of starvation are evaluated.

Methods

This study was carried out in part of a large mixed colony of Lesser Black-backed Gulls *Larus fuscus* (LBBG) and Herring Gulls *Larus argentatus* (HG), in the Kelderhuispolder on Texel (Frisian Wadden Sea islands, The Netherlands 53°00'N, 4°43'E). Within the colony at large, approximately 11,500 pairs of Lesser Black-backed Gulls and just over 5000 pairs of Herring Gulls are breeding. The breeding colony is situated at the crossroads of the western Wadden Sea and the southern North Sea. Strong tidal currents flow through a narrow passage between the mainland (Den Helder) and the island, and the main foraging areas for this population include open sea (fish and benthic fauna, including fisheries discards), freshwater ponds, tourist resorts (including restaurants), agricultural land, sewage plants, rubbish tips and mainland cities.

Ecological data were collected from April to August, 2006-2012. Prior to egg-laying the colony was visited with increasing frequency until the first eggs were found along a preset trail leading through the prime breeding habitats. Data on timing, clutch size and hatching success were collected annually from *c*. 80 marked nests in each species (Camphuysen & Gronert 2010a). In order to monitor chick development and survival after hatching, *c.* 20 (HG) or *c.* 40 (LBBG) randomly chosen nests were surrounded by a 50 cm high, about 16-25m^2 wide enclosure of 2cm mesh chicken wire halfway incubation. Nests were monitored every third day, until all enclosed young had either died or fledged (at 40d of age). Rainy days were avoided by conducting a control one day earlier or later (weather dependent). To minimise disturbance within the colony the observers (max 4 per visit) stayed close together during the work and chicks were removed from their enclosures during the measurements. Measurements included age since hatching (d), various assessments of structural size and development (head length, bill length, wing length, tarsus length, moult) and body mass (g). Food samples (spontaneously regurgitated prey remains) were collected from territories throughout each breeding season. In this paper, frequencies of occurrence of main prey types are presented (Barrett *et al.* 2007), based on 10,647 food samples (5143 LBBG, 5504 HG) collected in 2006-2012, only to demonstrate species-specific differences in main prey types prior to an post-hatching at the study colonies. A full analysis of the diet is beyond the scope of this contribution.

During 2006-2012, total of 376 nests were monitored from hatching to fledging or failure (263 LBBG, 113 HG), holding 799 chicks (565 LBBG, 234 HG). Body mass increments (g d^{-1}) were based on two subsequent weighings within 3d intervals (range 1-4d). The three day measurement rhythm resulted in a more or less even coverage of effort over the week (2006-2012, 149 field days in total, Mon, 21x; Tue, 22x; Wed, 25x; Thu, 21x; Fri, 23x; Sat, 17x; Sun, 20x). A total of 10,786 weighings of developing chicks were performed (6656 for Lesser Black-backed Gulls, 4130 for Herring Gulls), leading to 5393 assessments of body mass increments. Chicks that died or were predated at a very young age (<15d) were excluded from the analysis of the occurrence of mass losses with increasing age in Table 1. Due to a more favourable survival of Herring Gull chicks, on average 8.8 mass increments chick^{-1} were assessed in Herring Gulls, against 5.9 chick^{-1} in Lesser Black-backed Gulls. Individual pairs ('nests') cared for 1, 2 or 3 offspring. For each measuring date, therefore, the overall mean growth increment was calculated using mean growth increments for each nest as individual values.

Synchronised starvation events were characterised as dates on which litters, overseeing all monitored nests of a species (including all chicks, irrespective of later fledging success), on average had lost mass from one weighing session to the next (a negative overall growth increment). On the other extreme end, collective 'growth spurts' (mass gain) were dates on which, on average, litters had gained at least 30 g day^{-1} from one weighing session to the next. At least 5 nests per species needed to be monitored to obtain an acceptable value on collective decline or increase. To illustrate examples of synchronisation in mass increments (collective mass losses or gains), the body mass measurements for all chicks known to have fledged were plotted against date of measurement. A mean body mass was calculated for all these chicks combined, from the point that most chicks had hatched.

Actively breeding Lesser Black-backed Gulls were known to forage mainly within an 80km range around the colony; relatively rarely at greater distances (unpubl. GPS data monitoring >2000 foraging trips of 34 individuals; Shamoun-Baranes *et al.* 2010, Camphuysen *et al.* 2012, Shamoun-Baranes *et al.* 2012). Information on fishing fleet presence within a 80km radius around the colony was obtained from the Ministry of Economics, Agriculture and Innovation (black-box data). Summer data (April-August) were selected from daily information covering 2006-2010. All vessels used for the analysis were bottom trawlers (shrimpers and larger beam trawlers). The number of vessels present per day within that area was used as a proxy for the availability of discards within the foraging range.

Results

Egg laying and hatching - Mean egg-laying (± SD) in Lesser Black-backed Gulls varied from 10 May ± 4.2d in 2008 to 18 May ± 4.9d in 2012. Mean egg-laying in Herring Gulls was always earlier and this varied from 4 May ± 4.5d in 2011 to 10 May ± 5.5d in 2006. The difference in laying peak between the two species amounted to 5d in 2006, 2d in 2007, 3d in 2008, 6d in 2009, 9d in 2010 and 2011 and 11 d in 2012. The mean date of hatching differed more or less accordingly: a variation between 5 Jun (2008) to 14 June (2012) in Lesser Black-backed Gulls and 31 May (2011) to 6 June (2006). The difference in timing between the two species, was smaller in the first four seasons (2-6d difference) than in the last three (9-11d difference).

Chick growth - The body mass of chicks would typically slowly increase immediately after hatching, conform the expected sigmoid growth curve, and this increase accelerated between 5-20d of age (a period of near-linear growth). Few chicks that would survive at least two weeks of age were found to have lost mass between two subsequent weighings in the first 15 days of their lives (2.3% of 915 observations of body mass increments in Lesser Black-backed Gull chicks were negative, 0.9% of 655 records in Herring Gull chicks). Body mass losses between subsequent weighings became more frequent with increase age, until between one third (Herring Gull) or nearly half (Lesser Black-backed Gulls) the increments close to hatching were negative (Table 3.1). Between hatching and fledging (at 40d of age), in total 14.3% of all body mass increments of Lesser Black-backed Gulls (n= 2390) and 13.4% of all Herring Gulls (n= 1824) turned out to be negative. Fledging chicks that could be measured had attained a mean (± SD) body mass of 674 ± 136g (max 920g, n= 76) in Lesser Black-backed Gulls and 791 ± 144g (max 1063g, n= 91) in Herring Gulls.

Table 3.1. Measurements of body mass increments (n), the average and peak increments (g chick d^{-1}) with age, and the occurrence of weight losses (n, %) calculated for chicks that reached at least two weeks of age, Kelderhuispolder colony, 2006-2012.

	Age	**1-5**	**6-10**	**11-15**	**16-20**	**21-25**	**26-30**	**31-35**	**36-40**
Measured increments	LBBG	187	362	366	442	364	290	233	146
	HG	152	242	256	308	252	250	217	147
Average gain (g chick d^{-1})	LBBG	11.5	20.2	23.5	21.6	16.5	13.3	10.0	3.3
	HG	12.7	21.2	27.9	27.6	21.8	10.9	7.8	8.9
Peak gain (g chick d^{-1})	LBBG	26.7	78.5	56.7	82.0	70.0	70.3	74.3	62.0
	HG	35.0	54.7	60.7	75.0	115.0	71.7	80.0	75.0
Mass losses (n)	LBBG	4	5	12	32	71	76	76	66
	HG	1	1	4	11	29	72	75	52
Mass losses (%)	LBBG	2.1	1.4	3.3	7.2	19.5	26.2	32.6	45.2
	HG	0.7	0.4	1.6	3.6	11.5	28.8	34.6	35.4

Table 3.2. Events of collective body mass reductions (mean <0 g chick day^{-1}) in Lesser Black-backed Gulls and Herring Gulls, Kelderhuispolder 2006-2012. Increments are expressed as g chick mass day^{-1}, and the number of monitored nests, the mean age of chicks under care and the proportion of nests (%) in decline are provided.

Species	**Date**	**Day**	**Nests**	**Age**	**Increment**	**Nests in decline**
LBBG	29/06/2008	Sun	7	26.2 d	-9.4 g d^{-1}	57%
	13/07/2008	Sun	7	35.6 d	-3.7 g d^{-1}	71%
	05/07/2009	Sun	15	26.2 d	-3.6 g d^{-1}	47%
	11/07/2009	Sat	14	32.8 d	-3.5 g d^{-1}	43%
	11/07/2010	Sun	24	33.0 d	-8.4 g d^{-1}	67%
	03/07/2011	Sun	24	23.4 d	-1.0 g d^{-1}	42%
	09/07/2011	Sat	21	28.9 d	-0.9 g d^{-1}	67%
	15/07/2011	Fri	15	34.0 d	-21.8 g d^{-1}	100%
HG	04/07/2006	Tue	6	25.8 d	-1.8 g d^{-1}	67%
	13/07/2008	Sun	5	35.7 d	-16.7 g d^{-1}	100%
	05/07/2009	Sun	9	31.9 d	-14.3 g d^{-1}	89%
	27/06/2010	Sun	16	26.1 d	-7.5 g d^{-1}	63%
	03/07/2010	Sat	14	31.9 d	-1.1 g d^{-1}	43%
	03/07/2011	Sun	9	32.8 d	-1.6 g d^{-1}	67%
	01/07/2012	Sun	17	28.5 d	-9.8 g d^{-1}	76%

Collective growth reductions and growth spurts - Even in the earliest years, it was noted that substantial mass losses, but also substantial mass gains (growth spurts), often involved many chicks at the same time, but not necessarily both species simultaneously (examples in Fig. 3.1). Serious starvation events (overall chick mass increment negative, usually more than 50% of all monitored nests involved) were recorded 8x for Lesser Black-backed Gulls and 7x in Herring Gulls (Table 3.2). The starvation events typically occurred on Saturdays and Sundays and three events involved both species simultaneously (Sun 13/07/2008, Sun 05/07/2009, and Sun 03/07/2011). The mean age of chicks involved was rather high (30.2 ± 4.0d, range 23-36d). By contrast, 23 events of particularly strong body mass gain (overall >30g chick day^{-1}) were recorded (10x LBBG, 13x HG; Table 3.3). Growth spurts typically occurred on weekdays (Tue-Fri) and five events involved both species simultaneously (Wed/Thu 21-22/06/2006, Wed 28/06/2006, Thu 12/07/2007, Wed 18/06/2008, and Tue 06/07/2010). On average (±SD), 59 ± 11% of all monitored nests were involved in these spurts and the mean age of chicks involved was on average slightly lower than in starvation events (21.9 ± 8.6d, range 10-35d).

A cycle in growth spurts and periods of poor provisioning - Highlighted events appeared to be exponents of a consistent trend with reduced growth in weekends and enhanced growth rates

Table 3.3. Events of substantial body mass gain (mean >30 g chick day^{-1}) in Lesser Black-backed Gulls and Herring Gulls, Kelderhuispolder 2006-2012. Increments are expressed as g chick mass day^{-1}, and the number of monitored nests, the mean age of chicks under care and the proportion of nests (%) involved in growth spurts are provided.

Species	Date	Day	Nests	Age	Increment	Nests involved
LBBG	22/06/2006	Thu	18	14.3 d	32.5 g d^{-1}	61%
	28/06/2006	Wed	14	19.4 d	37.4 g d^{-1}	79%
	22/06/2007	Fri	10	16.5 d	32.5 g d^{-1}	70%
	12/07/2007	Thu	9	35.3 d	30.0 g d^{-1}	44%
	18/06/2008	Wed	38	12.6 d	30.4 g d^{-1}	50%
	06/07/2010	Tue	28	28.3 d	35.2 g d^{-1}	64%
	14/07/2010	Wed	14	35.2 d	33.5 g d^{-1}	50%
	30/06/2011	Thu	26	19.9 d	30.2 g d^{-1}	46%
	06/07/2011	Wed	21	25.9 d	30.4 g d^{-1}	71%
	04/07/2012	Wed	11	19.4 d	32.6 g d^{-1}	45%
HG	21/06/2006	Wed	6	11.4 d	32.9 g d^{-1}	67%
	28/06/2006	Wed	8	17.1 d	34.2 g d^{-1}	63%
	15/06/2007	Fri	9	14.5 d	32.1 g d^{-1}	33%
	12/07/2007	Thu	6	31.5 d	31.5 g d^{-1}	67%
	12/06/2008	Thu	15	10.2 d	31.1 g d^{-1}	53%
	18/06/2008	Wed	17	15.2 d	32.4 g d^{-1}	59%
	25/06/2008	Wed	17	22.2 d	33.1 g d^{-1}	59%
	10/07/2008	Thu	9	35.0 d	34.0 g d^{-1}	67%
	17/06/2009	Wed	13	16.2 d	33.0 g d^{-1}	54%
	08/07/2009	Wed	8	34.1 d	39.1 g d^{-1}	75%
	15/06/2010	Tue	17	15.5 d	30.9 g d^{-1}	53%
	06/07/2010	Tue	12	34.2 d	35.1 g d^{-1}	67%
	21/06/2011	Tue	11	20.7 d	31.4 g d^{-1}	64%

on week days (Fig. 3.2). In both species, this pattern was strong in older chicks (>15d of age). Only in Lesser Black-backed Gulls was this pattern apparent also in chicks of the younger age groups. The observed pattern in growth must result from substantial and structural differences in chick provisioning during weekends relative to week days.

Diet - The most frequently encountered prey items in Lesser Black-backed Gulls, in the prospecting and egg phase just as well as during chick care were marine roundfish and flatfish (Table 4). Common prey items, considerably less important in energetic terms, were insects, polychaetes (mostly nereid worms), and crustaceans (mostly swimming crabs *Liocarcinus* spp.). Birds (mostly eggs and chicks of conspecifics or Herring Gulls), mammals, plant materials and domestic refuse all contributed to the diet. In Herring Gulls, the most frequently encountered prey items were bivalves (mostly mussels *Mytilus edulis*, crushed in pellets or intact in chickfeeds), crustaceans (mostly shore crabs *Carcinus maenas* and brown shrimp *Crangon crangon)*, and fish. Domestic refuse, birds (again, mostly gull chicks and eggs), insects, plant material, mammals, polychaetes and various other less important items all contributed to the diet. In energetic terms, bivalve prey, fish, crustaceans and domestic refuse formed the bulk of their diet. In both gull species, the most frequently encountered fish prey species (in declining order) were Whiting *Merlangius merlangus*, Plaice *Pleuronectes platessa*, Dab *Limanda limanda*, Dover Sole *Solea solea*, Horse Mackerel *Trachurus trachurus*, sandeels *Ammodytes* spp., Grey Gurnard *Eutrigla gurnardus*, and Dragonet *Callionymus lyra*. With the exception of perhaps Horse Mackerel but certainly sandeels, these are all species that were most likely taken as discards behind bottom fishing trawlers (beamtrawlers and shrimpers).

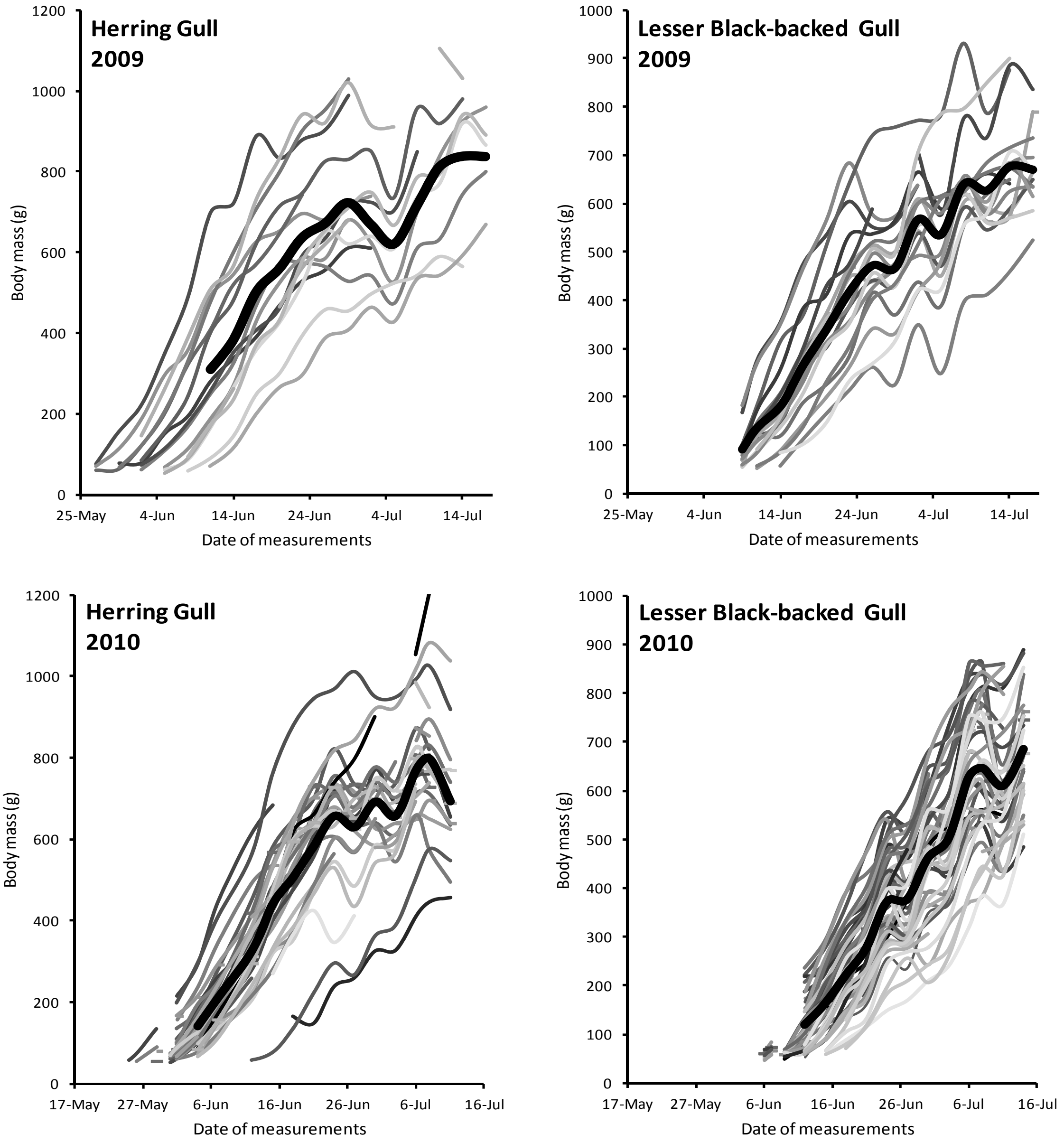


Figure 3.1. Examples of synchronised starvation events in Herring Gulls and Lesser Black-backed Gulls in 2009 and 2010. Body mass measurements of individual chicks known to have fledged (or reached 40d of age), connected by (smoothed) lines to highlight synchronisation in starvation events. The thick black line provides the overall body mass development of all (fledged) chicks combined; sharp declines indicate starvation events as in Table 1.

Fleet activities - Fleet activities (the presence or absence of beamtrawlers and shrimpers) were derived from the VISSTAT database of the Dutch Ministry of Economics, Agriculture and Innovation (EL&I). Within a wide radius around the island, from April to August, 2006-2010, the number of active fishing vessels was fairly constant within and between seasons. A slight peak in fishing effort in June occurred (mean ± SD 64.8 ± 49.3 vessels day^{-1}), relative to the other months (mean 53-54 vessels day^{-1}; Fig. 3.3). In anyone season, however, a very strong weekly pattern in fleet size occurred, with high numbers of boats at sea Monday through Thursday, a much reduced number (mostly homeward bound) on Friday, and near to nothing on Saturdays and Sundays (Fig. 3.4). This pattern clearly matches the common routine of Dutch fishing fleets: marketing fish on Fridays, ship repairs and provisioning on Saturdays, a rest for the crew on Sundays and a return to sea either Sunday night or Monday morning for a week (effectively 4-5 days) of fishing.

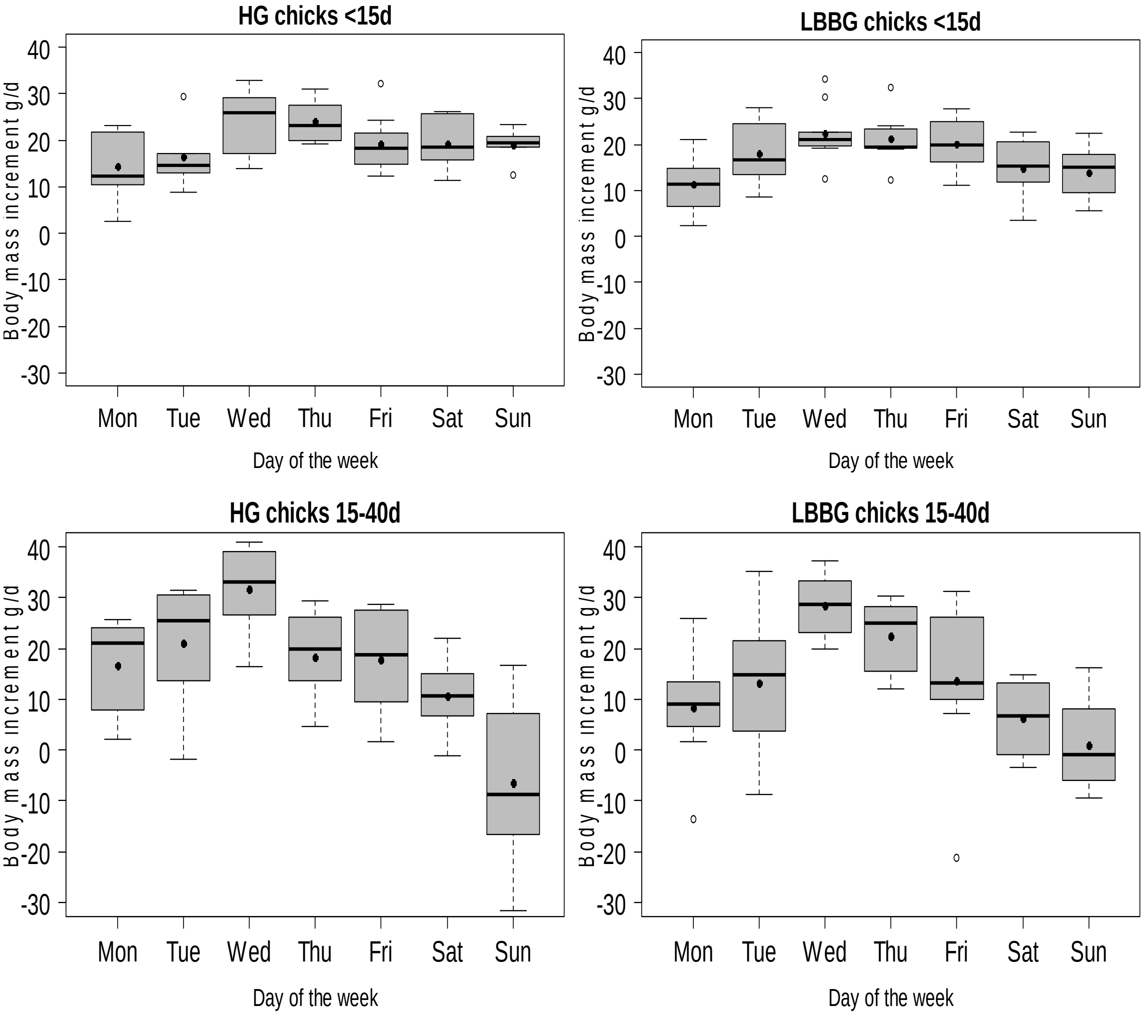


Figure 3.2. Mean chick body mass increments (g d^{-1}) during the week in young (1-14d) and older chicks (15-40d) of Herring Gulls and Lesser Black-backed Gulls at Texel, 2006-2012.

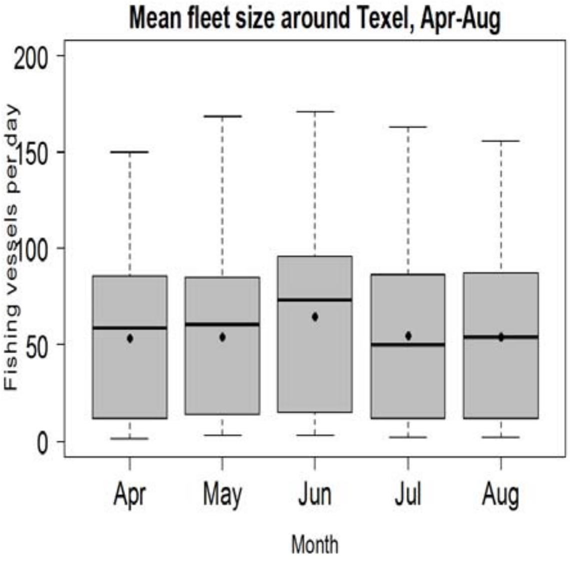


Figure 3.3. Bottom trawl fisheries around Texel (mean vessels per day per month), from black box data Apr-Aug, 2006-2010).

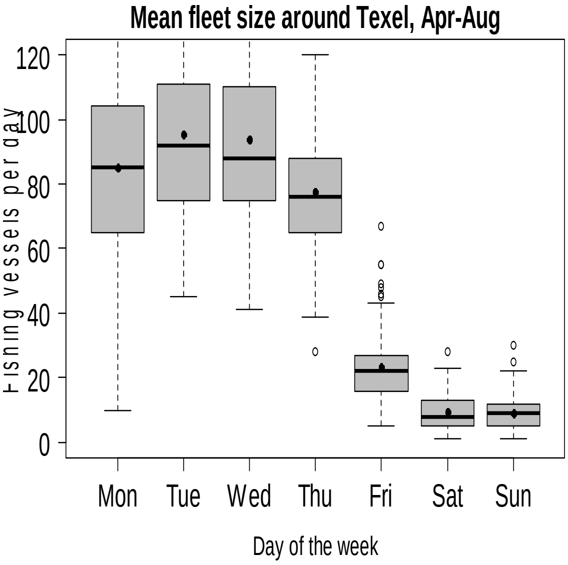


Figure 3.4. Bottom trawl fisheries around Texel (vessels per day), from black box data Apr-Aug, 2006-2010).

Table 3.4. Diet of Lesser Black-backed Gulls and Herring Gulls in the prospecting and egg phase (Pre-Hatching) and during chick care (Post-Hatching) based on frequency of occurrence (%) of prey items encountered in pellets, chickfeeds and boluses; Kelderhuispolder colonies 2006-2012.

	Lesser Black-backed Gull		**Herring Gull**	
	Pre-Hatching	Post-Hatchingt	Pre-Hatching	Post-Hatching
Insects	22	14	5	5
Polychaetes	24	9	2	1
Oligochaetes	4	3	1	1
Echinoderms	-	0	1	3
Snails	1	1	1	0
Gastropods	3	1	1	0
Bivalves	0	1	77	58
Cephalopods	0	0	-	0
Crustaceans	20	26	11	24
Marine roundfish	64	61	8	19
Freshwater roundfish	0	0	3	2
Marine flatfish	60	41	5	15
Birds	3	8	8	11
Mammals	1	1	2	1
Plants	9	11	6	6
Domestic refuse	6	6	8	18
Miscellaneous	1	1	1	2
Number of samples examined	2503	2640	2838	2666

Discussion

The period of exponential growth in the Dutch Lesser Black-backed Gull population followed, with some delay, a major fleet conversion from otter trawlers to beamtrawlers as the dominant fishing vessels in the Dutch fleet (Spaans 1998b, Rijnsdorp *et al.* 2008). Beamtrawlers are notorious in their excessive discards production (Jennings & Kaiser 1998, Innes & Pascoe 2010), and Lesser Black-backed Gulls became dominant scavengers at beamtrawlers in summer in the southern North Sea (Camphuysen 1995a, Garthe *et al.* 1996). An exponential growth in Herring Gulls was thought to result mostly from increased protection in combination with an ample supply of anthropogenic prey resources (particularly open refuse dumps) in the 1970s and 1980s (Spaans 1998c). Breeding success deteriorated and numbers declined in recent decades and although refuse dumps became less and less accessible in that same period, it is unclear if this is the sole explanation for that trend (hence the studies at Texel).

Many factors may influence food availability and in generalist seabirds it may be particularly difficult to assess which factors are most important. Strong winds may hinder fishing at sea, high tides may reduce the availability of intertidal prey, rain may enhance earthworm availability, sunny and warm weekends may provide ample opportunities to exploit tourist resorts, to name just few factors affecting foraging opportunities. The results of this study suggest that, despite a wide range of feeding opportunities and prey types, some (shared?) key resources affect provisioning rates and ultimately also the fecundity of Lesser Black-backed Gulls and Herring Gulls heavier than others. With chick growth rates (reflecting fluxes in provisioning by the parents) as proxies for prey availability, the observed weekly cycle must reflect a similar fluctuation in this resource. Apart from synchronised episodes of starvation (always during weekends) did we find synchronised growth spurts (always on week days). Only commercial fisheries have a periodicity that can explain the strong, cyclic synchronisation in chick growth as found during the studies on Texel. The three day rhythm in measurements meant that a chick mass measured on Monday was normally based on provisioning rates of the chicks on Friday night, Saturday, Sunday and Monday early morning. High body mass increments coincided with a large fishing fleet at sea, whereas low values were found when the fleet was more or less completely off effort and in harbours. Other factors, such as adverse weather, certain rich alternative resources or shifts in fleet distribution may either mask or enhance the effects of weekly reductions (weekends) and increases (during the week) in discards production, but there is no other key resource or influencing factor with the same consistent periodicity. The effect became stronger in later phases of chick care (chicks >15d of age), which will be a reflection of the increased energetic demands of the offspring and increasing difficulties for parents to collect sufficient prey to provision the chicks.

For Lesser Black-backed Gulls, a strong reliance on discards does not come as a surprise. The starvation events suggest that in the absence of discards, alternative prey is not readily at hand. The long series of years with poor reproductive success at Texel (Camphuysen & Gronert 2010a and seasons thereafter; Camphuysen *unpubl. data*) could indicate that discards as a resource is not as plentiful as before. For Herring Gulls, in which intertidal shellfish and crustaceans are important prey items, the effect of a periodicity in discards provisioning comes more as a surprise. Apparently, alternative prey resources can again not compensate for the reductions in supplies during weekends. Spaans (1971) and several other authors reported shifts in diets of breeding Herring Gulls after hatching and these shifts invariably meant that more fish was taken during chick care than in the egg phase (Pierotti & Annett 1987). Camphuysen (*in press*) found that prior to hatching, most Herring Gull pairs breeding at Texel focussed entirely on bivalve prey, but 25% of the pairs had distinct dietary biases. The overall dietary spectrum and the incidence of dietary specialisation changed when the energetic demands increased during chick care: chick growth and fledging rates were strongly correlated with the amount of fish prey provided, prey spectra diversified overall and fewer specialists were detected. Fish prey during chick care is apparently crucial to boost breeding success, despite several hundreds of other, alternative prey types. Fisheries discards are thus important for both gulls, which explains the synchronised patterns of growth and starvation in the two species.

The annual cycle of birds is made up of a sequence of life-history stages: breeding, moult and migration (Dawson 2008). Each stage has evolved to occur at the optimum time, and there is selective pressure to restrict breeding attempts to the time of year when food on which young are dependent is sufficiently abundant (Dawson 2008). The results presented here suggest that while two species relied on the same or a similar resource during chick care, the onset of laying (and thus the timing of hatching and chick care) varied independently. Seasonalities in fisheries effort could influence the timing of breeding, but in fact, the data show that fishing effort was fairly constant through the summer. Perrins (1970), found that many birds laid too late for the offspring to profit fully from seasonal peaks of food abundance, and suggested that the proximate cause was a shortage of food for the female when forming the eggs (the food constraint hypothesis). Drent (2006) suggested in response that laying date may be best considered as an individually based compromise, with exact timing subject to local environmental control (individual optimisation hypothesis). Lesser Black-backed Gulls are a migrant species (Ens *et al.* 2009, Hallgrimsson *et al.* 2012), whereas Herring Gulls are at best dispersive (Camphuysen *et al.* 2011). Migratory birds can be affected by other aspects influencing the timing of laying than more or less resident or dispersive species, and the observed differences in timing between the two may have another background. The earlier laying date of Herring Gulls would make the observed June peak in fishing effort more beneficial for this species than for the later breeding Lesser Black-backed Gulls.

The importance of discards for certain species of seabirds has been described in many parts of the world (Furness *et al.* 1992, Oro & Ruiz 1997, Votier *et al.* 2004). Predicting the response of seabird communities to changes in discard rates is problematic and requires additional data to elucidate the confounding effects of other, more ‘natural' ecological processes (Votier *et al.* 2004). According to Camphuysen (1995a), Lesser Black-backed Gulls (offshore) and Herring Gulls (nearshore) in the southern North Sea would lean on different fleet segments for as far as discards are concerned. Subtle dietary differences (not reported here) would support that suggestion:

brown shrimp and very young flatfish (typical shrimper discards/spills wihin the Wadden Sea and nearshore) are commoner prey for Herring Gulls than they are for Lesser Black-backed Gulls. By contrast, *Polinices polianus* (syn. *Lunatia alderi*), a marine gastropod and secondary prey (taken by flatfish or gadoids as prey), is commonly encountered in Lesser Black-backed Gull prey samples, but rarely in Herring Gulls. This gastropod has the highest biomass values (and, hence, the highest encounter rates) at greater distances from the shore, where large beamtrawlers operate.

Beamtrawl fisheries in general, but particularly the larger offshore beamtrawlers, are an inefficient fishing technique in terms of gasoline consumption per kg fish marketed (Thrane *et al.* 2009). Environmental concerns (excessive amounts of discards produced, effects on the seafloor, gasoline consumption) and soaring gasoline prices have made this type of fishing progressively less popular in recent years. The European Common Fisheries Policy now actively stimulates reductions, or even a total ban, in discards production and promotes more sustainable, “environmentally friendly”, fishing techniques (Penas 2007). As a result, more and more beamtrawlers are currently being decommissioned (Rijnsdorp *et al.* 2008), first and foremost the large, offshore vessels. Given a reduction in fleets size and a future reduction in the amount of discards, a contraction of scavenging seabirds towards the fewer remaining discards producing vessels may be foreseen, enhancing the inter-specific competition at trawlers, much as it was expected to occur by Noordhuis & Spaans in the late 1980s (Spaans & Noordhuis 1989, Noordhuis & Spaans 1992). A re-analysis of seabird distribution data in the southern North Sea could already show that the two species today mix more frequently in competing groups at trawlers than they did some decades ago (Camphuysen 1995a). The observed periodic declines in provisioning rates within the breeding season are likely to deepen in future years in both species of gulls, except where alternative resources could be exploited. The current shifts in attention by these gulls to inland prey types (and recent inland colonisations) may be signs of a shift in attention resulting from the recent gradual reductions in fleet size and a decline in the amount of discarded material (Camphuysen *et al.* 2010).

Overexploitation by fisheries is one part of the huge dilemma that humans face in an increasingly resource-limited world (Clover 2004). Many seabirds, around the world, have profited from overfishing, either as a consequence of removing large predatory fish by commercial fisheries, or as scavengers, utilising the excessive amounts of discards produced (Camphuysen & Garthe 2000, Tasker *et al.* 2000). We must seek sustainability, even if we may not be able to diversify our consumption indefinitely (Heffeman 2009). The current breeding population of large gulls in the western Wadden Sea, insofar sustained mostly by discards from bottom trawlers, may be seen as unnaturally high. A substantial population decline following a significant reduction in discards production can be foreseen but may be an acceptable price to pay.

4. Effects of supplementary feeding on parental nest attendance in a colonial seabird: excessive chick predation rates not reduced

Reviewed **Journal of Avian Biology** [in revision]

J. Ouwehand[1,2] & C.J. Camphuysen[1*]

[1]Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands; [2]Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands; *Corresponding author: kees.camphuysen@nioz.nl

Abstract We used a supplementary feeding experiment to investigate if parents would decrease provisioning effort in response to a reduction of the nutritional requirements of their chicks in a large colony of Lesser Black-backed Gulls *Larus fuscus*. Previous breeding seasons were characterised by high levels of chick predation (60-65% of hatchlings) and low fledging rates (0.26-0.45 chicks pair^{-1}). Food supply often limits aspects of reproduction in seabirds and by supplementing chick provisioning, we hoped to increase parental nest attendance and to reduce chick predation rates. To measure nest attendance, adults were instrumented with radio-transmitters. The results were ambiguous: nest attendance of supplemented pairs was enhanced in one study plot, but reduced in another. Our hypothesis that food provisioning would increase the time available for nest attendance (lowering predation rates and elevating fledging success) was not supported. Chick predation was high and growth rates were not enhanced by the supplementary feeding. Although supplemented birds fledged more young than controls, the difference was not significant. Chick predation and fledging success were significantly different between study plots. Factors such as autocatalytic interactions and collective, site-specific differences in the ability to defend chicks successfully from attacking adults will need more attention in future research.

Key words: *Larus fuscus*, Laridae, trade-off, food stress, ARTS, feeding experiment, chick mortality, seabird, population decline, high colony density, chick production, autocatalytic interactions

Introduction

A considerable proportion of pre-fledging mortality in gull colonies is attributed to cannibalism and inter-specific chick predation (Parsons 1971, Davis & Dunn 1976, Fetterolf 1983, Watanuki 1988, Velarde 1992). Chick predation is one of the apparent disadvantages of coloniality (Hunt & Hunt 1976, Gochfeld 1985, Wittenberger & Hunt 1985). It can be widespread and involve many adults (Hunt & Hunt 1976) or restricted to a few, specialised individuals (Parsons 1971). Chick predation includes infanticide, cannibalism (chicks of conspecifics) and predation of chicks of related species breeding sympatrically (Moreau 1923, O'Connor 1978, Urrutia & Drummond 1990).

Feeding conditions can alter trade-off decisions between current & future reproduction and within the current reproduction (Martin 1987; Linden & Møller 1989; Stearns 1992; Roff 2002). Under poor feeding conditions adult birds may not breed at all, lay smaller or fewer eggs, delay breeding until sufficient energy reserves are stored, decrease chick provisioning or chick defence, or reduce energy investment for their own maintenance at the cost of adult survival (Martin 1987, Safina *et al.* 1988; Monaghan *et al.* 1989, Pons & Migot 1995; Suddaby & Ratcliffe 1997, Dijkstra *et al.* 1990, Hanssen *et al.* 2005, Nager *et al.* 2001). Parental birds have to balance energy budgets between nest attendance to prevent chick predation, and time spent foraging to maintain themselves and their chicks. A balance between time allocated to nest attendance and foraging activities by breeding adults can significantly affect fledging rates (Bukacinski *et al.* 1998; Hatch 1990; Weidinger 1998; Weimerskirch 1995; Weimerskirch *et al.* 1995). The optimal response to food stress can differ between species, individuals and specific conditions (Stearns 1992). Long-lived species are expected to invest less in current reproduction when this comes at the expense of adult survival and life-time reproductive success (Drent & Daan 1980; Goodman 1974; Williams 1966). Food limitation is therefore thought to influence trade-off decisions mainly within the current reproduction of long-lived birds (Stearns 1992).

The Lesser Black-backed Gull *Larus fuscus* population in NW Europe has increased exponentially in recent decades, leading to numerous new colonies with high nesting densities (Spaans 1998b, van Dijk *et al.* 2010). Demographic studies in 2006 and 2007 showed that Lesser Black-backed Gulls breeding in one of the largest colonies in the Wadden Sea at Texel (The Netherlands) had, at peak population levels, very low reproductive success (0.26-0.45 chicks fledged pair^{-1}) mainly as a result of exceptionally high levels of chick predation (60-65% of hatchlings predated; Camphuysen & Gronert 2010a). Reductions in breeding success in colonial nesting birds are often related to high nesting densities through competition for resources such as food or nest sites.

In this study we examined whether food stress contributed to the elevated levels of chick-predation at Texel via a reduction in the levels of nest attendance, assuming that food limitation reduced the time available for parental nest attendance during chick care. Food availability and food limitation are very difficult to determine for generalist species such as Lesser Black-backed Gulls (Cramp & Simmons 1983), but by carrying out a supplementary feeding experiment, we artificially enhanced chick provisioning. Supplemented pairs were expected to increase the time spent at their territories (a reduction of foraging time), thereby reducing chick-predation risks, resulting in higher survival rates for their offspring and higher fledging success (nest-attendance hypothesis). Alternatively, if parents would not adjust their territory attendance, we expected that chicks in supplemented nests profited directly from an increase in food supply, thereby leading to higher growth rates (chick growth hypothesis).

Methods

Study area and monitoring - This study was carried out in a mixed colony of Lesser Black-backed Gulls and Herring Gulls *Larus argentatus* in the Kelderhuispolder on Texel (Frisian Wadden Sea islands, The Netherlands 53°00'N, 4°43'E). The breeding colony is situated at the crossroads of the western Wadden Sea and the southern North Sea. Strong tidal currents flow through a narrow passage between the mainland (Den Helder) and the island, and the main foraging areas for gulls include open sea (fish and benthic fauna, including fisheries discards), freshwater ponds, tourist resorts (including restaurants), agricultural land, sewage plants, rubbish tips and cities. Within the study area, approximately 11,500 pairs of Lesser Black-backed Gulls and just over 5000 pairs of Herring Gulls are breeding. Lesser Black-backed Gull nests were monitored within two study plots of flat grassy terrain ('*Foot Sea dunes'* and '*Valley'*), located in prime breeding habitats with high nest densities (*c.* 0.08 nests m^{-2}) but differing in reproductive output.

Ecological data were collected from April to August 2008 (Table 4.1). Prior to egg-laying the colony was visited with increasing frequency until the first eggs were found along a preset trail leading through the prime breeding habitats. For all study plots, data on timing, clutch size, hatching success, chick growth and fledging success were collected, in accordance with methodology used in 2006 and 2007 (Camphuysen & Gronert 2010a). Nest cover was classified using standardised criteria, ranging from no cover to well covered by vegetation (categories coded 1-7). To monitor chick development and survival after hatching, groups of nests were surrounded by a 50 cm high, about 16-25m^2 wide enclosure of 2cm mesh chicken wire in mid- incubation. Chicks were re-ringed just before fledging, with a steel tibia ring and engraved colour-ring with four letters on the tarsus, to allow individual identification at distance in later stages of life (Camphuysen 2008c). Nests were monitored until all enclosed young had either died or fledged (at 40d of age). Young missing chicks were logged as 'predated' when enclosures did not show any signs of possible escapes, or as 'unknown' when the chick wire fence was clearly damaged and

Table 4.1. Egg laying, clutch size and clutch volumes, egg predation, hatching success, chick predation and fledging rates in Lesser Black-backed Gulls breeding in Kelderhuispolder, Texel, 2006-2008 (from Camphuysen & Gronert 2010a). Only results for non-supplemented nests are shown.

		2006	**2007**	**2008**
Egg laying	Median egg laying	11-May	08-May	09-May
	25-75% laying dates	9-13 May	4-15 May	7-12 May
Clutches	Clutch size± SD	2.75±0.54	2.73±0.52	2.84±0.49
	N nests	(57)	(79)	(98)
	3-egg clutch volume ± SD (cm^3)*	226±17	224±17	224±15
	N nests	(46)	(61)	(87)
Eggs	Predation	29.0%	15.0%	14.4%
	Hatched	61.2%	78.1%	73.4%
	N eggs	(183)	(233)	(278)
Chicks	Predated	60.3%	66.7%	63.4%
	Fledged	14.3%	21.0%	16.9%
	N hatchlings	(63)	(81)	(71)
	Fledged $pair^{-1}$	0.26	0.46	0.35
	N nests	(35)	(37)	(34)

* Following Barth 1968 and Spaans & Spaans 1975

escapes were likely. Nests with ‘unknown’ chick fate were excluded from data analysis (n= 1). The recorded fate was changed if later evidence proved the initial description was wrong. Nests were monitored every third day. Rainy days were avoided by either conducting a visit one day earlier or later. To minimise disturbance within the colony the observers (max 4 per visit) stayed close together during the work.

Supplementary feeding experiment - A supplementary feeding experiment was conducted in both study plots. In each, four enclosures were erected fencing off four nests each (32 nests in total). Nests of adult birds within the prime breeding areas of the colony were selected based on similarity of geographical position, nesting density, laying date, clutch size, egg volume and nest cover. Two enclosures with 4 nests in either study plot received additional fish, while the two other, otherwise similar enclosures served as controls. Supplementary feeding commenced three days before expected hatching and continued until the chicks had died or fledged (i.e. 40 days of age). Clusters of nests rather than individual nests were enclosed and received the same treatment.

To reduce the risk of food stealing by conspecifics or Herring Gulls, thawed fish was provided in portions next to the nest under an artificial shelter (wooden cover on sticks, 0.1.x 0.2 x 0.1 m). Supplemented food was accessible for both adults and chicks within a territory. Supplemental feeding was carried out mainly in the afternoon when routine nest visits took place, to avoid extra disturbance of the colony as well as immediate regurgitated food supplements. We used Capelin *Mallotus villosus*, a non-native fish of the smelt family as food supplement, with a high energy content (5 kJ g^{-1}), comparable to fatty, high quality fish species like Sprat *Sprattus sprattus* and Herring *Clupea harengus*, which are common Lesser Black-backed gull prey. Capelin remains could easily be distinguished and tracked back in pellets or food boluses. Observations of supplemented nests and dietary analysis of food remains throughout the study area revealed that food stealing must have been very rare (Camphuysen *et al.* 2008).

A food supplement comprised 50% of the daily energy demands of one parent and the number of chicks that were alive during the previous nest visit. Supplements were provided only every third day, thus corresponding to approximately 1/6 of the daily energy requirement per nest. The mass of fish needed per supplement was calculated based on the energetic content of Capelin, an assimilation efficiency of 80% (Drent *et al.* 1992; Ritz *et al.* 2005), energy requirements using the field metabolic rate during the breeding season for parental demands (Camphuysen 1996), and the metabolisable energy for chick energy demands (Drent *et al.* 1992). To adjust food supplements to specific energy demands within the breeding season, we estimated the maximum chick demand over a weekly period to the nearest 50 kJ from a diagram available for the closely related Herring gull (Drent *et al.* 1992), because similar data is lacking for Lesser Black-backed Gulls. Food supplements ranged from 206g fish at the start of the feeding experiment to 806g fish for a nest with three chicks just before fledging.

Nest attendance - To investigate parental attendance at the nest site, we taped a 2g radio transmitter (0.3% of body mass) onto two central tail feathers. Nest attendance, which is assumed equal to the time present in the colony, was detected continuously in a 'scan' of available radio frequencies (20sec per frequency, 32 frequencies, 10min scan) using an automatically recorded radio station (ARTS) fed by a solar panel and rechargeable batteries (Rogers *et al.* 2006). Breeding results of 2006 and 2007 showed that the chance of nest desertion was relatively high when both parents were captured for ringing or tagging. To minimize the chance of nest desertion, only one parent per nest was caught and equipped with a radio transmitter, using nest cages during the incubation period. All radio tagged birds were also ringed and colour-ringed to allow for individual identification at distance. Nest attendance is defined here as the proportion of time an adult bird spends near the territory relative to the total time during the chick care period while the transmitter was operational.

Using large scale graphical inspection of daily means for the signal, noise and ratio of signal/noise, we determined the reception range for each radio. Radio tagged birds that either lost their transmitter or with very poor radio signals, were excluded from the analyses (n= 9). For radio transmitters that worked only part of the chick rearing period, only data from the non-operational period was excluded from analysis (n= 3). To control for quality differences between radio transmitters, we defined for each radio transmitter an individual threshold-ratio level (range 1.3-1.5) to determine presence-absence of a bird near the nest site. This was based on detailed graphical inspection of the deviance for signal, noise and ratio signal/noise together with calibration sightings of radio transmitted birds in the colony (n= 11 birds, n= 28 sightings).

Statistical analysis - In order to confirm our assumptions of low colony productivity and the spatial discrepancies in productivity between plots we compared results from 2006 and 2007 with 2008, for all non-supplemented nests monitored. Differences in breeding success, chick starvation, and chick predation rates between study plots and seasons were examined using using Maximum Likelihood ANOVA (Generalized Linear Models, GLM), assuming a Poisson distribution. Chick predation rate and breeding success were expressed as proportions of the number of hatched eggs in a nest.

Excluding 9 nests with poor radio data, only 23 nests could be used for a more rigorous statistical analysis. To avoid pseudo replication and to account for the fact that nests within enclosures are not independent, we used mixed models with enclosure included as a random intercept (Crawley 2007; Quinn & Keough 2002; van de Pol & Wright 2009). We first tested whether nests in our treatment groups and study plots differed à priori in nest quality, by fitting Linear Mixed Models (LME) separately for laying date, hatching date, egg volume and nest cover, with treatment, study plot and treatment*study plot as fixed factors and enclosure as a random intercept. Nest cover was the only term that differed à priori and was therefore included as a covariate in the starting models during hypothesis testing (Treatment*Study plot $F_{1,4}=25.29$, $P= 0.007$). A Generalized Linear Mixed Model (GLMM) with binomial distribution and logit link function was used to analyze the effects of feeding treatment and study plot on attendance, chick predation and breeding success. To examine if our food treatment enhanced the level of nest attendance during the chick phase we used a starting model for nest attendance that contained treatment, study plot, treatment*study plot and sex as fixed factors and enclosure as a random intercept. To investigate whether chick predation and breeding success were affected by treatment via nest attendance, the starting models contained treatment, study plot, treatment*study plot as fixed factors, enclosure as a random intercept, nest attendance during chick rearing and nest cover as a covariate. All models were reduced to minimal adequate models using backwards elimination of non-significant terms in order of their significance (Table 4.2). Significance was assessed by comparing models differing in one term pair-wise using Maximum Likelihood. Significance levels were set at $P < 0.05$, and all tests where 2-sided. Treatment, study plot and the random intercept were always kept in the model. Statistical packages used were SPSS 12.0, 16.0 and the R-package 'lme4'. Because estimated degrees of freedom for GLMMs with binomial errors are not calculated in the R-package 'lme4' , exact test statistics and *P*-values cannot be given. Parameter estimates, approximations of *P*-values and test statistics obtained by REML describe the effects of terms within the final model.

Conventional growth curves could not be fitted, because a large amount of the chicks died early in this study, and only a small number of growth measures were available (Gallego Garcia 2008; Bolton 1991). Instead, we used the linear phase of the growth curve of body mass to describe chick mass increment. Although this phase actually occurs between chick age 5-20d (Bolton 1991; Gallego Garcia 2008), we used data only until age 15d since not many chicks in our experiment survived to 20d. To ensure the independence of chick measurements, one mass measure per chick was randomly selected (*cf.* Oro *et al.* 1996). Since our data on chick mass increment with age is very sparse and graphical inspection showed strongly overlapping regression lines for both treatment groups and study plots, these data were not further analysed.

Results

Reproductive performance and cannibalism in the Kelderhuispolder colony - Three-egg clutch volumes (cc), hatching rates (eggs nest^{-1}), levels of chick predation (chicks nest^{-1}) and fledging rates (chicks pair^{-1}) for 2006-2008 according to the monitoring programme are presented in Table 4.1. All parameters were similar between seasons. The difference in reproductive performance between the two study plots in 2008 (*Foot Sea Dunes* 0.07 and *Valley* 0.83 chicks pair^{-1}) was similar to 2006 (0.09 and 0.58 chicks pair^{-1}, respectively) and 2007 (0.07 and 0.73 chicks pair^{-1}, respectively). The difference between the two study plots over the three-year period was almost ten-fold and highly significant (Foot Sea dunes 0.09, Valley 0.82 chicks pair^{-1}, GLM $X^2_1 = 26.7$, P< 0.001). The difference in reproductive success between the two study plots was primarily caused by differences in predation rates (GLM $X^2_1 = 7.45$, P< 0.01; Fig. 4.1). The number of chicks that died from starvation or disease was similar between the two study plots (GLM $X^2_1 = 1.36$, n.s.). In 2008, successful nests were clumped together in the Foot Sea dunes study plot. Within the Valley study plot, a successful cluster of nests occurred, but successful nests were more or less randomly distributed over the entire area. Successful patches in an otherwise failing subcolony characterised the breeding results in the Foot Sea dunes study plot also in 2006 and 2007.

Cannibalised eggs or chicks were found at 35% of 85 monitored Lesser Black-backed Gull nests and at 37% of 73 nests of Herring Gulls in 2008. Specialised cannibals feeding on chicks included two Herring Gulls and two Lesser Black-backed Gulls, all breeding in the high density parts of the Lesser Black-backed Gull colonies. Otherwise, such prey items (gull eggs and chicks) were widespread and involved many individual pairs. As in other seasons, many chicks were killed away from territories, and were often scavenged only much later. The involvement of many individual adult birds was further illustrated by various sightings of active kills with more than one attacking bird involved, including sightings of guarding adults that were outnumbered by attackers and that failed to protect more than one chick at the time.

Nest attendance - We examined whether our food treatment enhanced nest attendance levels of parents (Table 4.3). Only treatment*study plot had a significant effect on nest attendance (GLMM binomial $X^2_1 = 4.258$, P= 0.039), while treatment, study plot, sex of the parent and nest cover did not (Table 4.3, Table 4.2A). On average, food-supplemented parents carrying a radio-transmitter in the colony did not spend more time at the territories than control pairs (Fig. 4.2A), but the response appeared to differ between study plots (Fig. 4.2B; Table 4.3A). Nest attendance in supplemented pairs was higher than in control nests in the *Valley* study plot (supplemented: 0.47±0.07; controls: 0.36±0.05 relative time spent near the nest). In contrast, supplemented nests in the Foot Sea Dunes study plot showed lower attendance levels compared to control nests (supplemented: 0.26±0.03; controls: 0.32±0.07 relative time spent near the nest). The observed difference of treatment as a main effect was not significant, however (t-test: Valley: t_{10} =-1.351, P= 0.206; Foot Sea Dunes: t_9 = 0.793, P= 0.458). The relative time that parents spent near the nest site was slightly higher in the Valley study plot than in the Foot Sea Dunes area (Fig. 4.2C), but the difference was again not significant (P > 0.1; Table 4.3A).

Table 4.2. Shown are all parameters used to select the minimal adequate model to examine the effects of food supplementation on (A) nest attendance, (B) chick predation, (C) breeding success. Terms expressed in bold stayed in the final model.

	Variable	**X^2**	**df**	**P**
A	Nest cover	1.818	1	0.366
	Sex of the parent	0.635	1	0.426
	Treatment * Study plot	4.258	1	**0.039***
	Treatment			
	Study plot			
B	Treatment * Study plot	0.209	1	0.647
	Nest cover	0.640	1	0.424
	Nest attendance	1.712	1	0.191
	Treatment	1.745	1	0.187
	Study plot	4.462	1	**0.035***
C	Nest cover	0.085	1	0.771
	Treatment * Study plot	0.435	1	0.510
	Nest attendance	1.756	1	0.185
	Treatment	1.982	1	0.159
	Study plot	4.333	1	**0.037***

X^2-Values and significance levels were obtained using Maximum Likelihood during model selection, when a term was deleted from the model. Terms are presented in the order they dropped from the model. * level of significance P< 0.05. Enclosure is always included as random intercept.

Table 4.3. Effect of experimental feeding on (A) Nest attendance, (B) Chick predation and (C) Breeding success in a population of Lesser Black-backed Gulls at Texel. Presented are: parameter estimates and approximations of significance levels of fixed effects and interactions in the minimal adequate model obtained by GLMM using REML. Symbols refer to significance levels of $P_{approximations}$: *** = P< 0.001, ** = P< 0.01, * = P< 0.05, · = $P \sim$ 0.05.

	Parameter	**B**	**SE (β)**	***z*-value**	**$P_{approximation}$**	
A	Intercept	-0.621	0.189	-3.291	**0.001**	***
	Treatment*Study plot	0.892	0.377	2.368	**0.018**	*
	Treatment	-0.317	0.267	-1.189	0.234	
	Study plot	-0.145	0.267	-0.543	0.587	
B	Intercept	4.829	2.192	2.203	**0.028**	*
	Treatment	-2.343	1.909	-1.227	0.220	
	Study plot	-3.792	1.983	-1.912	**0.056**	·
C	Intercept	-4.804	2.112	-2.275	**0.023**	*
	Treatment	2.421	1.834	1.321	0.187	
	Study plot	3.596	1.903	1.889	**0.059**	·

Model summary of the minimal adequate model with enclosure as random intercept.

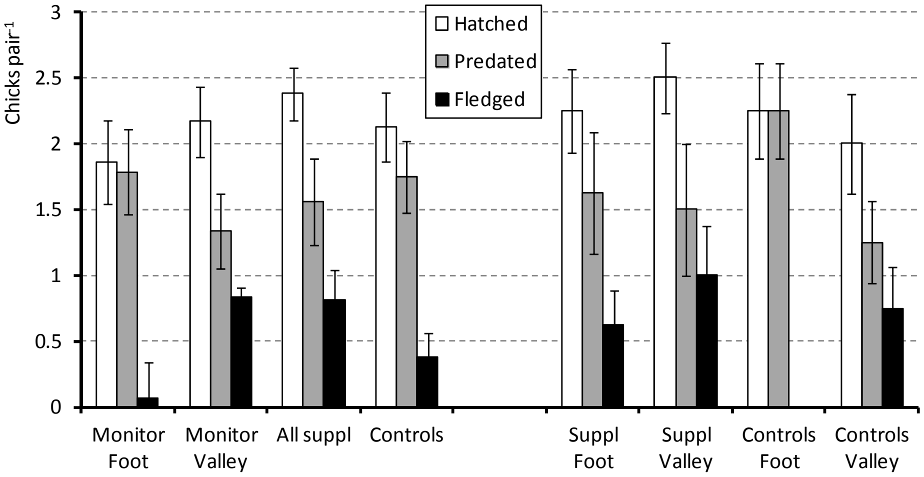
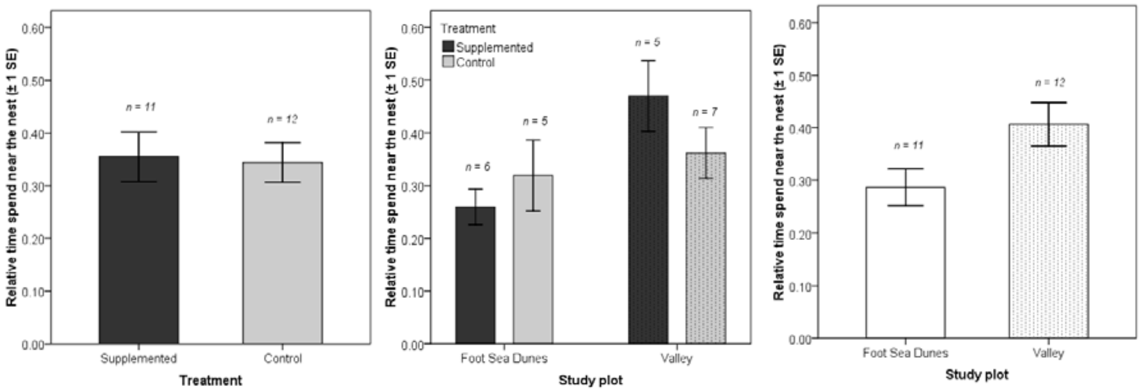
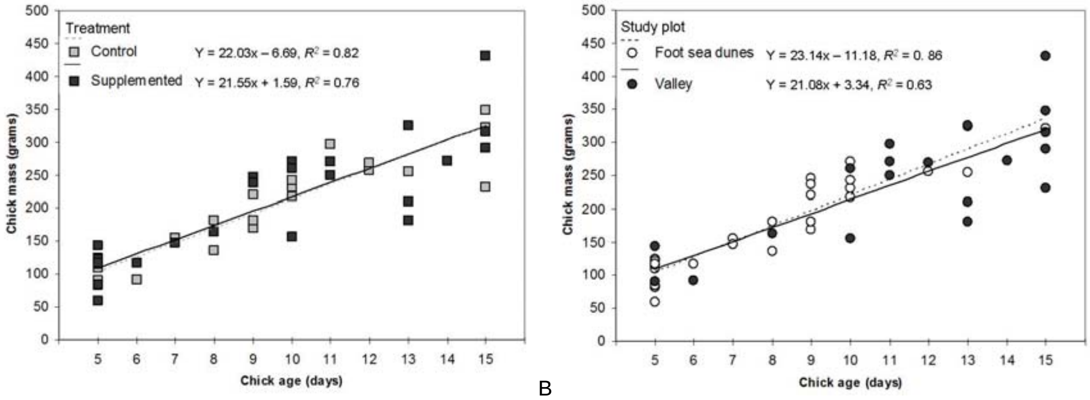


Figure 4.1 Hatching, predation and fledging success according to the monitoring programme in the Foot Sea Dunes (14 nests) and the Valley (12 nests), for all supplemented pairs (16 nests) and all controls (16 nests) and for supplemented pairs and controls in either Foot Sea Dunes or Valley Study (mean ± SE).



A B C

Figure 4.2. Mean nest attendance rates (± SE) over the whole chick rearing period in which transmitters were operational as obtained by 10 min intervals in relation to (A) Feeding treatment, (B) Feeding treatment in each study plot, and (C) Study plots.



A B

Figure 4.3. Chick growth rates of mass increment of chick during age 5-15 days in relation to (A) Feeding treatment, (B) Study plot. Dots represent one randomly selected mass measurement per chick during the linear growth phase.

Predation & breeding success - Supplemental feeding did not lead to a significant reduction in chick predation (*P* > 0.1; Table 4.3B), even though chick predation levels were on average much higher in the control nests (78±8%) than in the food supplemented nests (53±14%) in both studyplots. On average, 0.91±0.29 chicks pair^{-1} fledged per supplemented nests and 0.50±0.23 chicks pair^{-1} fledged in control nests, but the difference was not significant (Table 4.3).

The difference between study plots in predation rates and breeding success is also present in our restricted experimental dataset of 23 nests (respectively *P*= 0.056 and *P*= 0.059; Table 4.3B), and fits the large spatial discrepancy in productivity seen in the last 3 years. Predation rates were particularly high in the Foot Sea dunes, where controls did not fledge a single chick and where even supplemented pairs produced fewer fledglings than controls in the Valley study plot (Fig. 4.1). In the Valley, 47.2±11.8% of chicks fledged compared to 16.7±9.8% in the Foot Sea Dunes. This corresponded to 1.08±0.29 chicks nest^{-1} in the Valley and 0.27±0.14 chicks nest^{-1} in the Foot Sea Dunes (Fig 4.1).

Nest-attendance versus chick growth hypothesis - We expected nest attendance and chick predation to be negatively correlated, but we could not confirm this hypothesis. A model including nest attendance did not significantly explain any more variation in predation rates than a model with only treatment and study plot (GLMM binomial: *P*> 0.19). Also, the model positing effects of food supplementation on fledging success via changed levels of nest attendance performed worse than the same model without nest attendance (GLMM binomial: *P*> 0.15; Table 4.2C). The mass increment was on average 21.6 g d^{-1} (R^2= 0.78) during the linear period of chick growth. A graphical inspection of chick mass increment over the age period 5-15 days revealed strongly overlapping growth rates for the treatments (Fig. 4.3A) and study plots (Fig 4.3B). Therefore, we did not perform further statistical tests.

Discussion

The reproductive performance of Lesser Black-backed Gulls in 2008 in our study area was similar to the earlier seasons (2006-2007), with low fledging rates, high chick predation rates, widespread cannibalism and a huge difference in breeding success between the two study plots. By supplementing chick provisioning, we hoped to increase parental nest attendance and to reduce predation rates as a side effect. Cook & Hamer (1997) investigated the existence of a causal relationship between the nutritional status of nestlings and the subsequent rates of food provisioning by their parents in Atlantic Puffins *Fratercula arctica*. Chicks given supplementary food received less frequent meals than controls, with the effect that the total amount of food received by the experimental group (parental delivery plus supplementary food) was similar to the amount delivered by parents in the control group, indicating compensatory regulation of provisioning by parents in the experimental group. A similar response was reported by Gjerdrum (2004). Our own results were more ambiguous: nest attendance of supplemented pairs was enhanced in one study plot, but slightly reduced in the other. Attendance levels of control nests during the experiment amounted to 32% in the Foot Sea Dunes and 36% in the Valley. These values are similar to attendance levels reported for Lesser Black-backed Gulls during chick rearing at Terschelling (Dutch Wadden Sea) in the mid-1990s (Bukacinski *et al.* 1998). With similar nest attendance, Bukacinski's study revealed considerably lower predation rates than our study and higher reproductive success (Bukacinski *et al.* 1998).

In a supplementary feeding experiment at Terschelling (Bukacinski *et al.* 1998), pairs in which chicks provided additional food fledged significantly younger than control pairs (Bukacinski *et al.* 1998). In our study the results were not significant, even though food supplementation on average doubled the breeding success. Given lack of significance in the treatment effect in our experiment, one might wonder if enough food has been supplemented to detect differences. The amounts of fish supplemented in our study, *c.* 1/6 of the daily energy requirement of the whole nest, were similar to supplements provided in other feeding experiments that yielded significant effects of treatment on reproductive success (Bukacinski *et al.* 1998; Ritz *et al.* 2005; Verboven *et al.* 2003). In our studies, supplemented chicks were evidently hungry and eagerly consumed all food supplements almost immediately after provisioning. Possibly, the parents in our experiments have experienced the additional food as an “unpredictable resource” (food was supplemented every third day and not on a daily basis), and therefore did not change their attendance behaviour much.

Model selection indicated that attendance levels did not help to explain chick predation and fledging success of Lesser Black-backed Gulls in our experiment. Thus, our main expectation that reduced foraging would increase birds’ nest attendance and lead to lower predation rates and higher fledging success, could not be supported. Although we designed a balanced experiment that contained 32 territories initially, several nests and radio-tagged birds had to be excluded from the analysis, resulting in a total of only 23 nests. This reduced the power of the analysis and the possibility to confirm any effect that was present. Because differences between treatment groups seem rather large (e.g. 78±8% predation rates in control nests vs. 53±14% in food supplemented nests) and most often tended in the expected, we cannot confidentially reject the ‘attendance’-hypothesis.

In our feeding experiment, daily chick mass increments appeared unaffected by our treatment. In contrast, in an otherwise very similar experimental set-up at Terschelling in the 1990s, Bukacinksi *et al.* (1998) found, that in supplemented nests, chicks showed higher daily mass and wing-length increments resulting in a higher fledging mass at an earlier age than control chicks. In our study area, chick growth measurements of 2006-2008 showed that the most pronounced fluctuations in development and mass occurred after *c.* 20 d of age (Gallego Garcia 2008). Gallego Garcia (2008) suggested that this is the time when chicks in our study area undergo a critical period. Since very few chicks survived the first 15 days, a response of growth rates to food limitation may have been missed. In that case, we expect already shortly before d15 to see a differentiation between treatment groups and study site, which is not the case. We therefore reject the ‘growth’-hypothesis provisionally.

Trade-offs appear when resources are limited (Stearns 1992). Lesser Black-backed Gulls are food generalists, utilising a wide range of prey items (Cramp & Simmons 1983), and are assumed to be relatively well adapted to food limitations. When part of their prey spectrum is scarce, they could potentially shift their attention towards a resource that is more plentiful. Nevertheless, high quality food is very important in the chick-rearing period to meet the energetic demands of chicks, and intra-specific competition may be high in large colonies. Food samples at Texel revealed that Lesser Black-backed Gulls concentrated their foraging efforts on (marine) fish prey throughout the season (Camphuysen *et al.* 2008). Studies at the nearby island Terschelling (Noordhuis & Spaans 1992) have demonstrated that higher quality prey (i.e. fatty fish) was most important in the chick-rearing period. A switch to prey types of a higher calorific content was not found, or was at best very weak, at Texel (Camphuysen *et al.* 2008). Throughout the breeding season, a large proportion of prey consumed and provisioned to the chicks at Texel were discards, produced by commercial beamtrawlers off the Dutch coast: rather lean fish with calorific values <4 kJ g^{-1} such as flatfish and gadoids.

Poor reproductive output and high levels of chick predation are important indicators of food limitation in seabird colonies (e.g. Hamer *et al.* 1991; Martin 1987; Strann & Vader 1992). Very low breeding success of Lesser Black-backed Gulls in northern Norway (72-100% chick mortality) was attributed to food shortages (Strann & Vader 1992). Fetterolf (1983) found that food-stressed chicks in Ring-billed Gulls *Larus delewarensis* were subjected to the highest levels of intra-specific attacks and predation. The breeding success of Lesser Black-backed Gulls at Texel was very low in comparison with that in other European colonies (range 1.8-2.4 fledglings $pair^{-1}$; Garthe *et al.* 1999; Nager *et al.* 2001; Royle 2000; Royle & Hamer 1998; Verboven *et al.* 2003). That food supplies may have limited the reproductive success at Texel in 2006-2008 is not unlikely, given the recent population increase that continued over several decades (Spaans 1998b, van Dijk *et al.* 2010). Meanwhile, since the early 1990s, fishing effort around Texel has declined steadily

(Rijnsdorp *et al.* 2008), which will have increased the intra- and inter-specific competition at trawlers (Camphuysen *et al.* 2008). In fact, in recent years, fishing effort in a wide radius around the colony declined seasonally in the course of July (Camphuysen et al. 2008), so that the intra-specific competition for discards must have increased particularly in the critical phase of chick-rearing (Drent et al. 1992; Gill & Hatch 2002).

Study plot differences and chick defence - The low fledging rates were caused by very high predation rates, which were consistently much higher in one study plot than in the other (2006-2008; Table 4.1). Thus, the observed inconsistencies of the effect of supplementary feeding between two study plots deserve attention. Adults in the Valley showed an increase in nest attendance when supplemented with food, while the opposite occurred in the Foot Sea dunes. Chick growth rates were similar between the two study plots, suggesting that provisioning rates were similar. Also, nest attendance at control nests was similar in both study plots, while chick predation and fledging success differed significantly. Parents in the Foot Sea Dunes study plot were apparently less effective to prevent chick predation and several field observations indicated that many adults were actively involved in the attacks. In the Foot Sea Dunes, successful nests in all years (2006-2008) were clumped in an otherwise more or less completely failing subcolony, while in the more productive Valley, successful nests were more randomly distributed (scattered in between unsuccessful breeding attempts). Possibly, pairs in the Valley were more capable to fledge a brood alone, while Foot Sea Dunes pairs only managed to defend and fledge broods when clustered with other pairs that also defended territories. Individual birds may differ in numerous aspects, including foraging efficiency, diet, parental quality, acquisition and allocation of energy, or in many other aspects (Stearns 1992). But while individual birds may differ in their trade-off decisions, it would require a collective response to explain the structural differences in breeding success between the two areas.

The study plots at Texel were selected in 2006 for their apparent similarities (nesting densities, species composition, habitat, geographical position within the colony), knowing that colony studies using poorly chosen study plots may end up with non-representative data for the population at large (Stowe 1982). We have no information on age composition, individual quality or experience of the birds breeding in either area, but breeding birds in immature plumage are entirely absent. Habitat selection is a hierarchical decision-making process (Kim & Monaghan 2005b), and it is not unlikely that birds of similar quality live together within a sub-area in large colonies.

Autocatalytic interactions between members of an animal group can be an important factor in the organisation of their collective activity (Deneubourg & Goss 1989). The interactions between individuals and their environment allow different collective patterns and decisions to appear under different conditions, with the same individual behaviour. This could lead to situations where the same stress factors have a different outcome. A consideration of social dynamics and an analysis of apparently collective decisions in breeding seabirds may enhance our understanding of group behaviour.

5. The annual cycle of a scavenging seabird: a change in phenology

Manuscript, to be submitted

Camphuysen C.J.[1*], G. Aarts[2], F. Cottaar[3], A. Gronert[1], K. Verbeek[3] & A.L. Spaans[4]

[1*] Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, kees.camphuysen@nioz.nl; [2]IMARES-Texel, Postbus 167, 1790 AD Den Burg, Texel; [3]IJmuiden ringing group, Lutulistraat 42, 2037 CB Haarlem; [4] Alterra, Postbus 23, 6700 AA Wageningen; *present address:* Sylvalaan 12, 6816 RB Arnhem

Abstract Selective pressure will restrict breeding attempts to the time of year when food on which young are dependent is sufficiently abundant. Lesser Black-backed Gulls mostly utilise (offshore) marine habitats and fisheries discards are the most important source of food. Seasonalities in fisheries effort could thus influence the timing of breeding. We examined the timing of first returns, prospecting, egg-laying, hatching, chick care, when the breeding areas were abandoned in autumn, and changes therein over the years in Lesser Black-backed Gulls. The birds were geographically segregated by age throughout the annual cycle. Southward autumn movements had a different start in immatures (early), adults (intermediate) and juveniles (late), and juveniles wintered furthest to the south. The timing of spring migration was early in adults, intermediate in immatures, and late in juveniles. We found no evidence that one of the sexes returned earlier and prospecting breeders in the colony were synchronised with Herring Gulls. Herring Gulls, however, laid on average well in advance of Lesser Black-backed Gulls and have advanced the onset of breeding since the late 1960s with two weeks. Median laying in Lesser Black-backed Gulls has not advanced in recent years. The seasonality in fisheries effort could not adequately explain the onset of breeding, but an annual rise in effort in June coincided with the earliest phase of chick care. A comparison between older (<2000) and more recent data (≥2000) indicated a marked change in the timing of migration in autumn and spring and an overall shortening of the time spent at breeding latitudes by one month. Since 2000, adult Lesser Black-backed Gulls departed earlier and returned later on breeding latitudes than before, while there was no delay in laying date. There was no evidence for a *seasonal* shortage of food from fisheries sources in spring, but a general decline of fisheries is expected to have intensified intraspecific competition at trawlers and must have been responsible for the low reproductive success found in recent years. Apparently, returning breeding birds have utilised foraging opportunities while under way in spring (energy minimising migration strategy) or in wintering areas in recent years, rather than on resources that are now available in shorter supply around their colony. A later return did not compromise the timing of laying.

Key words: *Larus fuscus* – annual cycle – timing of breeding – migration strategy – trawl fisheries

Introduction

The annual cycle of birds is made up of a sequence of life-history stages: breeding, moult and migration (Dawson 2008). Seasonal differences in food availability often lead to a life-history strategy that includes migration (Ramenofsky & Wingfield 2007). Each stage has evolved to occur at the optimum time, but migratory birds can be affected by shifts in global climate patterns or prey resources. This emphasizes the need to know how events throughout the annual cycle interact (Sillett *et al.* 2000). When early breeding would be advantageous, spring migrants may be time stressed (Drent *et al.* 2006). There is intense selective pressure to restrict breeding attempts to the time of year when food on which young are dependent is sufficiently abundant (Dawson 2008). Perrins (1970), however, found that many birds laid too late for the offspring to profit fully from seasonal peaks of food abundance, and suggested that the proximate cause was a shortage of food for the female when forming the eggs (the food constraint hypothesis). Laying date may therefore be best considered as an individually based compromise, with exact timing subject to local environmental control (individual optimisation hypothesis; Drent 2006).

Lesser Black-backed Gulls *Larus fuscus* are relative newcomers as breeding birds in The Netherlands (Spaans 1998b). They are migratory birds, wintering mainly in France, the Iberian Peninsula, and northwest Africa (Harris 1962, Speek & Speek 1984, Rock 2002). Lesser Black-backed Gulls currently breed sympatrically with Herring Gulls *Larus argentatus* in The Netherlands, often in large, mixed colonies. Herring Gulls have a comparatively restricted wintering range (The Netherlands, Belgium and northern France; Camphuysen *et al.* 2011), which could be a disadvantage for the migratory Lesser Black-backed Gulls when territories have to be secured in spring.

Lesser Black-backed Gulls breeding in The Netherlands have been described as piscivorous seabirds, mostly utilising marine habitats (Spaans & Noordhuis 1989, Camphuysen 1995a). In fact, considerable amounts of food are taken from terrestrial sites (Cramp & Simmons 1983, Chapter 14, Appendix 9), but fisheries discards are the most important source of food for these birds (Camphuysen 1995a, Camphuysen *et al.* 1995, Garthe *et al.* 1996). A more thorough knowledge of the seasonality, area use, population size, and timing of breeding (chick care) is vital to comprehend the effects of seasonal trends and current declines in fishing effort and fleet size (Poos 2010). Proposals in the European Common Fisheries Policy aim at modifying beamtrawl fisheries into a more environmentally friendly industry (Rijnsdorp *et al.* 2008, 2011; Schou 2011). One aspect of this modification will be to significantly reduce the production of discards, which would radically alter food availability from this relatively predictable, anthropogenic resource in future years. This may have a profound effect on the annual cycle and breeding performance of Lesser Black-backed Gulls in the (near) future.

We were interested if early returns would facilitate early laying dates, and if the timing of departure and return to the breeding grounds were correlated with seasonal variations in resources. From a 25 year colour ring programme (1986-2011) and recent colony studies (2006-2011), we explored the timing of breeding and differences in timing and migratory range between age categories (juveniles, immatures and adults) and sexes, and between failed and successful breeders. We assessed when the birds returned to their breeding grounds, when prospecting birds arrived within the colony, the timing of egg-laying, hatching and chick care, and when the breeding areas were subsequently abandoned in autumn.

Methods

Between 1986 and 1988, 94 Lesser Black-backed Gulls were ringed opportunistically as chick during a large campaign to colour-ring Herring Gulls (50 individuals in 3 colonies in 1986, 32 birds in 4 colonies in 1987, and 12 birds in 3 colonies in 1988; Camphuysen *et al.* 2011). Two of these chicks were ringed in Callantsoog, 1 in Europoort, 4 in Schoorl, 28 at Terschelling, and 59 in Wassenaar. Between 1989 and 2005, another 369 birds were colour-ringed: 69 in Europoort, 89 at Maasvlakte, 182 in IJmuiden, 4 at Texel, and 25 at Terschelling. Of these 369 birds, 62.3% were ringed as fledglings, 3.8% as immature breeding birds, 27.6% as breeding adults, and age at ringing was unknown for the rest (6.2%). During 2006-2011, as part of yet another ringing scheme, 1112 Lesser Black-backed Gulls were colour-ringed: 3 in Leiden, 307 in IJmuiden, 741 at Texel, and 61 at Vlieland. Of these, 32.3% were ringed as breeding adults, 0.1% as breeding immature, and 67.6% as fledglings. Total ringing effort over this 25 year period (1986-2011) amounted to 1575 individual birds (68.3% ringed as chicks or fledglings). Of 450 breeding birds that were sexed during ringing, 51.6% were females, and 48.4% were males. With two clusters of data as a result of more intensified ringing effort (450 birds ringed 1986-1996, 1112 birds ringed since 2006; only 13 birds ringed 1997-2005) we could explore differences in timing over the years. Seasonal patterns were evaluated separately for adult Lesser Black-backed Gulls seen prior to 2000 and since. Because the subsets of colonies between these two periods were rather different (see above), mean distances to the natal colonies (km) rather than mean latitudes were calculated.

Sightings of colour-rings were all entered into our database by a central database manager upon receipt, while each entry was immediately examined in the context of previous sightings. Because the movements of many individual birds were characteristic, ''unusual'' records (outliers in time or space) were double-checked, and observers were consulted, where needed, to confirm sightings. During this procedure, misreportings were found where misreadings or colour-fading had been an issue. Where uncertainties remained, records were omitted. To correct for individual and area-specific differences in sighting-frequencies, we calculated the annual/monthly mean geographical position of sightings for all individual birds. Exact sightings locations were used to study the overall direction (°) of migratory movements and distances (km) away from the colony or wintering sites. We calculated the mean (SD, median, 1st and 3rd quartiles, *n*) latitude (°N) of sightings for each month to study the approximate distance away from the natal colonies of particular groups of birds (age, sex).

The age categories used included juveniles (first year birds, from fledging in July through June in the 2nd calendar year), immatures (from July in 2nd calendar year until Dec in 5th calendar year) and adults (>5th calendar year, or fully adult plumage if ringed as a breeding bird with unknown age). Adult breeding birds were sexed when captured by using biometrics, following procedures described by Coulson *et al.* (1983). Differences in mean latitudes between periods, sexes or age groups were investigated with a *t*-test assuming independent samples (two-tailed tests).

Returns of prospecting birds within the colony were studied only at Texel in recent years (2007-2011). The breeding biology and timing were studied in a large mixed colony in Kelderhuispolder, a dune area south of De Geul at Texel (53°00'N, 04°43'E). Lesser Black-backed Gulls became established as breeding birds in 1970, when about 1000 pairs of Herring Gulls nested in the area. The study area was visited every three days from mid-April to early August to record the presence of colour-ringed birds, laying and hatching dates, the period of chick care, diet, chick growth and fledging success (Camphuysen & Gronert 2010a). Visits from late March on were to record the earliest presences of colour-ringed birds prior to egg-laying. The total number of individual colour-ringed birds seen between March and July was used as a proxy of the returned birds and serial sessions of ring-reading from late March through May (the prospecting phase) were used to assess when the majority (*c.* 90%) had first arrived in the colony. Colony visits in April 2008 (3x) were less frequent than in the other seasons (2007 14x, 2009 12x, 2010 17x, 2011 18x). Colony visits in May were more frequent (2007 36x, 2008 19x, 2009 24x, 2010 23x, 2011 26x), but relatively less time was available for ring reading due to all other activities.

To quantify the fishing effort, data from the VISSTAT database were used. VISSTAT is a database for logbook data implemented by the Dutch Fisheries Inspection (AID) from 1990 onwards. It contains trip data from all vessels landing and marketing in Dutch harbours. Trip data consist of a vessel identification, vessel length and power (kW), gear type, days at sea, departure and arrival time, ICES rectangle in which most fishing occurred and marketed volume (mass) of fish. Gear types extracted for this study were beam trawls (TBB), bottom otter trawls (OTB), bottom pair trawls (PTB), Nephrops trawls (TBN), bottom shrimp trawls (TBS), non-specified bottom trawls (TB), mid-water otter trawls (OTM), mid-water pair trawls (PTM), mid-water shrimp trawls (TMS), non-specified mid-water trawls (TM), otter twin trawls (OTT), non-specified otter trawls (OT), non-specified pair trawls (PT), non-specified other trawls (TX), miscellaneous gear (MIS) and gear not known or not specified (NK). Only fishing effort data from ICES rectangles 34F3, 34F4, 34F5, 35F3, 35F4, 35F5, 36F3, 36F4 and 36F5 (*i.e.* an area north of 52°30'N, south of 54°N, east of 3°E and west of 6°E) are considered here. Fisheries in the area are essentially day and night activities, lasting 5 days (Mon-Fri) or 11 days (Mon-Sun-Thu) per trip. By summing the number of vessels at sea around mid-day (i.e. 12:00h), we derived a daily measure of fleet presence (effort expressed as 'vessel days'), which was assumed to be a proxy of discards production.

Results

Annual migration from colour-ring sightings - Adult Lesser Black-backed Gulls abandoned breeding latitudes in August (starting late July), immediately after fledging (Fig. 5.1). There was no difference between the sexes (mean latitude August t_{380}= 1.43, n.s.), and no difference between failed and successful breeders (mean latitude July t_{60}= -1.03, n.s., August t_{27}= -0.77, n.s.). Wintering sightings locations, without exceptions and all age categories included, were at lower latitudes than breeding areas and 90% of wintering observations in Nov-Feb (n= 700) occurred in a narrow range of angles to the south-southwest of the breeding colonies (mean ± SD 200° ± 23.0°, median 201°, 90% within 177°-221°). In mid-winter (Dec-Jan), the majority of adult birds had reached wintering latitudes (mean *c.* 42°30'N, Table 5.1, *i.e.* Portugal and south Spain). There was no difference between the sexes in mean latitude until March (t_{314}= -2.12, $P<$ 0.05) and April (t_{672}= -3.36, $P<$ 0.001), when females tended to be observed slightly closer to the breeding grounds than males. A single January sighting (13 Jan 1996, IJmuiden), three reports from 1-10 February, 5 from 11-20 February, and 13 from 21-29 February are the earliest documented returns to The Netherlands. Nearly

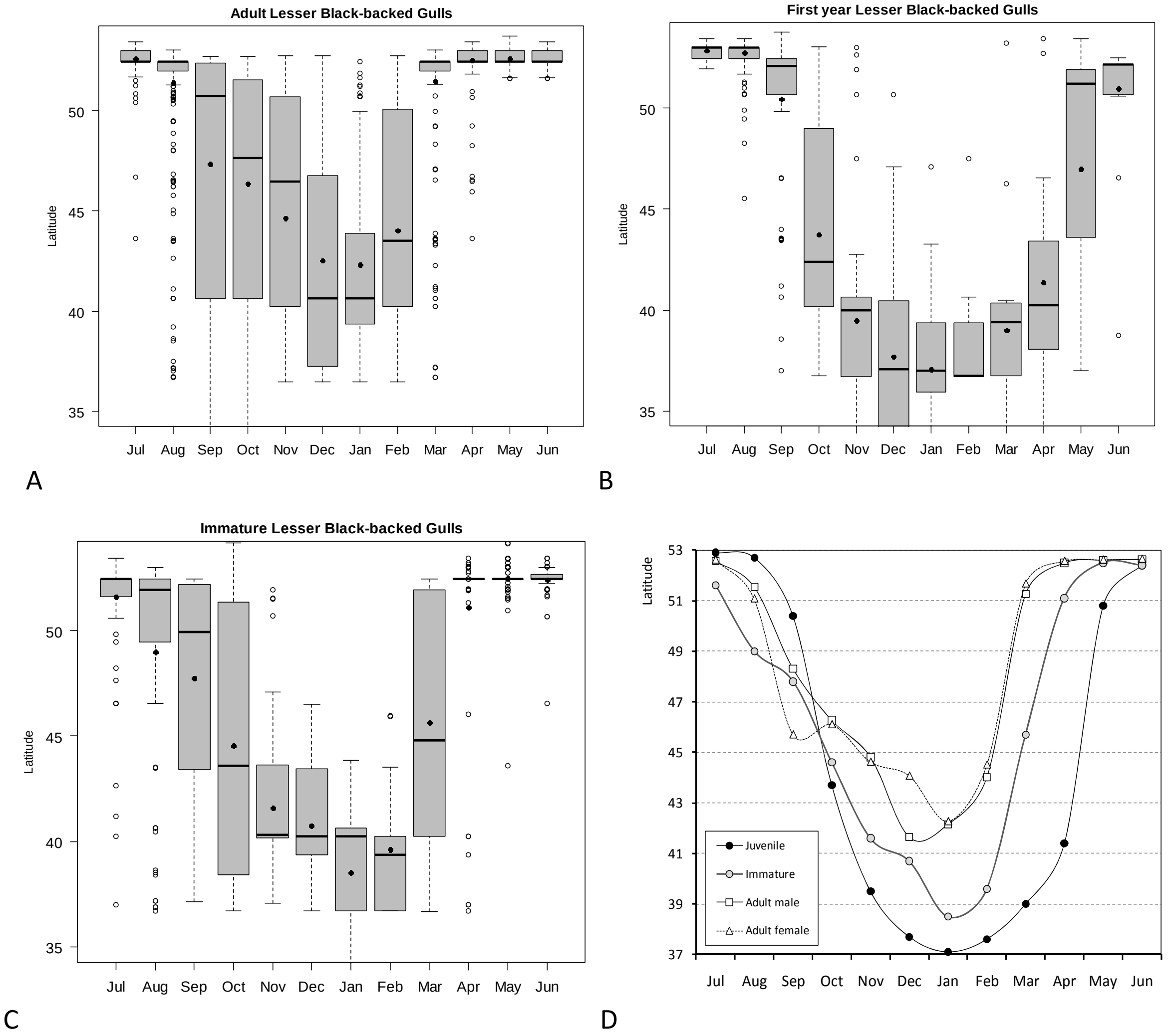


Figure 5.1. Boxplot of the annual cycle of migration in (A) adult, (B) juvenile, and (C) immature Lesser Black-backed Gulls based on colour-ring sightings through the year by latitudes (°N). Mean latitudes (as indicated by black dots within the boxplots), are combined in (D) to further illustrate differences and similarities between the different age groups. Adults are now split into females and males.

Table 5.1. Mean ± SD degree latitude (°N) and number of monthly sighting-positions (n) of juvenile, immature and adult Lesser Black-backed Gulls colour-ringed during 1986-2011 in The Netherlands. The difference in mean latitude between juveniles and immatures, adults and immatures and adult females and adult males was tested (t-test; significance: *** = $P< 0.001$, ** = $P< 0.01$, * = $P< 0.05$, n.s. = $P\geq 0.05$).

	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Juveniles	52.9±0.3	52.7±0.5	50.4±3.9	43.7±5.3	39.5±6.4	37.7±5.7	37.1±4.2	37.6±4.0	39.0±6.8	41.4±7.0	50.8±4.2	52.4±0.9
n	907	536	79	40	33	20	24	15	11	11	56	406
Juv/imm	***	***	*	n.s.	n.s.	*	n.s.	n.s.	*	***	**	n.s.
Immatures	51.6±2.5	49.0±5.4	47.8±5.2	44.6±6.3	41.6±5.0	40.7±3.6	38.5±4.3	39.6±3.0	45.7±5.6	51.1±4.3	52.5±1.0	52.4±0.8
n	119	77	37	50	37	30	23	21	24	62	121	89
Ad/imm	***	***	n.s.	n.s.	**	*	***	***	***	*	n.s.	*
Adults	52.6±0.5	51.4±3.2	47.4±6.1	46.4±6.1	44.7±6.1	42.5±5.9	42.3±4.7	44.0±5.5	51.5±3.0	52.5±0.7	52.6±0.4	52.6±0.4
n	702	443	187	143	111	106	97	68	311	908	1288	978
Ad female	52.6±0.5	51.1±3.6	45.7±6.4	46.1±5.8	44.6±6.4	44.1±5.8	42.3±5.6	44.5±5.6	51.7±2.9	52.6±0.4	52.6±0.4	52.7±0.4
	301	181	65	62	51	36	25	24	141	404	558	418
Fem/male	n.s.	n.s.	**	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Ad male	52.6±0.6	51.5±3	48.3±5.8	46.3±6.4	44.8±5.7	41.6±5.9	42.1±4	44±5.4	51.3±3.2	52.5±0.7	52.6±0.3	52.6±0.3
	366	240	109	69	53	62	62	39	150	460	665	519

Table 5.2. Timing of breeding of Lesser Black-backed Gulls at Texel, 2007-2011.

	2006	2007	2008	2009	2010	2011	2006-11
First egg	04 May	29-Apr	01 May	30-Apr	04 May	01 May	29-Apr
Peak egg-laying	10-15/5	6-15/5	7-12/5	9-15/5	11-16/5	10-16/5	8-15/5
Median egg-laying	12 May	09 May	10 May	12 May	14 May	13 May	11 May
Breeding period	16/5-5/6	16-31/5	13/5-2/6	16/5-5/6	16/5-5/6	17/5-5/6	16/5-4/6
Incubation (d)	26.7±1.6	26.7±1.3	26.5±1.4	27.2±0.7	26.6±1.6	26.3±1.5	26.7±1.4
First hatchling	01-Jun	22 May	29 May	28 May	30 May	27 May	22 May
Peak hatching	6-11/6	1-11/6	3-13/6	6-13/6	6-12/6	6-12/6	5-11/6
Median hatching	08-Jun	05-Jun	06-Jun	08-Jun	09-Jun	09-Jun	08-Jun
Chick care (40d)	12/6-22/7	12/6-22/7	14/6-24/7	14/6-24/7	13/6-23/7	13/6-23/7	12/6-22/7
First fledgling	17-Jul	10-Jul	10-Jul	14-Jul	11-Jul	10-Jul	10-Jul

all birds had returned to at least the vicinity of the breeding grounds in April and only very few sightings are known from areas far south of the breeding area in May and June (Fig. 5.1).

Juveniles (fledglings) tended to linger around in the breeding areas until late August (adults versus juveniles t_{463}= -8.83, $P< 0.001$), were still on average significantly to the north of adults in September (t_{224}= -4.78, $P< 0.001$; Table 5.1, Fig. 5.1). Significantly lower mean latitudes were reached by juveniles in October (t_{71}= 2.68, $P< 0.01$), illustrating a fairly rapid long-distance movement during September (late September – early October) which continued in October and November. Juveniles wintered on average 600 km further to the south/southwest than adults (juveniles Dec-Jan *c.* 37°30’N, Table 5.1).

Immatures moved towards the breeding grounds in summer, but as cohort they never quite made it to the latitudes of their natal colonies (adults and immatures were closest in June, t_{91}= 2.54, $P< 0.05$; Fig. 5.1). A distinct southward movement was detected in July, ahead of most adults (t_{120}= 4.34, $P< 0.001$). The difference between adults and immatures faded away in September (t_{58}= -0.51, n.s.) and October (t_{84}= 1.77, n.s.), possibly as a result of shared stop-over use in France or Northern Spain (44-49°N latitude). Immatures travelled on average further to the south than adults, to mean latitudes (*c.* 39°30’N) that were intermediate between wintering latitudes of adults and juveniles. The difference in mean wintering latitudes between juveniles and immatures was not significant, however (Table 5.1). Return movements of immatures towards the breeding grounds (or areas nearby) were *c.* one month later than returns of adult birds, but one to two months earlier than juveniles. Only in June were mean latitudes of sightings of juveniles (2^{nd} calendar year birds) similar to those of immatures (t_{141}= -0.07, n.s.).

Prospecting birds in the colony at Texel - The earliest confirmed returns into the Texel colony were colour-ringed birds observed on 22 March 2009 (2) and 31 March 2008 (4). Sightings of colour-ringed birds from Texel elsewhere within The Netherlands (nearby colony locations) point at first returns from the wintering areas in late February (22 February as earliest date). Some of the birds that were first seen in late March in the colony had already returned to The Netherlands more than three weeks earlier. More than 85% of all colour-ringed birds that returned to Texel in anyone season were detected in April (Fig. 5.2). Around egg-laying (median 11 May), over 95% of adults that returned in anyone season had been detected.

We failed to detect a difference in return dates between the sexes (mean ± SD first colony sightings females 17 Apr ± 16.3d, males 18 Apr ± 16.9d, t_{328}= -0.92, n.s.; Fig. 5.3). Sightings of prospecting recruits have been uncommon events during the studies at Texel, but included 3cy (4x), 4cy (10x), and 5cy (6x) individuals. One particularly early 3cy bird was first observed 13 April 2009,

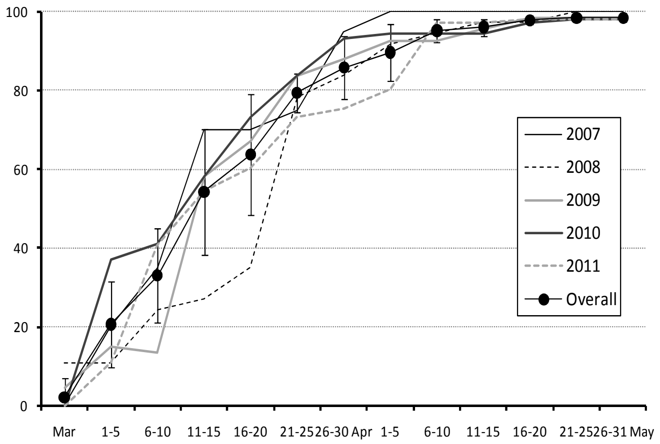


Figure 5.2. Return rates (cumulative %, SD) of individual colour-ringed Lesser Black-backed Gulls ringed as adults (2006-2010) in five-day periods during late March, April and May at Texel, 2007-2011. Return rates were based on the total number of colour-ringed individuals known to have returned at least once to the colony (Mar-Aug).

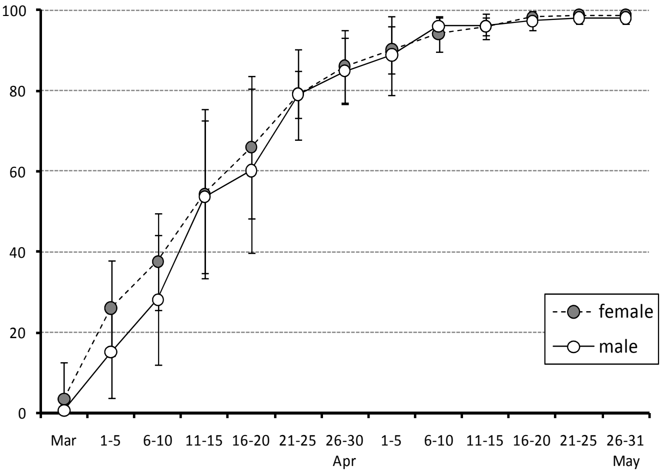


Figure 5.3. Return rates (cumulative %, SD) of colour-ringed male and female Lesser Black-backed Gulls ringed as adults (2006-2010) in five-day periods during late March, April and May at Texel, 2007-2011. Return rates were based on the total number of colour-ringed individuals known to have returned at least once to the colony (Mar-Aug).

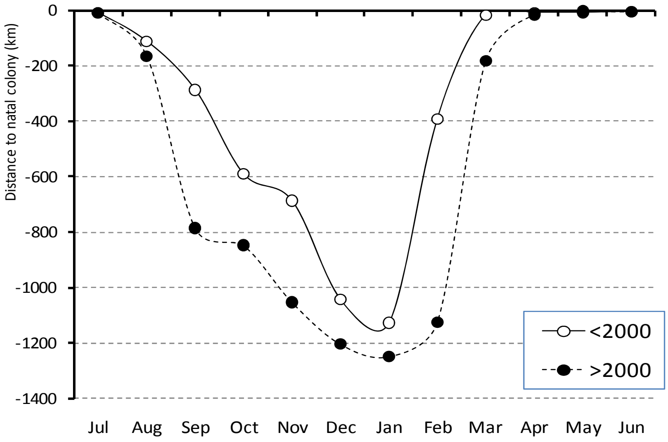


Figure 5.4. The annual cycle of migration in adult Lesser Black-backed Gulls by distance to natal colonies (km), prior to and since 2000, based on colour-ring sightings through the year (see Table 5.3 for standard deviations and sample sizes).

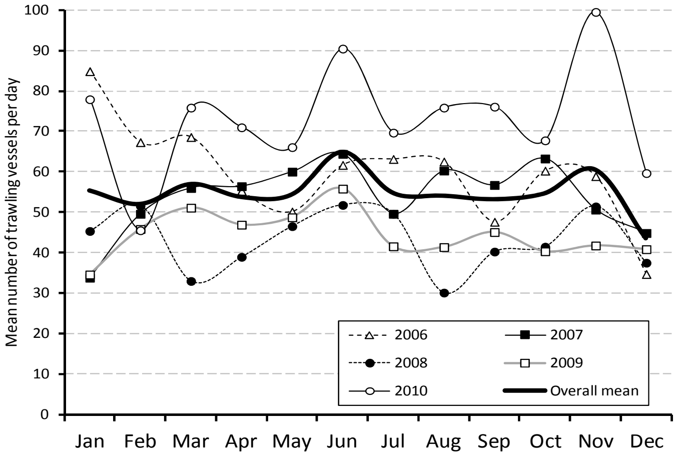


Figure 5.5. The annual cycle of trawl fisheries around Texel (vessel days), 2006-2010.

four 4cy individuals were first seen during the last week of April. First (confirmed) returns could be as late as 25 July (a 4cy individual), however. First confirmed returns tended to advance with increasing age (3rd calendar year 18 May ± 33.8d, n= 4; 4th calendar year 16 May ± 28.3, n= 10, 5th calendar year 20 April ± 13.0, n= 6), but the sample size is too small to draw firm conclusions.

Timing of breeding - Breeding was highly synchronised, with a laying peak (1st-3rd quartile around the median) of eight days (2006-2011 range 6-10 days; Table 5.2). There were very few relaying attempts when nests were plundered (10% of 539 nesting attempts failed to produce hatchlings; range 2006-2011 7-18%). Only 3% of all nesting attempts were new attempts after an earlier clutch had been lost (range 0-10%). Median egg laying was consistently in the second week of May (median 11 May, 1st-3rd quartiles 8-15 May). The mean incubation period for all monitored eggs, irrespective of laying sequence (n= 1188) amounted to 26.7±1.4 days (range for individual eggs 21-36 days; Table 5.1). Median hatching was consistently around 8 June (2006-2011 range 5-9 June, overall median 8 June, 1st-3rd quartiles 5-11 June), but the first hatchlings could be found as early as 22 May (Table 5.1). Chicks were (arbitrarily) considered to have fledged at an age of 40d after hatching, which would lead to a main period of chick care from 12 June to 22 July and early fledglings around 10 July.

Early returns (colour-ring sightings) into the colony did not involve birds with a particularly early laying date. The mean (± SD) laying date of first eggs in early birds (prospecting confirmed prior to 10 April; 12 May ± 4.8d) was not significantly different from the overall, colony mean (11 May ± 5.2d; t_{85}= 0.62, n.s.).

Table 5.3. Mean ± SD distance (km) from natal colony and number of monthly sighting-positions (n) of adult Lesser Black-backed Gulls observed during 1986-1999 (old data) and 2000-2011 (new data). The difference in

mean distance between "old" and "new" sightings was tested (*t*-test; significance: *** = *P*< 0.001, ** = *P*< 0.01, * = *P*< 0.05, n.s. = P≥ 0.05).

	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
1986-1999	9±28	112±275	287±453	591±703	687±631	1043±630	1128±999	391±568	17±80	9±46	8±25	5±16
n	171	148	77	53	31	29	20	22	174	411	418	281
Old/New	n.s.	n.s.	***	*	**	n.s.	n.s.	***	***	n.s.	***	n.s.
2000-2011	9±68	165±426	786±842	848±791	1053±771	1204±765	1248±546	1124±624	182±466	15±91	3±17	4±18
n	570	351	135	106	98	95	95	63	209	672	1006	740

Changes over time - Adult Lesser Black-backed Gulls ringed and observed prior to 2000 were characterised by a slower departure and towards higher wintering latitudes than birds in recent years, followed by an earlier and highly synchronised return to the breeding grounds (a V-shaped curve; Fig. 5.4). Since 2000, adult Lesser Black-backed Gulls have moved earlier and faster away from the colonies, but returned (also highly synchronised) about one month later (a U-shaped curve). Observed distances away from the natal colonies during autumn and spring migration in the older and more recent data were highly significant (Table 5.3).

Trends and seasonal fluctuations in resources - The seasonal pattern in fishing activity around Texel, based on 29,808 trips during 2006-2010, is illustrated in Fig. 5.5. Fisheries effort was fairly constant over the year, but was slightly more variable in winter than in summer. Fleet size around Texel in March (R_S= 0.50), April (R_S = 0.20), nor in May (R_S = 0.30, all n= 5, n.s.) correlated with the median laying date in each of these years. In many years, summer fisheries effort peaked in June (hatching of eggs and early chick care of Lesser Black-backed Gulls at Texel) and subsequently declined over July and August (final stages of chick care and fledging). Total effort of the Dutch beamtrawl fleet (the main offshore fishery in the area) steadily declined with 6.5 ± 5.9% per annum between 1995 and 2008 as a result of decommissioning and other factors (overall decline 59%; Rijnsdorp *et al.* 2008, A. Rijnsdorp *pers. comm.*).

Discussion

Lesser Black-backed Gulls were geographically segregated by age throughout the entire annual cycle, rather than showing a geographic age-related cline only in the wintering areas (*cf.* Jorge *et al.* 2011). The autumn movement to the south had a different start in immatures (early), adults (intermediate) and juveniles (late). The finding that immature (non-territorial) birds travelled earlier southward than failed breeders (the timing of which was similar to successful breeders) could point at the importance of a prolonged presence at established territories. Future possibilities to breed may be enhanced in failed breeders, if territories are continued to be occupied and defended throughout the breeding season. Juvenile birds were found to winter significantly further to the south than adults, and had no tendency to migrate towards the natal colony region until very late in spring or early summer. Juveniles arrived some four months later than adults near the latitudes of their natal colonies (in summer rather than spring), following a rather slow spring movement to the north. Immatures left the breeding latitudes ahead of adults, used the same stop-over latitudes in autumn, wintered further to the south/southwest, and returned to the breeding grounds approximately one month later than adults. In October adults, immatures and juveniles were reported from similar latitudes, in Britain and northern France, where stop-overs were used by many birds, prior to the final leg to the wintering grounds further to the south. Colour-ring readings in autumn were mostly at landfill areas, sewage plants, pig farms, and in roosts at beaches in England and France. October is the only month in which there was no significant difference in latitude of sightings between age groups (Table 5.1). For adult and immatures, these stopovers could be important to finalise the post-nuptial (complete) moult, the onset of which is during chick care and fledging in breeding adults (Barth 1975, Verbeek 1977c, Cramp & Simmons 1983).

With increasing age, the annual cycle of Lesser Black-backed Gulls appeared increasingly synchronised towards long-distance movements in a shorter time span. Spring migration comprised a rapid, highly synchronised (sexes) movement to the north. Adults returned to the vicinity of breeding colonies in the course of a few weeks during mid-Feb to mid-Mar. The onset of breeding (egg-laying) followed a prospecting phase of well over one month during which territories gradually became occupied (late March to early May). We found no evidence that one of the sexes returned ahead of the other, and the prospecting phase of males and females for as far as appearances within the colony are concerned was identical. As potential competitors for breeding space with Herring Gulls, the disadvantage as a result of long-distance migration in spring was apparently limited. Adult Herring Gulls return to breeding latitudes from December and January onwards, with a more complete return not before March and early April (Camphuysen *et al.* 2011). The first actual colony visits at Texel by both species occurred in late March and early April were more or less simultaneously. Such early presences within the terrain had a short duration, the birds involved were wary and easily flushed, and they did not stay overnight (*cf.* Spaans 1971). Herring Gulls, however, laid on average well in advance of Lesser Black-backed Gulls (average 4 days, range 2-9 days 2006-2010; Camphuysen & Gronert 2010a). In line with earlier studies (e.g. Calladine 1997), Camphuysen & Gronert (2010a) found that the breeding habitat characteristics were different in either species, so that the actual inter-specific competition for territories may not have been particularly intense.

Bukaciński *et al.* (1998) reported a median laying date of 10-12 May in Lesser Black-backed Gulls nesting at Terschelling in 1992, which is similar to the current median laying date at Texel (Table 5.2). Sympatric Herring Gulls have significantly advanced the onset of breeding since the late 1960s (mean laying first eggs Terschelling 1967-69: 19-20 May (Spaans & Spaans 1975), Terschelling 1983-84: 12 May (Spaans *et al.* 1987), Texel 2009-11: 3-5 May (Camphuysen & Gronert 2010a and *unpubl. data*)). Historical information for Lesser Black-backed Gulls is short in supply, but data collected by Bukaciński *et al.* (1998) and ourselves do not indicate a similar trend: median laying in Lesser Black-backed Gulls has not advanced in recent years.

Klaassen *et al.* (2011) found that migrating Lesser Black-backed Gulls stopped frequently on travel days to forage, both in autumn and in spring. These frequent and long migratory stopovers resulted in a low overall migration speed; among the lowest recorded for migratory birds. Hence, female Lesser Black-backed Gulls may be able to replenish body stores needed for laying while underway to the breeding grounds (capital breeders rather than income breeders; Drent & Daan 1980, Drent 2006). Yet, a one and a half month pre-laying period at the breeding latitudes, as found in our study, should be sufficient to add the body stores needed for egg formation and still lay timely (income rather than capital breeders).

A comparison between older and more recent ringing data suggest that there has been a marked change in the timing and progress of migration both in spring and in autumn. Prior to 2000 (when populations increased exponentially), birds returned about one month earlier on breeding latitudes than they did in recent years (when populations were stabilising). After breeding in recent years, adult Lesser Black-backed Gulls moved earlier and faster to the wintering areas than they did in the recent past. Effectively, this change means that foraging areas at breeding latitudes were fully used by adult Lesser Black-backed Gulls for at least 5 months prior to 2000, but only for 4 months in recent years. The difference was apparently primarily at the expense of the pre-laying (prospecting) period (Feb-Mar).

If the timing of breeding in a generalist feeder as a Lesser Black-backed Gull had anything to do with the (peak) availability of resources during chick care and fledging, we may need to focus on the most important resource. The population increase of Lesser Black-backed Gulls in The Netherlands follows an earlier, steep increase in beam trawl fishing effort in the southern North Sea that took place between the early 1960s and the late 1990s (Rijnsdorp *et al.* 2008). Even though the exact contribution to the energetic demands of Lesser Black-backed Gulls breeding in coastal colonies in The Netherlands is unknown, it is evident that discards produced mostly by beam trawlers is a very important resource (Camphuysen 1995a, Camphuysen *et al.* 1995, Garthe *et al.* 1996). Recent studies at Texel have confirmed that marine fish is the single most important prey of breeding Lesser Black-backed Gulls, of which 69% were probably discards (mainly demersal gadoids and flatfish), 28% were possibly discards and only 3% were most likely non-discards (Camphuysen *et al.* 2008). Discards were also the most important prey in Lesser Black-backed Gulls studied at Terschelling in the 1980s and 1990s (Spaans & Noordhuis 1989, Noordhuis & Spaans 1992, Bukaciński *et al.* 1998). Most these fish were obtained at offshore fishing vessels (Camphuysen 1995a, Camphuysen *et al.* 1995), an industry that is essentially year-round with fleet distribution patterns governed by catch rates, economic factors, and public holidays (Fig. 5.5; Poos 2010). Fishing effort within the foraging range of the study colony at Texel did not peak around breeding such that seasonal fluctuations in fishing effort could not explain any aspect of the annual cycle of area usage by Lesser Black-backed Gulls. Within seasons, fisheries effort peaked in June and (slightly) declined later in summer. This decline may have led to higher levels of intraspecific competition during later phases of chick care, while the annual peak coincided with early chick care. The high price of fuel and the relatively low biomass of flatfish jeopardised the survival of the large beam trawl fleet in the area, which declined since the late 1990s (Rijnsdorp *et al.* 2008). The prospects of the fleet are further threatened by attempts to reduce the impacts of this fishery on the ecosystem (e.g. reduce discards; Schou 2011), which will increase the intraspecific competition for prey in breeding Lesser Black-backed Gulls and put pressure on the breeding population as it is now. Other resources may gain importance during this process, which may affect the timing and seasonality of Lesser Black-backed Gulls in future years.

Adult Lesser Black-backed Gulls have delayed their return to breeding latitudes in recent years (Fig. 5.4), but there is no evidence for a delay in laying date. Fishing effort early in the season is not very different from effort later in summer, and there is no evidence for a *seasonal* shortage of food from fisheries sources in spring. The overall trend of a fisheries decline, however, is likely to put pressure on resources of a population that has increased exponentially for so many years. An earlier departure and later return of adult Lesser Black-backed Gulls is therefore interpreted as an adjustment to relatively poor resources on the breeding grounds in recent years (which is consistent with poor reproductive success in recent years; Camphuysen & Gronert 2010a). Female gulls will have to rely more on foraging opportunities while under way in spring or in wintering areas (capital breeders), which could explain the energy minimising strategy reported by Klaassen *et al.* (2011).

6. Colony- and age-specific seasonal dispersal of Herring Gulls *Larus argentatus* breeding in The Netherlands

Published **Journal of Ornithology** 152: 849-868 (2011)

Kees (C.J.) Camphuysen[1], H.J.P. Vercruijsse[2] & Arie L. Spaans[3]

[1]Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands, E-mail: kees.camphuysen@nioz.nl; [2]Girostraat 38, 5038 DN Tilburg, The Netherlands; [3]Alterra Wageningen UR, The Netherlands; present address: Sylvalaan 12, 6816 RB Arnhem, The Netherlands

Abstract The Herring Gull population in The Netherlands went through phases of exploitation, protection, persecution, and again (partial) protection during the 19th and 20th centuries. Numbers of breeding pairs peaked in the 1980s at *c.* 90,000 pairs, at which point a colour-ringing campaign was organised to evaluate dispersal and distribution patterns. Herring Gulls were ringed as chicks, predominately near-fledglings, in 12 colonies in 1986 (1,247 individuals), 13 colonies in 1987 (1,354 individuals), and 14 colonies in 1988 (1,396 individuals). Between 1986 and 2009, of 3,997 Herring Gull chicks colour-ringed, 3,124 individuals (78.2%) were seen and reported at least once, while 453 (11.3%) were recovered dead. In total, 86,247 ring-readings of living gulls were received and processed, originating from 1,358 locations by 868 observers. One-fifth (20.5%) of all sightings originated from the home-ranges (areas within a radius of 5km around the ringing place). Only 691 sightings (0.8%) were reported at over 300km from the natal colony (10.7% at 6-10km, 8.9% at 11-25km, 17.7% at 26-50km, 22.9% at 51-100km, 14.4% at 101-200km, and 4.1% at 201- 300km). Colony-specific differences in travelling distance, dispersal rate, and direction of movements suggested a grouping of colonies in three: (1) eastern Wadden Sea islands (Rottumeroog-Vlieland), with significantly higher dispersal rates and movements mostly towards south-west to south-east, (2) Texel and the four colonies along the mainland coast (Callantsoog-Wassenaar), with shorter mean range and movements mostly to the south, and (3) colonies in the Delta area (Europoort- Saeftinghe) with rather short range movements and dispersal in many directions. The maximum distance travelled did not vary much between adults, immatures, and juveniles, but the timing of outward and return movements was different for each of the age categories. Adult birds reached their greatest mean distances on average one month earlier than immatures, which in turn arrived at this point one month earlier than juveniles. These age-specific differences were enhanced in spring, when birds were moving towards the (natal) colonies, but when adults moved on average closer and two months ahead of immatures, which in turn moved earlier and closer to the natal home-range than juveniles. With reference to studies in other European countries, Herring Gulls breeding in The Netherlands occupied a mid-position between dispersive and sedentary tendencies.

Key words: *Larus argentatus* – colour-ringing – dispersal – timing – distribution – long-term trends

Introduction

Palaearctic Herring Gulls *Larus argentatus*, with the exception of more migratory populations breeding in northern Scandinavia and Russia, are known as either resident or dispersive to a varying degree (Glutz von Blotzheim & Bauer 1982, Cramp & Simmons 1983). Seasonal dispersal patterns have been shown to vary with age as well as with breeding area (Landsborough Thomson 1924, Eaton 1933, Schüz 1933, Coulson & Butterfield 1985, Calladine 2002). In The Netherlands, where the species is generally regarded as a common resident or at best a short-distance migrant (CNA 1970, Bijlsma *et al.* 2001), a review of migratory movements and dispersal patterns of Herring Gulls has thus far only been undertaken on the basis of metal ring recoveries (Spaans 1971). Tinbergen (1952) reported an apparent discrepancy between the results of an early analysis of ringing results (Drost & Schilling 1940), describing Herring Gulls as residents with some dispersal in all directions after the breeding season, and observations of endless streams of southbound Herring Gulls along the coast and called for data. Spaans (1971) also concluded, that during the 1950s and 1960s, after the breeding season, Herring Gulls dispersed in all directions, "more or less random around the ringing localities", and that only birds from Texel in their first year moved predominantly to the south.

Herring Gull population in The Netherlands went through phases of exploitation, protection, persecution and again (partial) protection in the late 19th and throughout the 20th centuries (Spaans 2007). In the early 20th century, the breeding population was small (*c.* 2,500 pairs) and colonies were frequently raided by humans in search of eggs (food) and feathers (fashion). This changed around 1912, when protective measures were implemented to safeguard colonies from egging and other forms of disturbance and the demand for seabird feathers had come to a halt. The population increased from the mid-1910s to *c.* 15,000 pairs in the late 1930s (12.2% increase per annum; Spaans 1998c). By that time, however, even conservationists became concerned about the impact of what was called an "overpopulation" of Herring Gulls. Measures to restrict the number of nesting Herring Gulls were taken and in the absence of immediate success, this developed into a systematic campaign of destruction. From 1947-1966, some 90,000 adults were either shot or poisoned and some 500,000 eggs were destroyed (Spaans 2007). In the mid-1960s, this type of destruction came to an end. It stopped because the effect of culling was 'disappointing', but also because of an alarming decline in breeding success of a number of seabirds and marine mammals in the Wadden Sea area, due to intoxication, following continuous leakages of pesticides (e.g. dieldrin, aldrin) by Shell Chemie in Botlek near the mouth of the River Rhine (Koeman *et al.* 1969). The Herring Gull population, which had peaked at 24,000 pairs in 1954 when the persecution was intensified, had dropped to some 16,000 pairs in the mid-1960s.

Following the relaxation of persecution, after the late 1960s, the population rapidly increased, to reach an all time high of nearly 90,000 pairs in 1984 and 1985 (11.5% increase per annum; Spaans 1998c). Now that the Herring Gull population was so large, investigations into the whereabouts of gulls from each of the major colonies were instigated. A large-scale colour-ringing programme (plastic colour-rings with inscriptions that could be read from a distance, for gull studies a rather novel tool at the time) seemed the most appropriate approach to achieve that goal (Spaans & De Wit 1985, Noordhuis 1989). The colour-ringing campaign, in which *c.* 100 large chicks were marked annually in each of 12-14 participating colonies, lasted from 1986 through 1988. The colonies have been rather different in their fate since this project started: some are still intact and with roughly the same number of breeding pairs, others were abandoned within a few years after the ringing campaign, others increased markedly and again other colonies declined (Spaans 1998c). The wealth of information that has accumulated over the years following this colour-ringing campaign is now fit for analysis and this paper evaluates the first results.

The sightings of colour-ringed individuals observed between 1986 and 2009 were analysed in search of patterns of dispersal and seasonal movements, and differences between colonies, cohorts and age categories therein. Specific questions addressed are: (1) Is there evidence for migration (i.e. regular seasonal journeys) in Herring Gulls that fledged from colonies in The Netherlands, or are movements usually irregular and mostly in response to for example weather or prey resources? (2) Do these Herring Gulls move in all possible directions away from the natal colonies, or is there a tendency to travel in a set direction? (3) What is the difference between annual and seasonal movements of juvenile, immature, and adult Herring Gulls? (4) Is there a difference between colonies or regions with respect to the distance and direction of (annual or seasonal) movements (*cf.* Coulson and Butterfield 1985)? Finally, (5) do Herring Gulls in winter completely mix, or is there a difference in wintering areas for birds originating from different breeding colonies or breeding regions?

Material and methods

Herring Gulls were ringed as chicks, mainly near-fledglings, in 12 colonies in 1986 (1,247 individuals), 13 colonies in 1987 (1,354 individuals), and 14 colonies in 1988 (1,396 individuals).

Table 6.1. Numbers of Herring Gull chicks colour-ringed during 1986-1988, and estimated breeding populations between 1985 and 2005 (rounded figures; SOVON & Waterdienst *unpubl. data*). Trends in breeding numbers of colonies since colour-ringing took place are indicated as well, and qualified as either increasing (+), stable (±), declining (—), or having collapsed (†). Strong trends are indicated by double symbols. The bottom line refers to the total number of chicks colour-ringed (left) and the total Dutch breeding population estimates (pairs), including other colonies as well (right).

	Numbers ringed				**Number of breeding pairs**					
Colony	**1986**	**1987**	**1988**	**Totals**	**1985**	**1990**	**1995**	**2000**	**2005**	**Trend**
Rottumeroog	103	103	105	311	5,600	3,500	3,200	2,400	2,800	—
Rottumerplaat	105	105	100	310	2,800	6,200	2,100	1,700	1,300	——
Schiermonnikoog	105	105	105	315	5,000	5,200	4,800	7,200	3,100	±
Ameland	102	105	104	311	2,000	3,000	2,500	3,600	4,900	++
Terschelling	103	105	105	313	16,900	16,000	11,700	5,000	3,200	——
Vlieland	105	105	106	316	12,500	10,000	8,000	3,100	4,700	——
Texel	103	104	105	312	8,800	9,500	7,600	6,500	6,100	±
Callantsoog	105	104	104	313	1,500	730	1,400	510	350	——
Schoorl	102	99	103	304	3,200	1,200	25	0	0	†
IJmuiden			105	105	300	1,400	1,100	1,400	1,500	++
Wassenaar	105	104	40	249	5,100	200	0	0	0	†
Europoort	104	105	105	314	1,300	5,000	7,800	7,000	5,000	++
Schouwen	105	105	104	314	7,250[1]	7,400	4,000	3,000	2,300	——
Saeftinghe		105	105	210	6,100	7,000	8,500	8,000	8,000	±
Total	1,247	1,354	1,396	3,997	88,850	77,150	70,000	62,800	53,000	—

[1] a 1987 count was preferred over an unreliable estimate of 13,000 pairs in 1985 (see Vercruijsse 1999 for further details).

The 14 colonies (Fig. 6.1), the number of chicks ringed in each colony, and the years during which colour-ringing took place in of each of the sites are listed in Table 6.1. Colonies were categorised as having *collapsed* (†) if they ceased to exist within 15 years after ringing (Wassenaar and Schoorl), as *declining* (—) when 50% or less of the population remained in the early 21st century when compared to the late 1980s and early 1990s (Rottumeroog, Rottumerplaat, Terschelling, Vlieland, Callantsoog, and Schouwen), *stable* (±) if the population remained within ±50% of the number of breeding pairs during ringing (Schiermonnikoog, Texel, Saeftinghe), and as *increasing* (+) if the number of breeding pairs had more than doubled in recent years in comparison with the situation during the ringing campaign (Ameland, IJmuiden, Europoort; Table 6.1).

Colour-rings - The rings used, one on each tarsus, were large and conspicuous; colours deployed included blue, red, green, orange, white, yellow, and black (Camphuysen 2008c). Inscriptions were a single letter (A, B, D, G, H, J, L, N, P, S, T, X, Y and Z), a number (1, 2, 4, 7, 9) or one to three parallel bars (-, =, Ξ). The inscription was repeated three times so that a ring could be read from all angles of observation; the bars ran around the ring (horizontally). For notation, the protocol suggested to mention the left ring first, followed by the right ring, and to use B for blue and Z for black. Furthermore, it was suggested to write — for single bar, F for double bar and 3 for triple bar inscriptions. No metal ring was added. The position of the rings (left or right tarsus), the colour, and the inscriptions formed unique code combinations (further referred to as 'ring-codes').

The plastic rings were prone to wear and many rings were eventually lost. Incomplete codes were omitted from the analysis (1,706 sightings of 170 incomplete ring-codes), except in rare cases where local knowledge permitted us to enter the correct original code for sightings of well-known individuals that had lost one of their rings. Fading colours formed a second problem. Ring loss became a frequent issue after 10 calendar years, ring fading occurred in some colours after six years. Colours of rings were not randomly distributed over the various colonies/ringing years. Yet, differences in sightings probability were site-specific rather than colour-specific, and sightings rates were rather similar for colours with different 'hardiness' (dark rings being apparently slightly stronger than light colour rings) within subregions, while they were rather different between areas with similar ‘hardiness’ of the rings.

Sightings of colour-rings were all entered by a central database manager upon receipt, while each entry was immediately examined in the context of previous sightings. Because the movements of many individual birds were characteristic, ‘‘unusual’ records (outliers in time or space) were double-checked and observers were consulted where needed, to confirm sightings. During this procedure, numerous misreportings were found where colour-fading had been an issue. Where uncertainties remained, records were omitted. It was soon found that individuals were so site-faithful throughout their annual cycle (both in winter and in summer), that outliers were easy to spot. In later years, therefore, with more prolonged individual dispersal patterns at hand, further checks for consistency were performed during which at least several hundreds of records (probably <0.5% of all reported sightings) were either corrected or deleted. All these thorough checks have made that the database, despite its large size and numerous contributors, is now relatively ‘free’ of errors.

Age and plumage - Herring Gulls were labelled as juveniles during the entire first year since ringing (July of 1st calendar year until June of 2nd calendar year). Immatures are Herring Gulls in 2nd (Jul-Dec), 3rd (Jan-Dec), and 4th (Jan-Dec) calendar year, whereas older birds were referred to as adults. For the summer analyses (Apr-Aug or Apr-Sep), however, all 2nd calendar year individuals (at least 10 months old in that season) were included with the immatures.

Analysis - With all gulls ringed as chicks, the exact age was known for all birds of which a complete ring code could be read during later encounters. For each sighting, date, observer, and location were logged, while distance (km) and angle (°) from the natal colony were calculated for each locality and used for further analysis. Angles were subsequently grouped into octants (N, NE, E, SE, S, SW, W, and NW), while distances were either used as they were measured (km), or grouped into categories. Data were analysed on the basis of spatial or temporal patterns in sightings. Reported sightings were either plotted exactly (latitude-longitude co-ordinates; 1’ resolution), or grouped (within certain popular ring-reading locations, or particular distance zones) for analysis. All sightings within 5km from the ringing location were labelled as ‘home-range’ records. For each of the sightings, distance to the nearest North Sea coast was calculated (km), in order to facilitate the analysis of inland movements. Distances were grouped into categories for analysis. Sightings within 5km from the North Sea coast were taken as ‘coastal reports’.

In order to analyse the dispersal rate (*r*) from the natal colonies, sightings within the home-range were omitted. The rate of dispersal has been calculated using the method described by Coulson and Brazendale (1968) for Cormorants *Phalacrocorax carbo*. The sightings were grouped into equal distance zones from the natal area (50km intervals). To avoid pseudo-replication and to have individual birds as units rather than individual sightings, the representation of birds, as a proportion (%) of all sightings of that individual, within each of the distance bins was assessed and the average representation for all individuals within each of the distance bins was subsequently determined. The percentage of birds recorded within each zone, plus those recorded at greater distances from the natal colonies were determined, and the logarithm of these numbers plotted against distance. A linear relationship would imply that a constant proportion of the birds which enter a zone remain in it, irrespective of the distance to the colony. This constant (*r*), or the rate of dispersal, may vary between different age categories of gulls, or between gulls from different colonies or areas, and can be calculated (± standard error) in the same manner as the average annual survival rate in birds (Lack 1943, Parsons and Duncan 1978). The dispersal rate *r* is provided to illustrate and quantify whether the dispersal of a particular category of birds was greater or smaller than another.

Some sites were particularly productive with sightings (‘mega-sites’). For example, a frequently explored site such as the Tilburg refuse tip alone yielded 8,606 observations of 795 ring-codes. Another site, IJmuiden harbour, yielded 4,529 sightings of 557 individual birds over the years. Twelve clusters of such 'mega-sites' (i.e. groups of particularly productive sites within the same general area; Fig. 6.1, Table 6.2) were analysed to investigate the representation of individual colonies in each of them, in a further attempt to discover colony-specific dispersal and movements. Some of these clusters produced sightings over a distinctly shorter period of years than the others (Wieringermeer 1987-1995, inland areas southern Netherlands 1988-1996, Belgian refuse tips 1986-1995; Table 6.2). Because in some colonies fewer chicks were ringed than in others, correction factors were needed to avoid underrepresentation of certain ringing sites in the analysis: Rottumeroog (x0.92), Rottumerplaat (x0.92), Schiermonnikoog (x0.91), Ameland (x0.92), Terschelling (x0.91), Vlieland (x0.90), Texel (x0.92), Callantsoog (x0.91), Schoorl (x0.94), IJmuiden (x2.72), Wassenaar (x1.15), Europoort (x0.91), Schouwen (x0.91), and Saeftinghe (x1.36; see Table 6.1).

Table 6.2. Clusters of 'mega-sites' (sites from where at least 100 sightings of colour-ringed Herring Gulls were reported; see Fig. 6.1), with for each cluster the number of sightings and ring-codes during winter and summer, and in total.

			Winter (Oct-Mar)		**Summer (Apr-Sep)**		**Total**
Nr.	**'Mega-site' clusters**	**Period**	**Sightings**	**Codes**	**Sightings**	**Codes**	**codes**
1	Germany, refuse tips and sewage works	1987-2003	168	85	2	2	86
2	Groningen and Drenthe, refuse tips	1986-2009	3,462	599	1,354	468	744
3	Central Wadden Sea and refuse tip Terschelling	1986-2003	179	58	2,184	341	360
4	Wieringermeer, refuse tip	1987-1995	1,444	296	1,413	259	396
5	Coast northern Noord-Holland	1986-2009	4,341	476	9,471	786	901
6	Amsterdam	1986-2003	217	59	72	36	79
7	Mainland coast from IJmuiden to the south	1986-2006	9,425	1,020	10,154	903	1,301
8	Inland areas southern Netherlands, refuse tips	1986-1996	7,863	739	3,092	516	883
9	Zeeland, refuse tips and coastal sites	1986-2008	2,745	474	3,466	465	621
10	Inland refuse tips Belgium	1986-1995	666	318	163	105	348
11	Belgian coast (coastal sites)	1986-2009	555	134	748	170	225
12	French coast (coastal sites)	1988-2008	919	189	240	95	205

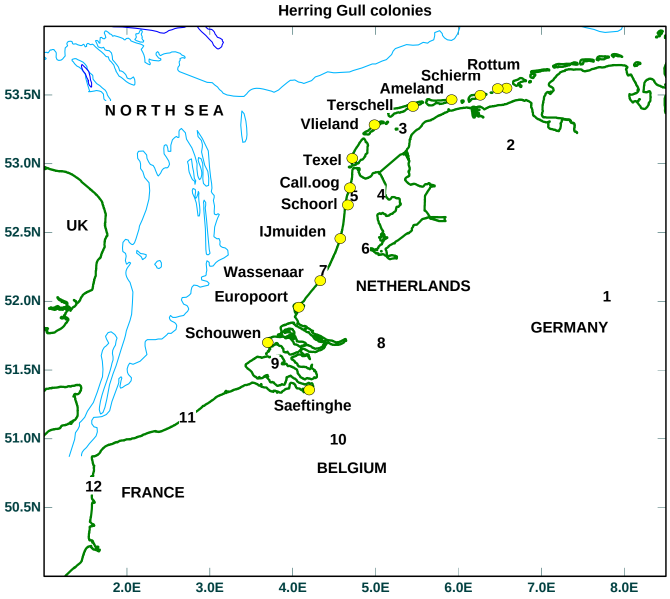


Fig. 6.1. Colonies (Rottum through Saeftinghe) of Herring Gulls where chicks were colour-ringed during 1986-1988 (see also Table 1).

Rottum refers to Rottumerplaat and Rottumeroog in the east. Figures refer 'mega-sites', including (1) German refuse tips and sewage works, (2) refuse tips Groningen and Drenthe (Usquert, Veendam, Wijster), (3) central Wadden Sea, also including refuse tip at Terschelling, Harlingen harbour, and Griend, (4) refuse tip in Wieringermeer, (5) northern Noord-Holland (Julianadorp-Camperduin, coastal sites), (6) Amsterdam, (7) mainland coast south of and including IJmuiden (IJmuiden-Hoek van Holland, coastal sites), (8) inland areas southern Netherlands (refuse tips Breda, Geldermalsen, Tilburg, Waalwijk), (9) Zeeland (refuse tips and coastal sites), (10) inland refuse tips in Belgium (Antwerpen, Helchteren, Mont-Saint-Guibert, Vlierzele), (11) Belgian coast (coastal sites), and (12) French coast (coastal sites).

Table 6.3. Sightings with age of Herring Gull chicks colour-ringed in The Netherlands during 1986-1988 (number and proportion of ring-codes).

Colony	Juvenile	Immature	Adult	N ringed
Rottumeroog	231 (74.3%)	138 (44.4%)	79 (25.4%)	311
Rottumerplaat	171 (55.2%)	115 (37.1%)	62 (20.0%)	310
Schiermonnikoog	195 (61.9%)	126 (40.0%)	72 (22.9%)	315
Ameland	162 (52.1%)	96 (30.9%)	55 (17.7%)	311
Terschelling	259 (82.7%)	120 (38.3%)	87 (27.8%)	313
Vlieland	264 (83.5%)	129 (40.8%)	74 (23.4%)	316
Texel	262 (84.0%)	164 (52.6%)	119 (38.1%)	312
Callantsoog	244 (78.0%)	197 (62.9%)	137 (43.8%)	313
Schoorl	243 (79.9%)	213 (70.1%)	183 (60.2%)	304
IJmuiden	100 (95.2%)	78 (74.3%)	64 (61.0%)	105
Wassenaar	99 (39.8%)	76 (30.5%)	58 (23.3%)	249
Europoort	238 (75.8%)	208 (66.2%)	142 (45.2%)	314
Schouwen	268 (85.4%)	202 (64.3%)	153 (48.7%)	314
Saeftinghe	157 (74.8%)	120 (57.1%)	70 (33.3%)	210
Total	2,893 (72.4%)	1,982 (49.6%)	1,355 (33.9%)	3,997

Results

Sightings and recoveries - Between the summers of 1986 and 2009 (23 years), of 3,997 Herring Gull chicks colour-ringed, 3,124 individuals (78.2%) were read and reported at least once, while 453 (11.3%) were eventually recovered dead. In total, 86,247 ring-readings of living gulls were received and processed, originating from 1,358 locations and by 868 observers. In all, 72.4% were reported at least once as juveniles (range 39.8-95.2%), 49.6% as immatures (30.5-74.3%), and 33.9% as adults (17.7-61.0%; Table 6.3). Rottumerplaat (colony declined), Ameland (increased), and in particular Wassenaar (collapsed) produced relatively few ring-readings in all age categories (Table 6.3). Most reported sightings came from coastal areas (in particular the mainland provinces of Noord-Holland and Zuid-Holland), and from refuse tips in the north-eastern part of the country and in the province of Noord-Brabant. An overwhelming majority of 93.6% of all sightings came from The Netherlands (n= 86,247; 3,073 ring-codes), 3.5% from Belgium (614 ring-codes), 2.1% from France (292 ring-codes), and 0.7% from Germany (214 ring-codes). Only five sightings were reported from Denmark (3 birds), 1 from Poland (1 bird) and 3 from the United Kingdom (3 birds).

Distances - One-fifth (20.5%) of all reported sightings (n = 86,247) originated from the home-range areas. Only 691 sightings (0.8%), including 144 birds (3.6%) were reported at distances of over 300km from the natal colony (10.7% 6-10km, 8.9% 11-25km, 17.7% 26-50km, 22.9% 51-100km, 14.4% 101-200km, 4.1% 201-300km). Wintering birds were reported on average at *c.* 80-95 km from the natal colonies, with a tendency for birds from the Wadden Sea area to travel further away (Table 6.4). Adults in summer were normally seen within 20-40 km from their natal colonies, but long-distances (200-500 km) were still frequently reported during the breeding season for all colonies (Table 6.5).

Exceptional distances (>500 km) were covered by three individuals. O2WJ (ringed at Rottummeroog) was seen as a juvenile at the refuse tip of Boismont, Somme (506 km from natal colony), and as an adult on the mudflats near Le Crotoy, Somme (504 km), France. WLZA (Callantsoog) was found dead in its 3rd calendar year at Courseulles-sur-Mer, Calvados (529 km), France. WTZB (Callantsoog) was sighted in its 4th calendar year at Kolobrzeg, Baltic coast (736 km), Poland. The two birds seen alive were re-sighted later, much nearer to the natal colony: O2WJ until 2008 (20 yrs), WTZB until 1995 (7 yrs).

Table 6.4. Mean and maximum distances (km) from the natal colony in winter (Oct-Mar) with age of Herring Gulls ringed as chick in The Netherlands during 1986-1988.

Colony	**Juvenile**		**Immature**		**Adult**	
	mean	max	mean	max	mean	max
Rottumeroog	98	506	69	478	107	504
Rottumerplaat	97	370	95	484	128	300
Schiermonnikoog	101	451	103	485	152	442
Ameland	137	426	159	461	156	432
Terschelling	119	406	133	412	167	412
Vlieland	101	417	143	404	151	414
Texel	99	388	105	388	95	357
Callantsoog	69	327	77	736	56	333
Schoorl	68	350	78	339	54	349
IJmuiden	53	292	52	326	24	327
Wassenaar	27	172	52	289	66	287
Europoort	54	431	60	262	64	264
Schouwen	80	366	90	262	63	354
Saeftinghe	57	221	52	264	44	199
Overall	83	506	91	736	95	504

Table 6.5. Mean and maximum distances (km) from the natal colony in summer (Apr-Sep) with age of Herring Gulls ringed as chick in The Netherlands during 1986-1988.

Colony	**2 cal yr**		**3 cal yr**		**4 cal yr**		**Adult**	
	mean	max	mean	max	mean	max	mean	max
Rottumeroog	105	473	72	349	44	274	20	504
Rottumerplaat	101	376	72	373	61	237	61	237
Schiermonnikoog	132	338	81	354	86	399	57	338
Ameland	142	426	57	330	79	265	74	264
Terschelling	79	406	72	397	59	226	53	203
Vlieland	63	380	63	292	52	222	59	419
Texel	74	351	64	376	65	344	49	376
Callantsoog	37	327	39	327	39	327	28	350
Schoorl	43	308	43	315	45	313	28	347
IJmuiden	46	292	53	327	17	282	5	327
Wassenaar	40	182	69	167	45	187	50	287
Europoort	60	429	59	231	50	231	45	264
Schouwen	78	223	72	227	51	213	18	227
Saeftinghe	49	224	52	225	49	177	40	198
Overall	75	473	62	397	53	399	42	504

The mean distance from the natal colony through the year fluctuated most strongly in Herring Gulls from the eastern Wadden Sea islands (Rottumeroog-Vlieland), with a mean range of 160 km away from the natal colonies in winter and a gradually closer approach of the home-range areas in summer with increasing age (Fig. 6.2A). Herring Gulls from Texel and the four colonies along the mainland coast (Callantsoog-Wassenaar) were seen at a mean distance of 80-100km in winter and at considerable shorter distances to the natal colonies in immature stages in summer than seen for immatures in the previous group (Fig. 6.2B). In the Delta area (Europoort-Saeftinghe), rather smaller differences in mean range between summer and winter were found, particularly in younger birds (within 50-70km from the natal colonies), but a more distinct seasonal pattern in distances was found in adults (Fig. 6.2C). Long-distance movements (>200km from the natal colony) were more common in the first group of colonies (12.9% of all sightings, 20.6% of all ring-codes) than in colonies situated along the mainland coast (2.6% and 16.5%, respectively), and in the Delta area (1.4% and 11.7%, respectively).

Dispersal rates (*r*) in winter (Oct-Mar) and summer (Apr-Sep) according to age for each of the 14 colonies are shown in Table 6.6. Winter dispersal rates were remarkably similar for each of

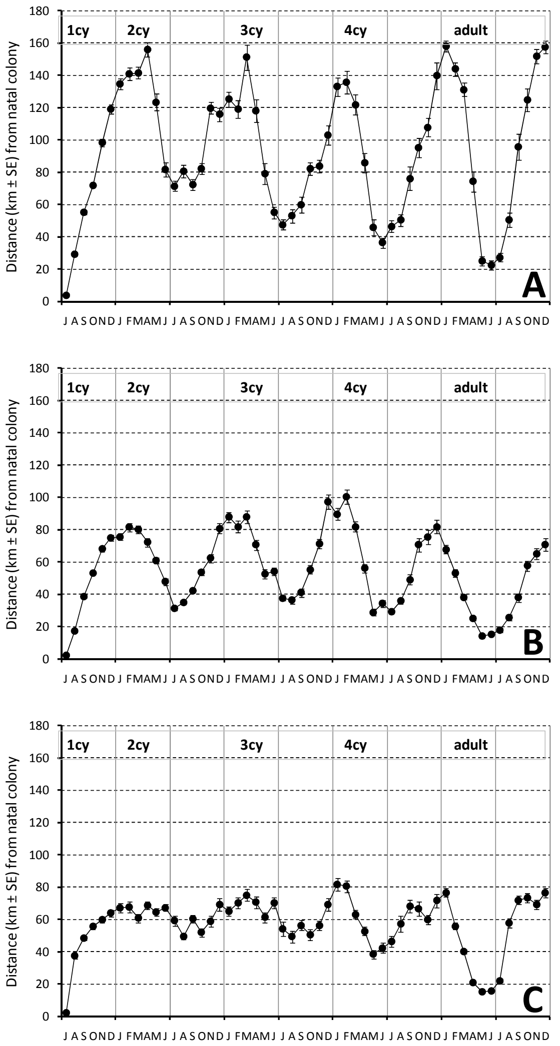


Fig. 6.2. Mean distance (km ± SE) from natal colony from fledging up to and including adult stage (A) for Herring Gulls colour-ringed as chick at the eastern Wadden Sea Islands Rottumeroog-Vlieland (n= 18,902 sightings), (B) at at Texel and in the mainland coast colonies Callantsoog-Wassenaar (n= 45,467 sightings), and (C) in the Delta area colonies Europoort–Saeftinghe (n= 21,869 sightings) during 1986-1988. The x-axis gridlines indicate 9 half-yearly periods (from July of the year of ringing).

the three age categories (adults versus immatures, t_{26} = 0.1, n.s.; immatures versus juveniles t_{26} = 1.13, n.s.), but in summer, immatures dispersed further than adults (t_{26} = 1.84, $P<$ 0.05). In all age categories and seasons, dispersal rates of Herring Gulls from Rottumeroog-Vlieland significantly exceeded those of the other colonies (Texel–Saeftinghe; Table 6.6).

The mean distance of winter movements away from the natal colony did not change with age (0-23 years, log-transformed mean distances in winter, excluding home-range sightings (y) against true age in years (x); y= 0.52x + 74.273, r^2_{23} = 0.03), but the maximum reported distances declined gradually, suggesting a progressively smaller winter range at older age (y= -14.627x + 555.09, r^2_{23} = 0.49). The difference in dispersal range between colonies in the north-east and those in the rest of The Netherlands (north-west and south-west; see Fig. 6.2) and the annual cycle of departure and return towards the home-range remained intact during at least the first 10 years of life, after which a seriously reduced sample size (a combination of ring loss and mortality) led to a more confusing picture (Fig. 6.3). The difference in dispersal distance between colonies in the north-western region (Fig. 6.2B) and those in the south-west (Fig. 6.2C) disappeared when the birds matured, leading to a highly similar seasonal pattern in range of adult birds in either region.

Direction of movements - The analysis of flight directions away from the natal colonies showed that most colonies, with the exception of those situated in the Delta area (Europoort-Saeftinghe), have a distinct southerly or south-westerly component (occasionally south-east)

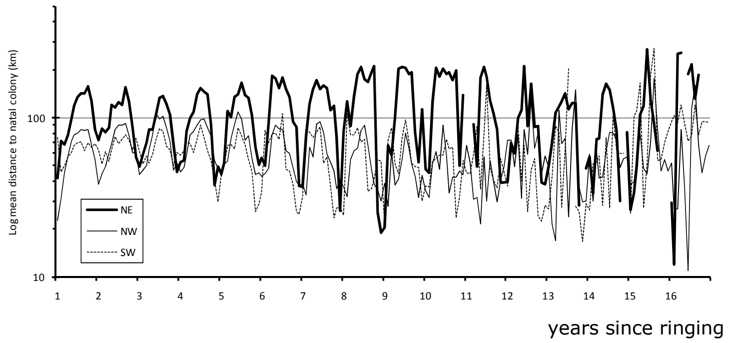


Fig. 6.3. Mean distance (km, log^{10} - transformed) from the natal colony with increasing age for Herring Gulls colour-ringed as chick at the eastern Wadden Sea Islands Rottumeroog-Vlieland (NE), at Texel and in the mainland colonies Callantsoog–Wassenaar (NW), and in the Delta colonies Europoort–Saeftinghe (SW). Mean distances were calculated for each month over a period of 16 years.

Table 6.6. Dispersal rates (r ± SE; see methods for explanation) for various categories of Herring Gulls colour-ringed as chick in The Netherlands during 1986-1988, based on 50km distance bins up to 250 km away from the natal colonies. The three lower lines are groupings of colonies with highly similar values and t-test results (*P< 0.05, ** P< 0.01, *** P< 0.001).

Nr. Colony	**Winter dispersal rates (Oct-Mar)**						**Summer dispersal (Apr-Sep)**			
	Adult		**Immature**		**Juvenile**		**Adult**		**Immature**	
	r	SE	r	SE	r	SE	r	SE	r	SE
1 Rottumeroog	0.65	±0.13	0.60	±0.12	0.63	±0.12	0.35	±0.07	0.58	±0.13
2 Rottumerplaat	0.61	±0.12	0.62	±0.03	0.60	±0.07	0.48	±0.10	0.50	±0.07
3 Schiermonnikoog	0.64	±0.08	0.61	±0.07	0.64	±0.11	0.41	±0.07	0.57	±0.08
4 Ameland	0.74	±0.08	0.71	±0.10	0.60	±0.09	0.52	±0.09	0.62	±0.02
5 Terschelling	0.73	±0.06	0.67	±0.10	0.60	±0.09	0.47	±0.05	0.59	±0.07
6 Vlieland	0.66	±0.10	0.58	±0.12	0.44	±0.14	0.55	±0.10	0.47	±0.04
7 Texel	0.47	±0.12	0.52	±0.11	0.48	±0.14	0.38	±0.08	0.42	±0.09
8 Callantsoog	0.47	±0.12	0.51	±0.09	0.52	±0.15	0.25	±0.09	0.48	±0.09
9 Schoorl	0.41	±0.05	0.49	±0.08	0.52	±0.09	0.35	±0.05	0.46	±0.07
10 IJmuiden	0.50	±0.10	0.44	±0.12	0.42	±0.06	0.48	±0.07	0.39	±0.10
11 Wassenaar	0.42	±0.14	0.35	±0.11	0.24	±0.11	0.41	±0.09	0.24	±0.12
12 Europoort	0.53	±0.08	0.58	±0.09	0.48	±0.07	0.40	±0.12	0.46	±0.05
13 Schouwen	0.43	±0.14	0.50	±0.14	0.44	±0.10	0.32	±0.09	0.45	±0.10
14 Saeftinghe	0.29	±0.13	0.43	±0.08	0.36	±0.11	0.23	±0.11	0.34	±0.06
Colonies 1-6	0.67	±0.04	0.63	±0.04	0.58	±0.04	0.46	±0.03	0.56	±0.03
Colonies 7-14	0.44	±0.11	0.48	±0.10	0.43	±0.10	0.35	±0.09	0.40	±0.08
t_{12} 1-6 versus 7-14	6.59	***	4.62	***	3.28	**	2.58	*	3.86	*

Table 6.7. Direction of sightings (1986-2009) at distances of over 5 km from natal colonies during the winter period (Oct-Mar; %, n= 36,039 sightings) of Herring Gulls (all age classes combined) ringed as chick in The Netherlands during 1986-1988. Predominant directions (>25%) shaded and bold.

	N	**NW**	**W**	**SW**	**S**	**SE**	**E**	**NE**	**Sightings**
Rottumeroog	0		1	20	**76**	2	0	1	1,662
Rottumerplaat			1	**29**	**40**	20	9	0	1,480
Schiermonnikoog			2	21	**35**	**41**	1	1	1,825
Ameland			3	**44**	**26**	22	4	0	1,370
Terschelling	0		4	**23**	**39**	17	17	1	1,678
Vlieland				7	**79**	7	4	2	2,163
Texel				4	**79**	15	1	1	3,267
Callantsoog	1			13	**79**	0	5	1	5,694
Schoorl	9			11	**73**	2	5	0	5,359
IJmuiden	11			**56**	**29**	1	1	2	1,105
Wassenaar	11			**33**	4	18	1	**33**	1,828
Europoort	2	0	1	15	9	**28**	3	**41**	3,253
Schouwen			0	**32**	14	15	**28**	11	3,037
Saeftinghe	11	2	8	3	1	8	1	**64**	2,318
Total	3	0	1	18	**48**	12	6	11	36,039

in their movements, and this applies to both the winter (Table 6.7) and summer reports (Table 6.8). Most (78%) of the sightings during the winter were south from the natal colonies. The proportion was highest for the ten northern colonies. With longitudes ranging from 6°35’E (Rottumeroog) to 4°42’E (Callantsoog), some degree of spatial segregation in wintering areas between colonies is suggested. There was, however, a split in the main direction between colonies, with birds from Rottumeroog-Schiermonnikoog mainly moving to the south and south-east, and those from Ameland-Vlieland mainly to the south and south-west (Fig. 6.4). Vlieland could also be included in another cluster of colonies (with Texel, Callantsoog, and Schoorl, in which 70-80% of all winter sightings were directly south of the breeding colonies. Directions of gulls that had fled-

Table 6.8. Direction of sightings (1986-2009) at distances of over 5 km from natal colonies during the summer period (Apr-Sep; %, n= 32,488) of Herring Gulls (all age classes combined) ringed as chick in The Netherlands during 1986-1988. Predominant directions (>25%) shaded and bold.

	N	**NW**	**W**	**SW**	**S**	**SE**	**E**	**NE**	**Sightings**
Rottumeroog	0		10	23	**57**	8	0	1	866
Rottumerplaat			5	**36**	**41**	9	8	0	773
Schiermonnikoog			10	21	24	**32**	8	4	873
Ameland			8	**64**	11	8	9		839
Terschelling	0		7	**40**	**29**	11	13	1	1,085
Vlieland				14	**43**	1	**39**	3	1,571
Texel				3	**69**	19	6	4	3,584
Callantsoog	6			17	**67**	0	4	6	5,826
Schoorl	**29**			11	**50**	1	5	4	4,856
IJmuiden	21			**55**	14	1	1	9	930
Wassenaar	18			**42**	2	11	2	**26**	2,056
Europoort	6	0	1	15	6	21	1	**51**	3,554
Schouwen				**26**	21	7	**34**	12	3,827
Saeftinghe	21	6	13	1	0	6	1	**52**	1,848
Total	9	0	2	20	**37**	8	9	14	32,488

Table 6.9. Proportion (%) of colour-ringed Herring Gulls from 14 Dutch colonies within 12 clusters of 'mega-sites' (see Fig. 6.1, Table 2) in winter (Oct-Mar). Representation was based on the number of ring-codes, corrected for differences in ringing effort between colonies of origin. Colonies indicated in shaded and bold were particularly well represented (≥10%). For header abbreviations: see text.

	1 **FRG**	2 **Gr**	3 **WdC**	4 **Wr**	5 **NH**	6 **Ams**	7 **ZH**	8 **Brab**	9 **Zeel**	10 **Binll**	11 **Bcst**	12 **F**
Rottumeroog	**12**	**25**	3	3			1	3	1	3		1
Rottumerplaat	**30**	**20**	5	5	1	3	2	3	1	2	2	
Schiermonnikoog	**19**	**20**	2	4	2	2	2	4	2	3	3	2
Ameland	9	**11**	**17**	5	2	5	3	4	3	3	1	3
Terschelling	**12**	**13**	**20**	8	2		4	5	1	2		2
Vlieland	**10**	4	**26**	**9**	9	7	7	5	3	4	5	2
Texel	2	1	3	**17**	**13**	**22**	**10**	**8**	3	3	3	6
Callantsoog	1	1	**10**	**18**	**26**	**25**	**14**	**9**	4	6	9	6
Schoorl	2	2	5	**16**	**25**	**17**	**15**	**10**	6	8	**11**	7
IJmuiden			5	7	9		**20**	7	**13**	**10**	**15**	**14**
Wassenaar		1		2	4	8	7	6	4	3	3	3
Europoort	1	1	2	3	5	8	**10**	**13**	**10**	8	**11**	**14**
Schouwen	1		2	1	1		4	8	**23**	**12**	**27**	**29**
Saeftinghe							1	**14**	**27**	**33**	**10**	**11**
n=	78	551	55	286	469	55	1100	756	529	355	143	199
Area in grey (Σ)	82	89	73	60	64	64	69	55	72	55	75	68

ged in the five southern colonies (IJmuiden-Saeftinghe) were more to north and north-east than those that had fledged in the other colonies. In fact, in all but one colonies (the exception being IJmuiden), few birds moved straight to the south (Table 6.7; Fig. 6.4).

These patterns were more or less retained in summer (Table 6.8), when sightings from Herring Gulls originating from the easternmost three Wadden Sea islands were mostly to the south and south-east, from Ameland and Terschelling mostly to the south-west, from Vlieland, Texel, Callantsoog and Schoorl mostly to the south (but note 39% of the Vlieland birds to the east of the natal colony, and rather frequent sightings north of the natal colony of birds originating from Schoorl). Most sightings of birds from the Delta area were to the east and north-east. Summer sightings from birds originating from the (collapsed) Wassenaar colony were most diverse, with 44% to the north and north-east, and 42% to the south-west of the natal colony.

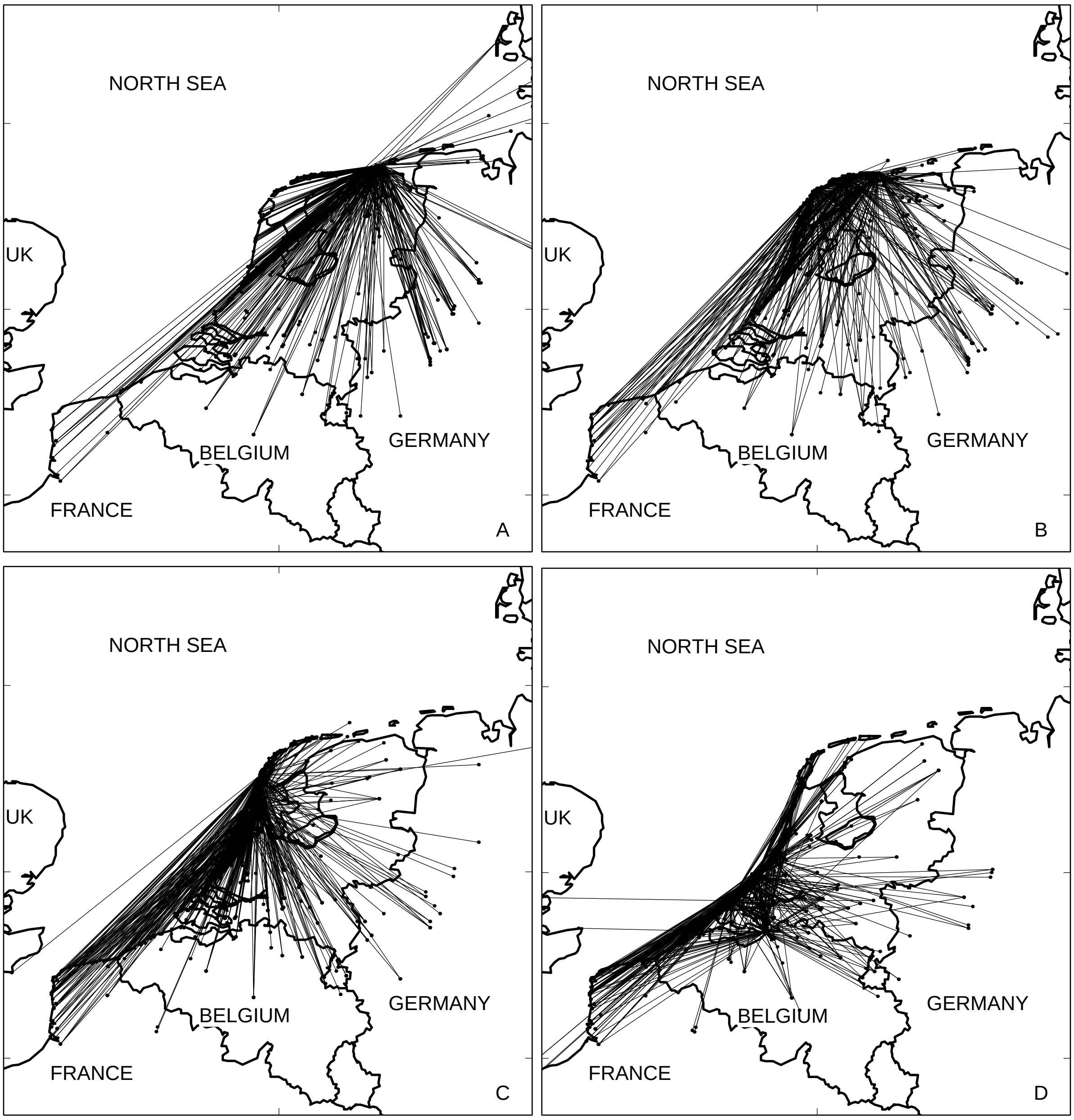


Fig. 6.4. Direction of sightings (1986-2009) at distances of over 5 km from natal colonies during the winter period (Oct-Mar; n= 36,039 sightings) of Herring Gulls (all age classes combined) colour-ringed as chick in Rottumeroog-Schiermonnikoog (A); Ameland-Vlieland (B); at Texel and in Callantsoog-IJmuiden (C); and in Wassenaar-Saeftinghe (D).

The results of travelling distances (Fig. 6.2), dispersal rates (Table 6.6), and directions of movements (Tables 7-8) suggest a grouping of colonies in three. The first group is formed by the eastern Wadden Sea islands (Rottumeroog - Vlieland), with the longest seasonal movements away from natal colonies in winter and a gradually closer approach to the natal colonies in summer with increasing age, significantly higher dispersal rates (Table 6.6) and movements mostly in directions varying from south-west to south-east. A second group of colonies comprises Texel and the four colonies along the mainland coast (Callantsoog-Wassenaar), with a mean range of 80-100km in winter, considerably shorter distances to the natal colonies in immatures in summer than in immatures from the previous group, and mostly moving strictly to the south. Finally, colonies in the Delta area (Europoort-Saeftinghe) show rather smaller differences in mean range between summer and winter in younger birds, a distinct seasonal pattern in adults, short range movements, and a dispersal in many directions.

Dispersal from the perspective of the main wintering areas - From the perspective of sites from where particularly large numbers of sightings were reported (clusters of 'mega-sites'; Fig. 6.1, Table 6.2), it is clear that most were visited during the winter by birds from all 14 breeding colonies. All clusters of 'mega-sites', however, were particularly important for certain (groups of) colonies (Table 6.9). Sightings of Dutch Herring Gulls at German refuse tips and sewage works (FRG, cluster 1) were dominated by birds originating from the Wadden Sea islands (Texel excluded; 91% of all reported rings). Only a handful of birds originated from colonies in the west. Refuse tips in Groningen and Drenthe (Gr, cluster 2) were dominated by Herring Gulls from Rottumeroog-Terschelling (89%), with only rare reports of birds from IJmuiden-Saeftinghe. Local birds were most frequently represented in the central Wadden Sea (WdC, cluster 3), with most Herring Gulls originating from Ameland, Terschelling, Vlieland, and, slightly odd, Callantsoog (73%). At the Wieringermeer refuse tip (Wr, 4), wintering Herring Gulls were dominated by birds ringed on Vlieland, Texel, and in Callantsoog and Schoorl (60% of all birds seen). The mainland coast between Julianadorp and Camperduin (NH, cluster 5) received mainly Herring Gulls from Texel, Callantsoog, and Schoorl (64%). In Amsterdam (Ams, cluster 6), sightings were dominated by birds from Texel, Callantsoog, and Schoorl (64%). The absence of birds from nearby IJmuiden is striking. The mainland coast between IJmuiden-Hoek van Holland (ZH, cluster 7) had sightings being clearly dominated by Herring Gulls originating from Texel, Callantsoog, Schoorl, IJmuiden, and Europoort (69%). Inland refuse tips at Breda, Geldermalsen, Tilburg, Waalwijk (Brab, cluster 8) were attended by a rather wide variety of birds (minimum colony representation 3%, maximum 14%), with 55% from colonies in the west, but as wide apart as Texel, Callantsoog, Schoorl, Europoort and Saeftinghe. In clusters 9-12, Herring Gulls originating from southern colonies (Schoorl–Saeftinghe) dominated: 82% in Zeeland (refuse tips and coastal sites; Zeel, cluster 9), 74% at Belgian refuse tips (Binll, cluster 10), 78% along the Belgian coast (Bcst, cluster 11), and 77% along the French coast (F, cluster 12). Birds from Wassenaar, even after correction for ringing effort, were not commonly represented in any of these 12 areas. Relatively high numbers were seen at some inland refuse tips (cluster 8, 6%), along the coast of Zuid-Holland (i.e. immediate surroundings of the home-range, cluster 7, 7%), and in Amsterdam (cluster 6, 8%; Table 6.9).

Using a similar approach, but with all sightings (including sightings outside the clusters of 'mega-sites' as well) within Germany (214 ring-codes reported), Belgium (614 codes), and France (292 codes), a clear split in regions was found. In Germany, 74% of all reported ring- codes originated from the easternmost five Wadden Sea Islands (85% from all Wadden Sea islands combined). In Belgium and France, the representation of Dutch colonies was rather similar, with 61% from the southernmost five colonies (IJmuiden-Saeftinghe) in Belgium and 64% in France (79% and 82%, respectively, when birds from the two next colonies in line (Schoorl and Callantsoog) are also included.

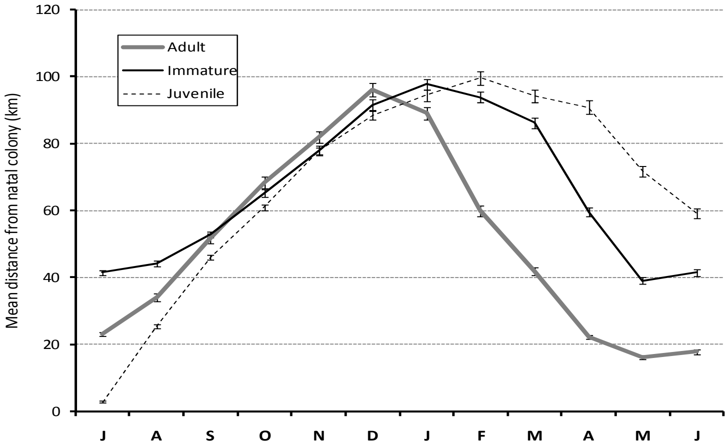


Fig. 6.5. Seasonality in mean distance (km ± SE) from natal colony (n= 86,247 sightings) for adult, immature and juvenile Herring Gulls (all colonies combined) colour-ringed as chick in The Netherlands during 1986-1988.

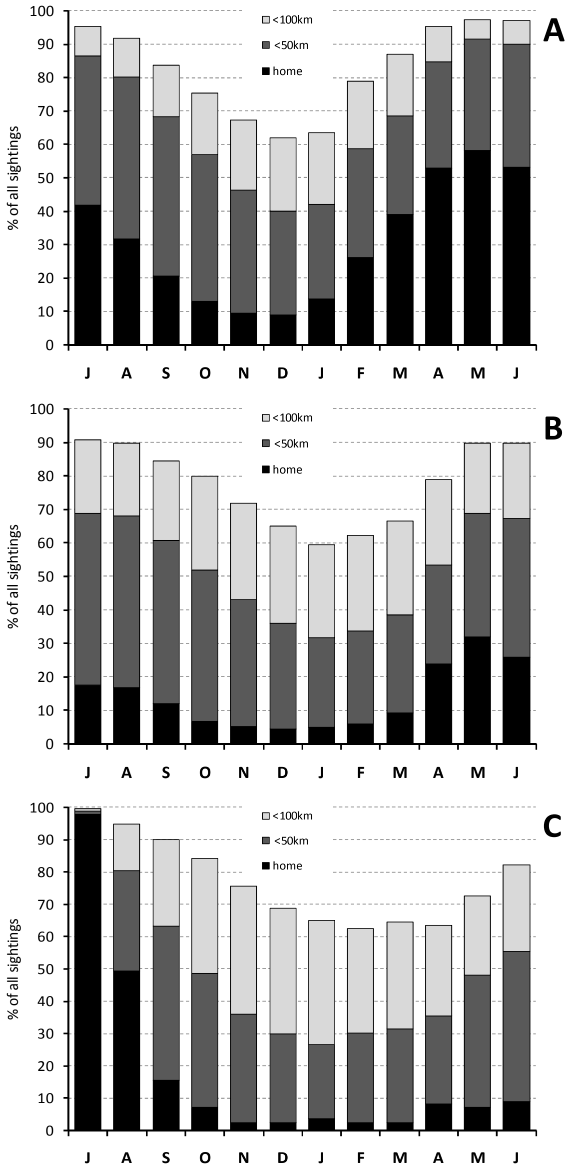


Fig. 6.6. Seasonality in dispersal for (A) adult, (B) immature, and (C) juvenile Herring Gulls (all colonies combined) colour-ringed as chick in The Netherlands during 1986-1988. Shown are proportions of sightings within the home-range and within 50 and 100km from the natal colony (n= (A) 26,158 sightings of adults, (B) 33,518 immatures, and (C) 26,258 juveniles).

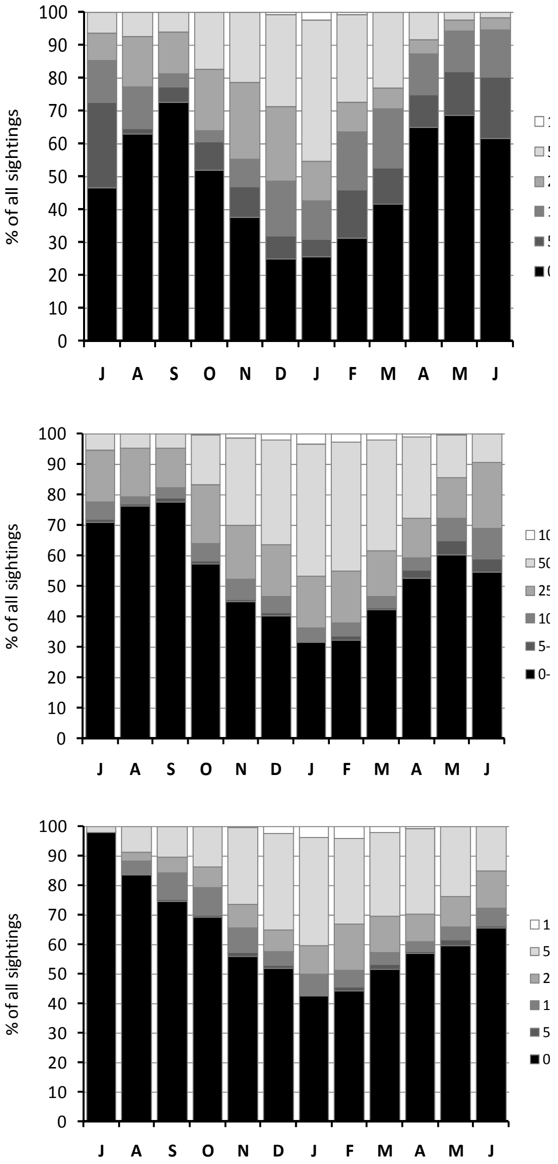


Fig. 6.7. Seasonality in inland dispersal for (A) adult, (B) immature, and (C) juvenile Herring Gulls (all colonies combined) colour-ringed as chick in The Netherlands during 1986-1988. Shown are proportions of sightings within distance bands measured from the North Sea shoreline (n= (A) 26,212 sightings of adults, (B) 32,456 of immatures, and (C) 30,268 of juveniles).

Seasonality and age - The maximum distance travelled away from the natal colony did not vary much between adults, immatures, and juveniles, but the timing of outward and return movements was different for each of the age categories (Fig. 6.2). Adult birds returned towards the colonies from December and January onwards, with a relatively fast return in March and April, whereas young immatures did not even tend to travel towards the natal colony region until very late in spring or early summer. Adult birds reached their greatest mean distances on average a month earlier than immatures, which in turn arrived a month earlier than juveniles (Fig. 6.5). These age-specific differences are enlarged in spring, when mean distances were progressively closer to the natal colony, but in which adults moved on average closer towards the home-range and two months ahead of immatures, which in turn were earlier and closer to the home-range than juveniles (Fig. 6.5).

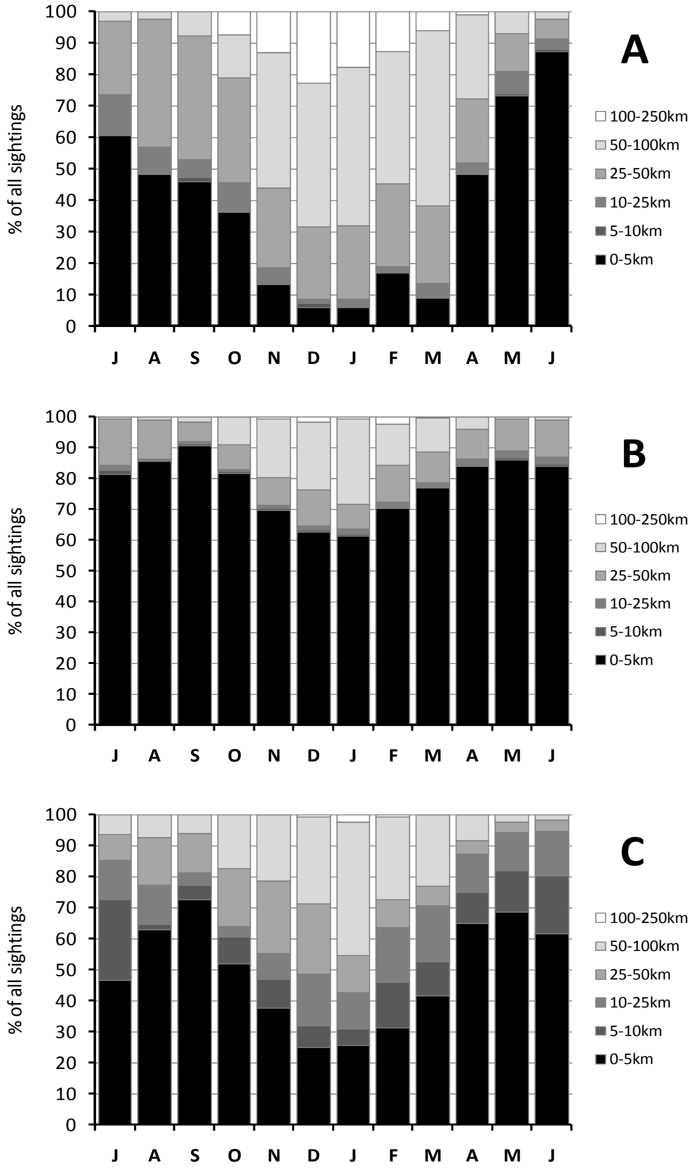


Fig. 6.8. Seasonality in inland dispersal (A) for adult Herring Gulls from eastern Wadden Sea colonies (Rottumerplaat-Vlieland; n= 2,814 sightings), (B) from Texel and the mainland coast (Callantsoog-Wassenaar; n= 16,653 sightings), and (C) from the Delta area colonies (Europoort-Saeftinghe, n= 7,745 sightings), colour-ringed as chick during 1986-1988. Shown are proportions of sightings within distance bands measured from the North Sea shoreline.

Home-range sightings of adult Herring Gulls peaked in May (nearly 60%) and were lowest in Nov-Dec (9%; Fig. 6.6A). Some 40% of all sightings of adult birds in winter were at distances over 100km from the natal colony. In immatures, considerably lower proportions of home-range sightings were found in all months, but the fraction seen within 100km from the natal colony was quite similar to that in adults (Fig. 6.6B). Juveniles abandoned the home-range later than the other age groups, and less than 10% of the sightings of juveniles originated from within the home-range in any month after August of the first calendar-year (Fig. 6.6C). The period in which 35-40% or more of the sightings came from distances at over 100km from the natal colony lasted from Dec-Jan in adults, from Jan-Feb in immatures, but from Jan-Apr in juveniles.

Inland movements - Adults and immatures, all colonies combined, showed a bi-modal pattern in sightings with respect to the distance to the nearest North Sea coast (Fig. 6.7). The peak at sites within 5km from the North Sea coastline in May can best be explained by home-range returns (all natal colonies being coastal), but a distinct second peak occurred in Aug-Sep, during wing moult, after the breeding season. The percentage of coastal sightings of juveniles declined gradually during the first autumn, and some return towards the coast was witnessed in April and May, as in immatures and adults, but with fewer sightings near the natal home-range areas (Fig. 6.7).

When it is clear that only mainland and Delta gulls (Texel-Saeftinghe) show the bi-modal seasonality, with the strongest tendency to stay in coastal habitats for birds originating from Texel–Wassenaar (Fig. 6.8). A high proportion of Herring Gulls from Rottumerplaat – Vlieland were observed at greater distances from the North Sea coast, particularly in winter, followed by a return in April through June. The post-breeding peak in coastal habitats was less obvious, although a decline in sightings occurred after September.

Discussion

Studies of the migratory movements of Herring Gulls in Europe have been based on field observations (Sluiters 1939, Tinbergen 1952, Meltofte and Faldborg 1987), ringing recoveries (Landsborough Thomson 1924, Spaans 1971, Jørgensen 1973, Prüter 1984, Calladine 2002), only occasionally on reported sightings of colour-rings (Rock 1999, Klein 2001, Markones and Guse 2007), and, more recently, on data downloads of electronic devices such as satellite and radio transmitters attached to free-flying gulls (Ens *et al.* 2009). Each method has advantages as well as disadvantages and the results are complementary rather than stand-alone descriptions of migratory pathways and dispersal patterns. Colour-ringing programmes have an advantage over traditional ringing recoveries given the multiple sightings of individual birds (without the need to retrap) over a large number of years, and generally provide a much larger sample size (number of individual birds monitored) than high-tech methods currently used to track individual birds (Ens *et al.* 2009). A disadvantage is that colour-ringing data are influenced by spatial and temporal patterns in observer effort, which is true for metal ringing data as well. As a result, colour-rings of Herring Gulls are seldom read at sea (birds usually in flight or swimming) or in other important foraging areas such as on mudflats in the Wadden Sea area, where birds occur in relatively low densities and where ring-reading is not very profitable from the point of view of the observers.

Bias resulting from ring-reading effort - Enthusiast ring-readers (volunteers, amateur bird-watchers mostly) tend to collect data in areas where the reward (*i.e.* the frequency of colour-ring

Table 6.10. Top-10 ring-readers (A-J) and individual number of ring codes observed, % of all ring-reports, number of individual ring codes found, % of all codes available, number of visited locations and % of all ring-report locations.

Observer	Rings read	% rings read	Codes	% codes	Locations	% locations
A	16,842	19.5	1,338	33.5	222	16.3
B	6,076	7.0	634	15.9	57	4.2
C	5,813	6.7	742	18.6	55	4.1
D	4,481	5.2	507	12.7	37	2.7
E	4,226	4.9	436	10.9	51	3.8
F	3,745	4.3	489	12.2	39	2.9
G	3,733	4.3	642	16.1	47	3.5
H	3,482	4.0	662	16.6	28	2.1
I	3,001	3.5	639	16.0	105	7.7
J	2,870	3.3	681	17.0	87	6.4
	54,269	62.9	1,975	49.4	501	36.9

Table 6.11. Top-10 ring reading sites and individual number of ring codes reported, % of all ring-reports, number of individual ring codes found, and % of all codes available.

Location	Type	Rings read	% rings read	Codes	% codes
Tilburg, refuse tip	Dump	8,606	10.0	795	19.9
IJmuiden, harbour	Harbour	4,529	5.3	557	13.9
IJmuiden, IJbunker colony	Colony	3,838	4.5	124	3.1
Wieringermeer, refuse tip	Dump	2,857	3.3	396	9.9
Camperduin, beach site	Beach	2,848	3.3	561	14.0
Schouwen, breeding colony	Colony	2,477	2.9	218	5.5
Scheveningen, harbour	Harbour	2,055	2.4	438	11.0
IJmuiden, beach site	Beach	2,021	2.3	502	12.6
Breda, refuse tip	Dump	1,959	2.3	444	11.1
Katwijk aan Zee, river mouth	Beach	1,924	2.2	477	11.9
		33,114	38.4	1,828	45.7

sightings) is considerable. Refuse tips, harbours, breakwaters, beaches, and other areas where gulls occur in groups and can be read rather easily are strongly preferred by them. The top-10 ring-readers of the Herring Gull programme described in this paper together have reported 54,269 sightings (62.9% of all 86,247 reports). They found nearly 50% of all ring codes ever deployed, while visiting 'only' 36.9% of all 1,358 sites from which colour-ringed Herring Gulls have ever been reported alive (Table 6.10). The top-10 ring-reading sites, where 33,114 sightings originated from (38.4% of all reported sightings), produced 1,828 ring codes (45.7% of all ring codes deployed). These locations included two harbours (IJmuiden and Scheveningen), three refuse tips (Tilburg, Wieringermeer, Breda), three beach locations (Camperduin, IJmuiden, Katwijk aan Zee), and two particularly well-studied colonies (Schouwen and IJmuiden; Table 6.11).

Because there are regional differences in the likelihood that colour-rings were found and reported, we have analysed the data not only from the perspective of the natal colonies ("where did they go"), but also from the perspective of the sighting areas from where many rings were reported ("from where did they come" and "how are different breeding areas represented within a sample of sightings somewhere"). After reviewing the data from these two angles, we feel confident that questions such as "is there evidence for migration in Herring Gulls breeding in The Netherlands" and "do Herring Gulls move in random directions away from their breeding grounds?" can be addressed.

Migration versus dispersal - Bird migration, as regular seasonal journeys undertaken by birds, is marked by its annual seasonality (Berthold 2001). Migrants tend to breed in area A and perform a seasonal migration to overwinter in area B. The seasonality of movements according to the colour-ring sightings was strong, as a characteristic of true bird migration, but the home-range and immediate surroundings of natal colonies were never completely abandoned outside the breeding period. Dispersal refers to movements away from an existing population through simply moving from one habitat patch into the next. If it is accepted that dispersal is a random movement with respect to distance, the distribution can be represented by a mathematical relationship which describes the smaller numbers of sightings at progressively greater distances from the natal colony. Coulson and Brazendale (1968) expressed this relationship as $p_j = r^j$, where j is the number of distance zones from the colony, p_j is the proportion of birds moving beyond the outer limit of zone j, and r is a constant for each colony being the proportion entering each zone and moving beyond (Table 6.6). A linear relationship between the percentage of birds recorded within each distance zone, plus those recorded at greater distances from the natal colonies (the logarithm of these numbers plotted against distance), would imply that a constant proportion of the birds which enter a zone remain in it, irrespective of the distance to the colony. In case of a true migration, it would be impossible to predict the extent and position of the wintering area from the more local sightings. The sighting data of our colour-ringed Herring Gulls have thus provided more evidence for colony- or area-specific dispersal than for true seasonal migration.

Distance and direction of movements - Dutch colour-ringed Herring Gulls were rarely observed at over 300 km from the natal colony, and predominately moved in a southerly direction away from their natal colonies. Note, however, that dispersal in northerly or north-westerly direction away from most colonies could not be recorded due to an absence of observation possibilities within the North Sea. Lack of observers also makes sightings within the Wadden Sea itself a rather rare event (Ens *et al.* 2009). Hence, while there is a strong seasonality in the whereabouts of Herring Gulls relative to the natal colonies, the observed patterns have been influenced by the (abundant or persistent) presence, scarcity, or even complete absence of observers; a problem for every ringing scheme. Our data suggest that there are distinct differences in wintering areas between birds originating from the North-east (longer range, predominantly south-west, south, and south-east), the North-west (intermediate range, predominantly to the south) and the South-west (shortest range, frequent movements in most directions; Fig. 6.2, Table 6.7). The overwhelming majority of winter sightings of the ten northernmost colonies (Rottumeroog-

IJmuiden) is south (south-west through south-east) from the natal colony, even despite suitable habitats to the east and north-east. With the same predominant direction of dispersal of Herring Gulls from different colonies, spatial segregation of main wintering grounds is inevitable and was indeed found. While the likelihood for an eastern bird was probably relatively higher in the central west of the country, as a result of differences in observer effort, we still find consistent patterns in dispersal between colonies (Table 6.9).

The fact that dispersal rates were higher in the more northerly colonies than in the southern subset also has some geographical context. Birds from colonies on Wadden Sea islands often roost on the mainland to the south of the colony, but these birds have to cover some distance in comparison with mainland birds, because of the mere presence of the Wadden Sea basin where they cannot roost. Suggested groupings based on range, dispersal rate, and directions of movements would include six colonies in the North-east (Rottumeroog-Vlieland), five colonies in the West and North-west (Texel-Wassenaar), and three colonies in the South-west (Europoort-Saeftinghe). The step between the first group of colonies and the second is larger than the step between the second group and the third. A geographical explanation for this difference could be the existence of the Wadden Sea. Ring-reading activity is low within that basin, so that the mean distance travelled calculated for birds from the Wadden Sea islands may be biased (exaggerated) as a result of a spatial gap in observer effort. Yet, the much greater tendency to abandon home-range areas by gulls from the Wadden Sea area could be an argument to label these birds as short-distance migrants rather than as dispersive.

Dispersal and age - With increasing age, Herring Gulls arrive earlier within the home-range each spring, until a regular pattern of approach (Feb-Apr), shortest range (May-Jul), departure (Aug-Oct), and longest range (Nov-Jan) relative to the natal colonies is achieved. Age-specific differences in mean travelling distance, however, were relatively small (Fig. 6.2), and winter dispersal rates were similar for all age groups.

Adults and immatures showed a bi-modal pattern in sightings with respect to the distance to the nearest North Sea coast (Fig. 6.7). Post-breeding peak numbers within 5km from the North Sea coast were found in Aug-Sep, just after the breeding season, when adults are engaged in post-nuptial (complete) moult. It is interesting to note that in this period at-sea sightings of Herring Gulls throughout the North Sea are at their lowest (Camphuysen and Leopold 1994, Stone *et al.* 1995). Lensink (2002) reports a coastal 'summer migration' from Jun through early Aug and explains these movements as 'birds abandoning colonies'. According to this author, autumn movements do not start before October, with a peak in early December and inland movements in autumn have a median value of one week later than coastal displacements. All this would fit the picture emerging from our colour-ring sightings (Fig. 6.7): Herring Gulls finalise their wing moult (which has commenced during breeding) at coastal sites, disperse to some extent and later in autumn and winter into inland habitats (colour-ring sightings) and to the open sea (as suggested from ship-based surveys; Camphuysen and Leopold 1994) and return to the coast (and colonies) in spring.

Since 1990, there were six years during which sightings from inland sites at 50-100km from the coast were frequently reported. Most sightings were from refuse tips, which became unavailable for gulls one after the other through changes in waste management (open refuse tips were closed or covered up, gulls were actively scared away with the help of falconers, and organic waste materials were increasingly separated from other waste products and processed elsewhere). In the next period (1997-2003), with many more deep inland sightings mostly at German refuse tips, the peak may have been an observer effect (most sightings are from only few dedicated, but apparently temporarily active observers).

The exceptional season, 1995-1996, with a very high proportion of winter sightings of adult Herring gulls at coastal locations, was the coldest winter in the entire series (IJnsen index De Kooy, data KNMI, De Bilt). For a second group of seasons with high proportions in coastal areas

(2001-2002 through 2003-2004), however, winter conditions were mild as in most of the other years. The colour-ring sightings cannot support the suggestion that Herring Gulls have a stronger tendency to disperse inland in mild seasons (SOVON 1987). After 2003, winter sightings of colour-ringed adult birds were typically within a narrow band of 25km from the North Sea coast.

Spaans (1971) high-lighted the attraction of inland refuse tips as 'relatively recent food sources'. Many of these sites are now defunct and therefore unattractive to Herring Gulls that have subsequently declined in numbers and must have redistributed themselves in winter since the 1980s and 1990s. If the observer bias cannot be held responsible for the decline in sightings at inland localities since winter 2001-2002, the stronger tendency to overwinter in coastal areas may have been the result of this change in waste management within the country. Between 1986 and 2001, the proportion of winter sightings from refuse tips has fluctuated between 25% and 63% (mean ± SD 39.8 ± 15.4%, n= 36,179 sightings; 1996 with only 5.1% excluded), but this fell to less than 1% in nearly all years since (9.3 ± 8.1%, n= 316 sightings). Van Waeyenberge (2003) reported that Belgian Herring Gulls tended to visit rubbish dumps less frequently in the course of their lifetime, suggesting a change in food choice with age rather than in food availability. A similar tendency was reported by Vercruijsse (1999), suggesting that adult Herring Gulls preferred a more natural habitat and natural (i.e. mostly intertidal) prey.

Herring Gulls breeding in The Netherlands seem to occupy a mid-position between being dispersive and sedentary; they certainly are not clearly migratory. Of all sightings, 99% were reported from distances less than 300km away from the natal colony. Yet, even within a small country like The Netherlands, there is evidence for a stronger tendency to cover some distance in winter for birds originating from the more northerly colonies than from colonies further to the south. The conclusions by Spaans (1971), that the gulls disperse in all directions and that the distribution of the autumn and winter recoveries is more or less random around the ringing localities, are not supported by the present study. We found colony-specific and age-specific patterns in dispersal and timing, and predominantly southward dispersal for most colonies after breeding. Belgian Herring Gulls also dispersed mostly in a southerly direction and generally covered only small distances (van Waeyenberge 2003). However, the Dutch Delta area was one of the main wintering areas, indicating northward and north-eastward dispersal similar to the birds nesting in Saeftinghe. Furthermore, the coastline of northern France and the Belgian coast itself were the most important areas. As in The Netherlands, immature birds returned later to the breeding grounds in spring than adults.

Landsborough Thomson (1924) described the movements of Herring Gulls in Britain as dispersal, with every gradation of distance but mostly within the limits of the British Isles. The greatest distance travelled found by him was *c.* 960 km. He failed to find regularity in movements with regard to timing or direction. Parsons and Duncan (1978), however, found that dispersal was predominantly in a southerly direction. There was no difference between the proportion of young and adult birds recovered inland, nor in range, except in summer when adults had returned to their coastal home grounds. The seasonality and range found by Parsons and Duncan (1978) for juvenile, immature, and adult Herring Gulls ringed on the Isle of May was remarkably similar to that in The Netherlands. They also explained the movements in terms of directional dispersal, rather than a migration from the natal colony. Calladine (2002) confirmed that Herring Gull dispersal had a marked tendency for southward autumn movements. He also found slight regional variations in the distances moved between breeding and wintering areas, with birds from Ireland being more sedentary than birds from northern and south-west Britain. Drost and Schilling (1940) in an early analysis concluded that German Herring Gulls did not migrate but dispersed irregularly, with a maximum distance of 550 km from the natal colony. They also failed to find a structural difference in dispersal range for juvenile, immature, and adult gulls. Gabrey (1996), on the contrary, recorded a monthly mean distance of *c.* 1,600km in winter for juvenile Herring Gulls ringed in breeding colonies in the Great Lakes (USA), but distinctly shorter mean distances in immature (700km) and adult (500-800km) birds. We failed to find a difference between age groups in terms of travelling distance for Herring Gulls colour-ringed within The Netherlands.

Finnish Herring Gulls were found to migrate (abandoning breeding grounds), with a mean winter distance of winter recoveries of 737km in adult birds (range 24-1,336km) and 634km in juveniles (range 19-1,019km; Kilpi and Saurola 1984). As in the Dutch data, juveniles were found to perform a return migration in spring, but 2-3 months later than adults. Juveniles tended to stay far south of the natal area in their first summer (Kilpi and Saurola 1983a). So, again, no difference in range between adults and juveniles, but a difference in timing and in tendencies to return to home grounds in the first years after fledging.

Only three sightings, from the British Isles were received of three birds colour-ringed between 1986 and 1988, suggesting that the southern North Sea acts as an effective barrier for Dutch Herring Gulls. Speek and Speek (1984) listed quite a number of recoveries in the UK of Herring Gulls ringed within The Netherlands, but their analysis was seemingly ‘polluted’ by misidentified chicks (actually Lesser Black-backed Gulls, see also Spaans 1971). Stanley *et al.* (1981) listed 28 recoveries mainly in south-eastern counties of England. Calladine (2002) showed that many Herring Gulls originating from north-east Scotland and east England were recovered in The Netherlands and gave further indications for North Sea crossings by Herring Gulls from Scandinavia, The Netherlands, and Belgium. While it is probable that birds from Dutch colonies occur regularly on the south and east coasts of England (Stanley *et al.* 1981, Calladine 2002), we can only conclude that on the basis of our colour-ring sightings, the British Isles are normally off-range for Dutch Herring Gulls.

Klein (2001) reported on 14,500 sightings from Herring Gulls colour-ringed as chicks in Mecklenburg-Vorpommern (western Baltic, Germany) between 1991 and 1999. Winter sightings confirmed that *c.* 75% of the gulls remained within the western Baltic area, that 20% moved inland, and 5% travelled towards the North Sea coast and down to Pas-de-Calais in France. With a distinctly larger range (e.g. mean distances in winter 300-400km from the natal area in immature birds), similar aspects of timing were found, with juveniles departing later from the breeding grounds than older birds, and a less pronounced tendency (later and fairly distant to the home grounds) to return in the next spring for juveniles was obvious. He also found that gulls originating from the Rostock area dispersed less far than birds from other colonies and explained this fact by more readily accessible, year-round food sources. He finally concluded that female Herring Gulls had a greater ‘mobility’ than males, which also returned earlier in the home-ground regions. Most of these aspects (with the exception of a sexual difference in dispersal strategy) were corroborated by our work in The Netherlands, albeit at slightly different scales and with slightly different patterns due to local conditions.

Kilpi and Saurola (1983b) examined pre-migration movements of coastal Finnish Herring Gulls after the breeding season and found that adults primarily exploited the nearest possible feeding sites upon leaving the colonies. This finding resembles the peak in occurrence of adult birds in coastal sites (as profitable feeding areas close to the breeding colonies) in The Netherlands in early autumn, prior to the dispersal to winter grounds. It is likely that such areas provide easy meals for birds actively engaged in post-nuptial (complete) moult, minimising the needs for energetically expensive foraging flights.

The migratory movements of Lesser Black-backed Gulls breeding at Texel have not been analysed in sufficient detail yet (but see Klaassen *et al.* 2011 for birds breeding on the neighbouring Wadden Sea island Vlieland). Some preliminary results for the birds monitored at Texel are provided in Appendix 5 of this thesis. Some of the material presented in this Appendix, together with data collected in the Moerdijk colony (Noord Brabant), has been used as a contribution to a recently published study on the migratory movements of Lesser Black-backed Gulls breeding in Iceland:

Hallgrimsson G.T.[1,2*], H. Gunnarsson[3], O. Torfason[4], R-J. Buijs[5] & C.J. Camphuysen[6] 2012. **Migration pattern of Icelandic Lesser Black-backed Gulls *Larus fuscus graellsii*: indications of a leap-frog system**. J. Ornithol. DOI 10.1007/s10336-012-0816-4.

[1]Institute of Biology, University of Iceland, Sturlugata 7, 101 Reykjavik, Iceland; [2]Reykjanes Environmental Research Institute, Gardvegur 1, 245 Sandgerdi, Iceland, **Correspondence author* e-mail: gunnih@hi.is; [3]Bjarkaras 23, 210 Gardabaer, Iceland; [4]Alfholt 34, 220 Hafnarfjordur, Iceland; [5]Buijs Eco Consult, Philips van Dorpstraat 49, 4698 RV Oud-Vossemeer, The Netherlands; [6]Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

On the species level the non-breeding distribution and the migration patterns of most European birds are well known. In contrast, the knowledge of the contribution of different breeding populations to particular non-breeding sites (migratory connectivity) is far more limited. We studied the non-breeding distribution of individually colour-ringed Lesser Black-backed Gulls (Larus fuscus graellsii) from Iceland and aimed for information on their migration pattern (leap-frog, chain migration, random mix). Most birds were resighted in Portugal, inland Spain and northwest Africa. No statistical difference was found according to age on the latitudinal winter distribution although 1st winter birds were on average 2 farther south. Both 2nd and 3rd calendar year (cy) birds performed a northward spring migration but spent the summer at significantly lower latitudes than adults. The autumn migration for adults was earlier compared with 1st cy birds. A direct comparison of resightings from birds ringed in Iceland and the Netherlands showed that these populations are not likely to contribute much to the wintering population in the UK. A striking difference was discovered in proportions of resightings in France, Iberia and northwest Africa. Birds from the Netherlands and Iceland were equally likely to be found in Iberia while Dutch birds were much more likely to be seen in France and Icelandic birds more likely to be seen in northwest Africa. These results indicate that Icelandic birds leapfrog both the Dutch and UK populations to some extent.

7. Apparent survival and fecundity of sympatric Lesser Black-backed Gulls and Herring Gulls with contrasting population trends

Published **Ardea** 100: 113-122 (2012)

Camphuysen C.J.* & A. Gronert

Royal Netherlands Institute for Sea Research, NIOZ, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands,
**Corresponding author* E-mail: kees.camphuysen@nioz.nl

Abstract We investigated apparent survival (*i.e.* survival confounded by permanent emigration) on the basis of a colour-ring programme in which individual Lesser Black-backed Gulls *Larus fuscus* and Herring Gulls *Larus argentatus* could be monitored over time. The work was conducted in a large, mixed colony in the western Wadden Sea (Texel), where measures of fecundity were collected simultaneously. In Herring Gulls, we found a mean apparent annual adult survival of 79% in females and 86% in males. Additive year effects rather than sex provided highest model support in Lesser Black-backed Gulls, in which apparent survival for both sexes combined varied between 81% and 100% (mean ≈91%). The breeding success in Lesser Black-backed Gulls was significantly lower than that of Herring Gulls. Lesser Black-backed Gulls experienced four consecutive breeding seasons with very low fledging rates (2006-2009) as a result of cannibalism (60-67% of all hatchlings). Chick predation was generally lower in Herring Gulls. A strong population increase in Lesser Black-backed Gulls coincided with substantial population declines in Herring Gulls in the Wadden Sea in the late 20st and early 21st century. In Lesser Black-backed Gulls, apparent survival declined with about 10% in the last two study years, which could, in combination with the low fecundity, halt the current population increase. We suggest that future work should concentrate on underexplored aspects affecting fecundity and survival such as intermittent breeding and sexual differences in migration, foraging and breeding effort.

Key words: apparent survival, fecundity, *Larus fuscus*, *Larus argentatus*, population trends, sexual segregation, food limitation

Introduction

Lesser Black-backed Gulls *Larus fuscus* and Herring Gulls *Larus argentatus* nest sympatrically in several large colonies throughout the Danish, German and Dutch Wadden Sea (Hagemeijer & Blair 1997). In the late 20st and early 21st century a strong population increase in Lesser Black-backed Gulls coincided with a substantial population decline in Herring Gulls (Spaans 1998ab, Aarts *et al.* 2008, van Dijk *et al.* 2010). Inspired by these contrasting developments, a comparative study of the feeding ecology, breeding biology and demography of the two species commenced in 2006. Our studies were conducted in one of the largest of these mixed colonies, at Texel (The Netherlands) and involved measurements of phenology (arrivals, laying date), reproductive success (including clutch size, egg volume, egg and chick predation, chick growth and breeding success), plus a colour-ring programme to assess site-fidelity, recruitment rates and annual survival. Particularly relevant for studies of population dynamics are parameters such as fecundity (*i.e.* fledging rates), population densities, rates of immigration and emigration, recruitment, and survival (Clobert & Lebreton 1991).

Adult annual survival is a key parameter affecting population trends among long-lived, generally philopatric species (Tinbergen 1953, Harris 1970, Davis 1975, Perrins *et al.* 1991). We investigated apparent survival (*i.e.* survival confounded by permanent emigration; White & Burnham 1999, Allard *et al.* 2010) on the basis of our colour-ring programme in which individual birds could be monitored over time. We assessed the influence of year, year of capture, sex, and sex-year interactions on apparent survival and re-sighting probabilities using program MARK

(White & Burnham 1999, 2010), and compared our findings with previously published survival estimates of large gull species with similar or contrasting population trends.

Food supply plays a major role in animal population dynamics and is often an important factor limiting breeding success and survival (Martin 1987, 1995, Pons & Migot 1995). In generalist feeders, such as large gulls (Cramp & Simmons 1983), food supply is notoriously difficult to assess. The observed long-term declines in the Herring Gull population are generally assumed to have been caused by changes in human waste management (covering up landfill areas that provided easy accessible food; Spaans 1998b). The most marked changes therein occurred several decades ago, and the continuing population decline in recent years would suggest that other factors are currently important. The favourable breeding success of Herring Gulls in recent years (Camphuysen & Gronert 2010a) was not in accordance with current population trends and the present study was to investigate if levels of annual survival were perhaps reduced. The population increase of Lesser Black-backed Gulls, notorious scavengers at fishing vessels in the breeding season (Camphuysen 1995a), mirrored the increase in beamtrawl fleet capacity off the Dutch coast (Spaans 1998a). Breeding success of Lesser Black-backed Gulls was very low in recent years and this study aimed at investigating levels of annual adult mortality. This gull species face changes in the European Common Fishery Policy that are gradually effectuated (smaller fleets, less discards to be produced; Schou 2011) and high gasoline prices that will all lead to reductions in fishing effort (Rijnsdorp *et al.* 2008). Given these conditions, we expect negative effects on the tendency to breed (birds in poor condition may forego breeding), fecundity and on annual adult survival.

Methods

Study area and population trends - Ecological data were collected April to August, 2006-2011 in Kelderhuispolder, Texel (53°01’N, 04°43’E), western Wadden Sea, The Netherlands, in a large mixed colony with approximately 11,500 breeding pairs of Lesser Black-backed Gulls and 5000 pairs of Herring Gulls *Larus argentatus*. The colony is situated at the crossroads of the western Wadden Sea and the southern North Sea. Strong tidal currents flow through a narrow passage between the mainland (Den Helder) and the island. The main food resources are fish (including fisheries discards), benthic fauna, terrestrial infauna, and domestic refuse. The main foraging areas include open sea, intertidal areas (mudflats and coastal breakwaters exposed at low tide), freshwater ponds, tourist resorts (including restaurants) and agricultural land. And at slightly larger distance the gulls frequent sewage plants, rubbish tips and cities. Lesser Black-backed Gulls became established as breeding birds in the early 1970s, at a time when about 1000 pairs of Herring Gulls nested in the area. Herring Gulls increased to just over 10,000 pairs in 1986 and declined since to *c.* 5500-6000 pairs in 2006 and 2007, when our studies commenced. Since colonisation, Lesser Black-backed Gulls have slowly increased to some 2000 pairs in 1992, but the population exploded to just over 14,000 pairs in 2003-2006 (reconstruction from Staatsbosbeheer (State Forest Management) unpubl. ann. Rep. 1967-1990 and SOVON LSB seabird colony database 1991-2007).

The study area Kelderhuispolder is a valley of 8 ha surrounded by higher dunes (preferred by nesting Herring Gulls) covered with Marram *Ammophila arenaria*, Sea-buckthorn *Hippophae rhamnoides*, and Elder *Sambucus nigra* (Camphuysen & Gronert 2010a). The valley itself is mostly covered with grass, including stands with taller Marram, patches with short vegetation, and occasional Elder bushes. Field work commenced early April and lasted until mid August, covering the entire breeding period from prospecting to fledging. Prior to egg-laying (mid-April) the colony was visited with increasing frequency until the first eggs were found along a preset trail leading through each of the study plots into prime Herring Gull and Lesser Black-backed Gull habitats. Nests were marked with a numbered wooden pole and the geographical position (latitude, longitude) of each nest was recorded with a handheld Garmin V GPS.

Ringing and re-sightings - Breeding gulls were trapped at the nest, roughly half-way incubation after we had established that a clutch was completed and fully incubated. Each gull was ringed with an steel band on the right tibia, and on the left tarsus fitted with a 35mm colour ring of 10mm diameter made of Polymethyl methacrylate (PMMA; a thermoplastic), engraved with a white inscription of 4 characters (F.xxx for females, M.xxx for males). A total of 180 Lesser Black-backed Gulls and 119 Herring Gulls were ringed between 200s6 and 2010, but 26 Lesser Black-backed Gulls fitted with GPS loggers were excluded from the analysis (Table 7.1). Sex was assessed using head and bill measurements (Coulson *et al.* 1983) and the birds were aged using plumage characteristics (Olsen & Larsson 2003, Svensson & Grant 2009). All birds were weighed to the nearest gram.

Marked gulls were monitored (re-sighted) using spotting telescopes and binoculars during almost daily visits to the colony between April and August. For analysis, multiple observations of an individual were collapsed to a single ‘occasion’ per year, effectively requiring one single sighting to be recorded as ‘alive’. Nonetheless, frequent observations were made within the colony to minimise identification error and to reduce the possibility of missing ringed individuals. Sightings were also reported outside the colony, mostly by dedicated birdwatchers, both in The Netherlands and elsewhere in Europe and NW Africa (Camphuysen *et al.* 2011). Only sightings within the colony were used to estimates apparent adult survival, but the other reports were used to check whether particular individuals were still alive even if sightings within the colony were lacking (Table 7.1).

Table 7.1. Reduced m-array (Burnham *et al.* 1987) summarising capture–mark–re-sight data from Lesser Black-backed Gulls and Herring Gulls marked as breeding (sub-)adults and monitored at Kelderhuispolder, Texel, from 2006 to 2011. Releases include newly colour-ringed individuals and previously marked birds seen alive within the colony in a particular year. Confirmed survival in 2011 (n, %) was based on all sightings recorded (anywhere in Europe), for all birds.

Lesser Black-backed Gull			Encountered for the first time after release						Confirmed	
	Ringed	Released	2007	2008	2009	2010	2011	Total	alive 2011	%
2006	23	23	22	1				23	10	43.5
2007	24	46		40	2			42	18	75.0
2008	39	80			66	7		73	22	56.4
2009	53	121				97	1	98	38	71.7
2010	15	119					91	91	14	93.3
Totals	154	389						327	102	66.2

Herring Gull			Encountered for the first time after release						Confirmed	
	Ringed	Released	2007	2008	2009	2010	2011	Total	alive 2011	%
2006	7	7	4	2				6	4	57.1
2007	12	15		12	1			13	5	41.7
2008	19	33			23	3		26	11	57.9
2009	37	61				48	3	51	27	73.0
2010	44	95					65	65	34	77.3
Totals	119	211						161	81	68.1

Fecundity - We used fledging rates as measure of fecundity. To assess fledging rates, randomly chosen (groups of) nests in enclosures were monitored. A total of 368 nests were monitored (252 Lesser Black-backed Gulls, 116 Herring Gulls; Table 7.1). Nests were enclosed during late incubation, by fencing off an area of at least eight square metres using 50cm high, 2cm mesh opening chicken wire. Enclosures included vegetation to provide cover for the offspring to hide. Chicks were marked with a numbered aluminium ring on day 1 and subsequently measured and weighed every third day (outside the enclosure) until they were either dead (e.g. predated) or fledged. Chicks of around 30-40 days old and capable of leaving and entering the enclosures, were colour-ringed on the left tarsus (with similar rings as the adults but with a different code, starting with either P or K) and marked with a steel ring on the right tibia. Chicks of 40d of age were considered 'fledged', even when they sometimes refused to leave the enclosure at that age. The fate of chicks was assessed, separating birds that died from starvation or disease from those that were killed and predated. The latter category included small chicks (<30d) that disappeared without a trace from the enclosures, if no evidence for escape could be found. Reproductive success was expressed as the number of fledglings per (monitored) pair (fledglings pair^{-1}).

Statistical analysis - Following an assessment of goodness-of-fit (GOF), re-sighting and apparent survival probabilities were investigated using the capture/mark–re-sighting data. Single state, open-population, live-encounter, Cormack-Jolly-Seber (CJS) models specified in software program MARK were applied (White & Burnham 2010). Since only six summer seasons (or sampling occasions) were available and because sample sizes were fairly small, violations of the basic assumptions may have been difficult to detect with GOF tests (Choquet *et al.* 2009). Transience is a source of heterogeneity resulting from permanent emigration from the study area or death by some individuals following marking. Trap-dependence can originate from individuals in a population that are relatively easy ("trap-happy") or difficult ("trap-shy") to detect and observe in the field. Transience and trap-dependence were assessed using the GOF tests 3.SR and 2.CT in the U-Care 2.2 program (Choquet *et al.* 2009). The null hypothesis under these tests was that newly released and previously marked animals are subsequently re-sighted within the colony with the same probability. To test for the effect(s) of grouping data, we conducted GOF tests for pooled data for each species and separately for each sexes within species.

The CJS model accounts for differences in survival rates between successive time periods (in our case breeding seasons), cohorts or sexes (Lebreton *et al*. 1992). A 'life history' was compiled for all colour-ringed individuals, including releases (first year sightings) and re-sightings in subsequent years within the colony. On the basis of individual re-sighting histories, PROGRAM MARK calculates the likelihood that an individual is observed within a given period (p) and a survival rate (Φ), which is the likelihood that an individual has not left the population or is not dead. Various versions of the CJS model were examined, differing in the extent to which survival and re-sighting rates were held constant ($\Phi(.)$ and $p(.)$ respectively) or whether they were considered year-dependent, sex-dependent or year and sex dependent ($\Phi(t)$ and $p(t)$ respectively). The results were corrected for slight over-dispersion of the data using the value of the goodness of fit parameter $\hat{c}$ (based on 100 bootstraps; web-based manual to MARK; Anderson *et al.* 1994). Akaike's Information Criterion (AIC; Anderson *et al.* 1998, Anderson & Burnham 1999) was used to determine the version of the CJS model that gave the best fit to the data. In accordance with model weights and evidence ratios presented by Burnham & Anderson (2002), only models within 6 AIC_c units of the top model ($\Delta AIC_c = 0$) were considered for this assessment; all others were considered as unsupported by the data. Values reported are means ± SE. For tests of independence, the adjusted *G*-statistic (G_{adj}; Sokal & Rohlf 1981) and X^2-tests (White & Burnham 2010) were used.

Results

Age and sex of marked birds - Both species of gulls breeding at Texel seem to recruit at a relatively advanced age and incubating birds with immature plumage characteristics are relatively rare. All incubating Lesser Black-backed Gulls that were trapped were in full adult summer plumage. Seven (5%, n= 145) trapped and marked Herring Gulls were sub-adults (4th (5x) or 5th calendar year (2x)). One Lesser Black-backed Gulls trapped in 2009 appeared to have been ringed as a chick in 2005, but this bird did not show any plumage features indicating its age (5th calendar year), suggesting that some young breeders (recruits) may have been overlooked. One individual, trapped in 2008, had been ringed as an adult while wintering in Worcestershire (UK) in 1993 and must have been at least 19 years of age when it was colour-ringed at Texel. Another 11 trapped

Lesser Black-backed Gulls had been ringed as chicks elsewhere or in earlier years at Texel and these birds averaged 11.8 ± 1.9 years of age (range 9-15 years). Four Herring Gulls were captured that appeared to have been ringed as chicks, respectively 8, 10, 14 and 19 years earlier (average 12.8 ± 4.9 years of age). In total, 85 marked incubating Lesser Black-backed Gulls (55.2%, n= 154) and 57 Herring Gulls (47.9%, n= 119) were sexed as females. In either case, the sex ratio was not significantly different from even (G_{adj} = 0.83 and 0.10 respectively, df= 1, n.s.). Two documented cases of colour-ring loss occurred during 2006-2011, both of which were 'solved' by reading the metal tibia ring (one was re-ringed). Three further birds were re-ringed because the colour-ring was either damaged or too badly worn.

Table 7.2. Models and selection criteria used to determine support for competing models and their effects on Lesser Black-backed Gulls (top) and Herring Gulls (bottom).

Lesser Bl-backed Gull models	**AICc**	**Δ AIC$_c$**	**AIC$_c$ weight**	**Model likelihood**	**NP**	**Deviance**
(1) Φ(year) p(year)	423.09	0	0.573	1	9	53.156
(2) Φ(year) p(.)	424.06	0.98	0.352	0.614	6	60.388
(3) Φ(.) p(year)	429.44	6.35	0.024	0.042	6	65.762
(4) Φ(year + sex) p(year)	429.68	6.60	0.021	0.037	14	49.105
(5) Φ(.) p(.)	430.11	7.02	0.017	0.030	2	74.624
(6) Φ(sex) p(.)	432.14	9.05	0.006	0.011	3	74.620
(7) Φ(year capture) p()	432.14	9.06	0.006	0.011	3	74.624
Herring Gull models	**AICc**	**Δ AIC$_c$**	**AIC$_c$ weight**	**Model likelihood**	**NP**	**Deviance**
(1) Φ(.) p(.)	291.07	0	0.322	1	2	60.143
(2) Φ(sex) p(.)	291.43	0.35	0.329	0.839	3	58.437
(3) Φ(year capture) p()	293.07	1.99	0.145	0.369	3	60.078
(4) Φ(.) p(year)	294.62	3.55	0.067	0.169	6	55.340
(5) Φ(sex) p(year)	295.32	4.25	0.047	0.120	7	53.898
(6) Φ(year) p(.)	297.04	5.96	0.020	0.051	6	57.754
(7) Φ(year + sex) p()	303.59	12.5	0.001	0.002	11	53.387

Table 7.3. Estimates of apparent survival and re-sighting probabilities from year to year (2006–2011) from models 1 in Table 7.2 for Lesser Black-backed Gulls, and apparent survival between the sexes and re-sighting probabilities as a constant from models 2 in Table 7.2 for Herring Gulls.

Group	**Interval/occasion**	**Estimate**	**SE**	**95% CI**
Survival probabilities (Φ) Lesser Black-backed Gull				
	2006-2007	Fixed = 1.0		
	2007-2008	0.919	0.041	0.795-0.971
	2008-2009	0.932	0.033	0.831-0.975
	2009-2010	0.812	0.036	0.732-0.872
	2010-2011	0.874	197.1	nd
Re-sighting probabilities (p)				
	2006-2007	0.956	0.042	0.750-0.994
	2007-2008	0.949	0.035	0.820-0.987
	2008-2009	0.887	0.040	0.783-0.945
	2009-2010	0.988	0.012	0.918-0.998
	2010-2011	0.874	197.1	nd
Survival probabilities (Φ) Herring Gull				
	Females	0.787	0.049	0.676-0.868
	Males	0.864	0.038	0.771-0.923
Re-sighting probabilities (p)		0.871	0.036	0.784-0.927

Goodness of fit - Heterogeneity (due to, e.g. "transience" or "trap-dependence") was negligible in our dataset: 20 releases (11 Lesser Black-backed Gulls, 9 Herring Gulls) eluded detection on the first occasion following release (upper diagonals, Table 7.1). Otherwise, birds that returned were usually detected in the first season following release (lower diagonals, Table 7.1). The birds that did not return within two years were never seen again. Indeed the GOF test results indicated that there was no evidence for transience or trap-dependence in either species, whether tested separately for either sex or for pooled data (Transience test 3.SR: Lesser Black-backed Gull, standardized log odds-ratio (SLOR)^{females} = 1.18, P = 0.12, SLOR^{males} =-0.07, P= 0.53, SLOR^{pooled} = 0.57, P= 0.28; Herring Gull, SLOR^{females} = -1.50, P = 0.94, SLOR^{males} =0.57, P= 0.28, SLOR^{pooled} = 0.13, P= 0.4; Trap-dependence test 2.CT: Lesser Black-backed Gull SLOR^{females} = -0.81, P = 0.42, SLOR^{males} =n.d., SLOR^{pooled} = -1.28, P= 0.20; Herring Gull SLOR^{females} = 0.18, P = 0.86, SLOR^{males} =-0.99, P= 0.32, SLOR^{pooled} = -0.68, P= 0.50). We concluded that the CJS model was acceptable.

Factors affecting survival and re-sighting - Only models fitted to assess structure in the survival process within 6 AICc units of the top model were considered (Table 7.2). The simplest model (Φ(.) p(.)), yielded slightly but not significantly higher mean apparent survival estimates for Lesser Black-backed Gulls (mean 0.87 ± SE 0.03, CI 0.81-0.91, SE and CI corrected for $\hat{c}$ 1.85) than for Herring Gulls (0.83 ± 0.03, 0.76-0.88, $\hat{c}$ corr. 0.97). Re-sighting probabilities in Lesser Black-backed Gulls were 0.94 ± 0.02, (CI 0.87-0.97) and 0.87 ± 0.04, (CI 0.75-0.93) in Herring Gulls. In Lesser Black-backed Gulls, models including additive year effects (models 1 and 2) provided highest support; the simplest model, or models assessing the effects of sex or year of capture were not supported by the data (ΔAIC$_c$ >6 units). The top model, fitted to assess annual variation in re-sighting probability, was not significantly different from the slightly simpler, second best model in which a constant re-sighting rate was assumed (model 2, Table 7.2; X^2_1= 7.32, P= 0.06). We selected Φ(year) p(year) as top model for this species, and estimates of apparent survival and re-sighting probabilities from 2006 to 2011 are provided in Table 7.3. The large standard errors for the last survival and resighting probabilities suggest that these parameters were not identifiable (Lebreton *et al.* 1992).

Table 7.4. Fecundity (fledglings pair^{-1}) and chick mortality in Lesser Black-backed Gulls and Herring Gulls, Kelderhuispolder, Texel, 2006-2011.

Lesser Black-backed Gull	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**
Chick predation	60.3%	66.7%	63.4%	62.3%	35.4%	49.3%
Chick mortality	25.4%	12.3%	15.5%	17.9%	34.8%	19.7%
Chicks fledged	14.3%	21.0%	16.9%	17.0%	28.6%	31.0%
(n) hatchlings	63	81	71	106	161	71
Fledglings per pair	0.26 pr^{-1}	0.46 pr^{-1}	0.35 pr^{-1}	0.37 pr^{-1}	0.71 pr^{-1}	0.69 pr^{-1}
(n) nests	35	37	34	49	65	32
Herring Gull	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**
Chick predation	33.3%	39.1%	25.0%	51.2%	20.0%	16.7%
Chick mortality	42.4%	8.7%	25.0%	7.0%	21.8%	46.7%
Chicks fledged	24.2%	52.2%	50.0%	39.5%	58.2%	36.7%
(n) hatchlings	33	23	44	43	55	30
Fledglings per pair	0.62 pr^{-1}	0.80 pr^{-1}	1.10 pr^{-1}	0.81 pr^{-1}	1.33 pr^{-1}	0.48 pr^{-1}
(n) nests	13	15	20	21	24	23

In Herring Gulls, the simplest model provided an adequate description of the data. The model including a sex effect on survival scored second best, and was not significantly different from the simpler top model (Table 7.2; X^2_1= 1.76, P= 0.185). This second model deviated only 0.4 ΔAIC$_c$ units from the first model. Adding the effects of year of capture on survival or a year effect on re-sighting probability to our models did not lead to further improvements (models 3-5). Particularly those models in which a year effect on survival was assumed were not supported by the data (models 6-7; Table 7.2). We used the second model for this species (Φ(sex) p(.)), because it was not significantly different from the top model and biologically plausible (see Discussion). Estimates for apparent survival of each sex and pooled re-sighting probabilities are provided in Table 7.3. The reason for our choice is that we wish to explore the causes of an apparently fairly substantial sexual difference in apparent annual survival in our future studies (see Discussion).

Fecundity - The mean breeding success in Lesser Black-backed Gulls (mean ± SD 0.47 ± 0.19 fledglings pair^{-1}) was significantly lower than in Herring Gulls (0.86 ± 0.31) at Texel (t_{10}= -2.58, P=0.027; Table 7.4). This pattern was consistent, except in 2011 when the breeding success in Herring Gulls was exceptionally low, while Lesser Black-backed Gulls fledged relatively many chicks in comparison with most other seasons. Lesser Black-backed Gulls experienced four consecutive breeding seasons with very low fledging rates (2006-2009) as a result of high levels of chick predation (cannibalism; 60-67% of all hatchlings). Chick predation was generally lower in Herring Gulls, and the lowest reproductive success was found when levels of chick mortality as a result of starvation and or disease were high (2006, 2011).

Discussion

Overall adult survival in Lesser Black-backed Gulls were higher than in Herring Gulls, but declined in recent years. In Herring Gulls, the annual survival of adults was different between the sexes: notably lower in females. Documented longevity records based on ringing data show that both species are long-lived taxa (Schreiber & Burger 2002) and we had expected similar annual adult survival rates.

Year effects were found to mostly affect survival in Lesser Black-backed Gulls (ranging from 0.81-1.0; model 1). A mean value of 0.91 over this five-year study period agrees with an earlier estimate of 0.91 ± 0.12 for Lesser Black-backed Gulls in the United Kingdom (Wanless *et al.* 1996). Life history theory predicts that parents should value their own survival over that of their offspring in long-lived species such as seabirds (Erikstad *et al.* 1998, Ghalambor & Martin 2001). Data currently available on fecundity and adult survival in several seabird populations suggest a negative relationship between the two (Weimerskirch 2002). The shape of the relationship is likely convex, similar to the classical figure representing the optimisation of the trade-off between survival and fecundity or other vital rates (Cody 1966). Cody (1966) proposed a model in which by the "*Principle of Allocation*" maximum contribution to future generations would be achieved by those individuals which utilise, to increase K (carrying capacity), some of the energy conserved by reducing r (the reproductive rate). Hence, if food becomes scarce, adults should reduce their breeding effort rather than jeopardise their residual reproductive value (Drent & Daan 1980, Martin 1995). For Herring Gulls, annual estimates of apparent survival could not be provided based on the current datasets.

We have evidence that a substantial number of prospecting Lesser Black-backed Gulls at Texel did forego breeding in some years (no subsequent sightings during the breeding season, numerous empty nests in the colony where eggs were never laid). Our fecundity measure is based on birds that did breed (*i.e.* laid eggs), while the annual survival is measured over all colour-ringed adults that returned to the colony and were seen; whether they bred or not in later years. Given the observed trends and inverse relationship between fecundity and survival, we feel that more attention must be given to intermittent breeding in these birds (Calladine & Harris 1997, Cam *et al.* 1998). Non-breeding behaviour may constitute an adaptive mechanism which allows maximization of life-time reproductive success in a fluctuating environment (Aebischer & Wanless 1992).

In Herring Gulls, based on the second best model, we found a mean apparent annual adult survival of 0.79 in females and 0.86 in males (model 2). Other studies of the mean adult annual survival using capture/mark-re-sighting models in Herring Gulls arrived at similar or slightly higher rates as in our males: 0.87 ± 0.03 (Canada; Allard *et al.* 2006), 0.88 ± 0.13 (UK; Wanless *et al.* 1996), 0.88 ± 0.01 (France; Pons & Migot 1995), and 0.91 ± 0.02 (Canada; Breton *et al.* 2008). A sex difference in apparent annual survival in the Herring Gull came as an unexpected result. The studies at Texel, now using advanced GPS loggers, have demonstrated a strong sexual segregation in foraging Lesser Black-backed Gulls in summer (Camphuysen *et al.* submitted), a phenomenon that has unfortunately not been investigated for Herring Gulls. A sex difference in resource exploitation in the Herring Gull breeding at Texel is not unlikely, however. Greig *et al.* 1985 reported different foraging strategies in male and female Herring Gulls breeding in the UK. Bosman *et al.* (2012) examined whether, and to what extent, body size and/or sex-specific differences in competition for resources (e.g. breeding territories or winter food) shaped variation in migration distance and timing of sexually mature males and females of Herring Gulls breeding in Belgium. They found that the larger males migrated further from the breeding colony, whereas migration distance was independent of body size in adult females. Allometry partly explained the sexual segregation in migration behaviour Herring Gulls and the observed latitudinal segregation between wintering males and females may reflect sex-specific niche specialization, with potential repercussions for the annual survival. With our current data, an explanation for the observed differences in survival between the sexes remains speculative. Future work will need to reveal differences in breeding strategies or other traits between male and female Herring Gulls that could help explain the observed sexual differences in annual survival.

The lower survival in Herring Gulls than in Lesser Black-backed Gulls could result from different levels of emigration, the second component next to true survival determining apparent survival. We used only encounters within the colony for this study. There were no confirmed sightings of birds colour-ringed as adults breeding in any other colony (true emigration), but if we were to use *all* sightings, collected anywhere within the flyway of either species, 7% more encounters would have been available (6% more in Lesser Black-backed Gulls, 9% more in Herring Gulls). This difference was not significant; $G_{adj} = 0.13$, df =1, n.s.). and differences in (apparent) emigration rates did not explain the difference between the two species. Lesser Black-backed Gulls are migratory, wintering generally several thousands of kilometres south of the breeding grounds (in this case mostly at the Iberian Peninsula and in NW Africa; Camphuysen *et al.* 2009, Hallgrimsson *et al.* 2012). Herring Gulls are dispersive or short-range migrants, wintering mostly in The Netherlands, in Belgium or in northern France, and migrating hundreds of kilometres rather than thousands (Camphuysen *et al.* 2011). It is unclear how long distance migration or short-distance dispersal would influence annual adult survival differently. These gulls could potentially forage everywhere along their flyways: there are no crossings of endless deserts, vast stretches of water, or other inhospitable areas required in either species. The availability of resources in wintering areas or during autumn or spring migration could still be a factor of importance. Alternatively, differences in survival could be related to the food supplies and the effort exerted by individual birds during breeding. Several authors concluded that adult mortality in large gulls reaches its maximum at the end of the breeding season (Pons & Migot 1995 and references therein).

Changes in fishing practices are only gradually effectuated, and while Lesser Black-backed Gulls breeding at Texel are currently almost certainly food-stressed (Camphuysen *under review*), this did not (yet) translate into a reduced annual adult survival. The current reproductive success of both species, on average much higher in Herring Gulls than in Lesser Black-backed Gulls (Table 7.4), would suggest that the contrasting population trends may soon be reversed. However, the differences in adult survival between the two species are such that this conclusion cannot be drawn. For a breeding population to remain stable, parent birds have to produce enough young that survive to breed themselves, to replace adults that die (Perrins 1991). From the adult annual survival rate, it is possible to deduce the proportion of young that must survive to breed in a stable population (at equilibrium, the number of young surviving per pair to breed must equal twice the annual adult mortality). We will need to continue the concurrent colour-ringing programme of fledglings to be able to assess recruitment rates and age of first breeding, to be able to model current and forecast future population trends.

8. Time for a break: causes and consequences of unusually long or distant foraging trips in central-place foraging seabirds

Reviewed **Animal Behaviour** [in revision]

C.J. Camphuysen[1*], J. Shamoun-Baranes[2], E.E. van Loon[2] and W. Bouten[2]

[1]Royal Netherlands Institute for Sea Research, NIOZ, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands, [*]*Corresponding author*; E-mail: kees.camphuysen@nioz.nl [2] Computational Geo-Ecology, IBED, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands

Abstract Tracking studies of seabirds occasionally reveal exceptionally long or distant foraging trips that are difficult to explain within a context of optimal foraging theory. We examined the characteristics, the frequency, and the possible triggers of such unusual trips in comparison to thousands of other, more regular trips, and in the context of reproductive performance and chick growth in a central-place foraging seabird, the lesser black-backed gull *Larus fuscus*. The hypothesis that exceptional trips were conducted exclusively by failed breeders, but not by active breeders during incubation or chick care, had to be rejected. Exceptionally long and distant trips occurred irregularly but annually, in many individual birds and in all phases of breeding. Evidence is provided that additional time for individual maintenance (e.g. self-provisioning, replenishing exhausted resources) rather than extra effort in chick provisioning (a chick starvation hypothesis) was an important factor. Exceptional trips in active breeders were relatively rare when the chicks were still young and highly vulnerable (<10d of age). The reproductive success in birds that performed exceptional trips was not compromised, pointing at compensatory behavior of the mate and/or flexibility in the system.

Key words: tracking studies, *Larus fuscus*, central-place foraging, self-maintenance, foraging range

Introduction

In the last 20 years, bio-logging science has revolutionized the ability to record the fine-scale foraging behavior and habitat use of seabirds (Weimerskirch *et al.* 1994, 2003, Bost *et al.* 2008, McLeay *et al.* 2010). Seabirds constitute a group of marine top-predators that may disperse over wide spatial ranges on foraging trips or while on migration and that are therefore difficult to study with more conventional means. Deployments of satellite PTTs and GPS loggers have been instrumental in revealing migratory pathways (Ristow *et al.* 2000, Guicking *et al.* 2001, González-Solís *et al.* 2007), but also in temporal patterns and trends in the foraging range and time budgets of breeding seabirds during different phases of the reproductive cycle (Catard *et al.* 2000, Cherel *et al.* 2000, Boersma *et al.* 2002). The Lesser Black-backed Gull *Larus fuscus* is a seabird that has markedly increased in numbers in much of Europe over the past decades. Migration routes of several subspecies have been studied recently with satellite telemetry (Pütz *et al.* 2008, Klaassen *et al.* 2011), and satellite PTTs and GPS loggers have been used to study foraging distribution and behavior in the breeding season (Ens *et al.* 2009, Camphuysen *et al.* 2010, Shamoun-Baranes *et al.* 2010). In one of these studies, conducted in 2007 using Argos/GPS PTTs, unexpectedly long and distant trips were recorded (Ens *et al.* 2009). These extraordinary trips could last several days and covered hundreds of kilometers, while most of the documented foraging trips were considerably shorter in duration and covered much shorter distances (Ens *et al.* 2009, http://www.sovon.nl/default.asp?id=408). In a study focusing on migration of the same individuals, Klaassen *et al.* (2011) documented additional examples and described them as pre- and post- migratory trips. In the absence of comprehensive data on the breeding status of the tagged individuals, these outliers were assumed to involve individuals that had lost their clutch or chicks and that were therefore relieved of parental duties within the colony. The analysis of the data of foraging distribution was hindered by uncertainties regarding these unexpectedly long journeys and a clear question arose: what is an unusual trip and what is not?

In a seminal paper on the concepts of home range and territoriality Burt (1943) suggested the following definition of home range: *"…that area transversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range."* While such extreme excursions (sallies or forays) may not be common within a species, they do occur in numerous taxa although often excluded from analysis when the focus is on the home range or "normal" foraging movements of an animal (e.g. Salsbury and Armitage 1994; Gjertz *et al.* 2000; Guilford *et al.* 2008, Schofield *et al.* 2010). Our understanding of the functions of such movements is limited. In the context of breeding, it has been suggested that such excursions may help an individual replenish their own energy stores (Weimerskirch *et al.* 1997; Weimerskirch *et al.* 2003; Schofield *et al.* 2010), prospect for new breeding locations (Schofield *et al.* 2010), participate in extra-pair copulations (Norris & Stuchbury 2001) or simply to gather food for chicks in alternative, more distant areas when local resources are diminishing (Ashmole's halo; Birt *et al.* 1987).

Lesser Black-backed Gulls are omnivorous seabirds, with a wide variety of prey items (Cramp & Simmons 1983). Foraging in the breeding season occurs mostly at sea, but also on land (Camphuysen *et al.* under review). As many seabirds, Lesser Black-backed Gulls are long-lived species that have bi-parental chick care (Bennett & Owens 2002). In our study, the foraging whereabouts of active breeding birds were studied with advanced GPS loggers. Breeding status and reproductive success of the tagged birds were carefully monitored, and we aimed at documenting the duration and range of foraging excursions throughout each of the phases of breeding, throughout the breeding season. Given the experiences described for an earlier project (Ens *et al.* 2009), we were alert to carefully document breeding conditions (breeding status, clutch and chick condition) continuously. This would enable us to examine the context of "exceptionally" long or distant trips and to evaluate (probable) cause and effect.

The period of chick care is generally viewed as a bottleneck in the reproductive cycle, because of frequent feeding visits that are required to meet the energetic demands of developing offspring (Drent & Daan 1980). Exceptionally long or distant trips are difficult to understand in a context where foragers are assumed to optimize feeding efficiency and to minimize their absences from the colony, certainly during incubation (warming eggs) and early chick care (defending chicks; Stephens & Krebs 1986, Maurer 1996). We therefore hypothesized that exceptionally distant or abnormally long trips (such as those logged at Vlieland in earlier years) were conducted only by failed breeders, given the constraints imposed on active breeders raising chicks. If indeed active breeders were involved, we hoped that a combination of the breeding data (e.g. condition and survival of the chicks) and the trip destination (e.g. characteristics of foraging area) could provide support for one of two potential drivers of such trips: 1. extra parental effort to support chicks (chick starvation hypothesis), or 2. extra effort for self maintenance (self-care hypothesis).

Methods

Study area - The study was conducted in a breeding colony on the island of Texel The Netherlands (53°00'N, 04°43'E) at the crossroads of the western Wadden Sea and the southern North Sea. Strong tidal currents flow through a narrow passage between the mainland (Den Helder) and the island, and the main foraging areas include open sea (fish and benthic fauna, including fisheries discards), intertidal areas (mudflats and coastal breakwaters exposed at low tide; benthic fauna), freshwater ponds, tourist resorts (including restaurants), agricultural land, sewage plants, rubbish tips and cities. Within the study area, approximately 11,500 pairs of Lesser Black-backed Gulls and just over 5000 pairs of Herring Gulls *Larus argentatus* are breeding. Breeding data within the colony were collected during April to August over six consecutive breeding seasons (2006-2011). The birds were tagged in 2008-2011.

Breeding data - To monitor breeding status and breeding success in the colony, nests were marked each year during egg laying and marked nests were either monitored until hatching, or, after a random selection of nests, enclosed with 50 cm high chicken wire to assess chick growth and fledging rates (Camphuysen & Gronert 2010a). Nests were visited every third day, throughout the breeding season (laying to fledging), but only in favorable weather (i.e. not during rain or storm; visits could be entirely skipped or postponed/be earlier by as much as one day at most). During each nest visit the following attributes were recorded: date of laying and egg size, clutch size, egg losses, hatching date, chick growth, fledging rates and/or chick mortality. Breeding phases analyzed in this study in chronological order were (1) incubation, (2) hatching, (3) chick care (first 40 days after hatching) and (4) fledging (chick care within colony > 40 d). 'Active breeders' were involved in any of these four phases of egg/chick care. Individuals that lost eggs or chicks were considered 'failed breeders' from the date that all eggs or chicks were lost.

GPS tracking - Half-way incubation (with completed, incubated clutches), adult breeding individuals were trapped at the nest using a walk in trap, ringed and colour-ringed with a green 35mm polymethylmethacrylate (PMMA) ring (10mm diameter), on the left tarsus, engraved with a white inscription of 4 characters (F.xxx for females, M.xxx for males). Adult males are on average larger than adult females, and the sexes were separated on the basis of body measurements (head plus bill length) with only 5% expected misidentification (Coulson *et al.* 1983). In 2008 – 2011, 34 individuals (16 females, 18 males) were tagged with a GPS logger and tracked with the UvA-BiTS tracking system (see www.uva-bits.nl for more details about the tracking system). The GPS tracker was mounted with a harness on the back of a bird. Birds were released immediately after the tag was fitted on the bird. The tracking system enables changing the measurement frequency while the tag is on the bird. In general a GPS fix was taken every 5 – 15 minutes, during the day and night throughout the entire breeding season. Occasionally, high resolution measurements were taken (every 3 – 30 s). The tag is powered by four solar cells and a 65 mAh lithium polymer battery and gaps in the data occurred when the battery was not sufficiently recharged or the GPS timed out before a fix could be made. Trips with data gaps of more than one hour duration were omitted from the analysis. Single birds of individual pairs were tagged to avoid excessive stress during breeding attempts. To obtain some information on the activities of partners during incubation, a temperature logger (DS1921G Thermochron iButton, Maxim, USA) was placed in the nest that recorded nest temperature every 15 minutes.

Ethical notes – Following recommendations by Casper (2009), potential impact on the birds due to instrumentation with the GPS tags was minimised. During tagging, we captured single birds at the time, using a nest cage, which was continuously monitored and removed if the bird did not enter the trap within 20 minutes (considered "trap-shy"). Attempts to capture "trap-shy birds" were repeated no more than once (hours later, or the next day), before an attempt was abandoned altogether. Once a bird was trapped it was removed from the cage, carried in a dark bag (obstructing views to the outside), and immediately ringed, measured and weighed by a licensed ringer (<5 minutes handling time). During tagging, the bird was restrained by an assistant (holding wings, tail and feet together in one hand, head and bill in the other hand, while blindfolding the bird with a ringing bag while carefully preventing a blockade of the airways), and the harness adjusted to individual size and deployed by the ringer. After rigorous checks of the attachment (no restriction of wing movements and other body parts, proper fit of straps) the bird was released within 15-20 min after being captured (total handling, including ringing). The mass of the 18g tag amounted to 2.1% of the body mass of the average tagged individual (mean mass 862.5 ± 99g), or 2.8% of the body mass of the smallest tagged individual (650g). Birds normally returned to the nest within 1-2 hours after tagging. The loggers were retained on the birds after the breeding season to monitor migratory movements and wintering locations for at least one year. Once loggers stopped functioning they were removed if the bird could be recaptured. Removed loggers show only minor abrasion of back coverts and downy feathers, with no major skin lesions. In the first year of study, one bird was entangled in the harness and died a few days after release. The tagging protocols were subsequently reviewed and revised to ensure that the risk for entanglements was further minimised, and there were no further problems with the harness recorded. In the field studies, we did not observe abnormal behaviour by tagged birds; furthermore they did not abandon nests and continued to breed. However return rates the next year were slightly lower than controls (this paper). The disturbance of the colony during visits were minimized by using a small team that stayed together on all occasions and by shortening the visits to enclosures (and nest sites) by swiftly removing chicks from the pens, measuring them at distance in a quiet area, and by swiftly returning them after that. The effect of this procedure had been monitored from a hide in the 2007 seasons, showing that the effects of these disturbances were minimal (van Nus 2007).

Chick growth - Enclosures were visited every third day, and all chicks were captured, measured, weighed and returned to the enclosure (or collected when found dead). Gallego Garcia (2008) tested four growth models to describe changes in body mass and structural size with age of chicks of Lesser Black-backed Gulls at Texel. The best fitting growth model for body mass (using Akaike's information criterium, AIC), was a logistic growth model with 3 parameters:

$$y = \frac{a}{1 + b\ell^{-kt}}$$

where y is the mass (g) at time *t* (d), *a* is the upper asymptote (g), *b* is the value of *t* at the point of inflection of the curve and *k* is the growth rate. The logistic growth model predicts accelerating growth of chicks at an early age (which occurred between 5 and 20d of age in the data; Gallego Garcia 2008). Reduced growth rates occurred in older chicks. We used age-specific chick growth rates (g d^{-1}) measured when (or within a day) parents departed or returned from exceptional trips and during normal trips. The measurements around departure would indicate if chicks at that time were in a poor condition or if they developed normally according to the growth model. Growth rates that coincided with returns (again within 1 day) were seen as indicators of trends in chick growth during exceptional absences of the partner carrying a logger. These growth rates were calculated on the basis of mass differences between subsequent measurements (3 d).

Data processing - Following Camphuysen *et al.* (under review), the time-series of single GPS-points were grouped into three types of activity bouts per individual bird: 'nest bouts', 'short trips' and 'long trips'. We defined a 'nest bout' as a continuous period where an individual stays at its nest or territory (i.e. continuously within a circle with a 150 m radius around the nest, which is within the dune valley where the colony is located). We define a 'short trip' as a continuous period where an individual moves out of the 150 m circle but stays within a 3 km radius from the nest before returning to the nest (beaches, roosts and bathing places, but no important foraging areas within this ring). And finally we define a 'long trip' as a continuous period where an individual moves out of the 150 m circle and travels more than 3 km from the nest before returning (a long trip begins once the distance from the nest was >150m and ended once the bird was ≤ 150 m from the nest). Within the 3 km zone the birds spend almost all their time on bathing and resting, while foraging occurred nearly exclusively outside of the 3 km zone. The analysis for this contribution was based on completely logged 'long trips' only (i.e. excluding trips that were interrupted as a result of battery failures). If the breeding status of the individual bird was uncertain, these data were removed from further analysis: The current analysis is based on 2199 'long trips' performed by 34 different individuals, known to be either actively breeding or to have failed, during April-August, 2008-2011.

Terminology - For each individual data point (GPS position) we assessed the (great circle) distance (km) to the nest. For each trip, we calculated the total duration (h) of a trip and the range as the maximum distance to the nest (km). After assessing duration and range of all 2199 logged foraging trips, the upper 1% of each parameter were defined as ‘exceptional trips’. ‘Normal trips’ were all foraging trips that fell within 99% of trip durations or ranges. After preliminary analysis we included an extra class of trips, these were trips that were not only exceptionally long but also covered highly unusual distances (>250km from the nest) and were labeled as ‘freak trips’. Summary of trip definitions:

Range	maximum distance (km) from the nest per trip
Duration	duration (h) of trip from time it left the territory to the time it returned
Short trip	range <3 km from territory (presumed roost visit)
Long trip	range >3 km from territory (presumed foraging trip)
Normal trip	99th percentile of duration or range of long trips
Exceptional trip	>99th percentile of duration or range of long trips
Freak trip	exceptional trip, but with a range >250 km

Data analysis - We tested differences in the duration (h) and range (km) of normal long trips between sexes within each breeding phase and within each sex between breeding phases with a Student’s *t*-test. Differences between observed and expected frequencies of exceptional trips between sexes and between birds of different reproductive status were evaluated with an adjusted G-statistic (G_{adj}, Sokal & Rohlf 1981). Differences in habitat use on long trips (normal versus exceptional), based on the time spent (h) during long trips on the North Sea, within the Wadden Sea, on the Continental mainland (Netherlands, Germany, Belgium and France), within the United Kingdom, or on the island Texel were also evaluated with a G-statistic, comparing observed time budgets during exceptional trips with expected values based on normal trips conducted by the same individual birds.

We plotted and modeled chick growth rates (g d^{-1}) against age (d) for all chicks with parents carrying GPS loggers. Chick growth rates that coincided with ‘exceptional trips’ were compared with those measured when foraging trips were ‘normal’ using an analysis of covariance (ANCOVA). Differences in age distributions of chicks under care during ‘normal trips’ and chicks cared for during ‘exceptional trips’ were investigated with a two-sample Kolmogorov-Smirnov test.

Results

Foraging trip characteristics - In active breeding birds, nearly two–thirds of all trips had a total duration of less than 6 hours (69% in females, n= 1013; 57% in males, n= 866), while nearly all trips were complete within one day (98% in females, 97% in males). Trip durations were similar during the egg and the chick phase, within each sex (males: $t_{406.3} = 2.150$, P = 0.03, females $t_{977.0} = 0.762$, $P = 0.45$), but failed breeders made highly variable, but on average significantly longer trips (chick phase versus failed breeders, males: $t_{190.4}= -3.694$, $P< 0.001$; females $t_{185.7}= -4.230$, $P< 0.001$). Slightly less than half of all recorded trips in failed breeders had a duration of <6 hours (51% in females, *n*= 176; 44% in males, *n*= 144), while 85% of the trips in both sexes were completed within 24 hours. Only 25 trips (n= 2199) had a duration of more than 48 hours (‘exceptionally long’; Fig. 8.1A).

In active breeding females, 80% of all foraging trips were within 30km of the nest (n= 1013), while only 45% of the trips logged for males remained within that short range of the colony (n= 866). Nearly all trips of both sexes, however, remained within a maximum distance of 100km from the nest site (99% in breeding females and in males). Adult males travelled significantly further away from the nest site than females during the egg phase (mean ± SD 30.6 ± 34.7km, n= 256 for males, 17.2 ± 12.8 km, n= 325 for females; $t_{310.2}= -5.871$, $P< 0.001$) and during chick care (32.8 ± 19.5km, n= 610 for males, 21.5 ± 23.1km, n= 688 for females; $t_{1233.6}= -8.537$, $P< 0.001$). In females that had failed as breeding birds, 67% of all foraging trips were within 30 km of the nest (n= 176), while 50% of the trips logged for males remained within that short range of the colony (n= 144). The mean trip range was similar between the sexes in failed breeders (34.2±35.0 km, n= 144 for males, 27.0 ± 51.9km, n= 176 for females; $t_{307.5}$= -1.479, P= 0.14), and just as in the active breeding birds, nearly all trips of failed birds from both sexes remained within a maximum distance of 100km from the nest site (98% in females and in males). Only 21 trips (n= 2199) had a maximum distance of more than 100km (‘exceptionally distant’; Fig. 8.1B).

Exceptional trips - The distribution of all long trips according to range and duration is summarized in Table 8.1. In total 38 trips were designated as exceptional or freak trips (8x exceptionally long *and* distant, 17x long but nearby, 13x short but distant; Figs. 2-3). The number of exceptional trips (38 in total) recorded per year was in accordance with expectations based on the annual total number of foraging trips (G_{adj}= 0.92, df= 3, n.s.). Exceptional trips were particularly rare in birds engaged in incubation (1 case observed, 10 expected), commoner during chick care (18/23), but more frequent than expected in failed breeding birds (19/5; G_{adj} = 15.8, df= 2, P< 0.001). Trips of an exceptional duration (irrespective of range; n= 25) were logged for males and females according to expectation given the number of documented trips for either sex. However, exceptionally long trips were significantly more frequent in failed breeders (18 observed cases, 4 expected) than in active breeders (7 cases, 21 expected; G_{adj}= 17.5, df=1, P< 0.001).

Table 8.1. Foraging trips (n= 2199) sorted by range (max distance to nest, km) and duration (h), for breeding females and males (left) and for failed birds (right). Trips in shaded area are of exceptional range (>100km), long duration (>48 h), or both.

Breeding females	<1 h	1-6 h	6-12 h	12-18 h	18-24 h	24-48 h	48-96 h	>96 h	Σ	**Failed females**	<1 h	1-6 h	6-12 h	12-18 h	18-24 h	24-48 h	48-96 h	>96 h	Σ
0-10 km	46	262	33	2					343		1	49	9	2					61
10-20 km	5	245	51	16	2	2			321		1	23	10	4		1			39
20-30 km		79	49	10	1	2			141			6	7	2	2				17
30-40 km		51	40	16	5	2			114			9	11	1	3	11	4		39
40-50 km		8	17	11	3	1			40				3	1	2	3	2		11
50-60 km		2	10	4	3				19			1	2	1			1		5
60-70 km		1	3	2	2	2	1		11										0
70-80 km			5	4	2	1			12							1			1
80-90 km			1			2			3										0
90-100 km				1					1										0
100-250 km				3		3	1		7										0
>250 km								1	1									3	3
Σ	51	648	209	69	18	15	2	1	1013		2	88	42	11	7	16	7	3	176

Breeding males	<1 h	1-6 h	6-12 h	12-18 h	18-24 h	24-48 h	48-96 h	>96 h	Σ	**Failed males**	<1 h	1-6 h	6-12 h	12-18 h	18-24 h	24-48 h	48-96 h	>96 h	Σ
0-10 km	26	71	3						100		1	20	4	2		1			28
10-20 km	2	139	14	2					157			17	2	4			1		24
20-30 km		96	31	2	2	1			132			11	3	3	1	2			20
30-40 km		120	88	27	8	2			245			10	6	3	3	2			24
40-50 km		29	46	23	8	8			114			4	8	3	2	4			21
50-60 km		8	28	9	7	3	1		56				1	4	4	3	3		15
60-70 km		2	16	3	3	2	1		27				2	2	1				5
70-80 km		3	4	5	7	4	1		24				1				1		2
80-90 km		1	1	1		1			4							1	1		2
90-100 km									0										0
100-250 km			1	2	1	2			6							1	2		3
>250 km							1		1										0
Σ	28	469	232	74	36	23	4	0	866		1	62	27	21	11	14	8	0	144

Trips spanning an exceptional range (irrespective of duration; n= 21) were logged for males and females, active breeders and failed birds, according to expectation given the number of documented trips for either sex or reproductive status. Distant trips were slightly more frequent than expected in failed birds relative to active breeders, but the difference was not significant (G_{adj}= 1.17, df=1, n.s.). A total of 16 trips covered maximum distances between 100 and 250 km from the nest and these involved 7 breeding females, 6 breeding males, and 3 failed males. Of these trips, 13 were completed within 48 hours (12 by breeding birds, one by a failed bird), the other three trips took up to 74 hours (3.1d) to be completed (overall mean trip duration 31.2 ± 19.2h; range 12-74h, n= 16). All 19 exceptional trips by failed breeders had a relatively long duration, but 10 trips remained within a normal distance range. In contrast, only one out of 19 exceptional trips by active breeders were within normal range (1 long and nearby, 3 short and distant, 15 long and distant).

Table 8.2. Exceptional foraging trips by active breeding birds (n= 19), including 2 "freak trips" (see Fig. 8.3). Listed are colour-ring code of bird carrying GPS logger, duration (h) and range (km) of exceptional trip, mean±SD duration (h) and range (km) and total number (n) of 'normal' trips by that same individual, age (d) and number of chicks at departure, mean growth rate (g d^{-1}) of the chicks around departure and body mass developments (plus trend) measured after the exceptional trip (n.d. = no data). The number of fledglings for each breeding attempt is provided in the far right column.

	Exceptional trip		**Normal trips (mean±SD)**			**Chicks**	**Growth rates (g d^{-1})**			**n**
Ring	Duration	Distance	Duration (h)	Distance (km)	n=	age (n)	Dep	Return	trend[1]	fledged
F.AAU	13.3h	132km	5.0±6.0	17.7±13.8	88	26-27 (3)	+41.0	n.d.	↔	2
	46.8h	136km				27-28 (3)	n.d.	+7.9	↔	
F.ABN	35.6h	139km	7.3±6.6	23.7±17.5	73	33 (1)	-4.3	n.d.	?	1
F.AKK[2]	194.7h	357km	4.9±4.3	23.2±12.3	89	32 (1)	+38.3	+62.0[3]	↑	1
F.AKN	50.2h	61km	7.4±5.9	25.5±15.3	64	12-13 (2)	+28.5	+18.9	↔	2
F.AKV	13.6h	105km	4.9±4.0	23.0±18.0	101	13-14 (3)	+14.3	+33.1	↑	2
	16.1h	124km				19-20 (3)	-4.2	+40.5	↑	
	25.4h	169km				34 (2)	+0.5	+13.3	↑	
F.APP	62.1h	105km	4.7±4.0	16.7±17.2	57	15-16 (2)	n.d.	n.d.	?	0
M.ACV	67.5h	68km	8.8±6.9	26.8±14.4	32	8 (1)	+18.0	†	↓	0
M.AMJ	16.3h	101km	6.8±5.3	33.5±15.0	296	36 (1)	-12.7	n.d.	?	2
	52.9h	75km				54 (1)	n.d.	n.d.		
M.AMK	30.3h	109km	3.8±3.0	23.1±15.9	96	17 (1)	+19.0	+31.0	↑	1
	26.3h	115km				37 (1)	+8.0	-23.3	↓	
M.AMP	21.9h	105km	4.6±4.1	24.1±17.2	80	17 (1)	-3.0	48.0	↑	1
	10.8h	111km				20 (1)	+48.0	-1.0	↓	
	16.6h	112km				28 (1)	+5.5	+5.0	↔	
M.APJ	84.1h	58km	6.3±6.0	25.7±16.5	92	52 (1)	n.d.	n.d.		1
M.APN[2]	89.7h	533km	8.2±6.6	35.5±17.8	29	(eggs)	n.d.	n.d.		0

[1]) ↑ = substantial mass gain, ↔stabilized mass, ↓ substantial mass loss, † death; [2]) Freak trips: very distant and very long; [3]) Marked mass increase *prior to return* points at compensatory behavior of partner

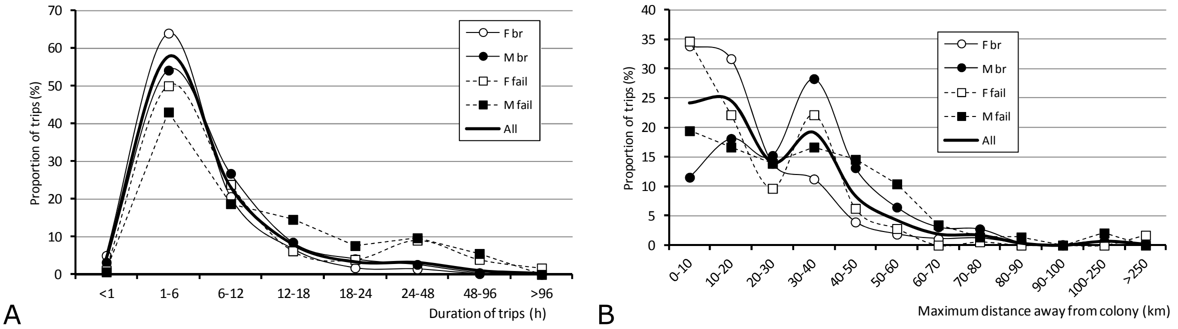


Fig. 8.1. (A) Trip duration (h) and (B) trip range (maximum distance away from the nest, km) in Lesser Black-backed Gulls, including actively breeding females (Fbr, n= 1013 trips) and males (Mbr, n= 866) and in failed breeders (Ffail, n= 176; Mfail, n= 144).

Within this dataset, five "freak trips" were identified (0.2%, n= 2199; Fig. 8.3). Three of these trips were documented for two females that were failed breeders at the time of the trips (colour-ring codes F.AAW and F.APP (2x), duration 5.0-7.3d, trips across the southern North Sea into England, maximum distance 409km). The other trips were completed by an incubating male (colour-ring code M.APN; duration 3.7d, range 533km and into the English Channel) and a female during chick care (colour-ring code F.AKK, prior to fledging of the chick; duration 8.1d, range 357km and into northern France).

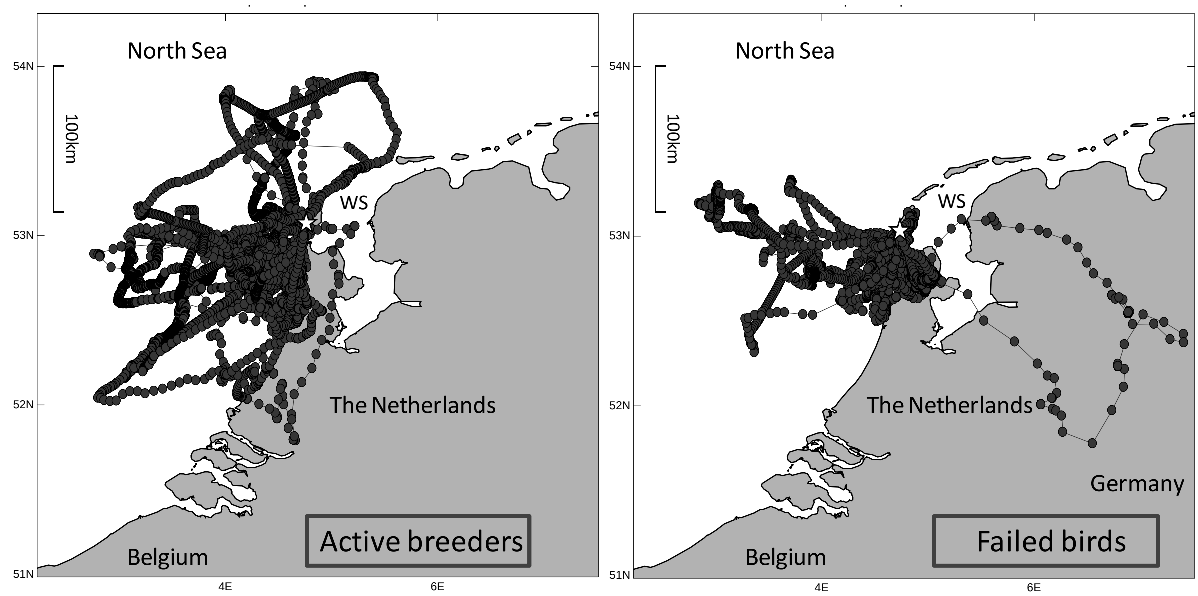


Fig. 8.2. Exceptional trips by Lesser Black-backed Gulls (duration >48 hours and/or distance 100-250 km distance from the nest site), left active breeders (n= 17 trips), right failed breeders (n= 16 trips); 2008-2011. The colony at Texel is indicated with an asterisk; WS = Wadden Sea.

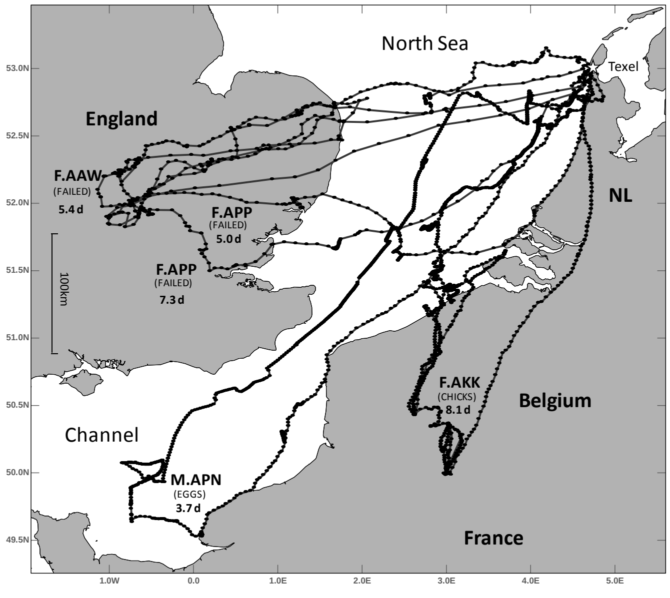


Fig. 8.3. "Freak trips" of Lesser Black-backed Gulls (>250 km distance from the nest site and duration > 48 h, n= 5). Colour-ring codes, breeding status and total duration (d) are indicated for each trip. The colony at Texel is indicated with an asterisk.

Exceptional trips by active breeding birds - Twelve different individuals (6 males, 6 females) embarked on 19 exceptional or freak foraging trips during active breeding (egg- or chick care; Table 8.2). One trip was in the egg phase and all other trips were during chick care. In the earliest phase of chick care (chicks <10d old), exceptional trips were still rare (a single case: an 8 d old chick that died during the absence of the parent; Table 8.2). The majority of the exceptional trips occurred when chicks under care were more than 10 days old and the age distribution of chicks during normal trips was significantly different from the age distribution of chicks during exceptional trips (Two-sample Kolmogorov-Smirnov test $D = 0.36$, P- = 0.004). Nine of these 12 pairs managed to fledge young (75%; Table 8.2), and among those that failed were pairs in which exceptional trips occurred in the egg phase and in the very early chick phase.

Chick growth rates around departure in the 18 exceptional trips that occurred during chick care were positive on nine occasions, negative or close to zero in five cases, and unknown in the other four trips. Chick growth rates associated with the return of parents that had conducted an exceptional trip were positive in nine cases, negative in three cases (including one chick that had died), and unknown in six cases. Growth rates associated with departures of exceptional trips (filled circles) and chick growth rates associated with 'normal' trips (open circles) are plotted against chick age (Fig. 8.4). The distribution of growth rates measured at the start of 'exceptional trips' did not deviate from growth rates measured during 'normal' trips (ANCOVA, $F_{3,\,390} = 1.242$, $P > 0.05$).

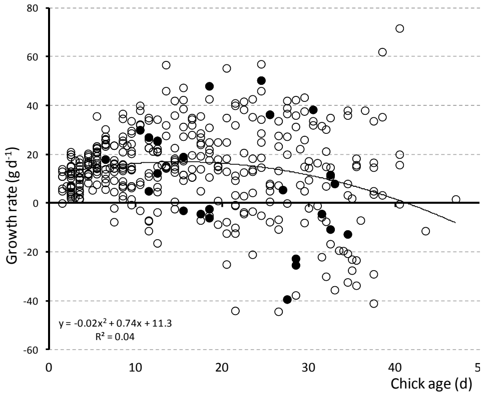


Fig. 8.4. Chick growth rates (g d^{-1}) with chick age (d), measured at 3-day intervals for nests with single parents carrying a GPS device. Growth rates for chicks at the start of exceptional trips and freak trips are indicated by filled symbols.

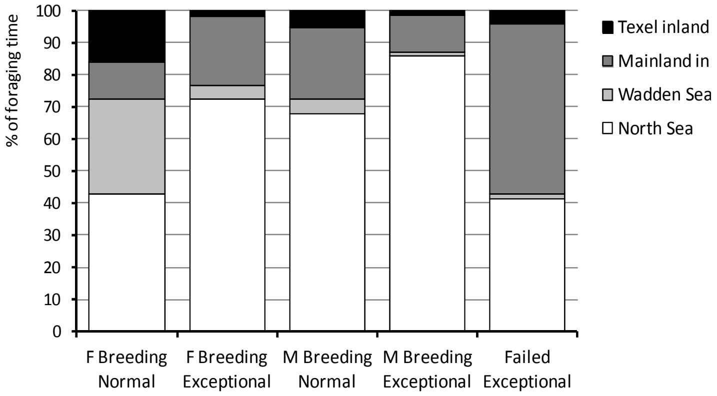


Fig. 8.5. Time spent (%) in terrestrial habitats on Texel or the Continental mainland, or within marine habitats in the Wadden Sea and the North Sea during 'normal' and 'exceptional' trips by Lesser Black-backed Gulls, male and females separated for active breeders, sexes combined for 'exceptional trips' in failed breeders. In failed breeders, 8% of the time was spent on land in the UK (included in "Mainland inland").

Habitat choice - Considering all logged foraging trips (2008-2011), actively breeding Lesser Black-backed Gulls concentrated their efforts on the North Sea (52.7%), followed by the Continental mainland (18.9%), the island Texel itself (14.6%), and the Wadden Sea (13.8%, n= 12,128h of trip time). Failed breeders spent more time on land during foraging trips in which they continued to visit the colony at regular intervals (North Sea 42.5%, terrestrial habitats on Continental mainland and in UK 40.3%, Texel 10.5%, Wadden Sea 6.7%; n= 4296h of trip time). Active breeders engaging in exceptional trips spent more time on the North Sea than they normally would, but in failed birds, individuals spent more time on land (Figs. 2, 5). The observed difference in time spent in the four main foraging habitats on normal trips versus exceptional trips was particularly strong in females (G_{adj}= 117.8, df=3, $P<0.001$), but highly significant also for males (G_{adj}= 33.0, df=3, $P<0.001$; Fig. 8.5). In breeding females, the time spent at sea during exceptional trips came mainly at the expense of time spent within the Wadden Sea and on Texel, but the relative time spent on the Continental mainland increased (a total time budget very similar to males on 'normal trips'), while in breeding males the increase in time spent at sea came at the expense of all other habitats (Fig. 8.5).

Partner response - Compensatory behavior by the partners was difficult to demonstrate with a 3-day interval of chick measurements (most exceptional trips during breeding were <72h in duration; Table 8.2). During the freak trip performed by male M.APN during incubation (duration 3.7d), however, the nest temperature remained more or less constant and well above ambient temperature (nest temperature logger data), indicating that his partner had fully compensated for his absence. During a freak trip conducted by female F.AKK that lasted more than one week (duration 8.1d, range 357km), an initial body mass decline in the single chick under care shortly after departure was followed by a marked growth spurt (body mass increase) prior to the return of the female parent, that must have been entirely caused by prey deliveries by the male partner (full compensation).

Discussion

Many earlier tracking studies have produced astonishing and often unexpected results regarding the duration and range of foraging trips by seabirds (Benvenuti *et al.* 1998, Prince *et al.* 1998, Birdlife International 2004, Casey 2005). Data loggers revealed that many animals travel further, dive deeper and apparently work harder than anyone ever had imagined and researchers may have had to reconsider traditional concepts and methods of estimating of home range and space use (Burt 1943; Kie *et al.* 2010). In the current study, we were particularly interested in the outliers; unusually long or distant foraging trips in comparison with the majority of trips conducted by a species. An overwhelming majority of the foraging trips of Lesser Black-backed Gulls breeding in one of the largest colonies in the Wadden Sea were within 80 km from the nest with a trip duration of (considerably) less than 48 hours (Fig. 8.1). Multi-day trips, certainly those beyond 100km from the colony, were rare. Our data show that trips of anomalously long duration or range were not the exclusive domain of failed breeders. For active breeders, trips of an exceptionally long duration could be risky (chicks unguarded for longer periods), while trips covering a particularly long distance could be at a higher cost to the adult, if energy expenditure would increase per unit time. We therefore focus the discussion on the exceptional trips by active breeders: what could have been the incentive, and what was the effect of the absences?

Foraging trips in breeding birds serve two prominent needs: self-maintenance (including rest, personal care and self-provisioning) and chick provisioning. In species with bi-parental care, the decision to return to the nest by any one parent is a compromise between an animal's own needs and foraging success, the energetic requirements of chicks under care, and the necessity to relieve the mate attending the clutch or chicks. This decision will be different in different phases of the breeding season: nest attendance is more urgently required during incubation (to keep eggs warm and guard from predation) and early chick phase (to guard and protect chicks from predation) than when chicks are close to fledging. If the participation of both parents is necessary for the breeding attempt to be successful, then parents should either compensate for decreased partner effort, or abandon the breeding attempt altogether (Jones *et al.* 2002).

Long trips to meet urgent needs of the offspring? - One reason for particularly long or distant foraging trips would be an urgent need to find adequate food for starving chicks that cannot be obtained in the traditional way (on “normal trips”): a chick starvation hypothesis. If the underlying problem would be local depletion, we would expect many active breeders to respond and change their foraging behavior. We have no evidence for concerted action indicating a colony wide response to prey depletion, and the exceptional trips were recorded irregularly in all study seasons and all phases of breeding. Individual specializations (in prey choice or feeding grounds), experience, or competitive abilities could lead to differences between pairs in chick condition. We assumed that disruptions in chick growth would provide indications of pair-specific reductions in chick provisioning in such cases. Body mass losses of the offspring, or reduced growth could trigger exceptional action. Our chick measurements suggest that while some trips occurred when growth rates of the offspring were low, the majority of the well-documented trips occurred when growth rates were favorable (Table 8.2). Periodic declines in chick growth were very common in this colony (Fig. 8.5), and only four exceptional trips commenced when chicks were actually losing weight. The distribution of chick growth rates corrected for chick age during departures of exceptional trips was not different from that during normal trips. Arguably, our selection of ‘exceptionality’ based on trip duration and distance may be a poor indicator for parental responses to food-stressed chicks. Increasing foraging effort in areas with ‘richer’ prey could be another parental response. In this study, active breeding birds spent more time at sea during exceptional trips than during normal trips (Camphuysen *et al.* under review), suggesting an increase in the proportion of marine prey items. However, based on the chick growth rates before and after exceptional trips and in comparison to normal trips, we can only reject the chick starvation hypothesis as an explanation for the occurrence of most exceptional trips.

Long trips for self-provisioning? - If the exceptional trips of the Lesser Black-backed Gulls in the present study were mainly for self-maintenance and the restoration of individual reserves, we could understand an increase in duration (extra care, extra self-provisioning as a time consuming factor). Why a trip should cover an exceptional range is less clear, however, except when this would lead to highly profitable feeding conditions, better than anything nearer the colony. Weimerskirch *et al.* (2003) found that Blue Petrels (*Halobaena caerulea*) alternated short foraging trips where they maximized food provisioning to chicks with long trips where the adults gained mass themselves. A similar strategy was also found in Wandering Albatrosses (*Diomedea exulans*), where adults initiated long trips when their mass declined (Weimerskirch *et al.* 1997). It would have been very useful to measure individual condition of the Lesser Black-backed Gulls tagged at Texel around departure and return (for example by weighing the adult birds), but that data is not available and would be difficult to collect without excessive disturbance. Long and distant trips, to explore alternative resources of food, at some distance to the most hectic of feeding frenzies nearer the colony, could suffice to restore reserves. Covering an exceptionally large distance *and* fight hard for prey would be an energetically expensive ‘solution’ to restore personal resources. However, the tracking data have also revealed that not all time spent at sea is used to forage and feed, but also to (seemingly) rest while afloat for hours on end (Shamoun-Baranes *et al.* 2010). Allocating time to rest on such trips could be an important aspect in the process of individual recovery from a stressful period.

Failed breeders, even those that keep frequenting the colony, often congregate on roosts, sometimes at considerable distances from the colony (in case of Texel, often on beaches and agricultural land on the Continental mainland). Sleeping, preening and molting are key activities on such sites. The increase in time spent on land in failed breeders (including those on exceptional trips; Figs. 2, 4) is consistent with these field observations. The sympatric breeding Herring Gulls *Larus argentatus* more or less avoid trips to the North Sea during the most intense period of post-nuptial (complete) molt (Jul-Sep; Camphuysen & Leopold 1994), probably because flight capacities are temporarily reduced (Hedenström & Sunada 1999). A similar inclination could emerge in Lesser Black-backed Gulls when the nesting attempt had failed: rest and personal care, molt and incidental colony visits, with a reduced incentive to forage at sea.

Consequences for the chicks - Our results indicate that most exceptional trips conducted by active breeders occurred when chicks were older than 10 days, which is after their most vulnerable period. Birds that performed trips earlier (eggs or young chicks) failed to fledge any offspring. Breeding failure was a common outcome of breeding attempts at Texel in recent years. Out of 225 pairs monitored during chick care (2006-2011), only 73 (32%) managed to fledge offspring (Camphuysen & Gronert 2010a, updated with 2011 data). Of 34 pairs with one parent bird carrying a GPS logger, 14 pairs (41%) fledged young. In the 20 birds that failed to raise chicks, only three conducted exceptional trips, while in 14 individuals that did fledge chicks, nine made at least one exceptional trip ($G_{adj} = 2.71$, df=1, $P > 0.05$). This would suggest that even if exceptional trips are not immediately beneficial for the young, they do not necessarily have a negative impact on the breeding attempt. Our sample size is small, but the results suggest that exceptional trips are postponed until the risks for chicks to remain unguarded have declined.

Consequences for the partner - In species with bi-parental care, there will often be a conflict of interest between the male and the female over the division of incubation, chick-provisioning and care (guarding). With limited resources to divide among reproduction, growth, and self-maintenance, this generally results in a trade-off for individual parents between current and future reproductive success (Stearns 1992, Jones *et al.* 2002). At Texel, at least in recent years, the risk for breeding Lesser Black-backed Gulls to lose eggs or chicks is very high; cannibalism is a widespread problem in this colony (≈54% of the young lost through predation) and breeding success is very low (Camphuysen & Gronert 2010a). Fairly frequent periodic and collective declines in growth rates of chicks and rather high rates of starvation (an additional ≈23% of the chicks starved to death; Camphuysen & Gronert 2010a) suggest that food is not always plentiful around Texel. In other words, in this colony there is a high risk of breeding failure with only a small decrease in parental effort.

Many models of bi-parental care assume that breeding success is a continuously increasing but decelerating function of parental effort (above a certain level of care, chick survival increases by diminishing amounts as combined parental effort increases). Alternative models have been proposed suggesting that in certain situations breeding success may be an accelerating function of biparental care (Winkler 1987, Ratnieks *et al.* 1996, Jones *et al.* 2002) and a small decrease in parental effort would could result in a high chance of breeding failure. It is in these cases that parents should fully compensate for their partner unless their condition falls below a certain threshold. Such a system can be expected in a dense seabird colony with a high predation level such as the colony in this study. If chick attendance is a key issue in the success of breeding attempts, the distance covered during an exceptional trip is of lesser importance (flight speeds over 70 km h^{-1} have been logged during our studies), but trip duration is important. Camphuysen (*et al.* under review) showed that males carrying GPS loggers tended to make significantly longer foraging trips, alternating with significantly longer bouts of nest attendance, than females in all stages of breeding (in failed breeders only the duration of nest bouts). If these differences persist within pairs, it is unavoidable that eggs and chicks are unattended at times. Thus during exceptional trips by any one of the partners, mates are expected to compensate for these absences by increasing the time spent within the colony, at the expense of self-maintenance and provisioning. Compensation may be partial (which is considered evolutionary stable in bi-parental care), or, as Jones *et al.* (2002) suggest for such systems, complete unless partners reach their abandonment threshold.

It is a serious flaw in our project that only one parent per pair had been tagged, but some of our data do demonstrate that partners did indeed compensate for prolonged absences of their mates ('freak trips' by incubating male M.APN and by female F.AKK during late chick care). Few of our exceptional trips were long enough to enable us to prove that partners compensated for the absences in terms of provisioning, and our nest sampling schedule was too coarse to monitor the effect of incoming parents after long excursions. Given that the colony is food-stressed as a whole, mono-parental care is probably insufficient to raise chicks, but our data suggest that none or few of the absences have been disastrous for the breeding attempts. In future studies we will have to reconsider the need to tag both partners at a nest, in order to shed more light on compensating behavior of partners facing exceptional trips performed by their mate.

The effect of tags - If the tags themselves would cause trouble, such that tagged birds made extraordinary foraging trips, is an issue that is difficult to test in the absence of controls. Phillips *et al.* (2003) examined the effects of satellite tag deployment in albatrosses and found that some individuals slightly extended their foraging trips, but affected birds nonetheless commuted to representative foraging areas. Other studies of albatrosses and petrels recorded extended trip durations and, in some cases, high rates of nest desertion following PTT attachment (literature review by Phillips *et al.* 2003). Breeding success and fledging rates of our study birds were not significantly different from control pairs (this study), but return rates of tagged birds (based on color ring re-sightings and logger data; 2008-2010 67%, n= 28) to the colony one year later were lower than expected from assessments of apparent survival (φ= 0.87 ± 0.02) and detection probabilities (p= 0.94, ± 0.18) within the colony (Camphuysen & Gronert 2012). Annual survival or return rates were apparently compromised in birds carrying GPS loggers. All recorded exceptional trips in our gulls, however, were isolated anomalies in otherwise "rhythmic" foraging routines (numerous shorter, less distant trips). Thus, these trips can be seen as sporadic incidents rather than continuous signals of prolonged physical stress. We did not find a negative correlation between breeding results and the occurrence of exceptional excursions, which would have supported the hypothesis of physical stress. Loggers (just as any other attachments) are likely to have at least some handicapping effect on the birds involved, however, and abnormal behavior induced by devices such as these can never be completely excluded.

In summary - The exceptional trips and freak trips as defined in this study were difficult to predict (for us), with likely repercussions for the partners. Anomalous trips occurred in active breeders as well as in failed birds. The exact characteristics of these trips were different between failed birds and active breeders, with an increased attention to marine resources in breeding birds as an important feature. From the data gathered in this study, we hypothesize that self preservation is an important trigger of exceptionally long/distant foraging trips and not the urgent needs of the offspring. Parents seemingly avoided the early phase of chick care, when chicks are most vulnerable for intra-specific attacks (cannibalism) within the colony. In future studies we propose that other, more modest deviations from "normal" routine flights are investigated in the context of chick growth rates with the highest possible resolution on the individual level. What is an extravagant action for one bird may be a default strategy for another. Evidently, optimality in foraging behavior is more than feeding efficiently and cutting foraging trip time as short as possible to rejoin the chicks.

Territorial Lesser Black-backed Gull carrying GPS logger and colour-ring, shortly after release (CJ Camphuysen)

Lesser Black-backed Gull carrying GPS logger in flight, 20 June 2009, Kelderhuispolder (CJ Camphuysen)

9. Incidence and fitness implications of foraging specialisations in a generalist feeder

Reviewed **J. Zool., London** [in revision]

C.J. Camphuysen

Royal Netherlands Institute for Sea Research, NIOZ, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands,
E-mail: kees.camphuysen@nioz.nl

Abstract Intra-population niche variation means that individuals within the same population are subject to different selective pressures, which can be beneficial in periods of environmental change. Inter-pair dietary specialisations were studied empirically and related to fecundity parameters in a generalist seabird recovering from a multi-decadal population crash. The overall dietary spectrum and the level and incidence of dietary specialisations changed when the energetic demands increased during chick care. Prior to hatching, most pairs focussed entirely on bivalve prey, but 25% of the pairs had distinct dietary biases. During chick care, both chick growth and fledging rates were positively correlated with the amount of fish prey provided. Prey spectra diversified overall during chick care and fewer specialists were detected. Particularly low chick growth rates were found in pairs that had a dietary bias towards crustacean prey.

Key words: Dietary specialization, intra-population niche variation, generalist feeders, fecundity, foraging strategies

Introduction

Many apparently generalised species are in fact composed of specialised individuals that use a small subset of the population's resource distribution (Bolnick *et al.* 2002). Individual specialisation has potentially important ecological, evolutionary, and conservation implications (Bolnick *et al.* 2003). Individual variation in the diet can affect components of fitness, such as fecundity and survival rates and may correlate with factors like timing of reproduction, clutch or litter size, and parental quality. It may affect the survival and growth of offspring through differences in provisioning rates, the calorific value of certain prey types, or through the amount of time available for parents to stand guard against predators (Watanuki 1992, Irons 1998).

Intra-population niche variation means that individuals within the same population can be subject to different selective pressures. "Phenotypically intermediate" individuals may experience stronger intraspecific competition and hence have lower fitness than dietary specialised conspecifics. The effect of individual specialisation is of particular interest when studying populations stressed by major environmental changes. Over a six year study period, patterns and biases in diet choice were investigated in relation to reproductive performance in a generalist seabird, the herring gull *Larus argentatus* in the western Wadden Sea. These herring gulls are currently recovering from a prolonged period of population decline, associated with major changes in resources (Spaans 1998, van Dijk *et al.* 2010). Reproductive success was found to vary considerably between seasons, but also within seasons between pairs (Spaans & Spaans 1975, Spaans *et al.* 1987, Camphuysen & Gronert 2010a). There was no *a priori* information on the level of dietary specialisation that occurred within the study colony, nor on any effects that this could have on reproductive success. The study was conducted under the expectation that the birds were ecological equivalents (Bolnick *et al.* 2003).

Variations in diet choice were investigated and related to timing (egg laying), clutch size, clutch volume, hatching success, cannibalistic pressure, chick growth and fledging rates. Dietary switches may be attributed to changes in the availability of resources, or to preferences of the predators themselves and are essentially state dependent (Houston 1993). A marked seasonal variation in the diet of wild animals can be expected, even within the breeding season itself (Spaans 1971, Pierotti & Annett 1987, Annett & Pierotti 1989). During breeding, parents adjust foraging efforts to meet the energetic demands of developing offspring. I therefore compared dietary specialisations during the pre- and post-hatching periods.

Materials and Methods

Study area - The study was conducted in a breeding colony on the island of Texel, The Netherlands (53°00′N, 04°43′E), at the crossroads of the western Wadden Sea and the southern North Sea. Strong tidal currents flow through a narrow passage between the Continental mainland and the island, and the main foraging areas include open sea (fish and benthic fauna, including fisheries discards), intertidal areas (mudflats and coastal breakwaters exposed at low tide; benthic fauna), freshwater ponds, tourist resorts (including restaurants), agricultural land, sewage plants, rubbish tips and cities. Within the study area, approximately 11,500 pairs of Lesser Black-backed Gulls and just over 5000 pairs of Herring Gulls breed sympatrically.

Reproduction - Breeding data within the colony were collected during April to August over six consecutive breeding seasons (2006-2011). To monitor breeding success in the colony, nests were marked during egg laying, and marked nests were either monitored until hatching, or, after a random selection of nests, enclosed with 50cm high chicken wire to assess chick growth and fledging rates (Camphuysen & Gronert 2010a). Nests were visited every third day, throughout the breeding season (prospecting to fledging). During these visits, the following attributes were recorded: date of laying and egg size, clutch size, egg losses, hatching date, chick growth, chick mortality, and fledging rates. Breeding phases analysed in this study in chronological order were (1) prospecting, (2) laying (3) incubation, (4) hatching, (5) chick care (first 40 days after hatching) and (5) fledging (chick care within colony >40d).

Hatchlings were marked with uniquely numbered aluminium rings (replaced by numbered stainless steel rings and engraved colour rings just prior to fledging). During enclosure visits, all chicks were captured, measured, weighed with an electronic balance to the nearest 2g and returned to the enclosure (or collected when dead). Growth rates (g d^{-1}) were calculated on the basis of mass differences between two measurements and the weighing interval. Chicks were considered to have fledged at 40 days of age. Several growth models were tested to describe chick growth. The best fitting model (using Akaike's information criterium, AIC) for body mass in chicks of Herring Gulls at Texel, based on pooled measurements collected in 2006-2008, was a logistic growth model with 3 parameters:

$$y = \frac{a}{1 + b\ell^{-kt}}$$

where *a* is the upper asymptote, *b* is the value of *t* at the point of inflection of the curve, ℓ for Euler's number and *k* is the growth rate (Gallego Garcia 2008). Body mass increments accelerated a few days after hatching and gradually slowed down after 20 days of age (sigmoid growth curve). In order to compare growth rates of chicks cared for by parents with different dietary specialisations, growth rate (g d^{-1}) was defined as the slope of the linear regression line between 5 and 20 days of age (Oro *et al.* 1996). This is a period during which the chicks of large gull species grow almost linearly (Vermeer 1963, Spaans 1971, Hunt & Hunt 1976, Gallego Garcia 2008). Only chicks that reached 20d of age were used in this analysis (5 measurements per chick).

Diet - Given that the net result of foraging efforts of both parents combined would affect breeding success (Herring Gulls have bi-parental care), the present study focused on nesting pairs rather than on individual birds. The diet study at Texel was based on regurgitated prey (pellets, other regurgitated matter, boluses during handling of the birds or chicks, and chick-feed deliveries; Barrett *et al.* 2007) found near the (marked) nests of individual pairs. Pellet analysis has been used widely on many species and the method has been tested extensively both with captive birds fed known diets, and against other diet study methods (Barrett *et al.* 2007 and references therein). The method is non-invasive, relatively simple and can provide large samples over time. "Frequency of occurrence" was used in this study, as recommended by Barrett *et al.* (2007), which is the percentage (frequency) of pellets ("sample-units") in which a particular food item occurred.

Samples were labelled with sample number, nest number and date and were stored frozen prior to analysis. The logged dates were assigned to the nest-specific breeding phase, later simplified to either "egg-phase" (pre-hatching, collected during prospecting, laying, and incubation) or "chick phase" (post-hatching, collected during hatching, chick care, and fledging). Nests (individual pairs of birds) selected for the analysis yielded at least 10 food samples during one breeding season (2006-2011, 172 nests studied, 4119 prey samples collected, mean 23.9 ± 16.1 samples per nest, range 10-143). The random selection of nest sites to monitor fledging success made that some pairs were included more than once for different seasons. These pairs were treated as independent samples (representing the population at large), just as the other pairs.

Samples were defrosted in the laboratory and food remains were collected and identified during a microscopic inspection (Olympus SZ51). All items were identified to the lowest possible taxon, measured and quantified (number of individuals) when possible. Relatively minor problems arise in pellet studies as a result of secondary consumption of prey (the pellet may contain remains of prey present in the digestive tract of the organism consumed by the bird). The problem is probably small, and some evident cases have been excluded from the analysis (Electronic Appendix). A second problem is the 'pollution' of samples with materials that were blown in by the wind (*i.e.* plant seeds from local flora), that were accidentally picked up from the ground while sampling (sand, grit, plant material, remains from other pellets), or that were ingested by the bird as a vehicle to regurgitate tiny hard parts (*i.e.* grasses to help excrete setae of earthworms, jaws of Nereid worms, or very small fish bones). Likely prey items such as vegetables, fruits, nuts and herbs from human waste materials, all countryside berries, and corn (Triticum, Poaceae and *Zea mays*) were included, but all other plant remains were excluded from the analysis.

After identification, prey items were grouped: Insects (including spiders and woodlice for convenience), Nematods, Polychaetes, Oligochaetes, Sponges, Echinoderms, Snails, Gastropods, Bivalves, Cephalopods, Barnacles, Crustaceans, Marine fish, Freshwater fish, Non-passerine birds, Passerine birds, Mammals, Plants, Seaweeds, Domestic refuse, Non-food, and Miscellaneous. The prey spectrum of the 172 selected nests was compared with the overall prey spectrum based on all samples taken in the colony in these years (n= 5542 samples). Based on the species identifications some further categories could be identified, including common fisheries discards, cannibalistic prey, freshwater fish prey, common intertidal prey, and agricultural land prey. The area of origin for individual prey items was assessed as either Marine (North Sea or Wadden Sea), Intertidal (Wadden Sea), Terrestrial (the island Texel or the Continental mainland), or Anthropogenic (selections in Electronic Appendix).

To investigate the dietary spectrum of pairs that failed to raise chicks and those that were successful, the present study pooled all food samples collected during chick care for nests that fledged young (n= 71 nests, 1428 food samples), for pairs in which all or most chicks were predated (n= 19 nests, 113 samples) and for pairs in which most or all chicks had starved to death (n= 18 nests, 179 samples). Because of the smaller sample size in failing pairs, only the top-4 prey categories were considered and the observed frequencies of occurrence of prey types in pairs that had failed were compared with an expectation based on the frequency of occurrence of prey types in successful pairs.

Statistical analysis - A hierarchical, agglomerative, polythetic cluster analysis in *r* (R Foundation for Statistical Computing, version 2.10.1; 2009-12-14) was applied to investigate the similarity of individual nests according to their dietary data (Legendre & Legendre 1983, Krebs 1989). The analysis was based on grouped diet data, in which the rarest groups were omitted (Terrestrial snails, Marine gastropods, Cephalopods, Barnacles, Plants, Seaweeds, and Non-food). The frequency of prey items for each individual nest was used as an independent observation. The first cluster analysis involved nests that produced sufficiently dietary information prior to hatching (mean ± SD 14.0 ± 11.2 prey samples samples, range 5-98), relevant for the egg phase; n= 134 nests) followed by a second cluster analysis based on nests that had produced sufficient samples during chick care and fledging (23.1±12.4, 5-63 prey samples), relevant for the chick phase; n= 73 nests). Characteristics of the groupings of nests, called the *dietary bias*, were indicated by listing the top three (max) dominant prey components in order of importance . The results were tabulated.

Dietary spectra were compared with a X^2-test. Rank Spearman Correlations were calculated to investigate trends in laying, Pearson correlation coefficients were calculated to investigate correlations between laying dates, egg volumes, chick growth rates and fledging rates and significance was accepted at the $P< 0.05$ level.

Results

Reproductive success - There were no significant differences between years in overall clutch size, brood size, and hatching success, but chick growth rates and fledging success were relatively low in 2006 and 2011 (Table 9.9.1). Overall, egg-laying was highly synchronised (1st and 3rd quartiles three days around the median), but the laying date advanced significantly between 2006 and 2011 ($R_S= -0.96$, df=6, $P< 0.01$, 1-tailed). There were no correlations between laying date and clutch size or mean egg-volume (or three-egg clutch volume). Fledging rates varied from 0.48 pr^{-1} in 2011 to 1.33 pr^{-1} in 2010 (Table 9.1). Growth rates ($g\ d^{-1}$) and fledging rates (fledglings $pair^{-1}$) were positively correlated ($r= 0.75$, $t_4= 3.17$, $P< 0.05$).

Prey spectrum and foraging habitats - The prey spectrum of Herring Gulls nesting at Texel is summarised in Table 9.2. Individual samples (pellets) could contain as many as 13 different prey species, representing up to 8 taxonomic groups, from all four areas of origin (n= 5542 samples). Based on the frequency of occurrence, the most important genuine prey items in declining order were marine bivalves (68.2%), marine fish (18.2%), crustaceans (16.9%), domestic refuse (12.8%), and non-Passerine birds (9.7%). Insects, freshwater fish, mammals, echinoderms, oligochaetes, and polychaetes were less frequent, but still relatively important prey items. The

Table 9.1. Summary statistics of Herring Gull breeding success and timing at Texel, 2006-2011.

	2006	**2007**	**2008**	**2009**	**2010**	**2011**
First eggs	02-May	26-Apr	25-Apr	23-Apr	26-Apr	24-Apr
Peak egg-laying	07-11 May	04-11 May	05-10 May	04-09 May	02-08 May	01-07 May
Median egg-laying	09-May	09-May	07-May	06-May	05-May	04-May
Clutch size	2.71 ± 0.51	2.58 ± 0.69	2.86 ± 0.43	2.69 ± 0.56	2.81 ± 0.48	2.77 ± 0.50
(n) nests	(42)	(55)	(69)	(65)	(58)	(56)
3-egg clutch volume (cc)	247.0 ± 23.3	241.9 ± 24.1	249.1 ± 22.4	241.3 ± 23.5	248.1 ± 20.2	248.4 ± 21.0
(n) nests	(31)	(38)	(58)	(48)	(49)	(48)
Eggs hatched	79.8%	63.7%	68.1%	70.3%	81.8%	64.9%
(n) eggs	(114)	(146)	(213)	(175)	(170)	(154)
Chick growth rate (5-20d)	23.0 ± 1.4 $g\ d^{-1}$	25.0±1.5 $g\ d^{-1}$	27.2±0.9 $g\ d^{-1}$	28.4±1.4 $g\ d^{-1}$	27.8±1.2 $g\ d^{-1}$	23.9±1.8 $g\ d^{-1}$
(n) hatchlings	12	18	32	23	37	19
Chicks fledged	24.2%	52.2%	50.0%	39.5%	58.2%	36.7%
(n) hatchlings	(33)	(23)	(44)	(43)	(55)	(30)
Fledglings per pair	0.62 pr^{-1}	0.80 pr^{-1}	1.10 pr^{-1}	0.81 pr^{-1}	1.33 pr^{-1}	0.48 pr^{-1}
(n) nests	(13)	(15)	(20)	(21)	(24)	(23)

Table 9.2. Prey spectrum of Herring Gulls breeding Kelderhuispolder, Texel, 2006-2011 based on prey samples at all studied nests (left) and at selected nests, in total, and prior to and after hatching of the eggs (see text). Nematodes, sponges, cephalopods, barnacles, and seaweeds (very rare taxa) were excluded from further analysis.

	All nests		**Selected nests**		**Selected nest and breeding progress**			
Group	Frequency	%	Frequency	%	Egg-phase1)	%	Chick-phase1)	%
Insects 2)	323	5.8	235	5.7	112	5.7	115	5.5
Polychaetes	81	1.5	40	1.0	13	0.7	25	1.2
Oligochaetes	55	1.0	42	1.0	9	0.5	31	1.5
Echinoderms	88	1.6	69	1.7	16	0.8	53	2.5
Terrestrial snails	52	0.9	40	1.0	27	1.4	11	0.5
Marine gastropods	25	0.5	12	0.3	9	0.5	3	0.1
Marine bivalves	3778	68.2	2733	66.4	1507	76.8	1191	57.0
Crustaceans	936	16.9	695	16.9	192	9.8	491	23.5
Marine fish	1010	18.2	746	18.1	178	9.1	557	26.6
Freshwater fish	145	2.6	123	3.0	61	3.1	47	2.2
Non passerine birds	538	9.7	478	11.6	249	12.7	221	10.6
Passerine birds	38	0.7	28	0.7	4	0.2	22	1.1
Mammals	92	1.7	72	1.7	53	2.7	17	0.8
Plants	344	6.2	274	6.7	138	7.0	121	5.8
Human waste	708	12.8	507	12.3	117	6.0	387	18.5
Miscellaneous	65	1.2	54	1.3	11	0.6	43	2.1
Non-food	831	15.0	635	15.4	483	24.6	140	6.7
Nematodes	1	0.0						
Sponges	1	0.0						
Cephalopods	3	0.1	3	0.1	1	0.1	2	0.1
Barnacles	8	0.1	8	0.2		0.0	7	0.3
Seaweeds	17	0.3	9	0.2	2	0.1	7	0.3
Sample size	5542		4119		1963		2091	

1) excluding 65 samples of "off-duty" birds that had lost their entire clutch or all chicks; 2) including spiders and woodlice

prey spectrum found in the colony at large was not different from that in the 172 selected nests with >10 prey samples per site available (X^2_{16}= 18.6, P= 0.288). When comparing the egg-phase and chick-phase periods at selected nest sites, it became obvious that the relative importance of bivalves and mammals declined during chick care, while the frequency of occurrence of marine fish, crustaceans and domestic refuse doubled or tripled (Table 9.2). The difference in prey spectra (egg-phase versus chick-phase) was highly significant (X^2_{16}= 785.3, P< 0.001).

By far the most abundant bivalves were Mussels *Mytilus edulis*, in which the frequency of occurrence declined from 71.5% prior to hatching of the eggs to 54.4% during chick care. The second (American razor clam *Ensis americanus*, 8.0% and 4.1%) and third most abundant bivalve prey (Cockle *Cerastoderma edule*, 3.1% and 0.5%) declined even more markedly after hatching. Trivial amounts of Brown Shrimps *Crangon crangon* were found prior to hatching (0.3%), while 5.3% of prey samples collected during chick care contained remains of shrimps. The frequency of occurrence of Common Swimming Crabs *Liocarcinus holsatus* (1.3 versus 6.9%) and Shore Crabs *Carcinus maenas* (7.6 versus 11.7%) increased more or less simultaneously. At least 36 species of marine fish were identified. Common fisheries discards were by far the most abundant fish prey encountered (91% of samples containing fish prey, n= 746), supplemented with clupeids Clupeidae, Horse Mackerel *Trachurus trachurus*, and sandeels Ammodytes.

Dietary biases in the egg phase - Prior to hatching, that is during prospecting, laying, and incubation, bivalve prey overwhelmingly dominated the collected samples (frequency of occurrence 77%). Gull eggs (13%), crustaceans (10%), marine fish (9%), and domestic refuse (6%) were

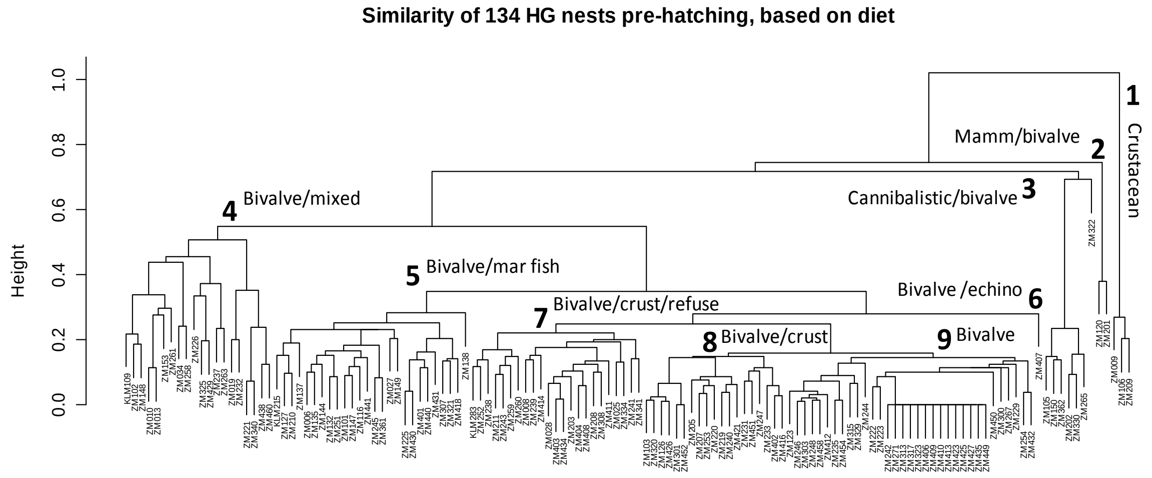


Fig. 9.1. Similarity of 134 Herring Gull nests based on dietary information (>5 prey samples analysed) collected during incubation, Kelderhuispolder (Texel), 2006-2011.

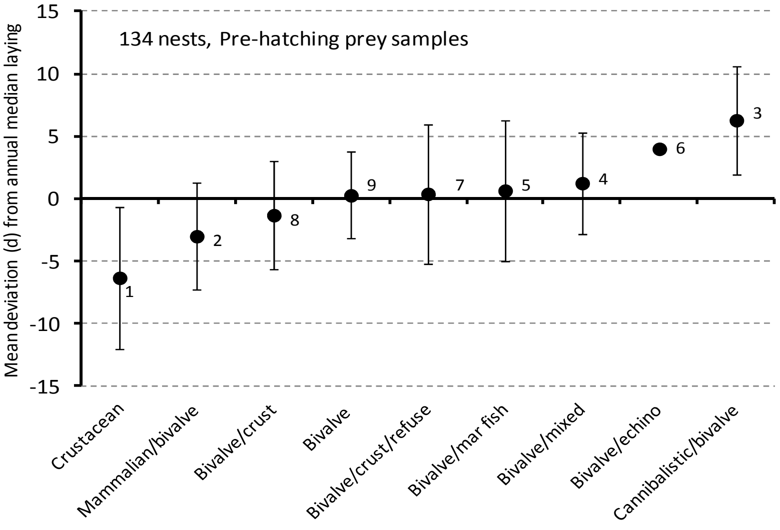


Fig. 9.2. Mean deviation in days (±SD) relative to the colony median laying date for 9 clusters of pairs of Herring Gull differentiated on the basis of their dietary bias (numbers refer to clusters indicated in Fig. 9.1). Negative values indicate advanced breeders, positive values indicate late nesting birds)

other common prey items. The cluster analysis revealed that most nests sites were characterised by high frequencies of bivalve prey, but with some small clusters of nests with more specialised pairs mainly feeding on crustaceans, mammalian prey or eggs (∑ 12 nests, clusters 1-3; Fig. 9.1). A group of 20 nests were characterised by a complex mixture of prey items (cluster 4), all other clusters were highly dominated by bivalve prey (Table 9.3).

Deviations of the median laying date were prominent in two clusters of rather specialised nests. Birds with cannibalistic preferences (cluster 3) commenced laying relatively late, whereas specialised pairs concentrating on crustacean prey (cluster 1) were rather advanced in comparison with the majority of pairs breeding at Texel; Fig. 9.2). The two outliers in laying date on either end (the advanced crustacean specialists and the delayed cannibals) were also characterised by larger clutches (3.3 resp. 3 eggs clutch^{-1}), larger eggs (3-egg clutch volume 288 ± 14.1 resp. 266 ± 24.5 cc, mean egg 89 ± 12.5 resp. 89 ± 8.3cc), higher hatching success (80.0 resp. 90.5%), and more hatchlings per clutch (both 2.7 clutch^{-1}) than all other clusters.

Dietary biases during chick care - The cluster analysis revealed a large number of nests with rather complex prey mixtures of (mainly) bivalves, crustaceans, marine fish, and domestic refuse in different compositions, and relatively few genuinely specialised pairs (Fig. 9.3). An exceptional pair concentrated on freshwater fish species (outlier cluster 1), only two pairs concentrated on crustaceans as prey (cluster 2; Fig. 9.3). A third cluster, characterised by cannibalistic prey (eggs and chicks of conspecifics and of Lesser Black-backed Gulls), comprised six territories. After hatching, the frequency of bivalve prey had declined markedly (54%), while marine fish (27%), crustaceans (23%), and domestic refuse (21%) gained importance (Table 9.4).

Chick growth rates were especially low (<25 g d^{-1}) in nest clusters with a dietary bias involving substantial amounts of crustaceans as prey (clusters 1, 2, and 9), except when also substantial amounts of marine fish were provided (cluster 5; Fig. 9.4). The fastest chick growth was recorded in pairs that provided substantial amounts of marine and/or freshwater fish (frequency of occurrence fish prey >24%; clusters 1, 5, 6, 7, and 8; Table 9.4). Fledging rates also varied markedly between the identified clusters, and a strongly positive correlation was found between the reproductive success (fledglings pair^{-1}) and the frequency of occurrence of fish prey (Fig. 9.5).

Successful pairs versus failing pairs - From pooled data (all food samples collected during chick care), it appeared that 71 successful pairs provisioned their chicks mainly with bivalves (frequency of occurrence 52.2%), marine fish (27.9%), crustaceans (23.4%), and domestic refuse (23.1%, n= 1428 prey samples; Table 9.5). Based on these frequencies of occurrence, pairs that failed provided the offspring with more than expected bivalves and less than expected domestic refuse (Table 9.5). Marine fish and domestic refuse were poorly represented in diets of pairs that

Table 9.3. Dietary biases based on a cluster analysis of prey samples collected at 134 Herring Gulls during incubation where at least 5 samples could be checked: cluster, bias characterisation, frequency of occurrence (%) of 13 prey types, and number of nests involved (see Fig. 9.1).

Cluster	Bias	Insect	Polych	Oligoch	Echino	Bivalve	Crust	MarFish	FrFish	Cannib	Aves	Mamm	Waste	Miscell	Nests
1	Crustacean	0	0	0	0	7	98	2	0	5	0	5	2	0	3
2	Mammalian/bivalve	2	0	0	0	30	6	6	4	2	0	69	7	0	2
3	Cannibalistic/bivalve	5	0	0	0	38	3	10	0	72	0	0	1	1	7
4	Bivalve/mixed	15	2	2	0	63	29	18	19	4	1	2	13	2	20
5	Bivalve/mar fish	7	1	1	1	87	9	21	1	5	0	1	10	1	26
6	Bivalve/echino	0	0	0	27	95	5	0	0	0	0	0	0	0	1
7	Bivalve/crust/refuse	6	2	0	1	92	6	6	0	3	0	1	9	0	23
8	Bivalve/crust	5	0	0	0	95	5	3	0	0	0	1	0	0	19
9	Bivalve	0	0	0	0	97	0	1	0	0	0	0	3	0	33
		6	1	0	1	77	10	9	3	13	0	3	6	1	134

Table 9.4. Dietary biases based on a cluster analysis of prey samples collected at 73 Herring Gulls during chick care where at least 5 samples could be checked: cluster, bias characterisation, frequency of occurrence (%) of 13 prey types, and number of nests involved (see Fig. 9.2).

Cluster	Dietary bias	Insect	Polych	Oligoch	Echino	Bivalve	Crust	MarFish	FrFish	Cannib	Aves	Mamm	Refuse	Miscell	Nests
1	Freshwater fish	0	0	0	0	11	6	0	80	0	0	0	3	0	1
2	Crustacean	0	0	0	0	19	100	0	0	2	0	0	0	0	2
3	Cannibal/bivalve	5	3	1	0	54	5	19	0	57	1	1	6	0	6
4	Crustacean/bivalve	0	0	0	9	64	73	6	0	0	0	0	3	0	2
5	Crustacean/mar fish	4	1	0	3	17	74	43	4	0	3	1	9	6	3
6	Mix	9	1	4	2	33	25	46	1	4	3	2	34	5	21
7	Bivalve/mar fish/crust	4	0	1	5	74	20	32	2	5	0	0	11	1	13
8	Bivalve/refuse/mar fish	6	1	1	1	62	11	21	0	3	0	0	48	3	12
9	Bivalve/crust	0	0	0	4	86	16	8	0	3	1	0	6	0	13
		5	1	1	3	54	23	27	2	11	1	1	21	2	73

had starving chicks. Growth rates of chicks from pairs that failed to fledge any offspring were notably lower than those from pairs that were successful, particularly so during the first phase of rapid growth (5-10d of age; Table 9.5).

Common additional prey types found around the nests of successful breeders were gull chicks and eggs (cannibalistic prey types; 10.9%), insects (4.7%), echinoderms (3.1%), and freshwater fish (2.7%, n= 1428). Chicks and eggs (cannibalistic prey) were particularly common around nests in which the chicks were predated (29.2%, n= 113), but uncommon around nests in which the chicks starved to death (3.9%, n= 179). Of twelve rather specialised pairs identified for the egg phase (Fig. 9.1, clusters 1-3), five pairs were monitored during chick care. One early nesting crustacean specialist persisted on that prey choice and failed to fledge offspring. Two late nesting pairs with a "cannibalistic/bivalve" bias (Fig. 9.3, cluster 3) persisted on that diet during chick care and managed to fledge young. Two further pairs switched to a diet that was rich in marine fish and both fledged young. Of nine rather specialised pairs identified for the chick phase (Fig. 9.3, clusters 1-3), only four had produced sufficient prey samples during the egg phase to be analysed; three of which are mentioned above. The most extreme outlier (cluster 1), however, focussed almost entirely on freshwater fish during chick care and raised two fledglings in 2011. This particular pair (with male and female colour-ringed) had also been monitored in 2009 (when one fledgling was raised), and that nest was included in cluster 5 (Fig. 9.3; Crustacean/marine fish bias). In 2009, freshwater fish made only a trivial contribution to the diet of this pair.

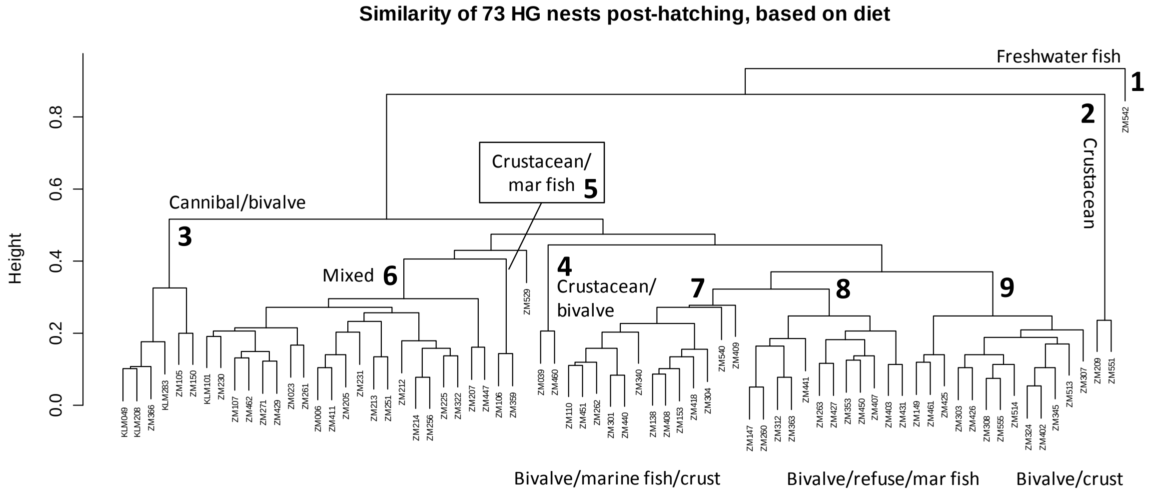


Fig. 9.3. Similarity of 73 Herring Gull nests based on dietary information (>5 prey samples analysed) collected during chick care, Kelderhuispolder (Texel), 2006-2011.

Discussion

Herring Gulls are generalist carnivores at a species level (Cramp & Simmons 1983), but individual birds may forage specifically at extreme ends of the entire prey spectrum (Harris 1965, Spaans 1971, McCleery & Sibly 1986, Pierotti & Annett 1987). Prior to hatching, most pairs (76%) concentrated on bivalve prey (frequency of occurrence >85%; Table 9.3) with little else ("ecologically equivalent" pairs; Bolnick *et al.* 2003). About one quarter of the studied pairs clearly deviated from this scenario (inter-pair "niche variation"; Bolnick *et al.* 2003). Twelve highly specialised pairs deviated not only in prey choice, but also in timing of laying (relatively early and late), clutch size (large), egg volume (large) and hatching success (high): non-trivial effects on ecological processes.

The next phase of breeding, chick provisioning, clearly required different skills, illustrating the importance of state (Houston 1993). Overall prey spectra diversified and fewer specialists were

Table 9.5. Observed and expected dietary composition of Herring Gulls that failed to breed successfully. The expectation of dietary composition was based on the frequency of occurrence of prey types (n, %) in food samples collected during chick care around 71 nests that did successfully fledge young (left data column). Estimates of chick growth were calculated for chicks that reached a minimum age of 10d and 20d, using growth rates (g d^{-1}) measured between 5-10d and 5-20d of age respectively.

Nest success	**Fledged**		**Predated**		**Starved**	
Nests (n)	71		19		18	
Food samples chick care (n)	1428		113		179	
Chick growth rate d5-10 (g d^{-1}±SE)	22.4 ± 1.3		17.9 ± 3.5		13.1 ± 3.9	
Chicks 10d (n)	160		32		36	
Chick growth rate d5-20 (g d^{-1}±SE)	25.1 ± 0.6		18.7 ± 2.0		21.7 ± 2.2	
Chicks 20d (n)	125		4		12	
Primary prey (freq)	n	%	obs (n)	exp (n)	obs (n)	exp (n)
Bivalves	746	52.2%	71	59	114	94
Crustaceans	334	23.4%	18	26	40	42
Domestic refuse	330	23.1%	10	26	12	41
Marine fish	398	27.9%	34	31	40	50
X^2_3			9.7	P= 0.02	18.4	P<0.001

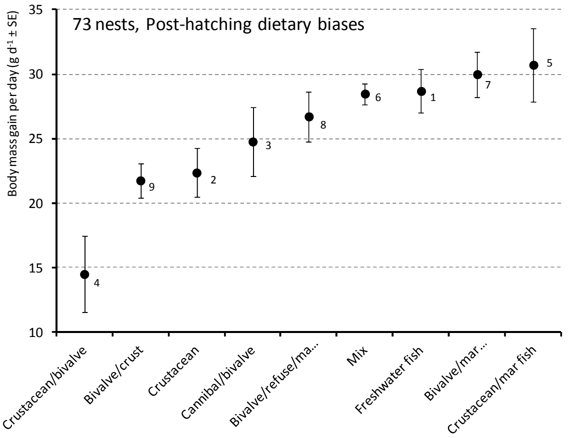


Fig. 9.4. Chick growth rates (g d^{-1} ±SE) for offspring between 5 and 20d of age for 9 clusters of pairs of Herring Gull differentiated on the basis of their dietary bias (numbers refer to clusters indicated in Fig. 9.3).

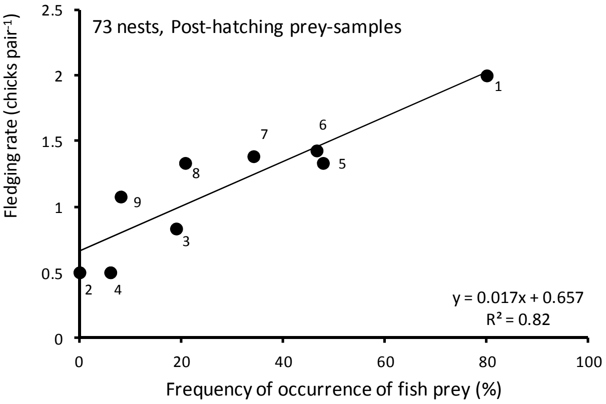


Fig. 9.5. Relationship between fledging rates and the occurrence of fish prey (%) in prey samples collected during chick care for 9 clusters of pairs differentiated on the basis of their dietary bias (numbers refer to clusters indicated in Fig. 9.3).

detected. The same or very similar dietary biases as in the egg phase, such as a preference for crustaceans, could now lead to poor growth rates of the chicks (Fig. 9.4) and lower fledging success (Fig. 9.5). Chick growth and fledging rates were strongly correlated with the amount of fish prey provided and pairs either switched to a dietary spectrum that included prey that was rich in energy, or they failed to fledge offspring. Earlier in the breeding season, a diet biased towards bivalve prey was apparently sufficient for self-maintenance (affecting the condition of the parents only). The advance in the onset of breeding relative to most other birds (Fig. 9.2), and the large clutches and high egg volume in crustacean-biased breeding pairs, did not translate into high breeding success, except when a dietary shift could be made to increase the amount of fish prey and/or domestic refuse during chick care.

The general importance of intertidal foraging habitats for Herring Gulls was evident in all phases of breeding. Nearly all marine bivalves, most crustaceans and numerous invertebrates must have been obtained in habitats that fall dry at low tide (North Sea shoreline breakwaters, Wadden Sea mudflats, gullies, and dikes). The dietary spectra were generally more complicated during chick care than during pre-laying and incubation, indicating that many Herring Gulls redirected at least some of their foraging flights to exploit alternative feeding opportunities. The bivalve prey bias in the dietary spectrum of the failed breeders was relatively strong, indicating that they either were unable to, or failed to switch to different prey. Intertidal invertebrates are often considered a less accessible (tidal regime), less energetic, generally more fluctuating resource than for example domestic refuse (Sibly & McCleery 1983ab, Pons 1994, Pons & Migot 1995), but of a high spatial and temporal predictability. Most fish prey that characterised the diets of successful birds must have been obtained at near-shore fleets bottom-trawlers (targeting flatfish and shrimps) within the western Wadden Sea and/or in the North Sea coastal zone (1-5km offshore), where Herring Gulls in summer are dominant scavengers and effective kleptoparasites (Hüppop *et al.* 1994, Camphuysen 1995a, Walter & Becker 1997). In the absence of suitable landfill areas within the home range, much of this must have been obtained in cities (*i.e.* on street markets or from rubbish bins), or from tourist resorts.

The current situation in the western Wadden Sea is a recovery of Herring Gull breeding success to historical values (Spaans & Spaans 1975). With the fledging rates now measured (all other demographic factors assumed the same), the population could resume growth (Camphuysen & Gronert 2010a). Annual adult survival is high, but there is currently no evidence for recruitment at an early age (virtually all nesting birds are in full adult plumage; Camphuysen & Gronert 2012). Domestic refuse is only sparsely available, compared to the 1960s and 1970s (Spaans 1971), because open refuse dumps within normal foraging range were covered up long ago (Werkgroep Afvalregistratie 2007). Fisheries are declining and so must the availability of discards (Rijnsdorp *et al.* 2008). Intertidal benthic prey has apparently (re-)gained importance for Herring Gulls breeding in the western Wadden Sea, but the molluscivorous landscape has changed markedly as a result of multiple factors (Beukema & Cadée 1996, Beukema & Dekker 2005, Dekker & Beukema submitted). The bivalve prey spectrum of Herring Gulls has altered more or less accordingly (Spaans 1971, Camphuysen *et al.* 2008, 2010, this study).

The pattern of food availability is an important environmental factor, influencing annual productivity, survival and thereby population dynamics (Kim & Monaghan 2006). Next to prey availability has prey quality received increasing attention in recent years (Bowen *et al.* 1995, Nehls 2001, Silva *et al.* 2001, Wanless *et al.* 2005, Whitfield 2008). To complicate things further: experience pays. Life-history theory predicts that, in long-lived organisms, effort towards reproduction will increase with age, and research from oviparous vertebrates largely supports this prediction (Paitz *et al.* 2006). None of these factors are mutually exclusive. Herring gulls breeding in The Netherlands, increased from a few thousand breeding pairs in the beginning of the 20th century to a maximum of 89,000 pairs during the mid 1980s (Spaans 1998), but numbers have declined since. Decreased food availability may have caused this decline, but supporting data are scarce. Spaans (1971) demonstrated the importance of domestic refuse as an additional source of food for Herring Gulls breeding at Terschelling (W Wadden Sea), at a time when the population increased rapidly (late 1960s). Covering up refuse tips has probably been an important factor influencing that recent population decline. Bukacinska *et al.* (1996) studying the same colony in that period of decline (early 1990s) highlighted the importance of fish in the chick phase: successful pairs ate more fish and chicks of conspecifics than unsuccessful ones.

The demographic implications of dietary specialisations are notoriously difficult to study in the field, because biases become only apparent over time, and may be expected to change in different phases of breeding. A further challenge will be to translate prey choice in energetic values and protein contents (Hughes 1993, Bowen *et al.* 1995) and to assess prey availability and prey-species specific intake rates. This study showed that genuine specialisations were relatively rare, but with varying fitness consequences in either direction. In the colony studied here, aspects such as age, experience and 'tradition' (or dietary consistencies and inconsistencies for individual pairs) may be evaluated in years to come, when more recruits have returned and when many more pairs can be monitored for a number of years. A striking result was the poor breeding performance in pairs that focussed on intertidal crustaceans (mostly common shore crabs) during chick care. Low energy and/or parasite infestations may play some role here, and field or laboratory experiments will be required to solve this issue. It is remarkable that in the population as a whole, crustacean prey increased in frequency of occurrence when comparing diets in the egg-phase with those in the chick-phase.

An important difference between successful breeders and failing pairs in the current study was the frequency of fish prey during chick care (cf. Bukacinska *et al.* 1996). About half the pairs monitored in the chick phase (clusters 1, and 5-7, Fig. 9.3) managed to boost chick growth rates above average (≈30 g d^{-1}) on a diet in which the frequency of occurrence of fish prey was well over 30% (Table 9.4). Annett & Pierotti (1999) reported that Western Gulls *Larus occidentalis* adopting a diet of fish had significantly higher long-term reproductive success than individuals specialising on domestic refuse. The fact that so few Herring Gulls returned with fish prey during prospecting and incubation, suggests that these prey are either hard to come by, or not essential for self-maintenance. The 2011 season was the worst on record for Herring Gulls in this study (0.48 fledglings $pair^{-1}$; Table 9.1), indicating a scarcity of suitable prey such as marine fish during chick care. It is therefore of interest to note that the outlier specialist pair (cluster 1, Fig. 9.3) deviated in 2011 from a dietary bias measured for the same pair in a previous season (cluster 5, with marine fish as important component in 2009). This pair focussed in 2011 almost entirely, and highly successfully (2 fledglings), on a generally rather rarely exploited resource: freshwater fish. A rare illustration indicating that individual pairs can indeed be flexible and may specialise to turn a potential disaster into success.

Colour-ringed Herring Gull foraging on moribund Ensis directus, 9 October 2011,Wijk aan Zee (Maarten van Kleinwee)

Appendix to Chapter 9.

Categorisation and grouping of prey items encountered in Herring Gull food samples, Texel, 2006-2011.

Group	**Origin**	**Observed species in Herring Gull prey samples**
Insects	Terrestrial	*Adelocera murina*, *Aelia acuminata*, Agonum, Aphodius, Carabidae, *Cidnopus aeruginosus*, Coccinellidae, Coleoptera, Curculionidae, Dermaptera, Diptera, Elateridae, Formicidae, Harpalus, Hymenoptera, Lema, Lepidoptera, *Melanotus rufipes*, *Micraspis 16-punctata*, unident. moth, *Musca domestica*, *Phyllopertha horticola*, *Prosternon tessellatum*, Pterostichus, Scarabaeidae, *Sigara* sp, Tipulidae, unident. insects, moths
Spiders	Terrestrial	unident. spiders [*rare; for convenience included under "insects" in analysis*]
Nematods	Undetermined	unident. Nematoda
Polychaetes	Marine	*Aphrodita aculeata*, *Lanice conchilega*, *Nereis* sp., *Nereis diversicolor*, *Nereis longissima*, *Nereis succinea*, *Nereis virens*
Oligochaetes	Terrestrial	*Lumbricus terrestris or any other abundant earthworm species*
Sponges	Marine	unident. Porifera
Echinoderms	Marine	*Asterias rubens, Echinocyamus pussillus, Ophiura ophiura*
Snails	Terrestrial	*Cepaea hortensis*, *Cepaea nemoralis*, *Cornu aspersum*, *Lauria cylindracea*, unident. snails
Gastropods	Marine	*Hinia reticulata*, *Hydrobia ulvae*, *Littorina littorea*, *Littorina saxatilis*, *Polinices catenus*, *Polinices polianus*
Bivalves	Marine	*Abra tenuis, Cerastoderma edule, Crassostrea gigas, Donax vittatus, Ensis americanus, Lutraria lutraria, Macoma balthica, Mya arenaria, Mytilus edulis, Petricola pholadiformis, Scrobicularia plana, Spisula solida, Spisula subtruncata*, unident. bivalve, *Venerupis senegalensis*
Cephalopods	Marine	*Allotheutis subulata, Loligo vulgaris, Sepia officinalis*
Barnacles	Marine	*Balanus* spp., *Balanus crenatus*
Crustaceans	Marine	*Cancer pagurus, Carcinus maenas, Carcinus/Liocarcinus, Crangon crangon, Hemigrapsus pensillatus, Hemigrapsus sanguineus, Idotea pelagica, Jassa marmorata, Liocarcinus depurator, Liocarcinus holsatus, Nephrops norvegicus, Pagurus bernhardus, Palaemon serrator*, parasitic Copepod, *Portumnus latipes*, unident. Decapoda
Crustaceans	Terrestrial	unident. woodlice [*rare; for convenience included under "insects" in analysis*]
Marine fish	Marine	All marine roundfish species: *Agonus cataphractus, Alosa fallax, Ammodytes, Ammodytes marinus, Ammodytes tobianus, Belone belone, Callionymus lyra, Clupea harengus, Cyclopterus lumpus, Dicentrarchus labrax, Echiichthys vipera, Eutrigla gurnardus*, fish eggs, *Gadus morhua, Hyperoplus lanceolatus, Merlangius merlangus, Myoxocephalus scorpius, Osmerus eperlanus Pholis gunnellus, Pomatoschistus minutus, Scomber scombrus, Sprattus sprattus, Syngnathus acus, Syngnathus rostellatus, Trachurus trachurus, Trigla lucerna, Trigla/Eutrigla, Trisopterus luscus, Trisopterus minutus*, unident. bony roundfish, unident. gadoid, *Zoarces viviparous* All marine flatfish species: *Arnoglossus laterna, Buglossidium luteum, Limanda limanda, Platichthys flesus, Pleuronectes / Limanda, Pleuronectes platessa, Scophthalmus maximus, Solea solea*, unident. flatfish
Freshwater fish	Terrestrial	*Abramis brama, Perca fluviatilis, Stizostedion lucioperca, Lepomis gibbosus, Rutilus* spp., *Rutilus erythrophthalmus, Rutilus rutilus*, unident. freshwater fish
Non passerine birds	Terrestrial	*Anser anser*, *Calidris maritima*, *Fulica atra* chick, *Larus argentatus* chick, *Larus fuscus* chick, unident.large gull egg, unident. large gull chick, *Morus bassanus* stomach [beached bird?], unident. non-passerine birds
Passerine birds	Terrestrial	*Anthus pratensis, Columba palumbus, Curvus monedula, Passer domesticus, Sturnus vulgaris, Turdus merula*, unident. passerines
Mammals	Terrestrial	*Erinaceus europaeus, Lepus europaeus*, mice droppings, *Microtus oeconomus, Microtus/Arvelicola, Mus musculus, Oryctolagus cuniculus, Rattus norvegicus, Talpa europaea*, unident. mammal
Plants	Terrestrial	*Claytonia perfoliata* seed, *Convolvus* sp seed, *Elaeagnus angustifolia*, *Epilobium hirsutum* seed, *Galium aparine* seed, *Stellaria media* seed, *Taraxacum* sp. seed, *Ammophila arenaria*, Carex seed, *Cornus mas* seed, *Empetrum nigrum* berries, Juncus seed, Poaceae, Poaceae seed, sheep pellets, Triticum seed, *Ulmus* sp. leaves, *Ulmus* sp. seed, unident grass seed, unident. Plantae, unident plant seed, *Zea mays*
Seaweeds	Marine	*Ceramium rubrum*, Enteromorpha, *Ulva lactuca*
Domestic refuse	Anthropogenic	*Actinidia deliciosa* seed, *Allium cepa*, aluminium foil, apple, apple seed, balloon, beef, bread, bread seeds, broken glass, cat food, cheese, chicken, chicken egg, chicken soup, chillipepper seeds, china, french fries, cigarette filter, crisps, deep fried fish, fishing hook, frikandel, garlic, gherkin, *Hippoglossus hippoglossus*, human vomit, mace (nutmeg), meat, meats and sausages, medal with ribbon, melon seed, metal waste, mobile phone, mutton, orange peel, *Panicum miliaceum* seed, paper, paraffin, party nuts, pencil, pistachio nut, plastic, plastic chips fork, plastic coffee stirrer, plastic doll, plastic fishing bait, plastic foil, plastic fragments, plastic line, thread, plastic objects, plastic packaging, plastic pellets, plastic toys, polystyrene, pork, potato, rice, rubber, salmon, sausage skin, sport-tape, tallow, textiles, tigerprawn, tomato, unidentif fruits, unident. refuse, vegetables, *Vitis vinifera* fruit, *Vitis vinifera* seed, walnut, wood, *Zea mays* seed
Non-food		Sheep wool, fossil shell grit, rock grit
Miscellaneous	Terrestrial	Miscellaneous unident. matter, unident. organic matter
Common fisheries discards		*Agonus cataphractus, Allotheutis subulata, Aphrodita aculeata, Arnoglossus laterna, Asterias rubens, Buglossidium luteum, Callionymus lyra, Cancer pagurus, Crangon crangon, Cyclopterus lumpus, Echiichthys vipera, Ensis americanus, Eutrigla gurnardus, Gadus morhua, Limanda limanda, Loligo vulgaris, Merlangius merlangus, Myoxocephalus scorpius, Nephrops norvegicus, Ophiura ophiura, Pagurus bernhardus, Platichthys flesus, Pleuronectes platessa, Polinices polianus, Scomber scombrus, Scophthalmus maximus, Sepia officinalis, Solea solea, Spisula subtruncata, Trisopterus luscus, Trisopterus minutus*, unident. flatfish, unident. gadoid, *Zoarces viviparus*
Cannibalistic prey		chick *Larus argentatus*, chick *Larus fuscus*, unident. large gull egg, unident. large gull chick
Freshwater fish prey		*Abramis brama, Perca fluviatilis, Stizostedion lucioperca, Lepomis gibbosus, Rutilus* spp., *Rutilus erythrophthalmus, Rutilus rutilus*, unident. freshwater fish
Common intertidal prey		*Abra tenuis, Carcinus maenas, Carcinus/Liocarcinus, Cerastoderma edule, Crassostrea gigas, Ensis americanus, Hemigrapsus pensillatus, Hemigrapsus sanguineus, Jassa marmorata, Lanice conchilega, Macoma balthica, Mya arenaria, Mytilus edulis, Nereis* sp., *Nereis diversicolor, Nereis succinea, Nereis virens, Scrobicularia plana*
Agricultural land prey		*Lumbricus terrestris*, sheep pellets, *Zea mays*, sheeps wool (most insects?), Triticum seed, Poaceae seed
Sample pollution (local flora)		*Claytonia perfoliata* seed, *Convolvus* sp seed, *Elaeagnus angustifolia*, *Epilobium hirsutum* seed, *Galium aparine* seed, *Stellaria media* seed, *Taraxacum* sp seed, *Urtica* sp
Presumed secondary prey		*Hinia reticulata*, *Hydrobia ulvae*, *Polinices polianus*

10. Sex-specific foraging strategies: physiological constraints or a sexually distinct reproductive role?

Reviewed **Ecosphere** (Ecological Society of America), *in revision*

Kees (C.J.) Camphuysen[1], Judy Shamoun-Baranes[2], Emiel E. van Loon[2] and Willem Bouten[2]

[1]*Corresponding author* Royal Netherlands Institute for Sea Research, NIOZ, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands, E-mail: Kees.camphuysen.nioz.nl; [2]Computational Geo-Ecology, IBED, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands, E-mail: shamoun@uva.nl, vanloon@uva.nl, w.bouten@uva.nl

Abstract Intra-specific differences in foraging behaviour can have fitness consequences, especially during the breeding season. We combined GPS tracking data from 34 individual Lesser Black-backed gulls (*Larus fuscus*) encompassing 2199 foraging trips with dietary information and reproductive status to test the influence of breeding status and sex as well as structural size on foraging behaviour. We found sexually distinct foraging strategies in a generalist seabird, that were maintained throughout incubation and chick-care. The marginally larger males travelled farther from the colony than females, spent more time in the North Sea, and remained longer at the nest during nest bouts. Males fed mostly on fisheries discards at offshore trawlers with few alternative resources nearby. Females foraged predominantly on land or in the Wadden Sea, where they had multiple foraging options including nearshore shrimpers. Individuals differed in foraging behaviour along a continuum of predominantly terrestrial to predominantly marine foragers. Foraging range, trip duration and the proportion of time at sea increased with wing length. Our findings did not support the usual inference that sexual segregation is mediated primarily by differences in competitive strength (i.e. differences in size) as both sexes foraged in competitive environments around fishing vessels. Females, accessed a wider variety of resources and a broad prey spectrum, by exploring a whole suite of foraging opportunities and habitats nearer the colony. Different behavioural strategies (a combination of individual specialisation and sexual segregation) during breeding may increase an individual's lifetime reproductive success through risk partitioning, by reducing resource competition between sexes (and within pairs), or by reducing the risk of unbalanced food provisioning, none of which is mutually exclusive.

Key words: breeding, foraging, GPS, individual specialisation, *Larus fuscus*, lesser black-backed gull, sexual dimorphism

Introduction

An important aspect of foraging ecology is the extent to which individuals within a population exploit food resources in a different manner (Bolnick et al. 2003). Levels of individual specialisation vary among species and populations, reflecting a range of behavioural, physiological, and ecological mechanisms that generate intra-population variation (Bolnick et al. 2003, Bearhop et al. 2006). Specialisation can be attributed to inter- or intraspecific competition and specialists may exclude generalists or opportunists if they use resources more efficiently (Enoksson 1988, Futuyma & Moreno 1988). Differences in foraging performance between species or between individuals within species are often ascribed to the influence of body size on foraging efficiency and competitive ability on feeding grounds (Greig et al. 1985, Pons 1994, Phillips et al. 2004).

Provision of food is a major component of parental investment. Many species have bi-parental care, but in sexually dimorphic taxa, male and females need not contribute equally to the provisioning of the young (Bennett & Owens 2002). Differences between the sexes may be related to sexual differences in ability to obtain food (Rose 1994, Remis 1999) or sexual segregation in habitat use (Conradt 2005), which are not mutually exclusive. Differences could result from social dominance and competitive exclusion (i.e. of smaller females by larger males), or niche specialisation arising from differences in morphology or reproductive role (Greig et al. 1985, Phillips et al. 2004, Bearhop et al. 2006, Székely et al. 2007).

Many studies of sexual segregation have been of species in which males and females can be distinguished visually (Scheel & Packer 1991, Gonzalez-Solis et al. 2000). With satellite transmitters and data loggers it has recently become possible to examine individual foraging behaviour and habitat specialisation of animals that are monomorphic, or in which sexes cannot be distinguished reliably in the field conditions (Lewis et al. 2002, Thaxter et al. 2009, Elliott et al. 2010). In the Lesser Black-backed Gull *Larus fuscus* adult males are on average only slightly larger than females (Coulson et al. 1983). Sexing these gulls visually in the field is at best unreliable. Lesser Black-backed Gulls are generalists with a wide variety of prey items, including vertebrates and invertebrates of suitable size, plant material, and rubbish (Cramp & Simmons 1983). Foraging occurs at sea as well as on land.

In this study we investigate the relative importance of different foraging areas and the influence of breeding status, structural size and sex on foraging behaviour, for Lesser Black-backed Gulls in the Wadden Sea. We used GPS tracking information to quantify individual utilisation of foraging habitats and combined this with the reproductive status of these birds throughout the breeding season. We studied the diet from regurgitated matter in the colony, and inferred individual dietary specialisations and foraging techniques from abundant and characteristic prey types encountered in each habitat. We explored individual variation in habitat usage and foraging behaviour, assuming that within the population of a generalist species, individuals may be specialised and that only between-individual variation could comprise the population's niche width (Bolnick et al. 2003). We expected that foraging behaviour or habitat selection could change during the breeding season or when compared to non-breeders, due to the varying constraints on time and energy between different breeding phases. As sexual dimorphism is not very strong in this species, we hypothesised that the overall foraging distribution between sexes would be similar.

Methods

The studies were conducted from a breeding colony on the island Texel (The Netherlands, 53°00'N, 04°43'E) at the crossroads of the western Wadden Sea and the southern North Sea. . Within the study area, approximately 11,500 pairs of Lesser Black-backed Gulls are breeding. The main foraging areas for this population include open sea, intertidal estuarine areas, freshwater ponds, tourist resorts, grasslands, arable land, and urban areas. Data were collected from April to August in four consecutive breeding seasons (2008-2011).

Breeding data - To monitor breeding status and breeding success, nests were marked during egg laying. Marked nests were visited every third day, throughout the breeding season (laying to fledging), to monitor reproductive status (condition of eggs and/or chicks) and fledging rates (Camphuysen & Gronert 2010a). Breeding phases used in this study were (1) incubation and hatching, (2) chick care (first 40 days after hatching) and fledging (>40 d), and (3) failed breeders (birds that had lost their clutch or brood from the day their breeding effort failed).

GPS tracking - A total of 34 breeding adult gulls (Appendix A) were tracked using UvA-BiTS GPS loggers (see Shamoun-Baranes et al. 2011 for details). Adult breeding individuals were trapped at marked nests half-way through incubation, using a walk in trap. The sexes were separated on the basis biometrics (head plus bill length) with only 5% expected misidentification (Coulson et al. 1983). Other measurements included bill depth (at base, 0.1mm), tarsus (mm), wing length (mm), and body mass (g). The birds were color-ringed and an 18g solar powered GPS tracker was mounted with a harness on the back of the bird. Device and harness weighed less than 3% of the body mass of the birds. Birds were released immediately after the tracker was fitted on the bird.
The tracking system enables changing the measurement frequency while the tag is on the bird. In general, a GPS fix was taken every 5–20 minutes during the entire breeding season. The tag is powered by four solar cells and a 65 mAh lithium polymer battery and gaps in the data occurred when the battery was not sufficiently recharged or the GPS timed out before a fix could be made.

Data processing - The time-series of consecutive GPS-points were grouped into three types of activity bouts per individual bird: (1) 'nest bouts', (2) 'short trips' and (3) 'long trips'. A nest bout was a continuous period at the nest or on territory (presence within a 150 m radius around the centre of the colony). Bathing places and roosts occurred within *c.* 3 km around the study colony (identified from visual observations of colour-ringed birds). Within this range there are very few suitable feeding areas except feeding opportunities within the colony itself (e.g. cannibalism), or berries and insects in the surrounding dunes. We defined a short trip as a period where an individual left the colony (moved out of the 150 m radius) but stayed within a 3 km radius from the nest before returning to the colony. Finally long trips were defined as continuous periods where an individual moved out of the 3 km radius before returning to the colony. As there are very few feeding opportunities within 3 km of the nest, foraging is associated almost exclusively with long trips. Any activity bouts with an interval of 60 minutes or more between two consecutive GPS-locations were excluded from further analysis. In addition, if the breeding status was uncertain for specific bouts these were removed from further analysis. In total, 6859 complete activity bouts were used in further analysis (3493 nest bouts, 1167 short trips, and 2199 long trips).

Potential foraging areas around the colony are (1) North Sea, including the coastal zone and beaches, (2) Wadden Sea, (3) Continental mainland areas and, (4) the island Texel. Each individual GPS position was assigned to one these four areas. The first two areas would provide marine or intertidal prey types, the other two would provide terrestrial prey. The time interval between consecutive GPS positions was used to calculate the proportion of time spent within certain habitats.

Data analysis – For each activity bout, we calculated the duration (h), and for each long trip we also calculated maximum (great circle) distance to the nest (km) as well as the proportion of time spent in one of the four main habitats described above. Using a linear generalised mixed effects model (Pinheiro & Bates, 2000) we tested the effect of sex and breeding status on the duration of nest bouts, short trips, long trips and on the foraging range of long trips. The response variables were available per trip and nested within each individual bird. Therefore, individual bird was treated as a random component, while the other predictor variables (sex and breeding status) were treated as fixed factors in the model. The response variables in our analyses have a skewed distribution, with means approximately equal to the standard deviation. These distributions were modelled using a Poisson model with over dispersion (in the normal Poisson model, the mean is equal to the variance) and were fit using the maximum likelihood criterion. After fitting the models, model residuals were evaluated graphically. Only models with acceptable residuals and significant parameters (at the 0.05 level) were retained. The results of the significant models are reported by listing the optimal parameter values for each variable on their normal scale (i.e. not log-transformed) with accompanying 0.95 confidence intervals. All calculations were conducted in R (Pinheiro et al. 2012, R Development Core Team, 2011).

Differences in time allocation (h) per habitat between sexes were evaluated with the adjusted G-statistic (G_{adj}; Sokal & Rohlf 1981). Furthermore, to explore individual variability in foraging behaviour (long trips) and the potential relationship with body size we compared mean foraging range (km) and trip duration (h) during long trips to the wing length (mm) of each individual using a linear model. We also compared the relationship between mean proportion (%) of time spent at sea or on land (%) to wing length (mm) using a generalised linear model with a logit transformation and a quasi-binomial link function. Comparisons with wing length were conducted for active breeding and failed breeders separately.

Linking diet and foraging areas - We inferred foraging strategies by combining information on general diet composition of gulls at the colony level with the habitats where these prey could be found. Tracking data were used to quantify where individuals spent their time. Diets were studied from spontaneously regurgitated matter (pellets, regurgitated indigestible food remains), from food boluses produced during handling of adults and chicks, and from chick-feed sub-sampled within the territories. During colony visits, marked territories were inspected for the presence of discarded prey items and these were individually bagged, numbered, and kept frozen for later analysis. A total of 5157 prey samples were collected, containing 240 different prey types. Prey samples were analyzed visually with a light microscope (Olympus SZ51), ensuring that even very small remains (such as earthworm setae, minute otoliths, and largely digested bread) were detected. With pellets, boluses and regurgitated matter, some easily and fully digested prey is overlooked (e.g. white bread, ice cream, soft tissue invertebrates), but none of these soft prey types was considered very important. A full analysis of the diet was beyond the scope of this contribution, and the occurrence of prey types or prey species is simply expressed as frequency of occurrence (%) calculated over all samples.

Table 10.1. Duration of nest bouts and short trips (h) in male and female Lesser Black-backed Gulls during different breeding stages. Values are mean ± SD, sample size.

	Incubation / hatching	**Chick care / fledging**	**Failed breeders**	**All phases**
Nest attendance				
Males	7.5 ± 6.3 n= 436	3.6 ± 3.3 n= 846	4.9 ± 4.4 n= 254	4.9 ± 4.8 n = 1536
Females	5.4 ± 4.7 n= 514	3.0 ± 2.8 n= 1008	3.4 ± 3.3 n= 435	3.7 ± 3.6 n = 1957
Short trips				
Males	0.8 ± 0.9 n= 145	0.9 ± 1.1 n= 226	0.8 ± 1.1 n= 98	0.8 ± 1.0 n = 469
Females	0.9 ± 0.7 n= 158	1.0 ± 1.0 n= 293	1.1 ± 1.4 n= 247	1.0 ± 1.1 n = 698

Table 10.2. Parameter values and 0.95 confidence intervals (i.e. the model-output translated to values (h) for each category) resulting from generalised linear mixed models on the combined effect of sex and breeding status on foraging trip characteristics and the duration of nest bouts (only significant models are listed in this table). (a) Duration of nest bouts, (b) duration of foraging trips (this model only includes breeding status, sex was not significant) and (c) foraging trip range.

	Parameter value (0.95 CI)
a) Duration of nest attendance (h)	
Female – Incubation	5.7 (5.0 – 6.4)
Female – Chick care	2.9 (2.7 – 3.1)
Female – Failed	3.3 (3.0 – 3.6)
Male – Incubation	7.5 (6.3 – 9.0)
Male – Chick care	3.9 (3.3 – 4.7)
Male – Failed	4.4 (3.6 – 5.2)
b) Duration of foraging trips (h)	
Incubation	7.0 (5.0 – 8.2)
Chick care	6.3 (5.6 – 7.2)
Failed	12.9 (10.7 – 15.6)
c) Range of foraging trips (km)	
Female – Incubation	18.3 (15.7 – 21.4)
Female – Chick care	20.7 (18.7 – 22.8)
Female – Failed	26.0 (22.5 – 30.1)
Male – Incubation	28.0 (22.6 – 34.6)
Male – Chick care	31.5 (25.5 - 39.0)
Male – Failed	39.7 (32.1 - 49.1)

Results

Nest bouts and short trips - The mean (± SD) duration of nest bouts was 4.9 ± 4.8 h (*n* = 1536) for males and 3.7 ± 3.6 h (*n* = 1957) for females (Table 10.1). For both sexes, mean nest bouts were longer during incubation and hatching than during chick care and fledging. The linear mixed model revealed that the combined effect of sex and breeding status on nest bout duration was relatively large and statistically significant (Table 10.2). For example during incubation, females spent on average 5.7 h per nest bout at the territory, whereas males spent 1.8 h (or

32%) per nest bout more in the colony. During chick care the nest bouts were significantly shorter for both sexes, but males still spent 1.0 h (or 35%) more per nest bout than females near the nest. Failed breeders continued to spend time at the nest, but failed breeders spent a little more time per nest bout during chick care but less time during incubation than active breeders during colony visits. The mean duration of short trips (assumed to be trips to roosts) was 0.8 ± 1.0 h for males (*n* = 469) and 1.0 ± 1.1 h for females (*n* = 698; Table 10.1). There was no statistically significant effect of sex or breeding status on the duration of short trips.

Table 10.3. Foraging trip characteristics of male and female Lesser Black-backed Gulls during different breeding stages. Upper panel mean and maximum foraging range, mean trip duration ± SD per sex and breeding phase. The mean foraging range is the mean of the maximum distance away from the nest calculated for each of the long trips. Middle panel shows northern-/southernmost and eastern-/westernmost geographical co-ordinates visited on foraging trips.

	Incubation / hatching		**Chick care / fledging**		**Failed breeders**	
	Males	**Females**	**Males**	**Females**	**Males**	**females**
Number of birds	18	16	11	15	6	7
Number of trips	256	325	610	688	144	176
Trip duration (h)	8.2±8.6	6.0±5.4	6.9±7.1	5.6±9.4	13.6±16.1	13.3±22.7
Mean range (km)	30.6±34.7	17.2±12.8	32.8±19.5	21.0±23.1	32.4±26.0	27.0±51.9
Max range (km)	532	69	115	357	195	409
Max latitude	53°20'N	53°23'N	53°56'N	53°34'N	53°20'N	53°23'N
Min latitude	49°32'N	52°28'N	52°05'N	49°59'N	51°47'N	51°30'N
Max longitude	04°56'E	05°18'E	05°37'E	05°24'E	07°25'E	05°08'E
Min longitude	01°09'W	03°54'E	03°09'E	02°34'E	02°50'E	01°52W
% time North Sea	78.4%	28.6%	65.4%	36.9%	66.4%	22.6%
% time Mainland	13.6%	21.2%	24.9%	14.2%	21.0%	56.4%
% time Texel	4.5%	29.3%	4.6%	23.7%	9.4%	11.5%
% time Wadden Sea	3.6%	21.0%	5.1%	25.2%	3.3%	9.5%

Foraging trip characteristics - The main characteristics of long trips (assumed to be foraging trips) are summarised per sex and breeding phase in Table 10.3. An overwhelming majority of the long trips (99% ; active and failed breeders included) were within 80 km from the nest with a trip duration of less than 24 hours (96%). Foraging areas were mainly to the southwest (North Sea), south (North Sea and terrestrial areas), southeast (Wadden Sea and terrestrial areas) and east of the colony on the island Texel. In active breeding birds, nearly two–thirds of all trips had a duration of less than 6 hours, while nearly all trips had a duration of less than 12 hours. The linear mixed model revealed that sex did not have an effect on the duration of long trips, whereas breeding status did (Table 10.2). The estimated trip duration during incubation was 7.0 h whereas failed breeders spent almost twice as much time per trip. The generalised linear mixed model for foraging range revealed that the combined effect of sex and breeding status was relatively large and significant at the 0.05 level (see the model coefficients with 0.95 confidence intervals in Table 10.2). In all phases, males travelled farther than females and both sexes travelled farther during chick care than incubation. The foraging range was longest for failed breeders. The proportion of time spent in different habitats varied between individuals representing a continuum of habitat use from almost exclusively terrestrial to almost exclusively marine (Fig. 10.1). The proportion of time spent in the main habitats was significantly different between the sexes, during breeding (incubation: G_{adj} = 1211.5, df=3, *P*< 0.001; chick rearing: G_{adj} = 1611.8, df=3, *P*< 0.001) as well as when comparing failed breeders (G_{adj} = 910.8, df=3, *P*< 0.001). Males spent between two-thirds and three quarters of their time at sea (North Sea), whereas females divided attention between each of the main habitats (Table 10.3). Actively breeding females spent, in total, half their foraging time within the Wadden Sea area: partly in the Wadden Sea itself (21% during incubation, 25% during chick care), partly on Wadden Sea island Texel (resp. 29% and 24%). Seven females that had lost either clutch or chicks substantially increased the time spent on terrestrial habitats on the mainland during long trips (56% relative to 16% when still actively breeding) and reduced their time spent within the Wadden Sea, on Texel and at the North Sea (G_{adj} = 448.1, df=3, $P < 0.001$). Six males that had failed spent less time at the North Sea and somewhat increased their time in terrestrial areas (Mainland and Texel; G_{adj}= 59.9, df= 3, $P <$ 0.001) in comparison with the time spent in each habitat while still actively breeding. Males spent very little time in the Wadden Sea during active breeding (4%) and after failing (3%).

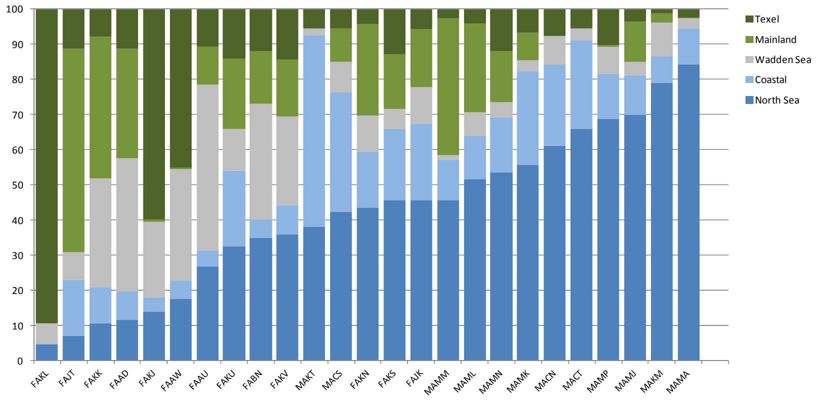


Fig. 10.1. Individual time spent (%) on long trips during active breeding (egg or chick care) in each of four main habitats (North Sea, Wadden Sea, terrestrial areas on the Mainland, and on the island Texel), sorted by an increasing amount of time spent at sea. Colour-ring codes (x-axis) of females start with F, males start with M (n = 34 individuals, 1879 foraging trips, 2008-2011).

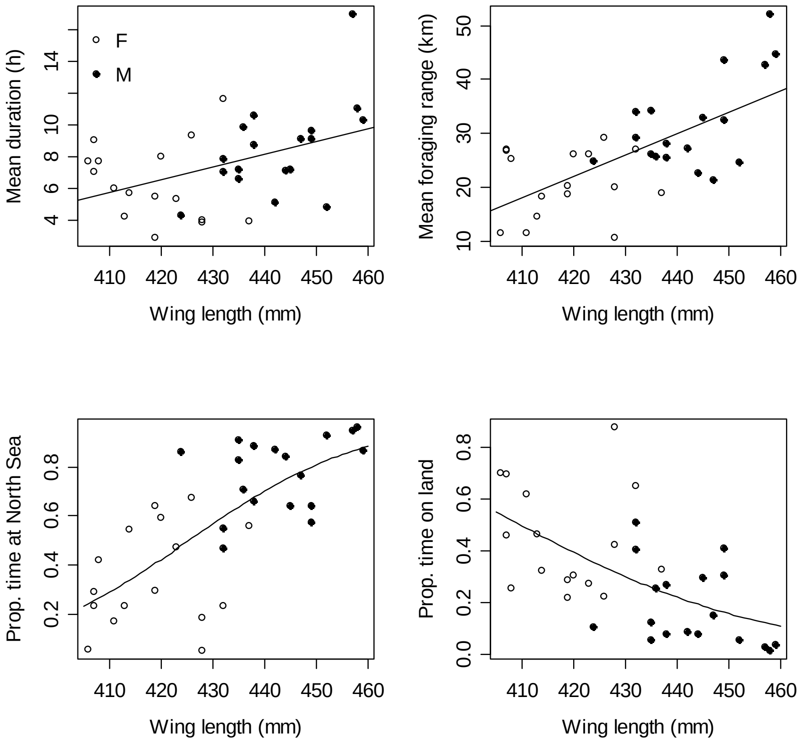


Fig. 10.2. Long trip characteristics versus wing length (as proxy for structural size) and sex of individual Lesser Black-backed Gulls carrying GPS loggers as active breeding birds (2008-2011). (A) mean trip duration (h), (B) mean range (km), (C) proportion of time on the North Sea, (D) proportion of time on land (Texel and continental mainland combined). Males indicated with filled symbols, females with open symbols (n = 34 individuals, 1879 foraging trips). Solid lines are predictions from linear (A,B) and generalised linear models (C,D), P < 0.01 in all subplots.

Morphology and foraging characteristics - In active breeding birds, significant positive correlations were found between wing length (as a proxy of structural size) and mean duration of long trips (LM, $F_{1,32}$ = 7.75, p < 0.01; t_{32}= 2.79, P < 0.01, Fig. 10.2A) and mean foraging range (LM, $F_{1,32}$ = 25.42, p < 0.001; t_{32}= 5.04, P < 0.001, Fig. 10.2B). No correlations were found between wing length and mean duration of long trips or mean foraging range in failed birds. In active breeding birds, a significant positive correlation was found between wing length and the proportion of time spent at sea during long trips (GLM, $F_{1,32}$ = 33.22, p < 0.001; t_{32}= 5.27, P < 0.001, Fig. 10.2C) and there was a significant negative correlation between wing length and the proportion of time spent in terrestrial habitats (i.e. on Texel and on the continental mainland)

(GLM, $F_{1,32} = 16.05$, $p < 0.001$; $t_{32} = -3.82$, $P < 0.001$, Fig. 10.2D). For failed breeders, no significant correlations were found between wing length and proportion of time at sea or on land.

Linking diet and foraging areas - Food samples (*n* = 5162) usually revealed a mix of species or prey types, often of different origin. Overall, 88% of all prey samples contained at least some prey of marine origin and the diet of Lesser Black-backed Gulls breeding at Texel was overwhelmingly dominated by demersal North Sea fish (Appendix B). Most fish must have been obtained while competing for prey behind beam-trawlers. Most of the marine crustaceans found were various species of swimming crabs, that commonly swim at the surface in the North Sea and that are captured by plunge-diving. Prey from intertidal resources was rather rare (represented in 2% of the samples). Intertidal polychaetes (43%), crustaceans (37%), and bivalve flesh (18%) were the most frequently encountered intertidal prey in these samples. On land, the diet and expected foraging conditions are considerably more complex. Prey types from terrestrial or anthropogenic sources were found in 1842 prey samples (36%). The most frequently encountered terrestrial prey were insects (50%), plant material, seeds or fruits (20%), seabirds (mostly other gull chicks; 20%), domestic refuse (16%), earthworms (11%) and small mammals (3%). On land, Lesser Black-backed Gulls had a varied prey choice with differences in resource accessibility and availability.

The frequency of occurrence of marine fish in the diet was higher than expected from the time spent by the tagged birds in the North Sea. By contrast, the amount of intertidal prey was much smaller than anticipated from the time spent (notably by females) within the Wadden Sea. From exploratory analysis it appeared that in the Wadden Sea, Lesser Black-backed Gulls spent almost no time over intertidal mudflats (not even at high tide), but focused almost exclusively at deeper gullies where trawlers operated. Shrimp trawling is the predominant trawling fishery in the Wadden Sea, producing superficially similar discards as North Sea trawlers.

Discussion

Our tracking studies revealed that the foraging activities of Lesser Black-backed Gulls from Texel were concentrated within a fairly limited range (< 80km), but with considerable individual variation in habitat preferences (Fig. 10.1). A clear sexual segregation in foraging habitats was found, with males spending significantly more time in the North Sea than females, and with females spending more time on land and within the Wadden Sea. Foraging males travelled on average further from the colony than females, although they did not spend more time away per trip. Males spent more time at the nest per nest bout than females. These differences persisted throughout the breeding stages. If breeding failed, both sexes spent more time away from the colony and travelled farther away. The habitat segregation persisted in failed breeders, with males spending more time at sea than females. Females that had failed spent relatively more time on the mainland than during active breeding.

Levels of parental investment are the product of a simultaneous resolution of conflicts of interest between parents and offspring (survival, fitness; Royle et al. 2004). We therefore had expected that, due to a trade-off between the amount of time allocated to different activities such as self-provisioning, chick provisioning and reduction of predation risk, certain characteristics of foraging behaviour would change in the course of a season. Nest bout duration declined significantly from incubation to fledging in both males and females, while roosting and bathing time (short trip duration) remained constant, thus more time could be spent on foraging during chick care. However, while trip duration also declined during chick care, mean foraging range increased in females and males during the breeding season. This suggests that individuals made more frequent yet shorter trips, while travelling further and spending relatively more time searching for food per trip. These changes in behaviour during the breeding season indicate an increase in foraging effort in response to increasing energetic demands of the developing chicks (Drent & Daan 1980). Similar changes in behavior between different stages of the breeding season have been noted in other seabirds (Clarke et al. 1998, Phillips et al. 2004, Paiva et al. 2008).

Contrary to our initial expectations, several aspects of foraging behaviour differed between the sexes. Foraging trip range differed significantly between the sexes during active breeding, but not in failed breeders. Males spent relatively more time in the territory than females per nest visit, which may indicate that males spent more time in nest (or chick) defence than females. Alternatively, the presence at the territory is important for males to safeguard a site for future breeding opportunities within the colony. A marked increase in nest-bout duration in males of which the breeding attempt had failed would be consistent with the latter hypothesis. Males generally travelled farther from the colony than females during active breeding and spent more time at sea, differences that were significant throughout the breeding season, but that were most prominent in the incubation phase (Table 10.3). The more distant foraging trips by males could result from a different foraging habitat preference between the sexes . A difference in habitat use could lead to habitat or niche segregation between the sexes at the macro-scale and our findings present evidence for both.

To gain a better understanding of individual specialisation and potential niche segregation between the sexes we combined information from tracking data on habitats visited with information from dietary analysis. Active breeders, overall, spent 67% of the time on long trips in marine habitats (North Sea and Wadden Sea combined) and 34% in terrestrial areas (Texel and Continental mainland). While not all that time is necessarily spent actively foraging and feeding (e.g. Shamoun-Baranes et al. 2011), three main foraging habitats call for attention: terrestrial, the North Sea and the Wadden Sea. Deduced from foraging locations, the tracking data indicate that individuals have dietary specialisations that are maintained over long periods. Nearly all prey samples collected in the colony contained at least some prey of marine origin, while just over one-third contained food that was most likely picked up on land. Prey items from the intertidal zone were rare. Most of the marine prey were demersal fish species, many of which are normally only available to Lesser Black-backed Gulls as discards behind beamtrawlers, the predominant offshore trawling fishery in this part of the North Sea (van Beek et al. 1990, Camphuysen 1994b) or behind shrimp trawlers, the predominant fishery in the Wadden Sea (Tiews 1978, Walter 1997). From the combined data (tracking and dietary data) we conclude that gulls (mostly females) foraging within the Wadden Sea did not or rarely exploited the area-characteristic intertidal resources available at low tide but must have mainly been scavenging behind shrimpers in that area. Foraging movements in the Wadden Sea area were highly concentrated in deeper gullies, the areas where shrimp trawler fleets operated, confirming that suggestion.

Differences between sexes might be considered ends along a continuum of individual variation in foraging behaviour (Bolnick et al. 2003). Even within only 34 tracked individuals, our tracking data revealed that habitat use varied between individuals along a range of almost completely terrestrial to completely marine habitat use (Fig. 10.1), suggesting a tendency of individuals to specialise on particular foraging areas, at least during the breeding season. While studies of resource use and population dynamics often treat conspecific individuals as ecologically equivalent, individual specialisation has been shown in a large range of species distributed across a broad range of taxonomic groups. A diverse array of physiological, behavioural, and ecological mechanisms could generate intra-population variation and between-individual variation in some cases may comprise the majority of the population's niche width (Bolnick et al. 2003). In our study, the structural size of the birds may at least in part influence individual specialisation. During active breeding, the proportion of time spent at sea, trip duration and trip range increased significantly with increasing wing length (Fig. 10.2).

Overall body size could be an aspect of importance driving sexual segregation in foraging habitats and foraging specialisation. Morphology, especially mass, wing load and aspect ratio, has important consequences for flight performance and flight energetics with cruising flight speeds and energy expenditure scaling with mass and wing load (Norberg 1990, Alerstam et al. 2007, Pennycuick 2008). Wind speeds at sea are often higher than over land, already close to the surface, due to the low surface roughness at sea (Stull 1988). Thus birds with higher cruising speeds may have an advantage at sea because they could compensate for a broader range of wind conditions (Chapman et al. 2011). Sexual differences in foraging behaviour of parents have been observed in a number of sexually size-dimorphic animals, with the usual inference that sex-specific differences are mediated primarily by differences in body size (Gonzalez-Solis et al. 2000, Phillips et al. 2004). Scavenging at fishing vessels does involve intense inter- and intraspecific competition (Furness *et al.* 1988, Camphuysen 1995a). Large, powerful seabirds, generally, forage more optimally under these conditions than smaller ones (Hudson 1989, Camphuysen et al. 1995), which could explain the more extensive use of marine resources (beam-trawlers) by (large) males than by (smaller) females. With larger seabirds foraging with greater success at trawlers, the observed differences in resource utilisation between male and female Lesser Black-backed Gulls may be driven by differences in physiological performance. However, while offshore trawlers (in summer) in the Southern North Sea are traditionally the domain of Lesser Black-backed Gulls with few competitors of equal strength (Camphuysen 1995a), flocks of scavenging seabirds associated with near-shore shrimp trawlers, certainly those within the Wadden Sea, are numerically dominated by larger, more powerful Herring Gulls (Walter & Becker 1994, Camphuysen et al. 1995). In other words, female Lesser Black-backed Gulls faced (and would normally be outnumbered by) even stronger competitors at shrimp trawlers than they would when they were joining male conspecifics at offshore beam-trawlers. A higher manoeuvrability of the small and relatively slender female Lesser Black-backed Gulls facing Herring Gulls around moving nearshore trawlers could be beneficial for them (cf. Strann & Vader 1992).

Foraging on land requires rather different skills. Several of the most frequently encountered prey items (insects, seabirds, plant material, oligochaetes, mammals; Appendix B) are not normally captured during mass feeding frenzies under stress from strong inter- or intra-specific competition. Most natural prey items on land are taken rather opportunistically, under the influence of particular weather conditions (insects, earthworms), seasonal trends (ripening fruits), or agricultural activities (small mammals, cereals, insects, worms). Anthropogenic resources included landfills (waste disposal), sewage plants (water treatment) and urban areas. Small feeding frenzies are formed in some of these conditions, where larger (more powerful) and smaller (more manoeuvrable) individuals have different prospects, but with abundant opportunities for profitable feeding for less competitive birds (Greig et al. 1985, Rock 2005).

In our study, differences in foraging behaviour, foraging areas and prey obtained in these areas suggest that, in general, males and females provision for their young differently and adults alter their foraging strategy when not breeding. Support for this hypothesis was provided by a marked shift in prey choice, deduced from foraging habitat utilisation, as well as foraging range in female Lesser Black-backed Gulls that had lost their chicks (Table 10.3). Sexual differences in parental care, foraging behaviour and food provisioning in some seabirds are well known but poorly understood (Weimerskirsh et al. 1997, Clarke et al. 1998, Thaxter et al. 2009). These differences cannot always be attributed to sexual dimorphism (Lewis et al. 2002). These and other findings (examples listed in Elliott et al. 2010) highlight the need to investigate sexual differences in the foraging behaviour of seabirds and other species more closely. Testing alternative hypotheses that do not rely only on differences in body size could provide better explanations of the observed differences between the sexes. Elliott et al. (2010) proposed that risk partitioning may contribute to the prevalence of sex-specific behaviours in monomorphic animals and that patterns are likely context specific rather than species specific. The possibility that the use of different behavioural strategies by each parent may increase reproductive success for both partners through risk partitioning is seldom considered. In Brünnich's Guillemots *Uria lomvia*, during the period of biparental care, males were feeding on “risk-averse” prey (consistent across time and space), whereas females fed on “risk-prone” prey. Models suggested that mixed-risk pairs had higher success than “risky” or “riskless” pairs. A similar scenario could be true for Lesser Black-backed Gulls, where the more powerful males tended to feed in a competitive setting at sea with few alternative resources nearby, but where females utilised fishing vessels nearer the colony, with a substantial risk of failure (when outcompeted by Herring Gulls), but near a whole suite of alternative foraging opportunities on land. In long lived species such as the gulls, the combination of individual specialisation and sexual segregation during the breeding season may increase an individual's lifetime reproductive success by reducing the risk of competition between sexes (and hence within a pair) or reducing the risk of unbalanced food provisioning, neither of which are mutually exclusive. Individual variation in body structure, experience and learning, will provide proximate drivers for individual specialisation.

Lesser Black-backed Gull pair, Kelderhuispolder 4 May 2011 (CJ Camphuysen)
Males (R) are on average larger, heavier and more powerful than females (L)

11. Herring Gulls and Lesser Black-backed Gulls feeding at fishing vessels in the breeding season: competitive scavenging versus efficient flying

Published **Ardea** 83(2): 365-380 (1995).

Camphuysen C.J.

Royal Netherlands Institute for Sea Research, NIOZ, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands,
E-mail: kees.camphuysen.nioz.nl

Abstract The distribution and feeding range of Herring Gulls and Lesser Black-backed Gulls breeding on the Dutch Wadden Sea islands were assessed, using results of ship-based surveys in the southern North Sea. The occurrence of both species in association with commercial fishing vessels is described in relation to distance to the coast and distance to the colonies. The feeding range of Lesser Black-backed Gulls (95% of all birds within 135 km of the colony) was considerably larger than that of Herring Gulls (95% within 54 km), and this difference could not be explained by differences in flight capacities. Feeding success and vulnerability to robbery of both species as scavengers at fishing vessels are described. Neither the vulnerability to robbery indices, nor the feeding success indices of both species did support earlier suggestions that Lesser Black-backed Gulls may have outcompeted Herring Gulls at (nearshore) fishing vessels. The feeding range of Lesser Black-backed Gulls could not solely be explained by a general avoidance of Herring Gulls near the coast, nor by the presence fishing vessels further offshore in comparison with the coastal zone. It is concluded that the large feeding range was motivated by a third, but unknown factor. The reduction of fisheries near the coast has probably led to a reduction in feeding opportunities for scavengers near the coast.

Key words: competitive scavenging, discards, beamtrawl fisheries, *Larus fuscus*, *L. argentatus*, flight capacity

Introduction

Breeding numbers of Herring Gulls *Larus argentatus* on Terschelling (one of the major gull colonies in the Netherlands) increased from 6-8000 pairs in the late 1960s to just over 21,000 pairs in 1982-83, but subsequently declined to less than 15,000 pairs in 1992 and 1993 as a result of poor breeding success (Noordhuis & Spaans 1992, Van Dijk *et al.* 1994, Koks 1994). Lesser Black-backed Gulls *L. fuscus* in the same colony increased from a few hundred in the late 1960s to 13,000 pairs in 1985 (68% of the total Dutch population) and subsequently stabilised on some 11,500-13,350 pairs in 1992 and 1993 (Van Dijk *et al.* 1994, Koks 1994). Hence, the ratio between numbers of gulls breeding on Terschelling has changed in favour of the latter species. Lesser Black-backed Gulls primarily feed on marine fish (Noordhuis 1987), whereas the diet of Herring Gulls is more diverse and includes many kinds of (marine) fish, marine invertebrates, terrestrial animals, carrion and refuse, grain and berries (Spaans 1971). During 1985-1987, the occurrence of marine fish in the diet of Herring Gulls amounted to only 14% of levels found in 1966-68 (Noordhuis 1987, Spaans & Noordhuis 1989). The diet of both Herring and Lesser Black-backed Gulls includes several demersal fish species which cannot normally be caught by plunge diving, but which commonly occur in the bycatch of beamtrawlers. It was therefore concluded that part of the fish brought ashore by these gulls was obtained at fishing vessels in the North Sea. The increase in numbers of breeding Lesser B1ackbacked Gulls on Terschelling was assumed to have forced Herring Gulls to concentrate more on other food resources than before (Noordhuis & Spaans 1992). This change in feeding habits of the Herring Gull and the increased intra-specific competition were hypothesized to have contributed to the decline in breeding success which has taken place compared to the late 1960s (Spaans & Noordhuis 1989). Studies in West Scotland, however, indicated that Lesser Black-backed Gulls were approximately two times more successful than Herring Gulls as scavengers behind fishing vessels (Furness *et ai.* 1988). In this paper an analysis of sightings of scavenging gulls at fishing vessels is presented, with special emphasis on feeding areas during the breeding season and around the breeding colonies, particularly off Terschelling. Results of experimental discarding of fish from a commercial beamtrawler in summer 1993 were analysed to obtain information on interspecific competition of these gulls at fishing vessels in the area. The analysis was meant to investigate whether the suggestion that interspecific competition between Lesser Black-backed and Herring Gulls at fishing vessels may have forced the Herring Gulls towards exploiting other sources of food could be supported.

Study area and methods

The area under study in this analysis was bordered by 53°-55°N latitude, and 3°-7°E longitude (Fig. 11.1), including the coastal zone of all Dutch Wadden Sea islands up to the Dogger Bank in the northwest. Shown in Fig. 11.1 are a system of *shipping lanes* off the Wadden Sea islands, which runs roughly from west to east and in which most shipping traffic is concentrated and the position of a *plaice-box,* established in the late 1980s to protect immature flatfish. Within the shipping lanes, fishing is not prohibited, but the area is unattractive to fishermen because of heavy traffic in a relatively narrow strip and because of specific traffic regulations which also apply to fishing vessels. Large beamtrawlers (>300 Hp) are not allowed to fish within 12 miles *(c.* 22 km) from land and heavy beamtrawlers are not allowed to use the Plaice-box in summer. Approximately between 53°30'N, 4°E and 54°N, 5°E, the Frisian Front area is located, an enriched zone which attracts piscivorous seabirds and fisheries (Leopold 1991).

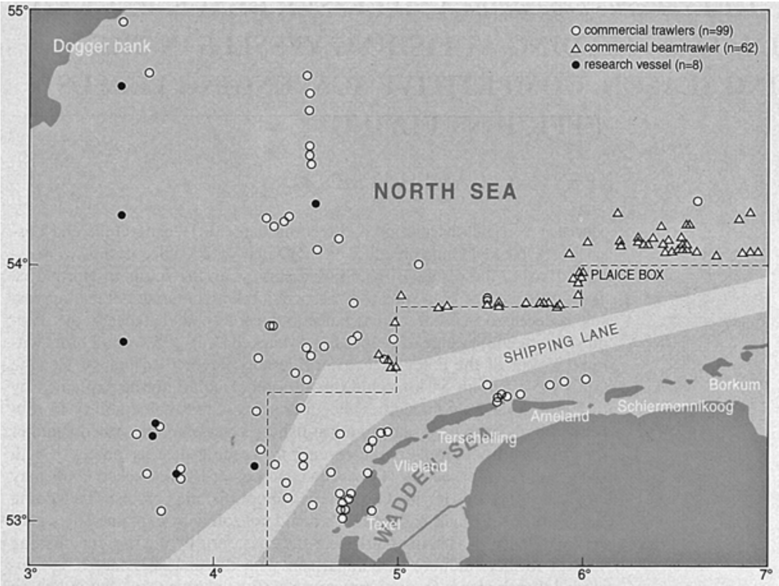


Fig. 11.1. Counts of groups of scavenging seabirds at commercial fishing vessels and research vessels in the southern North Sea in summer (May-August, 1987-1993, *n* = 169 counts). Shown are the outer borders of shipping lane north of the Wadden Sea islands and the plaice-box (dotted lines; see text). Plots include counts of seabirds onboard fisheries research vessels *(n* = 8), onboard a commercial beamtrawler *(n* = 62), counts of associated birds at nearby, actively fishing commercial fishing vessels during ship-based surveys at sea *(n* = 67) and birds associated with commercial fishing vessels as recorded from the shore *(n* = 32).

Since 1987, the distribution of seabirds in the southern North Sea has been studied by means of ship-based surveys, organised by the Netherlands Institute for Sea Research (NIOZ), the Dutch Seabird Group (NZG)/Tidal Waters Division of the Ministry of Transport, Public Works and Water Management (DGW) and the Institute for Forestry and Nature Research (IBN-DLO). Seabirds were counted during steaming in a strip-transect aside the ship (used to assess numbers per km^2) and in a 180° scan ahead of the ship (used to assess numbers per km travelled; *cf.* Tasker *et al.* 1984). During these surveys, fishing vessels were recorded when any seabirds were associated and all birds in these flocks were identified and counted (Camphuysen 1993a). In 1992 and 1993, additional information on the occurrence of scavenging seabirds was collected by means of observations of inshore commercial fishing vessels from coastal sites, during fishing onboard fishery research vessels, and onboard a commercial beamtrawler. For each count of seabirds attending a trawler during May-August, the distance to the nearest coast and the nearest (large) colony was calculated. Coastal colonies of Herring Gulls and Lesser Black-backed Gulls occur on most Wadden Sea islands (Table 11.1) and scattered along the mainland coast. In order to estimate feeding ranges during the breeding season, the distance to the nearest colony and the presence of adult Herring and Lesser Black-backed Gulls were assessed for each count of seabirds attending a trawler and for each 10-minute count during ship-based strip-transect counts at sea in summer (May-August 1987-1993). Densities at sea of Herring Gulls and Lesser Black-backed Gulls (around Terschelling only) in relation to the nearest colony were modelled. Densities were calculated in radial strata of 1 km width around colonies. The relative abundance of adults of these gulls at sea (n/km^2) with increasing distance to the colony were modelled, assuming that counts were Poisson-like-distributed by calculating the expected mean density as a function $\mu = \mu_0.e^{-a.distance}$ of the distance, obtained by maximising the likelihood. Dimensions needed for flight calculations were taken from adult gulls found dead on Texel and from literature. BASIC programmes were used to calculate fuel consumption in relation to distance of flight for both Herring and Lesser Black-backed Gulls (Prog_1a in Pennycuick 1989).

Table 11.1. Breeding numbers (pairs) and number of colonies of Herring Gulls and Lesser Black-backed Gulls on the Dutch Wadden Sea islands in 1993 (Koks 1994 and Dijksen 1996), and geographical positions of colonies used for feeding range calculations.

		Herring Gull		**Lesser Black-backed Gull**	
Waddensea islands		9 colonies	40,644 p	8 colonies	19,398 p
Rottumeroog	53°32.5'N, 6°35.0'E		3256p		145p
Rottumerplaat	53°32.5'N, 6°27.0'E		2525p		115p
Schiermonnikoog	53°30.0'N, 6°16.0'E		4295p		4295p
Ameland	53°27.5'N, 5°53.0'E		2609p		109p
Terschelling	53°26.0'N, 4°59.0'E		14,860p		13,350p
Vlieland	53°17.5'N, 4°59.0'E		9907p		1007p
Griend			30p		-
Texel, De Muy	53°08.5'N, 4°47.5'E		3162p		377p
Texel, De Geul	53°00.0'N, 4°43.5'E		8000p		1500p

Fishery waste comprises offal (waste from gutted, marketable fish), undersized roundfish, undersized flatfish, damaged marketable fish and benthic invertebrates. Onboard a commercial 2000 Hp beamtrawler in June-August 1993, samples of fish, offal and invertebrates were taken from the discards fraction of the catch. The items were identified, total lengths of fish were measured to the nearest cm, and discarded into the sea while the catch was sorted and gutted (thrown into to the steady trickle of discards produced by the ship's crew). Attempts by seabirds to pick up and swallow items were recorded into a tape recorder, noting the species and age class of the bird taking the item, whether the item was eaten, dropped or stolen. If it was stolen, the same notes were made for the second and subsequent birds, until the item was finally lost (sunk) or swallowed. During these discarding experiments the numbers and age classes of scavenging seabirds of each species were recorded so that fish consumption could be related to scavenging flock composition *(cf.* Hudson & Furness 1988, Camphuysen *et al.* 1993, Camphuysen 1993b). Feeding success of scavenging Herring Gulls and Lesser Black-backed Gulls at the trawl were compared, also in relation to other scavengers commonly occurring at the trawl (Fulmar *Fulmarus glacialis*, Great Black-backed Gull *Larus marinus* and Kittiwake *Rissa tridactyla*), and feeding strategies were described. Frequencies of robbing of experimentally discarded items by one bird from another were assessed, in order to evaluate the dominance hierarchies at the trawler. A 'vulnerability to robbery index' (number of experimental discards stolen from a species divided by the number of experimental discards stolen by that species) was calculated for all species commonly occurring at the trawler. Feeding'success rates' of scavengers are defined as the proportion of discarded items of a particular type that are consumed by a species, divided by the proportion of all scavenging birds at the vessel of that species. Thus, if all seabirds are equally successful in obtaining discards the success index will be 1.0 for each species. A success index greater than 1.0 indicates that the species in question obtained a greater proportion of the discards than expected from the numbers present. The number of discards expected to be eaten was calculated (on the basis of the numerical abundances of each scavenging seabird species) and compared with observed numbers using a X2-test (with the null hypothesis of equal success for all species).

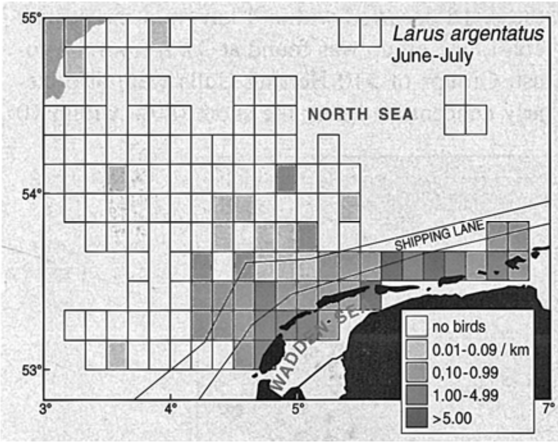


Fig. 11.2. Distribution of Herring Gulls at sea (n km^{-1} travelled) during chick rearing, June-July 1987-1993 (modified after Camphuysen & Leopold 1994).

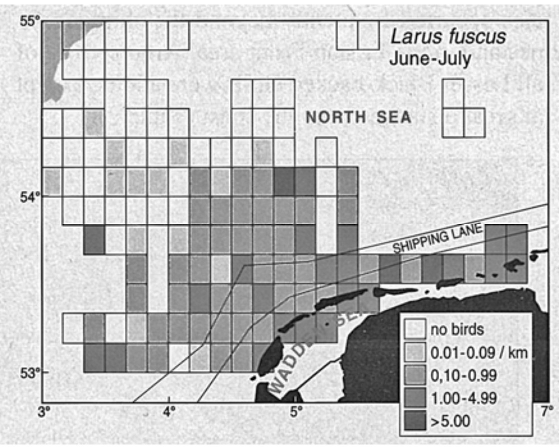


Fig. 11.3. Distribution of Lesser Black-backed Gulls at sea (n km^{-1} travelled) during chick rearing, June-July 1987-1993 (after Camphuysen & Leopold 1994).

Observations

Herring Gulls and Lesser Black-backed Gulls at sea - Herring Gulls were mainly restricted to the zone of 25 km from the nearest shore (Fig. 11.2, Table 11.2). Densities *(n/km2)* of adults during ship-based strip-transect counts declined with a rate of 8.2% per km away from the coast within the study area from a mean density of 1.74/km² within 1km from the coast (Poisson regression; $y = 1.735e^{(0.082 \cdot dcst)}$; where dcst= distance to the nearest coast in km). Beyond the shipping lanes, Herring Gulls were quite rare during most of the summer. Adult gulls predominated in most areas, but immatures were relatively numerous at over 100 km from the coast (Table 11.2). Comparatively large numbers were seen at over 50 km from the shore to the northwest of Texel and Vlieland, an area rich in offshore installations (Placid Field and associated installations). Large gulls are known to roost on oil and gas platforms in considerable numbers during most of the year (Tasker *et at.* 1986), but those associated with offshore installations during the breeding season are probably non-breeding birds. Lesser Black-backed Gulls were more widespread and occurred also in large numbers at substantial distances from the coast (Fig. 11.3, Table 11.2). Densities *(*n/km^2) of adult Lesser Black-backed Gulls during ship-based strip-transect counts declined at a rate of 2.9% per km away from the coast from a mean density of 1.74/km^2 within 1 km from the coast (Poisson regression; $y = 1.737e^{(O.029 \cdot dcst)}$). In contrast to Herring Gulls, this species occurred frequently beyond the shipping lanes and in the Frisian Front area. Around 90% of all Lesser Black-backed Gulls were adults, except at great distances from the coast (Table 11.2).

Table 11.2. Observer effort (number of 10-minute counts and km travelled), relative abundance of Herring Gulls and Lesser Black-backed Gulls at sea (n/100km), and the proportion of adults (%; sample size in parentheses) in six distance zones to the nearest coast, May-Aug 1987-93, 53-55°N, 03-07°E.

			Herring Gull		**Lesser Black-backed Gull**	
Zone	Counts (*n*)	Distance (km)	*n*/100km	% adult (*n*)	*n*/100km	% adult (*n*)
0-5 km	701	1710	228.7	88.8% (1843)	229.5	89.9% (1974)
5-10 km	370	988	107.0	91.8% (485)	220.6	97.1% (1047)
10-25 km	499	1614	37.2	83.1% (260)	95.5	90.3% (1610)
25-50 km	859	2768	10.4	78.9% (71)	85.2	94.4% (1370)
50-100 km	1362	4624	1.9	97.7% (861)	35.4	92.5% (1273)
>100 km	1141	4356	0.5	33.3% (15)	3.4	57.1% (98)

Zone	**Distance (km)**	**Fishing vessels (*n*)**	***n*/100km**
0-5 km	1710	13	0.8
5-10 km	988	5	0.5
10-25 km	1614	6	0.4
25-50 km	2768	15	0.5
50-100 km	4624	16	0.3
>100 km	4356	12	0.3

Table 11.3. Relative abundance (number per 100 km travelled) of commercial fishing vessels in six distance zones to the nearest coast, from ship-based surveys, May-Aug 1987-93, 53-55°N, 03-07°E.

Table 11.4. Observed and expected frequencies of occurrence of ~1O Herring Gulls or Lesser Black-backed Gulls in flocks of scavenging seabirds attending fishing vessels and proportion of adults (%; sample size in parentheses) in six distance zones to the nearest coast, May-Aug 1987-93, 53-55°N, 03-07°E. Stem counts include sightings of commercial fishing vessels during ship-based surveys and from the coast, counts at the stem of fishing research vessels and counts onboard a commercial beamtrawler (Fig 11.1). Expected frequencies are based on total number of counts at fishing vessels in each zone, within 100 km from the coast. The null-hypothesis of equal distribution of fishing vessels and groups of>10 gulls in this area was tested (X²-test).

		Herring Gull			**Lesser Black-backed Gull**		
Zone	Stern counts (*n*)	obs	exp	% adult (*n*)	obs	exp	% adult (*n*)
0-5 km	45	27	11.8	93.7% (1843)	16	27.1	99.6% (268)
5-10 km	5	5	1.3	98.3% (119)	3	3.0	99.2% (260)
10-25 km	6	3	1.6	90.0% (10)	4	3.6	72.7% (11)
25-50 km	51	2	13.3	93.6% (79)	37	30.7	94.2% (8526)
50-100 km	46	3	12.0	93.0% (43)	32	27.7	94.6% (6657)
>100 km	16	0	0	( )			
Total (<100km)	153	40	40	93.8% (3841)	92	92	94.6% (15,722)
X^2_4		22.1			3.6		
P<		0.001			n.s.		

Herring Gulls and Lesser Black-backed Gulls at fishing vessels - Commercial fishing vessels were widespread, but occurred in relatively high numbers within 5 km from the nearest coast and just around the edge of the plaice-box. The lowest number of fishing vessels observed per km travelled were found at >100 km from the coast (0.28/100km travelled; Table 11.3). Within 5 km from the shore, the chance of spotting a fishing trawler was 2.7x higher (0.76/100km). Herring Gulls were particularly abundant at inshore fishing vessels, with small numbers occurring in flocks of scavengers beyond the shipping lanes (Fig. 11.4). Of 81 records of Herring Gulls at fishing vessels, 17 records were of groups of over 100 individuals (21%). Of these, 16 occurred within 4 km from the nearest coast, one group was found at 7 km from the coast. Groups of >10 Herring Gulls were also clearly concentrated near the shore (80% within 10 km from the coast, *n* =40; Table 11.4). Observed frequencies of occurrence of such groups in five distance zones off the coast were significantly different from expected frequencies, based on total lumber of counts at fishing vessels in each zone :X^2_4 22.1, *P*< 0.001). The largest concentration of Herring Gulls at a trawler were 800 individuals associated with a shrimper off Texel (21 rune 1993). Adults predominated in all zones *:93.8%, n* = 3841; Table 11.4). Small numbers of Lesser Black-backed Gulls occurred at fishing vessels near the shore, but large groups were seen scavenging at fishing vessels in the vicinity of the major colonies at Texel and Terschelling (Fig. 11.5). Numbers of Lesser Black-backed Gulls in association with offshore fishing vessels were usually larger, often including several hundreds of birds in a single count. Observed frequencies of occurrence of groups of ≥10 Lesser Black-backed Gulls at fishing boats were not significantly different from expected frequencies, based on total number of counts at fishing vessels in each zone (X^2_4 =3.6, n.s.; Table 11.4). The largest concentration of Lesser Black-backed Gulls at a trawler comprised 1060 individuals at only 2 km from the shore (8 July 1987, unidentified trawler, off Ameland). In all areas, adults predominated (94.6%, *n* = 15 722; Table 11.4).

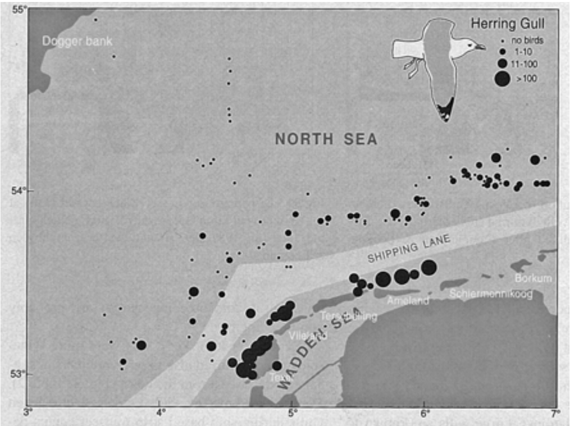


Fig. 11.4. Abundance of Herring Gulls at fishing vessels off the Dutch Waddensea islands, May-August 1987-1993 (n = 81 records). Counts of associated seabirds at fishing vessels where Herring Gulls were not positively identified are indicated by small dots.

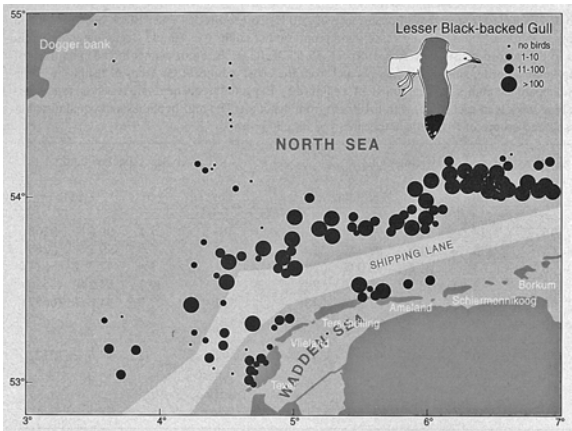


Fig. 11.5. Abundance of Lesser Black-backed Gulls at fishing vessels off the Dutch Wadden Sea islands, May-August 1987-1993 (*n* = 122 records). Counts of associated seabirds at fishing vessels where Lesser Black-backed Gulls were not positively identified are indicated by small dots.

Distance to nearest colony - Modelling the densities of adult Herring Gulls at sea in 1 km strata around the nearest colonies resulted in similar patterns as described for densities with increasing distance to the nearest coast ($y = 2.591 \,.\, e^{(-0.086 \,.\, dcol)}$,where dcol = distance to the nearest colony in km). Around Terschelling, distance to the coast was of greater importance than distance to the colony, as can be concluded from a decline of 8.4% per km away from the colony perpendicular to the coast and 0.4% per km away from the colony along the coast ($y = 2.07 \,.\, e^{(-(0.004 \,.\, dcol) - (0.084 \,.\, dcst))}$). The largest colony of Lesser Black-backed Gulls within the study area is found on Terschelling (nearly 70% of the Wadden Sea breeding population of 16,600 pairs in 1992; Van Dijk *et ai.* 1994). Densities (*y*) at sea around Terschelling dropped gradually, from 3.7/km^2 within 2 km from the colony with a rate of 3.5% per km away from the colony perpendicular to the coast and 2.1% per km away from the colony along the coast ($y = 3.706 \,.\, e^{(-(0.021 \,.dcol) - (0.014 \cdot dcst)}$; Fig. 11.6). Fuel consumption in relation to distance of flight Lesser Black-backed Gulls are relatively longer winged than the heavier Herring Gull (Table 11.5). As a result, Lesser Black-backed Gulls have potentially a 13% wider feeding range than Herring Gulls, using calculations from Pennycuick (1989). In both species, differences in wing length are significant between sexes (Table 11.5). Therefore, female Herring Gulls have potentially a 13% longer range than conspecific males, and female Lesser Black-backed Gulls have an 11% longer range than males of the same species. The differences in fuel consumption per unit distance, however, are rather small and are even quite similar in female Herring Gulls and male Lesser Black-backed Gulls (3.80 kJ/km at maximum range speed; Table 11.6). Hence, the different feeding range of both species around Terschelling, as ind-

Table 11.5. Biometrics[1] and energy requirements[2] during the breeding season of adult Herring Gulls and Lesser Black-backed Gulls.

Species		Herring Gull			Lesser Black-backed Gull		
	Sex	Mean ± SE	n	Sex	Mean ± SE	n	Source
Mass (Wales)	male	972 ± 13.1	47	male	894 ± 11.3	38	Verbeek 1977a
	female	835 ± 11.7	35	female	780 ± 11.9	41	
(Germany)	male	1051	80	male			Cramp & Simmons 1983
	female	864	80	female			
(Britain)	male	977 ± 11.3	36	male	880 ± 13.0	22	
	female	813 ± 12.2	32	female	755 ± 10.4	31	
Wing length	male	423 ± 1.2	75	male	425 ± 1.4	59	Verbeek 1977a
	female	400 ± 1.1	63	female	407 ± 1.1	71	
Span	male	1409 ± 6.5	29	male	1408 ± 6.2	35	Verbeek 1977a
	female	1325 ± 7.0	29	female	1332 ± 5.7	35	
Wing area	male	2106 ± 23.4	28	male	2053 ± 20.3	29	
	female	1838 ± 21.7	25	female	1848 ± 16.8	30	
Energetic requirements							
Mass	male	1000		male	890		
(for calculation)	female	850		female	770		
BMR	male	307.6kJ		male	282.4kJ		*cf.* Aschoff & Pohl 1970
	female	273.0kJ		female	253.9kJ		
Daily req.	male	1538kJ		male	1412kJ		*cf.* Drent & Daan 1980,
	female	1365kJ		female	1270kJ		Ellis 1984

[1] Measurements in mm; mass in grams; area in cm^2; wing load in g cm^{-2}; [2] The relationship between *BMR* (kJ) and mass (W in kg) in non-passerines is: $BMR = 307.6 \cdot W^{0.734}$ (Aschoff & Pohl 1970). Seabirds from high latitudes have a greater BMR than tropical seabirds (Ellis 1984): assumed is 1.25 BMR for this latitude. The energy requirements of adults during the breeding season are estimated at 4 (1.25 BMR) *(cf..* Drent & Daan 1980).

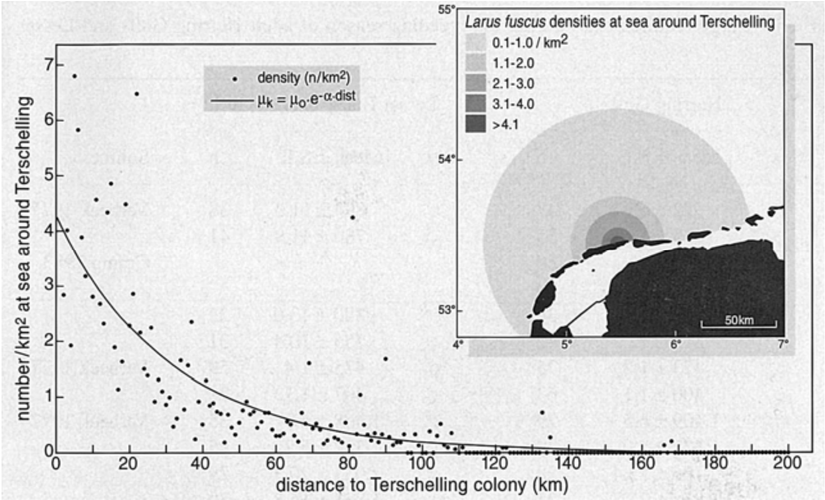


Fig. 11.6. Adult Lesser Black-backed Gulls at sea *(n km^{-2})* with increasing distance to the Terschelling colony, from ship-based strip-transect counts, May-August 1987-93 (data in Camphuysen & Leopold 1994). Shown are mean densities per stratum (+) and the expected mean density as a function $\mu = \mu_0 . e^{-\alpha . \text{distance}}$ of the distance, obtained by maximising the likelihood, assuming Poisson-like-distributed counts (solid line). Inset: impression of densities around Terschelling resulting from this analysis.

icated by a 8.4% decline in number per km perpendicular to the coast for Herring Gulls (95% of all gulls within 54 km of the colony) and a 3.5% decline per km for Lesser Black-backed Gulls (95% of all individuals within 135 km), is difficult to explain by interspecific differences in flight performance (Fig. 11.7). Feeding strategies at fishing vessels Behind fishing vessels, either Herring Gulls, or Lesser Black-backed Gulls were the numerically dominating species. The more powerful Great Black-backed Gulls formed a small minority and Kittiwakes occurred in numbers only near the colony at Helgoland. Fulmars were usually scarce and the individuals that turned up behind boats were usually moulting individuals *(i.e.* nonbreeding birds or failed breeders; Cramp & Simmons 1977) in poor physical condition (fat reserves depleted). Skuas were absent or occurred in very small numbers. As a result, many fights for scraps were between Herring Gulls and Lesser Black-backed Gulls (31.4% of all recorded fights, *n* = 806). Scavenging commenced when the trawler resumed towing after having brought a catch on deck. Sorting and gutting marketable fish took place at a speed of approximately 5-7 knots. Herring Gulls and Lesser Black-backed Gulls took discards mainly close to the ship, constantly being on the wing and making shallow plunge-dives into the water. Attempts to pick up and swallow discards were successful in 82.7% of all cases in Lesser Black-backed Gulls *(n* = 1956) and in 82.4% of all cases in Herring Gulls *(n* = 848). Prey selection and feeding success at the trawl The discards fraction in beamtrawl fisheries, estimated at 5-10 kg of fish and benthic invertebrates on each kg of landed fish (Van Beek 1990, Camphuysen 1993b), is dominated by benthic invertebrates and flatfish. Benthic invertebrates were usually ignored by both Lesser Black-backed and Herring Gulls (0.3% consumed, both species combined; *n* = 2540; Table 11.7). Overall consumption rates of flatfish, roundfish and offal by these two gulls were respectively 30.5% *(n* = 1044), 70.7% *(n* = 1101) and 65.9% *(n* = 1217). Herring Gulls and Lesser Black-backed Gulls overlapped with respect to species and size selection of fish at the trawl (Camphuysen 1994a). The number of flatfish taken by the two species was in accordance to expectation based on their relative abundance at the trawl (X^2_1= 3.0, n.s.). Herring Gulls, however, took significantly more offal particles than expected (X^2_1= 18.03, $P < 0.001$) and Lesser Black-backed Gulls took significantly more roundfish (X^2_1= 10.93, $P < 0.001$). Compared with other scavengers at the trawl, Herring Gulls could be classified as offal specialists, second only to the highly manoeuvrable Kittiwakes (Table 11.8). Herring Gulls obtained also more gadids than expected on the basis of numbers present at the trawl. Lesser Black-backed Gulls were particularly successful picking out gurnards, equalled only by Great Black-backed Gulls which tended to obtain the larger fish by robbing the smaller species.

Table 11.6. Comparison of mean wing span, mass, minimum power speed (V_{mp} in m s^{-1}), maximum range speed (V_{mr} in m s^{-1}) and fuel consumption (kJ km^{-1}) in Herring Gulls and Lesser Black-backed Gulls (cf. Pennycuick 1989).

Species	**Herring Gull**		**Lesser Black-backed Gull**	
	Sex	Mean	Sex	Mean
Span	male	1409	male	1408
	female	1325	female	1332
Mass	male	1000	male	890
	female	850	female	770
V_{mp}	male	9.1 m s^{-1}	male	8.7 m s^{-1}
	female	8.9 m s^{-1}	female	8.5 m s^{-1}
V_{mr}	male	15.1 m s^{-1}	male	14.5 m s^{-1}
	female	14.7 m s^{-1}	female	14.1 m s^{-1}
kJ km^{-1}	male	4.36	male	3.80
	female	3.80	female	3.36

Table 11.7. Consumption of benthic invertebrates, flatfish, offal, and roundfish by Lesser Black-backed Gulls and Herring Gulls scavenging at a commercial beamtrawler, southeastern North Sea, June-August 1993. Expected numbers are based on relative abundance of these gulls at the trawl (mean Lesser Black-backed Gull 338, Herring Gull 54 individuals).

		Herring Gull		**Lesser Black-backed Gull**		
	offered (*n*)	obs	exp	obs	exp	Consumption
Benthic invertebrates	2540	0	1	7	6	0.3%
Flatfish	1044	30	44	288	274	30.5%
Offal	1217	175	110	627	692	65.9%
Roundfish	1101	66	107	712	671	70.7%

Vulnerability to robbery - Of 342 fish handled by Herring Gulls and 959 fish handled by Lesser Black-backed Gulls, 50 and 104 fish respectively were stolen by other birds, 24 and 86 fish were dropped, and 268 and 769 fish were consumed (X^2_2= 4.275, n.s.). Up to seven scavengers handled individual discards. With regard to the first three birds handling a fish, numbers of Herring Gulls and Lesser Black-backed Gulls conformed expectation based on their relative abundance at the trawl (X^2_1= 0.023, n.s.). The number of Herring Gulls handling fish for the 4th-7th time was significantly higher than expected on the basis of numbers present (X^2_1=4.121, $P < 0.05$), suggesting that Lesser Black-backed Gulls gave up earlier. The vulnerability to robbery index of Herring and Lesser Black-backed Gulls, indicated that the latter lost 2.2x more fish through robbery than it obtained by robbing other species, whereas Herring Gulls obtained *1.4x* more fish by kleptoparasitising other species than they lost through robbery. Hence, Lesser Black-backed Gulls were clearly more vulnerable to robbery than Herring Gulls.

Table 11.8. Success indices of (common) scavenging seabirds at a commercial beamtrawler, June-July 1993. Success index calculated as number of items consumed divided by expected number of items based on numbers of birds at the trawl. The difference between the expected number of items consumed was compared with observed number, using a X²-test (with the null hypothesis of equal feeding success for all species).

Species	**Birds at the trawl** mean ± SE	**Offal** (595)	**Flatfish** (126)	**Gurnards** (275)	**Gadoids** (120)
Northern Fulmar	5.7 ± 0.7	0.96	0.00	0.69	2.38
Herring Gull	118.3 ± 19.2	1.33	1.09	0.35	1.34
Lesser Black-backed Gull	369.8 ± 46.1	0.73	1.00	1.27	0.87
Great Black-backed Gull	23.5 ± 4.9	0.00	1.65	1.26	2.12
Black-legged Kittiwake	26.4 ± 4.9	4.26	0.16	0.00	0.00
X^2_4		107.6	5.9	38.2	11.4
P<		0.001	n.s.	0.001	0.05

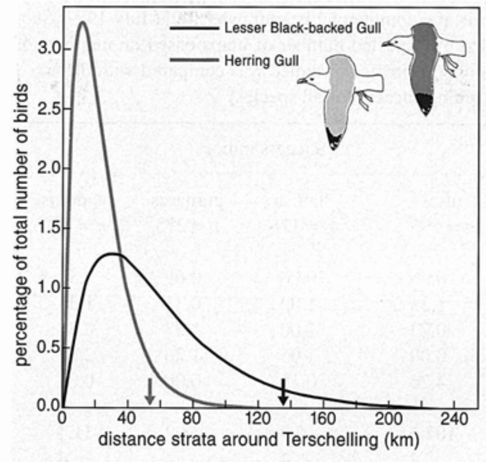


Fig. 11.7. Percentage of total numbers of adult Lesser Black-backed and Herring Gulls at sea per radial stratum (km) with increasing distance to the colony on Terschelling. Total numbers were calculated from the expected mean density per stratum, obtained by maximising the likelihood, assuming that counts were Poisson- like distributed. Arrows indicate the range within which 95% of the calculated numbers at sea were found (grey arrow = Herring Gull, black arrow = Lesser Black-backed Gull).

Discussion

Breeding success, and also breeding numbers, are probably regulated through a density-dependent reduction in reproductive output resulting from reduced rates of food provisioning of chicks *(cf.* Furness & Birkhead 1984, Brandl & Gorke 1988). The provision of Herring Gull chicks at Schiermonnikoog with supplementary food in 1987 led to increases in reproductive output, resembling that of gulls breeding on Terschelling in the 1960s (Van Klinken 1992). The provision with supplementary food of Lesser Black-backed Gulls on Terschelling in 1992 increased the reproductive output in comparison with a control group of gulls (Spaans *et al.* 1994). However, this was not the case in 1993, when Clupeids were more abundant off the coast than in 1992, indicating that the present low breeding success in most years is caused by a shortage of food. Reductions in the availability of marine fish may have been caused by changes in the shoaling behaviour of pelagic fish, fish stock collapses, declines in fishing effort and thus in the amount of discarded fish, or by increased intra- and interspecific competition of gulls at sea as a result of numerical increase of Herring and Lesser Black-backed Gull populations. Scavenging behind fishing vessels is a common feature in both Herring and Lesser Black-backed Gulls. The sightings of Herring and Lesser Black-backed Gulls at fishing vessels during the breeding season indicate that the coastal zone is shared by these birds with respect to trawler visits, but with Herring Gulls numerically predominating within 5 km from the shore. The absence of Lesser Black-backed Gulls at many fishing vessels with Herring Gulls in the coastal zone, except near large colonies such as on Terschelling, indicates that this species generally avoids the nearshore area where Herring Gulls predominate. Further offshore, Lesser Black-backed Gulls are dominating and considering the numbers found at sea off the Frisian islands and numbers associated with offshore fishing vessels, this gull is primarily an offshore species. For scavenging gulls, the advantages of visiting fishing vessels near the coast are obvious. Short feeding trips leave more time for adults to guard the chick, an important factor behind good breeding results *(cf.* Van Klinken 1992, Spaans *et al.* 1994). Birds that stay near land can soar along the dunes, waiting for fishing vessels within their field of vision, whereas the search for fishing vessels at sea requires prolonged periods of horizontal flapping flight. The energy requirements of horizontal flapping flight in large gulls may be as much as 7.5x the basal metabolic rate (BMR), whereas gliding flight costs only 3.lx BMR (Baudinette & Schmidt-Nielsen 1974, Ellis 1984). Finally, birds that stay near the coast have more possibilities to swap feeding areas (scavenging at fishing vessels, fishing at sea, feeding in the littoral zone, on land or in the Wadden Sea), whereas birds that fly out to sea can only choose between fishing and scavenging. Data presented in this paper suggest that many Lesser Black-backed Gulls venture much further out to sea than expected from Herring Gull densities or anticipated numbers of fishing vessels. Densities of Lesser Black-backed Gulls at sea declined 3% per km away from the colony on Terschelling (Fig. 11.6), indicating a maximum feeding range of over 135 km (95% of all birds within 135 km of the colony). Such a feeding range is well above that found by Pearson (1968) and a single feeding trip would take nearly 7 hours of constant flight (at 40 km/h). The ability of Lesser Black-backed Gulls to fly greater distances than Herring Gulls has been acknowledged before (Verbeek 1977a, Strann & Vader 1992) and the wing loading of Herring Gulls is such that they seem better off feeding closer to the colony (Verbeek 1977a). However, the differences in fuel consumption per unit distance are rather small (Table 11.6) and the differences in flying distance are much larger than can be explained from inter-specific differences in the energetic cost of flight. In each species, differences in wing length are significant between sexes, from which it can be concluded that females are better adapted to fly longer distances than males. Indeed, in Lesser Black-backed Gulls on Terschelling, the mean duration of absence of breeding adults ranged from 85-90 minutes in males and 110-130 minutes in females (Spaans *et al.* 1994). It is important to emphasize that feeding trips of a duration of 7 hours have not been recorded in the Terschelling colony (A.L. Spaans pers. comm.). Although large groups of scavenging adult Lesser Black-backed Gulls were common at the far end of the maximum feeding range, the breeding status of these birds is thus uncertain. Considering the breeding population of the two species on the Wadden Sea islands (Table 11.1) and the total number of gulls at sea calculated from densities derived from strip-transect counts, it can be estimated that a minority of the nesting Herring Gulls (approximately 1:7) and virtually all Lesser Black-backed Gulls feed at sea. However, the assumption that all adults at sea off the Wadden Sea islands are associated with any of the breeding colonies may be wrong. In Herring Gulls it was found that part of the mature adults which show up in a colony early in the breeding season fail to start breeding or lose the eggs before hatching (Drost *et al.* 1961). The mere presence of adult birds at great distances of breeding colonies could thus be misleading when feeding ranges of breeding adults are estimated. The differences in length of the feeding range of Herring Gulls and Lesser Black-backed Gulls, however, is clearly reflected in the spatial aggregation of (large) colonies of both species *(cf.* Furness & Birkhead 1984): far apart in Lesser Black-backed Gulls, close by in Herring Gulls (Table 11.1, Spaans 1987a, SOVON unpubl. data). Abundance estimates of Lesser Black-backed Gulls and fishing fishing vessels at sea showed that large numbers of gulls are found in areas which were not particularly rich in fishing vessels (Table 11.2-3), certainly not richer than the inner coastal strip. A long feeding range indicates that either inter-specific competition is intense over a wide area along the coast *(cf.* Brandl & Gorke 1988), or that the trips are initiated by something else. The reason for moving that far out to sea, which cannot be fully explained by the relative abundance of fishing vessels, nor by avoidance of Herring Gulls, would than probably be another, offshore food resource. Recent studies in colonies have indicated that pelagic shoaling fish such as small Clupeids feature prominently in chick diets of Lesser Black-backed Gulls (Spaans *et al.* 1994) and such fish become only rarely available as discards in beamtrawl fisheries. Moreover, breeding success on Terschelling collapsed in the mid-1980s and remained low since that time, with the exception of 1986 and 1993, years in which small Clupeids were rather abundant in food pellets of Lesser Black-backed Gulls (Noordhuis & Spaans 1992, Spaans *et al.* 1994). Future studies will have to show whether shoaling fish such as Herring are in fact the main target of Lesser Black-backed Gulls moving away from the coast, with discards at fishing vessels as an additional source of food. Fishing effort in the North Sea has increased enormously during this century particularly since the second World War (Daan *et al.* 1990). Despite an overall increase in fisheries, however, fishing effort in the southern North Sea has locally been reduced. The establishment of 'shipping lanes' in the late 1960s (changed in April 1987), may have removed quite substantial fisheries out of a ca. 15 km wide band off the Wadden Sea islands. Now that shipping intensities have increased during the last 25 years this effect may have gained importance. Secondly, in 1989, the regulation that large beamtrawlers were no longer allowed to fish within 12 miles (ca. 22 km) from land or within the plaice-box has removed substantial fisheries away from the coastal zone. These measures have probably reduced fishing effort and, hence, the availability of discards and offal for scavengers in the coastal zone. Breeding success of both Herring Gulls and Lesser Black-backed Gulls has declined in recent years and although food shortages were the key factor (Spaans *et al.* 1994), it is uncertain whether a possible reduction in fishing effort in the coastal zone has been responsible. Lesser Black-backed Gulls still feed mainly on marine fish, and may have expanded their feeding range, whereas Herring Gulls changed feeding habits and concentrated more on the littoral zone. Neither the vulnerability to robbery indices, nor the feeding success indices of both species did support the suggestion that Lesser Black-backed Gulls may have outcompeted Herring Gulls at (nearshore) fishing vessels. Future research will have to concentrate on natural feeding concentrations of these gulls off the Wadden Sea islands.

As can be seen throughout this thesis, fisheries discards are an important resource for both Herring Gulls and Lesser Black-backed Gull in the southern North Sea. The upcoming reform of the EU Common Fisheries Policy will be the biggest change in European fisheries management for a generation. A central plank of this reform is a proposed ban on discards, to aid the creation of economically and environmentally sustainable fisheries. This, together with a global trend for declining discards, may have unforeseen knock-on consequences for the large number of scavenging seabirds that consume this plentiful subsidy. A general expectation of the potential consequences of a EU discards ban on scavenging seabirds is provided in this paper.

Bicknell A.W.J.[1], D. Oro[2], C.J. Camphuysen[3] & S.C. Votier[1,4]* 2013. **Potential consequences of discard reform for seabird communities.** J. Appl. Ecol. DOI 11/1365-2664.12072

[1]Marine Biology and Ecology Research Centre, Plymouth University, Drake Circus, Plymouth, PL4 8AA, UK, [2] Institut Mediterrani d'Estudis Avançats IMEDEA (CSIC-UIB), Miquel Marque`s 21, 07190 Esporles, Mallorca, Spain, [3]Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands; [4]Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall, UK; **Correspondence author*: stephen.votier@plymouth.ac.uk.

Discards have shaped many aspects of seabird foraging, distribution, and population dynamics. Here we review these effects and consider the potential for both negative and positive impacts of discard reforms for seabirds, with particular focus on the EU, and propose recommendations for on-going research and conservation. EU seabird scavengers are dominated by a relatively small number of large generalist taxa. Many of these occur at globally significant numbers within the EU, but may be able to buffer a decline in discards by switching to feed on alternative foods. A discard ban may have negative consequences by creating a food shortage for scavenging birds. Some species may offset this by feeding more on other birds, with potentially negative population-level impacts, or by moving into novel environments. Benefits of a discard ban may be a reduction in seabird bycatch in fishing gears, as well as a reduction in populations of large generalist species that currently dominate some seabird communities. Synthesis and applications. Reform of the Common Fisheries Policy and global discard decline are essential components towards creating sustainable fisheries, but may have both detrimental and beneficial effects on seabird communities. The nature of these impacts is still poorly understood, highlighting the need for detailed long-term seabird monitoring, as well as building resilience into populations through policy measures that incorporate remedial action on major seabird conservation priorities. Research should focus on understanding how seabird foraging, in terms of functional responses and searching behaviour, are influenced by both changing discards and natural fish prey availability, and how they impact upon fitness. It is also essential to link individual-level responses with population, community and ecosystem-level change. Understanding these links is fundamental to on-going seabird management and conservation.

12. Riding the tide: intriguing observations of gulls resting at sea during breeding

Published **Ibis** 153: 411-415 (2010)

Judy Shamoun-Baranes[1*], Willem Bouten[1], Kees (C.J.) Camphuysen[2] & Edwin Baaij[3]

[1]Computational Geo-Ecology, IBED, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands, *Corresponding author, E-mail: shamoun@uva.nl; [2]Royal Netherlands Institute for Sea Research, NIOZ, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands; [3]Technology Centre, Science Faculty, University of Amsterdam, Science Park 904, 1098XH Amsterdam, The Netherlands

Abstract Adult Lesser Black-backed Gulls were followed during the breeding season using a high resolution GPS tracking system. Little is known about the foraging movements of these birds and what they do when they are away from the colony. The study revealed intriguing yet infrequent behavioural patterns showing that birds would sit on the sea surface drifting passively with the tidal current for several hours, resting at sea rather than in the breeding colony. The potential function of the observed patterns is discussed as well as the relevance of these observations for other species.

Keywords: drift, GPS tracking, *Larus fuscus*, resting at sea, tidal current

Introduction

With recent developments in high resolution GPS and other activity logging technologies, it is now possible to measure the movements and behaviour of animals in great detail providing exciting new opportunities for behavioural and physiological research of free ranging animals (Ropert-Coudert & Wilson 2005, Rutz & Hays 2009, Robinson *et al.* in press). Such detailed measurements can record infrequent yet fascinating behaviours that can reveal new aspects of behavioural ecology (e.g. Houghton *et al*. 2008a). As part of a long term study on gull resource selection and breeding success on Texel, a Wadden Island in the Netherlands, we studied the foraging movements of adult Lesser Black-backed Gulls *Larus fuscus* during the breeding season in 2008 using a novel GPS bird-tracking system. Although information exists about the prey preferences of different individuals in the colony as well as activity around trawlers for this area (e.g. Camphuysen 1995a, Garthe *et al.* 1996, Camphuysen *et al.* 2010), very little is known about the foraging movements of these birds and what they do when they are away from the colony. This paper describes an intriguing yet infrequent behavioural pattern revealed during the tracking study. During several trips to the North Sea smooth curved trajectories were recorded with very slow movement (< 4 km h^{-1}) lasting several hours. We explored this behaviour within the context of their daily movements and the local tidal currents.

Methods

The prototype bird tracking system used in this study was developed at the University of Amsterdam and consists of 18 g solar powered GPS tags, with a wireless ZigBee transceiver that communicates with a base station located in the centre of the breeding colony. Data logged on the GPS tags were downloaded to the base station and new measurement settings were uploaded to the tag. Thus the system enables remote measurement flexibility while the tag is on the bird. The GPS tag measures and logs GPS x,y,z positions (geographic position and altitude above mean sea level), sensor temperature and air pressure, and GPS diagnostics (e.g. fix time, number of satellites in view). The locations of the birds were measured at intervals ranging from 3–450 sec, during the day and at night. We varied the measurement interval to enable measuring movement at different temporal and spatial scales and capture different types of behaviour while minimizing gaps in the data due to temporarily low battery voltage, which can result from extensive high resolution measurements.

Five adult Lesser Black-backed Gulls, three males and two females were trapped and fitted with GPS tags between 24 May and 4 June, 2008 (Table 12.1) in the Kelderhuispolder breeding colony on the island of Texel (53°00'N, 04°43'E), The Netherlands. The GPS tags were attached to the back of the birds using a teflon 3-strap permanent backpack harness configuration with one strap fitting across each wing and one strap below the crop. Birds were immediately released following biometric measurements of the wing, tarsus and body mass and secure placement of the tags. The tags weighed less than 3% of the mass of each bird at the time of capture (mean 848 g, range 650-960 g). The birds continued to breed after being fitted with the tags and were tracked for several weeks until they left the breeding colony. Four of the five birds were observed in the colony and commenced breeding in the following season and one bird (tag 54) was found dead in a garbage dump in France with no external signs of cause of death.

Table 12.1. Overview of Lesser Black-backed Gull tracking data obtained from the GPS loggers during the 2008 breeding season. Data from the start of the tracking season until the last GPS record within the colony are included. Number of fixes includes fixes with and without altitude.

Logger ID	Sex	Deployment	Days tracked	Fixes	Max dist (km)	% at sea
45	M	31 May 2008	12	4784	82.0	45.5
51	M	24 May 2008	29	6651	78.6	33.5
52	F	4 June 2008	39	5391	83.7	43.6
54	F	2 June 2008	18	7161	44.6	6.0

Table 12.2. Overview of smooth curved trajectories during which birds sat at the sea surface and moved at speeds below 4 km/h (Fig. 12.1) for 4-6 hours. Start and end date and time (GMT) of the observation is recorded as well as the behaviour directly before and after the event. Measurements were collected in 2008. Passive drift of ID 45 and 52 are shown in Fig. 12.1.

Logger ID	Start date and time	End date and time	Activity before	Activity after
45	7 June 21:00	8 June 2:26	Flew from colony	Returned to colony
51	8 June 13:31	8 June 19:37	Foraged at sea	Foraged at sea
52	7 June 20:41	8 June 01:46	Foraged at sea	Foraged on mainland
52	11 June 20:49	12 June 03:10	Foraged at sea	Foraged at sea
52	23 June 20:24	24 June 01:59	Foraged at sea	Returned to colony
52	30 June 20:42	1 July 01:16	Foraged at sea	Foraged at sea

Speed and direction of the birds were calculated between consecutive GPS-positions. To calculate the amount of time spent in different locations, only data with an interval ≤10 minutes between fixes were used, to remove long time intervals if fixes were occasionally missing. A buffer with a 200 m radius around the colony was used to calculate the amount of time spent in or near the colony and to designate the start and end of a trip. Trips with a large gap between consecutive locations (>30 minutes) were excluded from the analysis of mean trip duration and maximum distance from colony. Following an exploratory analysis of speed distributions, speed was used to categorize behaviour as stationary (<1 km h^{-1}), floating or walking (1-4 km h^{-1}), or flying (>4 km h^{-1}). These thresholds were further supported by considering measured altitudes in combination with speed (in general measured altitude < 20 m AGL and speed <4 km h^{-1} were considered non-flight) and based on aerodynamic theory, these speeds would be too low to sustain flight (Shamoun-Baranes & van Loon 2006, Pennycuick 2008). Due to tag failure, one of the birds was only tracked for 2 days and thus removed from further analysis, although it was still observed breeding in the colony during the course of the study. The Zuno Model (Rijswijk, The Netherlands, Rijkswaterstaat) was used for assessing the tidal currents along the North Sea coast of the Netherlands. Currents were calculated with the Dutch Continental Shelf Model (Gerritsen *et al.* 1995) with a grid size resolution of 1/12°N and 1/8°E. The flow fields were linearly interpolated to the time and location of the bird provided by the GPS tags.

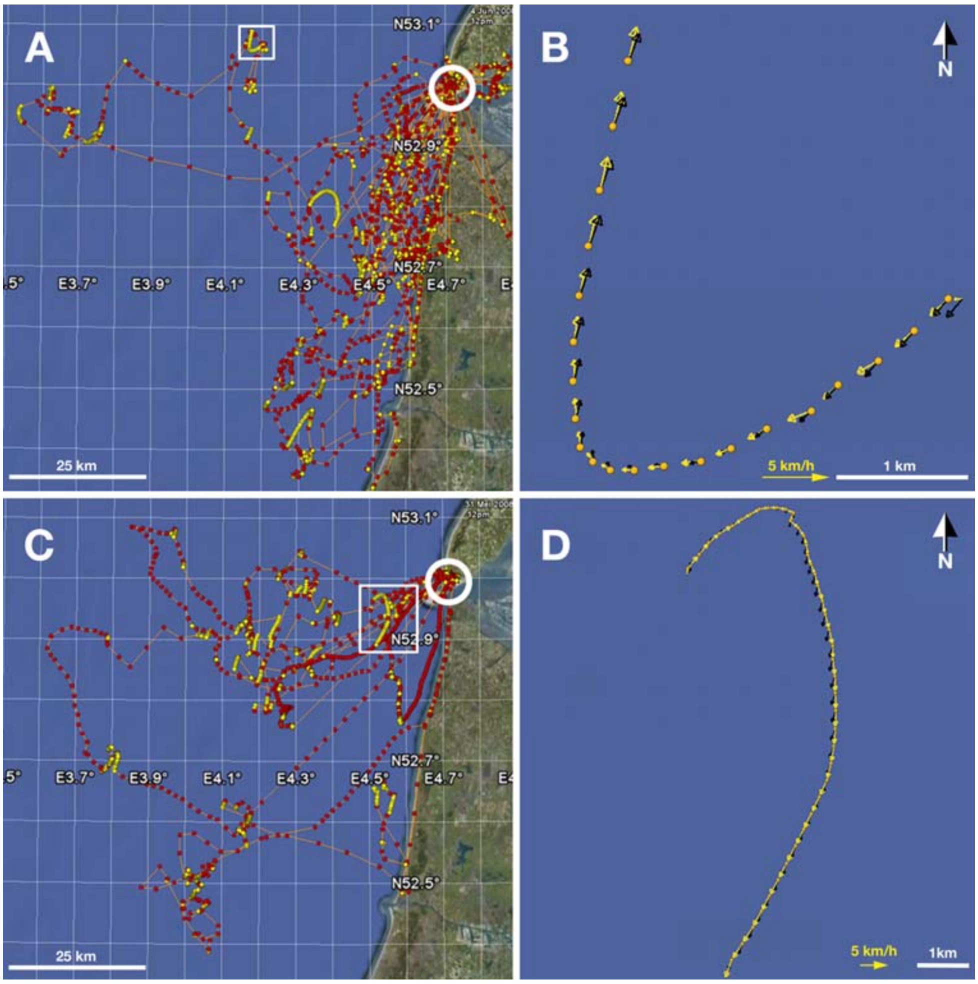


Fig. 12.1. Foraging and resting movements of Lesser Black-backed Gulls, breeding on Texel (white open circle), The Netherlands. Locations with an associated speed ≤ 4 km h^{-1} are indicated in yellow and represent when birds are stationary, walking or floating, higher speeds are indicated in red. (A) 4953 GPS positions of a female gull (logger ID 52) from 4 June 2008 through 15 July 2008 and there are four episodes of extended passive drift recognisable (drift lasting 4-6 hrs); (B) boxed area enlarged showing one case of passive drift of the gull (yellow points and arrows) superimposed on tidal current speed and direction (black arrows) 30 June 2008 20:42 GMT to 1 July 2008 1:16 GMT; (C) 4784 GPS positions of a male gull (logger ID 45) from 31 May to 11 June; (D) shows the one case of extended passive drift in this bird from 7 June 21:00 GMT to 8 June 2:26 GMT.

Results and discussion

During the breeding season, three of the four birds foraged regularly in the North Sea, up to 80 km away from their colony (Table 12.12.1, Fig. 12.1a and 12.1c) whereas one gull (tag 54, Table 12.12.1) spent most of its time on land. Although some trips lasted several days the mean trip duration for all birds was 7.9 ±9.0 h (SD, n = 78). Gulls spent 43% of their time in the breeding colony. Of the time spent outside of the colony 35 % was spent stationary, walking or floating.

During several trips to the North Sea intriguing smooth curved trajectories were recorded for 4-6 hours. Based on the very low speeds (<4 km hr^{-1}) and altitudes measured (<20m), birds sat at the sea surface during this time (Fig. 12.1). The movements occurred during both day and night and were only observed for birds regularly foraging at sea (tags 45, 51, 52). In total six of these trajectories were recorded (Table 12.2), however, trajectories of shorter duration were much more common although not included in the current study. We compared the speed and direction of the six trajectories to tidal current speed and direction. Based on the strong similarity between the bird movements and tidal currents, it is clear that the birds were passively riding the currents (Fig. 12.1b and d) for several hours. The movements coincided with slack tide, thus the turning of the tide resulted in curved trajectories. Although we did not have additional measurements of the birds' activity, the passive and long uninterrupted drift with the tidal current and lack of vertical movement strongly suggest that birds were resting during this period.

The movement patterns in this study were recorded during the incubation and hatching phase of breeding while colony attendance is assumed important to guard the clutch or newborn chicks (Cadiou 1999). Within the study colony, this seemed particularly relevant given the exceptionally high levels of chick predation observed (c. 60% of the hatchlings). However, similar to other colonial seabird studies (Irons 1998, Lewis *et al.* 2004) we found that partners did not always coordinate foraging trips leaving chicks unattended at times (C.J. Camphuysen, *unpublished data*). Animals and particularly birds can retain a certain level of vigilance during sleep and thus potentially reduce the risk of nest predation when resting in the colony (Lima *et al.* 2005, Siegel 2008). Bearing this in mind, and the fact that the maximum distance from the nest during foraging trips was 80 km, requiring less than 2 hours of flight to return to the nest, we would expect birds to rest in the colony when possible during the breeding season. This raises questions regarding the potential importance and function of such behaviour. Thus we also considered the activity of the birds before and after the resting period. If birds sleep during these trajectories and sleep is homeostatically regulated (Rattenborg *et al.* 2009), then a relationship might be found between the duration of resting and previous foraging activity (e.g. Weimerskirch & Guionnet 2002). In this study, different behaviours were observed: birds returned directly to the nest or continued to forage after drifting at sea; on one occasion a bird left the colony drifted at sea for several hours and then returned to the nest (Table 12.2). With our preliminary data we can only speculate about the possible function and advantages of such behaviour. Resting at sea may allow birds to reduce their vigilance providing an opportunity for more complete behavioural shutdown and hence improved brain maintenance (Lima & Rattenborg 2007). Resting and sleep is an important part of the daily time budget of animals, however, little is known about how often, where and when animals sleep and rest in the wild (Lima *et al.* 2005, Henson *et al,* 2007, Siegel 2008). Sleep is rarely measured directly in free-living animals (Rattenborg *et al.* 2008), although based on visual observations or activity sensor data (e.g. Ropert-Coudert & Wilson, 2005) it can be inferred from behavioural indicators such as posture, eye closure (e.g. Schwilch *et al.* 2002, Amlaner & Ball 1983), buccal oscillations (Houghton *et al.* 2008b) or diving behaviour (Miller *et al.* 2008, Mitani *et al.* 2010). Alternatively, resting at sea may reduce exposure to ectoparasites (Danchin 1992) or provide an opportunity to digest food before continuing with other activities such as foraging for chicks (Ropert-Coudert *et al.* 2004). Other colonial seabird species are known to rest and even drift for some time on the sea surface during the breeding season, although detailed information about the entire trajectory is often lacking (e.g. Weimerskirch *et al.* 2002, Ropert-Coudert *et al.* 2004, Guilford *et al.* 2008). Thus the phenomenon of long resting bouts at sea, away from the nest, may be more common than realized.

In future research we will include measurements of tri-axial acceleration and consider both long as well as shorter duration drift movements. When estimating foraging energetics and time-energy budgets of individuals, distinguishing different types of movement, such as passive drift from active movement or different flight strategies (e.g. Shamoun-Baranes & van Loon 2006), is essential. Advances in biotelemetry, exchange of data for comparative analysis, and analysis of common as well as rare events will greatly facilitate our understanding of behavioural ecology, stimulating new research questions and reviving old ones.

13. Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns

Published **Biological Conservation** 156: 22-29 (2012)

Kees (C.J.) Camphuysen*[,1], Judy Shamoun-Baranes[2], Willem Bouten[2], Stefan Garthe[3]

[1]*Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands,* *Corresponding author. *E-mail address:* kees.camphuysen@nioz.nl; [2]*Computational Geo-Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, PO Box 94248, 1090 GE Amsterdam, The Netherlands;* [3]*Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany*

Abstract The identification of marine areas of importance for seabirds is a challenge, because it is often unclear how birds are using the different areas in which they occur. Species differ in habitat choice, foraging behaviour and feeding range, but also in tendencies to roost at sea or to utilize resting places closer to or even on land. Because the designation of marine protected areas (MPAs) for seabirds should bear relevance to the ecological importance of these regions, simple presence/absence information is not sufficiently accurate and could even be misleading. Large amounts of data have been collected to assess distribution patterns of seabirds around the world. Two sources of data are highlighted here: ship-based surveys and sensor data from instruments attached to individual birds. Recently developed protocols to systematically record seabird behaviour at sea during ship-based surveys and novel tracking technology that facilitate spatio-temporal quantification of space use and identification of behaviour will be evaluated in the context of MPA designations. We present some limitations of traditional techniques and exciting possibilities of new protocols and the latest generations of electronic devices attached to seabirds. These advanced approaches in data collection and spatial analysis will reveal important ecological information that will enhance our understanding of offshore seabird distribution and activity which can guide the designation of marine protected areas.

Key words: Marine Important Bird Areas, Seabird behaviour, Census techniques, Data integration

Introduction

Though the benefits of marine protected areas (MPAs) are now widely accepted (Gaines et al. 2010a), less than one percent of the entire oceans' surface today is protected and only a small portion of this is managed effectively (Gjerde & Breide 2003; Halpern et al. 2010). MPAs have been described as a suite of tools developed in coastal waters to provide a framework for integrated area-based biodiversity conservation (Agardy 1994; Hoagland et al 2001; Gaines et al 2010b). Effectively managed, they can maintain ecosystem structure and function, protect habitats and species, and enable sustainable use of resources (Gjerde & Breide 2003). The identification of MPAs for highly mobile seabirds is a challenge. MPA designs, certainly when areas of ecological significance are aimed for, should be guided by at least some understanding of the natural history and habitat requirements of seabirds protected within these areas (Bernstein *et al.* 1991, Hyrenbach *et al.* 2000). Geostatistical interpolation methods often combine environmental, hydrographic, or even ecological parameters with abundance estimates to delineate sea areas of importance for seabirds (Skov et al. 2007; Wakefield et al. 2009). Information on key issues such as prey availability is usually lacking and certain proxies are chosen that would or could characterize the suitability of habitats (e.g. distance from the coast, water depth, frontal systems; Louzao *et al.* 2006, Yen *et al.* 2006, Garthe *et al.* 2007, Stevick *et al.* 2008), or be indicative of the presence of food (chlorophyll concentrations, salinity; Scott *et al.* 2010). These proxies may not be accurate and the results can thus be misleading. Moreover, abundance estimates of seabirds used in these models seldom discriminate between actively foraging animals and individuals that occur in certain areas for other reasons (e.g. on transit, resting, or otherwise).

Numerous papers report on observation protocols and techniques to enhance the accuracy of survey data (Gaston *et al.* 1987, Buckland & Turnock 1992, Spear *et al.* 1992, Spear *et al.* 2004). The geostatistical interpolation techniques applied to survey data have been scrutinised, further developed and refined to improve the results (Robinson & Metternicht 2006, Certain *et al.* 2007, Skov *et al.* 2007). However, rather few studies have addressed how the behaviour of the study animals could help identify the ecological significance of certain concentrations of animals, (Camphuysen & Garthe 2004). Would “high counts”, by definition, point at areas of ecological importance? We believe not, or at least not necessarily. High densities at offshore roosts, at crossroads in migratory pathways, in the main foraging areas, or along the flyways to and from major colonies would all show up as “important areas” on distribution maps. In the absence of behavioural information, the specific use (or ecological significance) of any of these areas is rarely evident.

Nowadays, seabird distribution data are collected more and more often with data loggers attached to individual birds. Concentrations of tracks have been used to identify areas of significance (e.g. Grecian et al. 2012). However, while numerous ecologists deploying these instruments have seen the need for behavioural or physiological information during such movements (e.g. diving, travel speed, flight altitude, flight strategy, resting, feeding bouts; Wilson *et al.* 1992, Ropert-Coudert & Wilson 2005; Rutz & Hays 2009), such data have only occasionally been used by conservationists. High abundances (i.e. high densities of data points) have usually been taken as indicators of “areas of importance”, worthy of protection (Freeman *et al.* 1997, Georges *et al.* 1997, Wilson *et al.* 2009). Assuming that a MPA would have to be of ecological importance as a feeding area, or rather as a roost or any other function, information on the actual behaviour of animals is crucially important. A more comprehensive analysis of the data, utilising the collected information about behaviour at sea, could lead to more precise delineations of areas of ecological importance.

The role and importance of incorporating animal behaviour in conservation biology is increasing (Buchholz 2007). Modern ship-based survey techniques and the latest generations of electronic devices attached to individual birds could easily provide information on animal behaviour. Collecting and using information on behaviour simultaneously with tracking/survey data would be the way forward. By doing so, a more comprehensive understanding of the ecological importance of marine areas with particularly high densities of seabirds would result. This would be an important step in an ecologically more meaningful designation of MPAs for seabirds. In this paper we provide examples of the type of information, apart from densities, about bird behaviour that can be extracted using different measurement techniques (tracking studies or at-sea surveys).

Examples are provided based on combinations of ship-based surveys and studies using tracking devices within the North Sea. These projects were all independent studies of seabird distribution and foraging activities in overlapping areas: in the NW North Sea (Northern Gannet; 1991-2004) and in the Southern Bight (Lesser Black-backed Gull; 1978-2010).

Data collecting techniques

Foraging distribution of Northern Gannets in the North Sea - The foraging range and feeding behaviour of Northern Gannets (hereafter simply ‘Gannets’) around the Bass Rock (SE Scotland, 56°06’N, 2°36’W) have been studied using ship-based surveys, in June–July during ten seasons between 1991 and 2004 in the northwestern North Sea (54–59°N, 3°W–2°E) (Camphuysen 2011d). These surveys covered most of the feeding range of Gannets nesting on the Bass Rock (Hamer et al. 2007). Counts were conducted in calm weather (wind speed <7 on the Beafort scale) when the vessel travelled at full speed (8–10 knots). A total of 9,972 km^2 were surveyed, travelling a distance of 33,601 km on effort, and 44,818 Gannets were observed. Standard counting techniques were applied (Tasker *et al.* 1984, Camphuysen *et al.* 2004), together with systematic recording of Gannet behaviour as an essential part of the protocols (Camphuysen & Garthe 2004). Inspired by Ashmole (1971), 10 types of (feeding) behaviour were commonly observed in Gannets: Actively searching, Deep plunging, Shallow plunging, Scooping prey, Surface seizing, Scavenging at fishing vessel, Resting or apparently asleep, Preening or bathing, Carrying nest material, and Being under attack by kleptoparasite (details in Camphuysen & Garthe 2004). Foraging flocks comprising more than one seabird species were named 'multi-species (feeding) associations', or MSFAs (Camphuysen & Webb 1999). Associations between seabirds and marine mammals were recorded and the type of behaviour was described and logged (Camphuysen 2011d). We will compare the survey data with a simultaneously conducted tracking study in which the at-sea distribution and behaviour of Gannets from the Bass Rock was monitored with satellite PTTs from Hamer *et al.* (2000, 2007). In these studies, unfortunately, the diving locations were not recorded, for example by means of time-depth recorders attached to the individual birds.

Foraging distribution of Lesser Black-backed Gulls in the Southern North Sea - Using very similar techniques and protocols, the at-sea distribution and feeding behaviour of Lesser Black-backed Gulls in the Southern North Sea was studied between 1978 and 2008 (European Seabirds at Sea database and C.J. Camphuysen *unpubl. data*). Systematic recording of behaviour was an essential part of surveys conducted since 1992. Behaviours commonly observed in Lesser Black-backed Gulls were: Actively searching, Shallow plunging, Scooping prey, Surface seizing, Scavenging at fishing vessel, Resting or apparently asleep, Preening or bathing, and Being under attack by kleptoparasites. Associations between gulls and fisheries were common and both the number of birds and the distribution and abundance of fishing vessels involved were assessed and the type of behaviour was described and logged. Foraging at anthropogenic resources and opportunities (discards in fisheries, associations with offshore installations) was distinguished from 'natural' foraging behaviour (i.e. independent of human activities).

In 2010, 14 adult Lesser Black-backed Gulls were trapped on nests and fitted with GPS tags (UvA-BiTS, Amsterdam) at the island Texel (53°00'N, 04°43'E), The Netherlands, to monitor the foraging distribution at sea and on land. The 17g GPS tags were attached to the back of the birds using a Teflon three-strap backpack harness configuration. The birds continued to breed after being fitted with the tags and were tracked for several weeks until they left the breeding colony and migrated south to their wintering areas. Data logged on the GPS tags were automatically downloaded to a base station within the colony (short range data transfer rather than the use of satellites). The tags measured geographical position, altitude, instantaneous speed (m/s), sensor temperature and GPS diagnostics. The locations of the birds were measured day and night at intervals ranging from 3 to 450s (settings remotely adjustable via the base station). The tag also included a tri-axial accelerometer which measures acceleration in three axes: heave (Z), surge (X) and sway (Y). The measured acceleration includes a static and a dynamic component. Static acceleration is a measure of the incline of the accelerometer with respect to the earth's gravitational field while the dynamic component is a result of body acceleration (see Shepard *et al.* 2008 for further details)..From the accelerometer data, different activities (behaviour) of the tagged individuals could be monitored.

Results

Gannets at sea - Ship-based surveys of gannets revealed a bell-shaped distribution pattern around the Bass Rock with gradual declines in densities with distance in any direction except towards land (Fig. 13.1). Mean densities of Gannets around the colony declined from >10 birds km^{-2} within 20 km of the colony to less than 0.2 birds km^{-2} at over 400 km. However, 66% of all recorded searching and actively feeding Gannets occurred in areas with very low densities of conspecifics, generally at more than 100 km away from the colony (Fig. 13.2). Because of the low densities of Gannets where most foraging occurred, feeding opportunities were typically exploited by relatively small flocks, with few competing birds. Intraspecific competition was thus less intense (and individual foraging success likely higher) than it would have been nearer the colony in areas with higher densities of conspecifics. Searching and feeding tactics of Gannets, as well as their foraging associations with other apex predators, were different between sea areas. Gannets joined nearshore multi-species foraging associations (MSFAs) around Wee Bankie and in a frontal zone bordering mixed nearshore waters off the east coast of Scotland (Fig. 13.2), where compact schools of small prey fish were herded towards the surface by diving auks (Alcidae). Associations of Gannets with marine mammals were typically an offshore phenomenon over thermally stratified water, generally at >100 km from the coast.

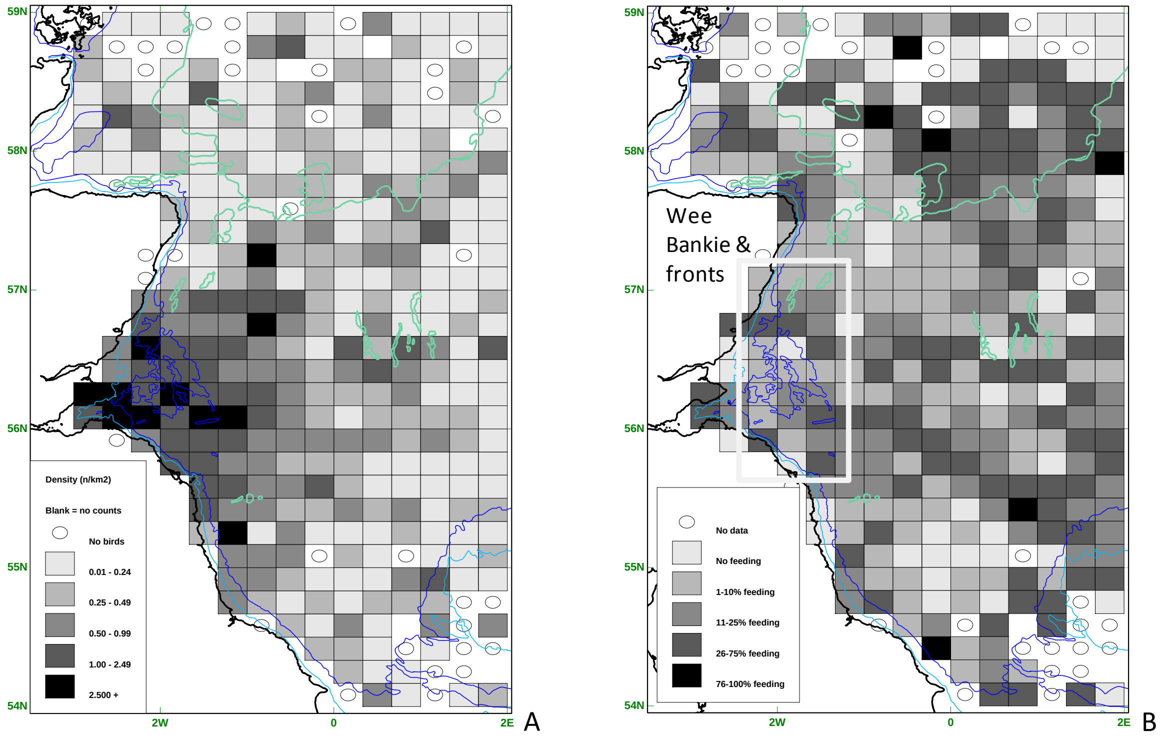


Fig. 13.1. A. Distribution pattern (n km^{-2} per 10'N x 20'E rectangle), and B. Proportion (%) of Gannets actively feeding around the Bass Rock (E Scotland, U.K.) in summer (June-July), based on ship-based surveys 1991-2004. Associations with fishing vessels excluded. A rectangle indicates the position of major fronts and Wee Bankie (see text); 30 and 50m depth contours are indicated.

A simultaneously conducted telemetry study confirmed that the entire range observed during ship-based surveys was indeed used by breeding birds originating from the Bass Rock colony. The maximum foraging range found was 540 km from the colony, and the mean furthest distance from the colony per trip was 232 km. Based on the assumption that Gannets feed throughout their foraging trips, Lewis et al. (2004) suggested that Gannets focused their foraging activity on areas that have characteristic bathymetric features and on tidal mixing fronts that were probably associated with high primary production. While the results indicated that birds searched for food in a wide range around the colony, all high-density areas, including those immediately around the Bass Rock, were interpreted as areas where foraging took place.

Lesser Black-backed Gulls at sea - Ship-based surveys revealed that during breeding, Lesser Black-backed Gulls off the Dutch coast were common within c. 40 km of the coast, with local clusters and peaks in abundance in response to feeding opportunities. Lower densities occurred at greater distances away from the coast (>40 km) and homing flights confirmed that breeding birds were also visiting the more distant areas (Camphuysen 1995a, Camphuysen *et al.* 2008). The distribution (densities) was patchy, largely as a result of large concentrations of birds recorded around fishing fleets (clumped distribution patterns, including actively feeding birds associated with fishing vessels and resting flocks that were engaged in a feeding frenzy at a trawler earlier on a survey day (Fig. 13.3). However, when naturally feeding behaviour (exact plots of plunge-diving in natural feeding concentrations of birds) was plotted, two rather discrete areas of ecological importance emerged: an area along the coast and within the 20m depth contour (influenced by eutrophic water from major rivers further to the south) and an area just beyond the 30 m depth contour in the north (the Frisian Front; a transition zone between mixed channel water and thermally stratified central North Sea water; Fig. 13.3). While using data on foraging behaviour, more ecologically relevant distribution data emerged than while using presence/absence data alone. These patterns were consistent over time.

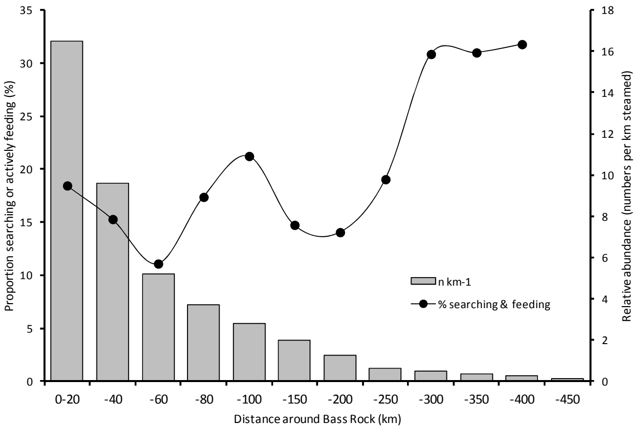


Fig. 13.2. Relative abundance (n km^{-1}; bars) of Northern Gannets and the fraction of actively foraging birds observed (%, line) with increasing distance from Bass Rock based on June-July ship-based surveys 1991-2004.

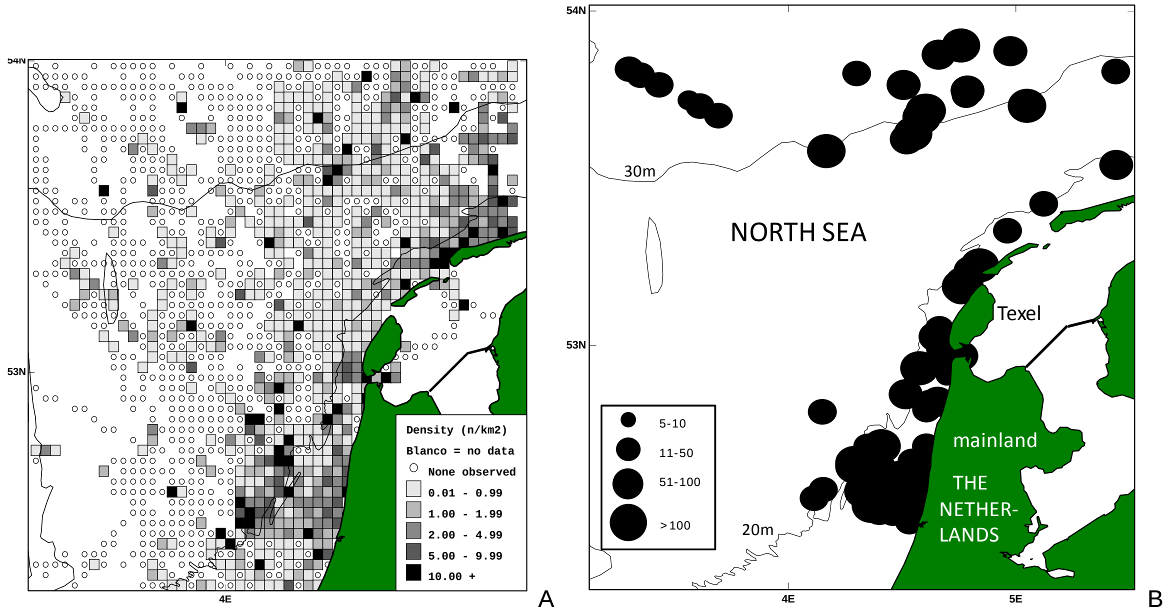


Fig. 13.3. (A) Abundance estimates of Lesser Black-backed Gulls at sea (densities per 2x3’ rectangle) and (B) plotted locations of natural foraging aggregations (dot size indicative of flock size) of Lesser Black-backed Gulls from ship-based seabird surveys in the southern North Sea, 1997-2008. In both subplots the 20m and 30m depth contours are shown.

The GPS tracking of actively breeding Lesser Black-backed Gulls revealed a fairly homogenous distribution pattern around the colony (Fig. 13.4). The maximum range and habitat utilisation (North Sea, Wadden Sea, mainland, the island Texel) were fairly constant between incubation and fledging, but was different in failed breeders (unusually long-distance trips occurred in the latter category). Active breeding birds spent a substantial proportion of time on foraging trips at sea (mean 34 % in females, 81% in males), but also foraged on land. The tracking data confirmed the frequent use of nearshore habitats, mostly to the south and southwest of the breeding colony. However, while a map of all tracks provides an indication of the spatial range of movements during breeding, there is no information on areas within that range that were of special ecological importance for the birds (Fig. 13.4). Again, higher abundance estimates were found nearer the colony, which is mainly the result of higher numbers of transient birds leaving and approaching the colony during feeding trips. Ground speed provided some indication if a bird was flying, stationary or floating on the sea surface, providing further insight into how an area was used (Shamoun-Baranes *et al.* 2011). More direct evidence of the locations of active feeding behaviour could in this case be derived from either the temperature of the device, or the accelerometer. Single trip examples in which either the temperature sensor (Fig. 13.5) or the accelerometer (Fig. 13.6) represented behavioural changes that indicate foraging activities are shown, to illustrate to potential of these instruments. By combining information on time and location with speed, temperature and/or acceleration, it can be determined where a bird is going, how long it spends in different places and what it is (likely) doing. By adding this information into the database, a quantitative analysis of (potential) feeding areas at sea is feasible.

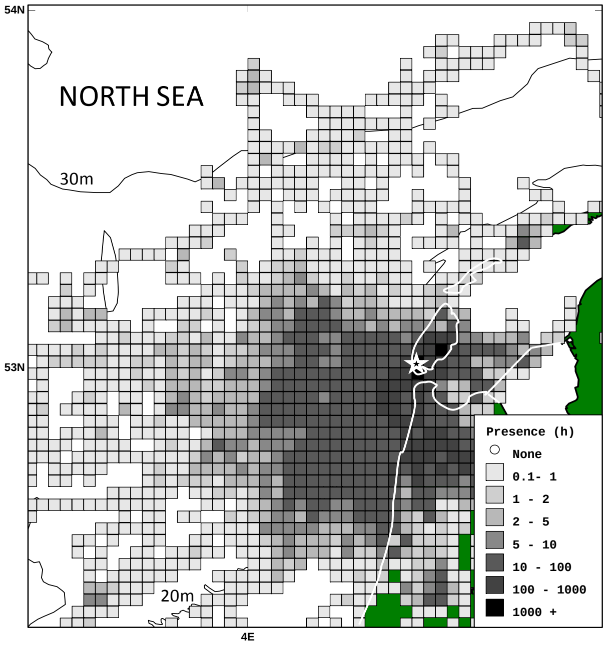


Fig. 13.4. Time spent (h) on foraging trips by Lesser Black-backed Gulls around the main breeding colony at Texel (asterisk), The Netherlands (southern North Sea), from GPS tracking studies in 2008-2010, summed for 2x3’ rectangles. Exact same area as in Fig. 13.3, but land “covered" with tracking data (coastline superimposed in white).

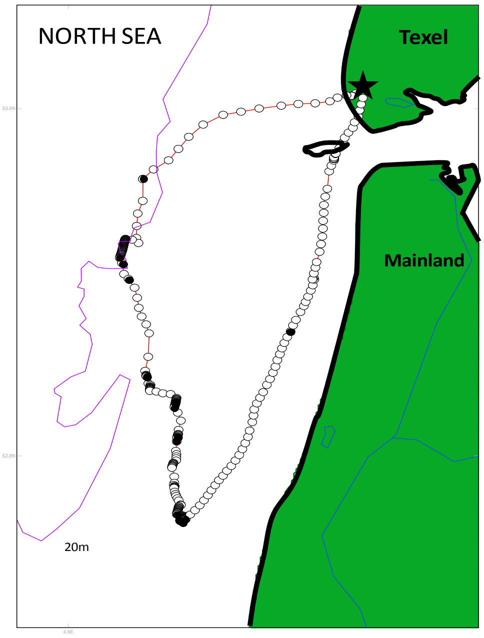


Fig. 13.5. Single foraging trip from the colony at Texel (asterisk). Circles indicate GPS positions recorded, abrupt drops in logger temperature caused by cold seawater on the logger are indicative of potential feeding bouts (solid circles). Green areas represent the mainland and Texel.

Discussion

In the past decades, ecologists have witnessed vast improvements in our ability to collect seabird movement and distribution data through aerial and ship-based surveys, through systematic observations of migrating birds from the shore and more recently through bird-borne technology, such as through GPS or ARGOS-satellite systems. However, more data does not necessarily yield more understanding of seabird ecology (Hebblewith & Haydon 2010). Within the North Sea, ship-based surveys have been designed *originally* to locate and quantify concentrations of seabirds that could be sensitive to sea surface pollutants, such as oil spills at sea (Tasker *et al.* 1984). Areas of high abundance were translated into areas of high sensitivity to oil spills when vulnerable taxa were involved, and researchers were most concerned with birds touching water (by either swimming or plunge diving; Carter *et al.* 1993). These same seabird distribution data were consulted in later years to enhance our understanding of ecologically important bird areas, even though the data had not been collected exactly for that purpose. The urgency to collect behavioural data simultaneously was realised only decades later (Camphuysen & Garthe 2004). Meanwhile, areas of high abundance were seen as areas of high (ecological) importance, and the first atlases identifying marine IBAs simply converted recorded densities into categories of 'general importance' to seabirds (Durinck *et al.* 1994, Skov *et al.* 1995).

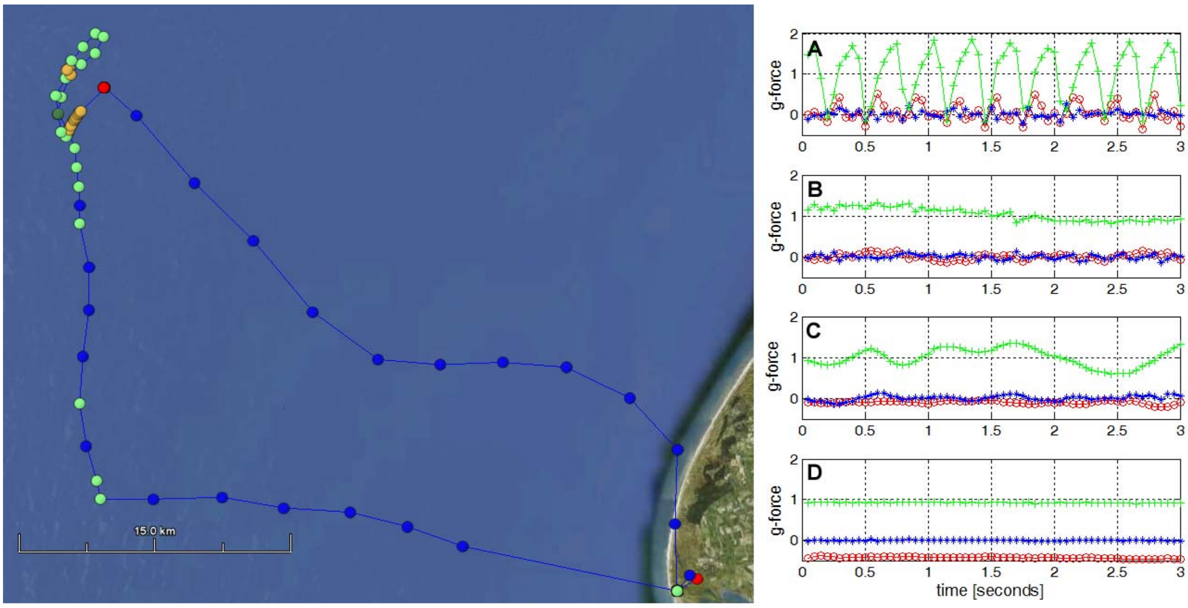


Fig. 13.6. Single foraging trip of Lesser Black-backed Gull leaving and returning to the colony at Texel, The Netherlands (southern North Sea), with typical accelerometer patterns representing specific behavioural features. In panels A-D acceleration (y axis) is shown in g-force and time is shown in seconds (x-axis), with heave, surge and sway represented by green, red and blue respectively. The following patterns are shown: (A) flapping flight, with a wing beat frequency of ~3.2 wing beats per second (blue symbols on map); (B) soaring flight (green symbols on map) (C) floating on the sea surface and bobbing in waves (yellow symbols on map), and (D) standing (red symbols on map). Potential feeding activities were exclusively recorded at the far NW end of the trip.

Case studies - The Gannet data described in this paper and published by Hamer *et al.* (2000, 2007) are clearly complementary. While both data sets are in agreement regarding the foraging range around the colony, information on the feeding activities of birds would require a more integrated analysis (in which the pros and cons of either method are evaluated) to reach firm conclusions. The combined results are promising, however, and regardless of whether or not the establishment of a marine protected area would be a sensible solution in Gannet conservation, the information on foraging activities would favour a different scenario than distribution data alone. Similarly, in a study of gannet colonies in eastern Canada (Montevecchi *et al.* 2012) different areas would be emphasized depending on how GPS and time depth data were analyzed. While all positional data acquired demonstrate general distribution patterns, different patterns were revealed when focussing on the areas where the birds were actually foraging (as measured by dives). From combined dietary analyses and investigations of prey presence the 'important' areas for gannets could be defined and understood much better (Garthe *et al.* 2007).

The data provided on Lesser Black-backed Gulls are also complementary in nature. The ship-based surveys, that included a behavioural module in the observation protocols, have been successful in outlining different areas of ecological importance (natural feeding concentrations in nearshore waters and in a frontal system north of the breeding colony; fisheries related distribution patterns elsewhere) potentially for multiple populations. The GPS loggers could illustrate which birds from a particularly large colony within that area utilised these foraging habitats. The frontal systems to the north of the colony, important feeding areas according to ship-based surveys, must have been exploited mostly by birds from other colonies or non-breeders. The information derived from temperature or accelerometer data on water contact, flight and rest will provide crucial further information on the at-sea activities and whereabouts of birds in tracking studies. Again, key areas identified on the basis of overall densities would be different from important areas based on densities plus behaviour: combining data leads to different and certainly more precise conservation proposals or management decisions.

Strengths and weaknesses of surveys and logger data - When designating and justifying marine protected areas, there is generally a need to know how many individuals use a particular area. One of the strengths of ship-based surveys is the capacity to estimate densities. However, densities may fluctuate due to factors such as resource availability, environmental conditions, or timing within the annual routine of individuals. Ship-based surveys should and can be repeated to at least account for inter and intra-annual environmental variability. Interpolation methods developed in recent years can be applied to reach standardised population estimates. In line with Camphuysen & Garthe (2004), we propose that behavioural data should always be collected as an integral part of seabird surveys with high priority. The European Seabirds at Sea database (ESAS database) was established to enhance the exchange of data between institutes and between countries and as a result large European sea areas have been mapped since the late 1970s. An integrated database, such as the ESAS database, can attract multiple users with diverse questions, and many users would profit from additional behavioural information stored in the database. While atlases tended to be based on presence/absence data, more recent publications increasingly focussed on offshore areas of ecological significance and the surveys that record seabird behaviour as part of the standard protocol have proven to be very valuable (Camphuysen & Webb 1999, Schwemmer & Garthe 2005, Camphuysen 2011d).

Seabird densities at sea are often influenced by other factors affecting the source population that are not directly observed in the survey area. Hence, information on where observed individuals are coming from is very useful. Information about the population source of the individual can be collected from individual tracking studies (satellite telemetry and GPS tracking). Individual tracking can provide information on what individual animals are doing and for how long. It can also provide information on how often birds visit specific areas in comparison to other areas. The benefits of deploying bird-borne technology for seabird research were appreciated first and foremost by ecologists working in seabird colonies. Radio-transmitters, satellite and GPS systems were used to reveal the generally unknown foraging areas of these species (e.g. Georges *et al.* 1997, Ropert-Coudert & Wilson 2005, Hamer *et al*. 2009). Later, a variety of sensors and even animal-borne cameras were attached to seabirds recording dive depth, temperature, prey ingestion, wing motion, speed, flight altitude and even underwater images (e.g. Ropert-Coudert & Wilson 2005, Rutz & Hays 2009). Accelerometers or other devices can be used to classify behaviour of tracked individuals. The down side of many of these studies was that the sample size was often small, the study period short, levels of individual specialisation of seabirds were often very high, and only a small subset of colonies was suitable to perform these studies, introducing a serious bias when sea areas have to be studied on large spatial scales, for example during the designation of a certain conservation status. Furthermore, initially, only large birds could be studied using such devices but technological improvements facilitated the development of much smaller devices so that now even much smaller seabirds can be instrumented. We may have overcome these problems now, or may do so in the very near future, now that more and more instruments are deployed.

Seabird densities from at-sea surveys as well as presence/absence indications from bird-borne loggers, without information about behaviour, can be misleading. In our examples, both tracking data and ship-based survey results point at high density areas near colonies. Here, in fact, the majority of the birds are only or mostly in transit; travelling to and from feeding grounds. A better notion of foraging whereabouts at sea, for example by logging feeding frenzies during surveys, or the areas where foraging behaviour is most frequently observed with birdborne devices, would give more exact indications as to where the designation of protected areas could be most effective. Protecting areas where MSFAs developed frequently would even be beneficial for a variety of seabirds, exhibiting different foraging techniques, rather than for a single species (Camphuysen & Webb 1999).

Ship-based survey and tracking data provided two distinct, yet complementary, perspectives of marine habitats (Louzao *et al.* 2009). Since tracking studies and ship-based surveys are often conducted independently it would be useful to merge these datasets to see if tracked individuals can be found in survey sites. When decisions have to be made, the specific qualities, opportunities but also shortcomings of either technique should be evaluated. Instrumented individual birds from one or more breeding colonies give no information about the whereabouts of the rest of the population: other breeding birds from nearby or distant colonies, non-breeding adult birds as well as immatures. Ship-based surveys can usually not be taken as conclusive for a specific breeding colony or for local breeding birds in general unless an isolated colony is studied (e.g. Leopold et al. 1995). Individual seabirds can be extremely site-specific and site-faithful. Distribution patterns at sea vary as a function of time of day, breeding stage, season, tide and natural and anthropogenic food availability, and data loggers are normally fully independent of observer effort (recording data also at night). Species interactions cannot (yet) be derived from logger data. With regard to important bird areas at sea, we would propose that natural foraging opportunities are a key issue to be addressed, as well as sea areas important for (flightless) moulting birds, given that most (on-land) breeding sites are now well protected.

Table 13.1. Pros and cons of different techniques used in this study to investigate the distribution of seabirds at sea for the designation of ecologically important marine protected areas. MSFA = multi-species foraging association.

	Densities at sea	Foraging range of breeding birds	Information related to breeding population	Information related to all birds at sea	Ecological significance (feeding area)	MSFAs, feeding associations, resources, biodiversity
Ship-based surveys – plain	**Very good**	Poor / indirect	Poor	**Very good**	Poor / indirect	Limited
Ship-based surveys + behaviour	**Very good**	Poor / indirect	Poor /limited	**Very good**	**Very good**	**Very good**
Satellite tracking plain	Very limited (sample size and representation)	**Very good**	**Very good**	Limited	Poor / indirect	Not known
Satellite tracking + time-depth recorder (only diving birds)	Limited (sample size and representation)	**Very good**	**Very good**	Limited	**Very good**	Not known
GPS logger + accelerometer	Limited (sample size and representation!)	**Very good**	**Very good**	Limited	**Very good**	Not known

Integration - Agardy (1994) stated that truly effective marine conservation will require conservation biologists to adapt a functional approach and direct their efforts to protecting key ecological processes that are responsible for maintaining specific marine structures. Such an approach requires more than collecting inventories, it requires insight into complex interactions at the individual, population and ecosystem levels. Integrating different observation and analytical techniques will facilitate this approach. Clearly each data source presented in this study provides information at different spatial and temporal scales but also at different levels of ecological significance, from the individual to the population. While each dataset has its own advantages and limitations (Table 13.1), we see great potential in combining these tools to provide a more complementary dataset that can be used to assess the ecological significance of different marine areas. Even the largest efforts dedicated to either of the methods cannot match the advantages from combining these different approaches. As most researchers have limited funds and generally cannot collect data from multiple sources directly, over long periods of time and for large samples, collaboration is essential. While the importance of collaboration is not new, a cyber-infrastructure for the collection, storage, exchange and joint analysis of heterogeneous datasets (in short e-science) is relatively new in ecology (Hey & Trefethen 2003; Halpin et al 2006; Coveney & Atkinson 2009) and can facilitate an integrative approach for conservation research.

Ship-based surveys of seabirds at sea, referred to above, in which the behaviour and the foraging interactions of seabirds and marine mammals were studied simultaneously have provided valuable insight in the exact role that species play in multi-species foraging associations (MSFAs). The constellations of feeding frenzies around trawlers were remarkably different from those in flocks of predators attacking more natural prey, even although the dominance hierarchies may have been similar (more powerful species taking larger prey and potentially outcompeting smaller species; smaller seabirds being more manoeuvrable and faster in obtaining relatively small, easily ingested prey). The significance of MSFAs for seabirds at sea has been described in a paper in which the role of Herring Gulls and Lesser Black-backed Gulls in feeding frenzies was touched upon as sideline:

Camphuysen C.J.[1*] & A. Webb[2] 1999. **Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment.** Ardea 87: 177-198.

[1]Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands, ***Correspondence author** e-mail: kees.camphuysen@nioz.nl; [2]Joint Nature Conservation Committee, Dunnet House, 7 Thistle Place, ABl0 1UZ Aberdeen, Scotland.

We studied the foraging distribution and the formation of multi-species feeding associations of seabirds and marine mammals off the British east coast. The local top-predator community comprised c. 34 species of seabirds, two pinnipeds and eight cetaceans. It appeared that multi-species feeding associations (MSFAs), with rather low species richness and diversity, were commonly formed around fishing vessels, were attracted by or otherwise associated with cetaceans (MSFAs with a generally low but more variable species richness and moderate diversity) and occurred over natural resources, apparently mainly fish shoals (MSFAs with the highest species richness and diversity). Small, short-lived MSFAs were the commoner type, particularly those over natural prey (sandeels and small clupeoids). Black-legged Kittiwakes acted as catalysts in these flocks, Common Guillemots and Razorbills as diving producers, apparently driving up fish towards the surface. The specific role of all other species joining in is described in general terms. MSFAs are prominent phenomena on the sea surface, guiding seabirds using visual cues for food finding. Secondly, the differentiation of feeding methods deployed in MSFAs may facilitate seabirds to reach prey that would otherwise be unavailable for them. The participation of scroungers in these flocks (e.g. Herring Gulls and Lesser Black-backed Gulls as common examples) normally ruined the MSFA formation in no time, because the disturbed auks gave up their synchronised feeding activities.

See also: Camphuysen C.J., B. Scott & S. Wanless 2006. **Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multi-species foraging assemblages and habitat-specific feeding strategies.** In: Boyd I.J., S. Wanless & C.J. Camphuysen (eds) Top predators in Marine Ecosystems: monitoring change in upper trophic levels: 82-97. Cambridge Univ. Press, Cambridge.

14. Mammalian prey in Laridae: increased predation pressure on mammal populations expected

Published **Lutra** 53: 5-20 (2010)

Kees (C.J.) Camphuysen[1], Peter de Boer[2], Willem Bouten[3], Arnold Gronert[1] & Judy Shamoun-Baranes[3]

[1]Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, the Netherlands, e-mail: kees.camphuysen@nioz.nl (corresponding author); [2]SOVON Vogelonderzoek Nederland, Rijksstraatweg 178, 6573 DG Beek-Ubbergen, The Netherlands; [3]Computational Geo-Ecology, Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, Nieuwe Achtergracht 166, 1018 WV Amsterdam, The Netherlands

Abstract The occurrence of mammalian prey in the diet of two species of large gulls, Laridae, was investigated in order to quantify and compare the predation on mammals from coastal and inland colony sites. Coastal nesting specialised individual birds and a majority of individuals in an inland colony were found to feed on mammals frequently. The encountered mammalian prey included Hedgehogs, shrews, voles, mice, moles, rats, Rabbits and Brown Hares. Most mammalian prey may have likely been obtained on inland fields, perhaps during ploughing or similar activities of farmers, some may have been captured within the colonies, and some will have been the result of scavenging at roadsides. Many coastal mainland colonies of gulls have recently collapsed as a result of persistent Red Foxes *Vulpes vulpes* predation. In addition, gulls breeding along the coast in the Netherlands increasingly suffer from shortages of food (mostly marine fish and intertidal invertebrates) during chick-rearing in recent years. Inland breeding did become more frequent and will further increase as a result of both factors, so that the gulls are expected to increasingly focus on alternative foraging habitats and prey species, mammals included.

Key words*: Apodemus sylvaticus, Arvicola terristris, Clethrionomys glareolus, Erinaceus europaeus, Lepus europaeus, Microtus arvalis, Microtus oeconomus, Mus domesticus, Oryctolagus cuniculus, Rattus norvegicus, Sorex araneus, Talpa europaea,* predation, Laridae, mammalian prey, diet

Introduction

Investigations into levels of predation of mammals would normally take the impact of raptors Falconiformes, owls Strigiformes, perhaps crows Corvidae, and certainly other (predatory) mammals into account (e.g. Lambin *et al.* 2000, Sundell 2002, Trout & Tittensor 2008). The reason why other potential predators have received much less attention could be that the mammalian part of their diets is considered to be trivial or at least insignificant. Recent work on the ecology of large gulls, generally considered omnivorous species (Cramp & Simmons 1983), has shown that this expected insignificance may not be true at all times or in all areas. For example, the food of coastal nesting Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus* in The Netherlands consists predominantly of tidal invertebrates and marine fish, but individuals from inland colonies can be completely terrestrial in their feeding habits (Spaans 1998ab). Camphuysen *et al.* (2006) showed that in one such case, a colony in Wormer & Jisperveld (Noord-Holland), juvenile meadow birds and in particular various species of mammals were in fact highly important prey.

Gull populations in The Netherlands are in a state of flux, both with regard to breeding numbers as with respect to their breeding distribution. Until recently, Herring gulls and Lesser Black-backed Gulls in The Netherlands were exclusively breeding in (large) colonies near the coast. Colonies of both species, that were established in dune areas along the mainland North Sea coast, have suffered from persistent predation by Red Foxes *Vulpes vulpes* since the mid-1980s and particularly in the 1990s, and many breeding areas were abandoned (Bouman *et al.* 1991, Spaans 1998ab). The species started nesting on buildings in towns up to 25 km from the coast and in other inland locations. Further and deeper inland breeding colonisations have occurred since (Hustings & Vergeer 2002, Poot 2008). On top of this: recent ecological studies have shown that coastal nesting Lesser Black-backed Gulls are increasingly facing food shortages during chick-rearing and experience currently very low breeding success (Camphuysen *et al.* 2008ab). The shortage of food is seemingly worsened by a decline in fishing fleet size and novel (more sustainable) fishing techniques, so that further inland colonisations may be expected in the near future. With a significant proportion of mammalian prey in inland breeding gulls, this could lead to a forecast for an increasing predation pressure on mammalian populations.

This contribution evaluates our current understanding of the dietary preferences of coastal nesting and inland breeding large gulls with regard to mammalian prey on the basis of recent diet studies. Which mammal species are taken, where and how could they be captured and what levels of dietary specialization were found to date are questions underlying the analysis. From the analysis we will speculate on possible changes in predation pressure on certain mammal populations as a result of the ongoing colonisation of inland breeding habitats by large gulls.

Methods

Foraging distribution and behaviour were assessed during direct field observations (1986-2009), from an analysis of colour-ringed Herring Gulls (Camphuysen *et al.* in press & unpubl. data; 1986-2009), and from high resolution positional data obtained with GPS-loggers on individual Lesser Black-backed Gulls (2008-2009). The diet was studied on the basis of food remains found in three breeding colonies (2005-2009):

Kelderhuispolder (Texel) – A well-established, mixed colony with Herring Gulls and Lesser Black-backed Gulls, studied since 2006, at the southern tip of Texel (Noord-Holland; 53°00'N, 04°43'E). Prior to egg-laying (mid-April) the colony was visited with increasing frequency along a preset trail through various study plots, leading through prime Herring Gull and Lesser Black-backed Gull habitats. Nests were marked with a numbered wooden pole. Randomly chosen groups of nests were fenced off with an enclosure, in order to monitor chicks until fledging. Diets were studied mainly from spontaneously regurgitated matter (pellets, large chunks of regurgitated matter, partly eaten food remains), from food boluses produced during handling of the birds, from chick-feeds sub-sampled within the territories and from stomach contents of animals found dead. During each of the nest visits, territories were inspected for the presence of discarded prey items, and each of the items was individually bagged, numbered, and kept frozen for later analysis. Food samples were collected from marked territories from the pre-laying phase until and including the fledging period (April to August), 2006-2009. The nesting stage was characterised for each individual marked territory, using the following terms: Pre-laying, Laying, Incubation, Hatching, Chick care, Fledging, or Predated. To enlarge the sample of prey-remains, colonies and associated club-sites were searched for pellets and prey remains at regular intervals of time. For these food samples, breeding stages were termed in accordance with the breeding stage of the majority of the monitored nests.

Vliehors (Vlieland) – A well-established, mixed colony of the same two species, in a dune valley of the Vliehors area (53°14'N, 04°55'E), studied irregularly since 2006 by SOVON. Food samples from marked territories of Herring Gulls were collected in 2006, stored in a similar way as described earlier, and analysed at NIOZ in 2008. The samples could in this case not be related to the breeding stage of the predators.

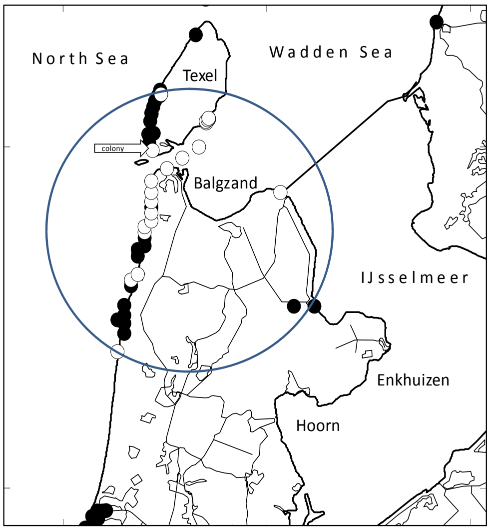


Fig. 14.1. Presumed main foraging range (based on colour-ring sightings) of Herring Gulls from Texel. Black dots are birds ringed as chicks 1986-1988 and seen as adults in summer since 1991, white dots are birds ringed as breeding adults in 2006-2009 and seen in summer. The arrow points at the colony location.

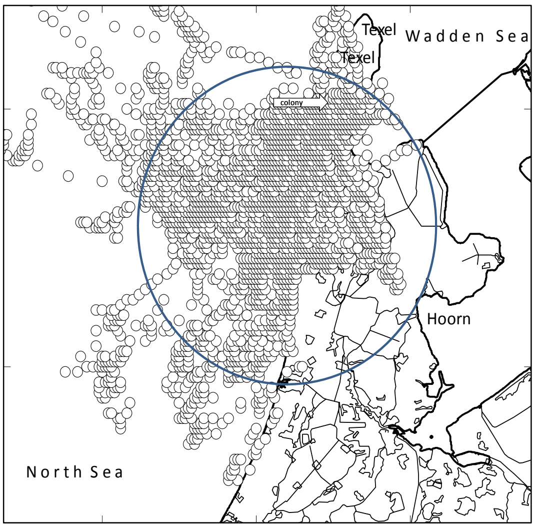


Fig. 14.2. Main foraging range based on GPS positions of Lesser Black-backed Gulls from Kelderhuispolder, Texel. White dots are simplified (rounded) positions of birds tagged with GPS loggers in 2008. The arrow points at the colony location.

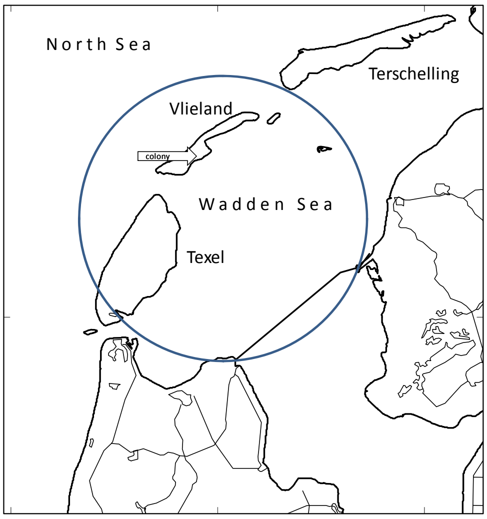


Fig. 14.3. Presumed main foraging range (based on Argos satellite tags) of Herring Gulls from Vlieland. Underlying data are not presented (see for details:

http://www.sovon.nl/default.asp?id=408)

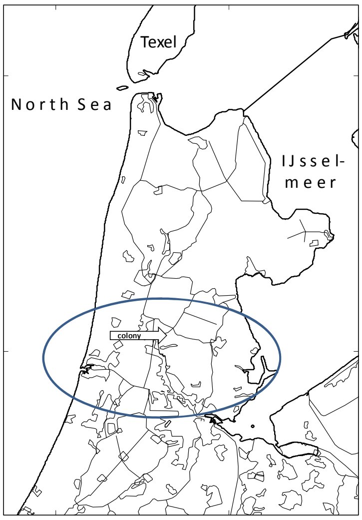


Fig. 14.4. Expected foraging range based prey items (marine discarded fish, pelagic shoaling fish, meadow birds, waterfowl, terrestrial mammals and freshwater fish) of Lesser Black-backed Gulls nesting in Wormer- & Jisperveld.

Wormer & Jisperveld (Noord-Holland) – A colony of Lesser Black-backed Gulls, situated in a nature area covering 18 km² (of which 0.7 km² is a protected area owned by Natuurmonumenten), between the towns De Rijp, Purmerend and Wormerveer (Noord-Holland; 52°31'N, 04°50'E). The area consists mainly of marshland, grassland and open fresh water channels and is situated at c. 15 km from the North Sea coast. Lesser black-backed gulls colonised the area in 2000 and the breeding population is rapidly increasing (Camphuysen *et al.* 2006). The site was visited and searched for regurgitated prey during three successive visits in 2005 (Camphuysen *et al.* 2006). All samples were taken during chick care from otherwise unmarked, non-monitored territories.

Table 14.1. Food samples analysed in search of mammalian prey in colonies of Lesser Black-backed Gulls (LBBG) in Wormer & Jisperveld and at Texel (Kelderhuispolder), in colonies of Herring Gulls (HG) at Texel (Kelderhuispolder) and Vlieland. Some prey samples were from a hybrid gull pair on Texel or from unidentified predators (Lesser Black-backed *or* Herring Gulls).

Species	**Location**	**chickbolus**	**chickfeed**	**pellet**	**regurg**	**bolus**	**stomach**	**territory**	**faeces**	***n***
LBBG	Wormer & Jisperveld			156				4		160
	Kelderhuispolder, Texel	205	253	3379	151	77	79	16	2	4162
Hybrid	Kelderhuispolder, Texel		3	5						8
spec	Kelderhuispolder, Texel			17	148	5		1	4	175
HG	Kelderhuispolder, Texel	120	686	2782	149	42	48	68	9	3904
	Vliehors, Vlieland		2	193		3				198
		325	944	6376	448	127	127	85	15	8447

Food sampling - The total number of food samples analysed, including 4322 samples for Lesser Black-backed Gulls, 8 for a hybrid pair, 175 for unidentified large gull, and 4102 for Herring Gulls are listed in Table 14.1. Prey items were defrosted, sorted and analysed under a Olympus ZN51 binocular microscope (8-40x magnification) in order to find even minute prey items. Mammalian remains were usually identified with Husson (1962) or Kapteyn (1999), occasionally by using ordinary field guides. Dental aspects, specific bones or external characteristics (claws, spines, fur), and sometimes even intact mammals could be found in regurgitated prey remains.

Foraging distribution and habitats - Unique colour-ring combinations or codes were used to individually identify birds within and outside the colonies (for details see Camphuysen 2008c; example on photo). Most ring-readings outside the colonies were by volunteers (amateur bird-watchers mostly), whereas within colonies the presence of ringed individuals was monitored as part of the overall research. Summer sightings (Apr-Aug) of colour-ringed adult birds around the natal colonies were used to assess the foraging range during breeding. Some Herring Gulls from Vlieland were fitted with colour-rings but also with Argos satellite transmitters in 2007 and 2008 (Ens *et al.* 2009). Results were downloaded from the internet to evaluate likely foraging areas in summer (http://www.sovon.nl/default.asp?id=408; accessed 28 October 2009).

For Lesser Black-backed Gulls, where colour-ring data are less useful, the foraging range and feeding habitats were deduced from GPS uploads obtained in two consecutive breeding seasons (2008-2009). Five (2008) and six (2009) breeding adults respectively were harnassed and fitted with a 17g GPS-logger, designed and developed by the Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam. Data were remotely downloaded from a base station erected within the colony and data-resolutions could be freely varied (via remote instructions) from one geographical position each three seconds at the highest rate to lower rates in order to save energy. Downloaded data were plotted on a Google Earth background, to obtain information on habitats and specific habitat-related activity patterns.

Results

Foraging range and feeding habitats - Herring gulls colour ringed at Texel were during the breeding season mostly re-sighted within 40-50km to the south of the colony (i.e. the northern part of Noord-Holland and the southern tip of Texel). The sightings were mostly confined to coastal sites, which is likely a reflection of observer effort rather than true distribution (Fig. 14.1). The entire range of the species in the northern part of Noord-Holland is characterised by the frequent, albeit irregular occurrence of feeding frenzies in nearshore waters, in the intertidal zone, on agricultural land, in cities, in sewage treatment centres and on various other locations. Few of these situations are suitable for consistent ring-reading. Herring Gulls from Vlieland with satellite tags were mostly utilising breakwaters at Vlieland and mudflats to the south and southwest of the island. The northern half of Texel fell well within their foraging realms (SOVON unpubl. data).

Colour-rings are a less suitable method to assess the foraging distribution of true seabirds, such as Lesser Black-backed Gulls, but GPS logger data revealed that terrestrial feeding habitats are visited by most, and virtually exclusively by some specialist birds (Fig. 14.2). The normal foraging range of tagged birds from Texel amounted to 40-80km to the south and southwest of the breeding colony at Texel. Terrestrial feeders often crossed the Marsdiep and entered mainland Noord-Holland through the Den Helder area, whereas return flights were mostly gliding flights along the dunes. Inland potential feeding areas were visited south to Hoorn (Noord-Holland) on regular feeding trips.

During the breeding season, Herring Gulls nesting on Vlieland were mostly found foraging at breakwaters on the beach, on intertidal mudflats to the south and southeast of the island, on the northern half of Texel and along the Afsluitdijk, a long barrier separating the Wadden Sea from the IJsselmeer (Fig. 14.3). There was relatively little evidence for terrestrial feeding from these satellite tracking data (http://www.sovon.nl/default.asp?id=408).

Lesser black-backed gulls nesting within the Wormer- & Jisperveld colony were ringed nor tagged and there is therefore no empirical data to assess their foraging range. The frequent occurrence of marine fish, the simultaneous (and frequent) occurrence of freshwater fish species and the overwhelming abundance of terrestrial prey in the form of mammals and birds would indicate that, centred around the colony, a considerable inland area, and some parts of the North Sea and the IJsselmeer were within normal feeding range (Fig. 14.4).

Individual tracks of Lesser Black-backed Gulls carrying GPS loggers demonstrated the frequent use of coastal but also inland roosts in Noord-Holland and on the south tip of Texel as well as the frequent use of inland fields for roosting and foraging. Linear patterns in tracks over agricultural areas suggested that the animals were following either linear structures (in a deep ploughed field for example), or a machine working the fields (Figs. 14.5-8). The logger data confirmed suggestions that Texel birds frequently joined inland concentrations of large gulls roosting or foraging in the northern part of Noord-Holland. There was little evidence for frequent use of land areas to the north of the breeding colony (i.e. most of Texel), but some gulls, incidentally, foraged on the island.

Table 14.2. Frequency of mammalian prey in food samples (see Table 14.1) of Lesser Black-backed Gulls (LBBG) in Wormer & Jisperveld and at Texel (Kelderhuispolder), in colonies of Herring Gulls (HG) at Texel (Kelderhuispolder) and Vlieland. There were no mammalian prey found in a hybrid gull pair on Texel, but for some the predator (Lesser Black-backed or Herring Gulls) remained unidentified.

	Location	**chickbolus**	**chickfeed**	**pellet**	**regurg**	**bolus**	**stomach**	**territory**	**faeces**	**Total**	**Mammalian**
LBBG	Wormer & Jisperveld			70				2		72	45.0%
LBBG	Kelderhuispolder		2	30	2					34	0.8%
Hybrid	Kelderhuispolder									0	
spec	Kelderhuispolder			2						2	
HG	Kelderhuispolder		4	77	2			3		86	2.2%
HG	Vlieland			2						2	1.0%
		0	6	111	4	0	0	3	0	124	1.5%
	mammalian (%)		0.6%	1.7%	0.9%			3.5%		1.5%	

Dietary composition - Mammalian prey remains were most commonly found in pellets, as regurgitated matter within territories (idenfied as either ‘chickfeed’, or ‘regurgitated matter’ or within territory samples of a mix of indigesitable prey remains labelled as ‘territory’; Table 14.2). Only a few hundred boluses (freshly regurgitated matter during handling) were examined, and mammalian prey were just never encountered. Because of the sheer number of pellets collected in each of the colonies, the analysis will therefore focus on these as a source of information. With pellets being the most readily available source of information in all study areas and (in all seasons), the quantification of the entire dietary spectrum was based on these data only (Table 14.3).

Table 14.3. Frequency of occurrence (n, %) of main prey types in pellets, as the most readily available and common source of dietary information in all study colonies. Worms include terrestrial, marine and parasitic types, Mollusca include gastropods (terrestrial and marine), bivalves and cephalopods (both marine), and under Fish both marine and freshwater types are included.

	Lesser Black-backed Gull				**Herring Gull**			
	Kelderhuispolder		Wormer & Jisperveld		Kelderhuispolder		Vliehors	
Group	n=	%	n=	%	n=	%	n=	%
Insects	609	18.2	6	3.8	245	8.9	13	6.7
Spiders	3	0.1		0.0	4	0.1		0.0
Worms	633	18.9	31	19.9	83	3.0	5	2.6
Mollusca	116	3.5	1	0.6	2036	74.0	127	65.8
Crustaceans	746	22.3	6	3.8	374	13.6	97	50.3
Fish	2741	81.8	30	19.2	596	21.7	54	28.0
Birds	227	6.8	33	21.2	252	9.2	2	1.0
Mammals	30	0.9	70	44.9	76	2.8	2	1.0
Plants	450	13.4	4	2.6	293	10.7	5	2.6
Seaweeds	1	0.0		0.0	10	0.4	1	0.5
Human waste	192	5.7	5	3.2	350	12.7	3	1.6
Miscellaneous	151	4.5	3	1.9	393	14.3	28	14.5
n=	3349		156		2750		193	

The dietary composition and the frequency of occurrence of mammalian prey was rather different between colonies (Texel and Vlieland as coastal colonies versus Wormer & Jisperveld as inland colony), and slightly different between species within colonies (Texel; Table 14.2). The food samples collected at the inland colony (45% of which with mammalian prey) are clearly different from those collected in colonies situated in coastal areas. Mammalian prey were fairly insignificant in Herring Gulls from Vlieland (1.0%, n= 193) and in Lesser Black-backed Gulls from Texel (0.9%, n= 3349), more substantial in Herring Gulls from Texel (2.8%, n= 2750) and very important in Lesser Black-backed Gulls from Wormer- & Jisperveld (44.9%, n= 156).

Within colonies at Texel, high levels of individual dietary specialisation could only be recognised in Herring Gulls. During four consecutive seasons, 2006-2009, 1039 pellets were collected at 231 individual Lesser Black-backed Gull nest sites. Mammalian prey were found on 8 sites (3.5%), whereas 11 of the pellets at individual nest sites (1.1%) contained mammalian prey. At the sites where mammalian prey were found at least once (n= 8), an average (± SD) of 1.38 ± 0.7 pellets (max 3) with mammal remains were picked up. The exceptional Lesser Black-backed Gull site with 3 pellets containing mammalian prey was found to provide two species of voles (Bank Vole *Clethrionemys glareolus* and Root Vole *Microtus oeconomus*).

In Herring Gulls in the same colony and years, 2399 pellets were collected at 225 individual nest sites. Mammalian prey were found on 25 sites (11.1%), whereas 72 of the pellets at individual nest sites (3.0%) contained mammalian prey. At the sites where mammalian prey were found at least once (n= 25), an average (±SD) of 2.88 ± 5.2 pellets (max 26 pellets with mammalian prey at a single site) with mammal remains were picked up. Five Herring Gull sites with more than 2 pellets holding mammalian remains included:

- ZM120, a territory marked in 2007, 26 pellets containing mammalian remains; all Rabbits *Oryctolagus cuniculus*.
- ZM201, 2008, 10 pellets, Rabbits (7), Brown Rats *Rattus norvegicus* (2), and unidentified mammals (1)
- ZM023, 2006, 4 pellets, Rabbit (1), Root Vole *Microtus oeconomus* (2), and Brown Rat (1)
- ZM261, 2008, 4 pellets, Rabbit (1), Root Vole (2), and House Mouse *Mus musculus* (1) and with Rabbit (1) and Brown Rat found in chickfeed samples
- ZM035, 2006, 3 pellets, Rabbits (2) and Root Vole (1)

A brief description of prey items, the type of remains and the frequency of occurrence for each of the main groups of mammalian prey:

Hedgehogs - European Hedgehogs *Erinaceus europaeus* were found twice in pellets near two different Herring Gull territories at Texel, both in 2008 (3 June and 25 July, Entry Dunes, Kelderhuispolder colony). The first sample contained a skull and teeth plus smaller fragments, the second pellet contained spines, bones, teeth and vertebrae. The remains were indicative for scavenged carcasses of mature Hedgehogs, rather than for prey swallowed whole (e.g. Hedgehog cubs). A scavenged carcass of a fully grown European Hedgehog was found 14 May 2007 right in the middle of the colonies near a Herring Gull club site. This find was not included in the diet studies and it must have been an animal that was either found dead or killed by gulls within the colony, rather than transported through the air.

Shrews - The Common Shrew *Sorex araneus* was the sole representative of this group and there was only a single occurrence of this species: Wormer & Jisperveld, Lesser Black-backed Gull, 23 June 2005 (complete regurgitated skeleton recovered). This prey item was found at a nest site of a bird clearly specialised in waterfowl and meadow birds (Mallard *Anas platyrhynchos* 2x, Lapwing *Vanellus vanellus* 1x, Black-tailed Godwit *Limosa limosa* 11x, and Redshank *Tringa totanus* 4x).

Species	Wormer & Jisperveld	Kelderhuispolder
Sorex araneus	1	
Talpa europaea	24	2
Arvicola terristris	8	1
Clethrionomys glareolus		1
Microtus arvalis	8	
Microtus oeconomus	2	10
Microtus/Arvelicola	21	10
Apodemus sylvaticus		1
Rattus norvegicus		1
Lepus europaeus	9	
Oryctolagus cuniculus	1	5
unidentified mammal	2	5

Table 14.4. Mammalian prey of Lesser Black-backed Gulls at Wormer & Jisperveld and in Kelderhuispolder at Texel (shown are total number of prey samples with each species represented).

Species	Kelderhuispolder	Vliehors
Erinaceus europaeus	2	
Talpa europaea	2	
Microtus oeconomus	7	
Microtus/Arvelicola	3	
Mus domesticus	2	
Rattus norvegicus	5	
Oryctolagus cuniculus	50	1
mice droppings	5	
unidentified mammal	10	1

Table 14.5. Mammalian prey of Herring Gulls in Kelderhuispolder at Texel and at Vliehors, Vlieland (shown are total number of prey samples with species represented).

Moles - The European Mole *Talpa europaea* was a common prey of inland nesting Lesser Black-backed Gulls (Wormer & Jisperveld, 24 (33%) out of 72 samples containing any mammalian prey; 15% of all 160 prey samples analysed for that colony). Many of the pellets with remains of European Moles contained some pitch-black fur and a subset of mole-bones, the humerus and jaws or skulls of which were used to assess the number of individuals taken. Single mole remains were spread over two individual pellets on at least two occasions. European Moles were found only incidentally in the Kelderhuispolder colonies, with two prey remains of Herring Gulls (2 out of 86 samples with mammalian prey; Table 14.4) and two further regurgitated parts of moles that could not be attributed to a particular gull species. There were few or no other prey species encountered in most “mole-pellets”, suggesting that the animals were swallowed whole and formed a near-complete meal prior to pellet production. However, one pellet from Texel contained remains of a mole, marine fish and Coleoptera (a mix of marine and terrestrial feeding activities) and at least two pellets from Wormer- & Jisperveld contained remains of marine fish next to skeletal parts and fur of European Moles. European Moles formed no more than a tiny fraction of prey types found in these coastal nesting gulls. Apart from the food samples collected, mummified remains of European Moles were found occasionally in and around the Texel colonies (moles do not occur naturally on the island); not attributed to a particular gull species.

Voles - At least four species were found: water vole *Arvicola terristris*, Bank Vole, common vole *Microtus arvalis*, and the endemic Root Vole *M. oeconomus arenicola*. Water voles were only found in pellets produced by Lesser Black-backed Gulls, including 8 samples (5%) from the inland colony Wormer- & Jisperveld (2005), and a single sample (0.02%) from Texel (2007). Common voles were exclusively found in the Wormer- & Jisperveld colony (200%), again being represented in 8 different samples (5%). The endemic Root Vole was represented in food samples from both gulls, including positive identifications in two samples from Wormer & Jisperveld (1.3%), 10 samples from Lesser Black-backed Gulls on Texel (0.2%), and 7 samples from Herring Gulls in that colony (0.2%). On Lesser Black-backed Gull pellet from Texel contained 4 lower jaws of Root Voles, but the other samples were all indicative for no more than a single vole in each. The Bank Vole was only once positively identified in a pellet from a Lesser Black-backed Gull at Texel (an intact individual regurgitated as chickfeed and rejected by the offspring, 20 July 2007). Unidentified voles were found in 21 samples (13.1%) from Lesser Black-backed Gulls in the Wormer- & Jisperveld colony and in 10 samples from Texel (0.2%), whereas only three pellets of Herring Gulls from Texel were found to contain unidentified voles (0.08%).

Mice - True mice were rarely encountered. A single Wood Mouse *Apodemus sylvaticus* was found in a pellet produced by a Lesser Black-backed Gull at Texel during laying (10 May 2009), while the House Mouse *Mus domesticus* was recorded twice, both from Herring Gulls pellets produced during egg-laying in May 2007 and May 2008 at Texel. All three mice were swallowed whole and the pellet contained most of the skeleton, teeth, and fur.

Rats - Brown rats *Rattus norvegicus* were found in Herring Gulls pellets collected at Texel in June 2006, June 2007, and May and June 2008 (laying, incubation, and chick-care), and in a single pellet produced by a Lesser Black-backed Gull in the same colony (May 2008, pre-laying). Within the colony large parts of rats were found occasionally, as rejected prey remains, not clearly associated with territories. Within pellets, teeth and bones were used for identification, while (grey) fur and nails were frequently encountered. Three of the 'mammal specialist' Herring Gulls produced pellets with remains of rats, which is a high representation given the small number (five) of pellets with rats found in the colonies as a whole.

Brown Hares and Rabbits - Brown Hares *Lepus europaeus* were found frequently (5.6% of all samples, n= 160), but exclusively, in the inland colony of Lesser Black-backed Gulls at Wormer- & Jisperveld. In most cases, some remains (mostly hind legs) were retrieved, of a size and with a bone structure suggesting that mostly very young individuals were taken and transported into the colony. A single Rabbit *Oryctolagus cuniculus* was retrieved in that same colony, but a mis-identification cannot fully be excluded in this case. Rabbits were common as prey for Herring Gulls in Kelderhuispolder (50 samples, 58% of all food samples of Herring Gulls with mammalian prey, 1.3% of all food samples), were occasionally found in food samples from Lesser Black-backed Gulls in the same colony (15% of all samples with mammalian prey, 0.1% of all food samples) and Rabbits were represented in the smaller sample of food samples collected at Vlieland (Table 14.4). Two Herring Gulls at Texel had clearly specialised on Rabbits (see above), and one produced at least 26 pellets with remains of Rabbits in one breeding season. This particular individual produced owl-like pellets, compact prey-remains, containing mostly fur and splintered bones. Young Rabbits (bone structure) were clearly represented, but ageing was not always possible.

Fig. 14.5. Foraging trips into mainland Noord-Holland of a Lesser Black-legged Gull with GPS logger from Kelderhuispolder, Texel. Dots represent individual GPS uploads.

Fig. 14.6. Foraging trips to agricultural land on Texel of a Lesser Black-legged Gull with GPS logger from Kelderhuispolder, Texel. Dots represent individual GPS uploads.

Fig. 14.7. Foraging activity on a field at Texel of a Lesser Black-legged Gull with GPS logger from Kelderhuispolder, Texel. Dots represent individual GPS uploads.

Fig. 14.8. Foraging activity and roosting (cluster on the right) on fields in mainland Noord-Holland of a Lesser Black-legged Gull with GPS logger from Kelderhuispolder, Texel. Dots represent individual GPS uploads.

Unidentified mammals - Most unidentified mammals were small rodents (voles or mice) or shrews, given the small bones and short fine fur encountered in Lesser Black-backed Gull pellets from Wormer- & Jisperveld (2x) and Kelderhuispolder (5x) and in pellets from Herring Gulls from the latter colony (9x). One Herring Gull pellet contained hairs of a large mammal (horse, deer?), while a single pellet found on Vlieland contained flesh and fur of an unknown mammal. Mice droppings (or at least droppings of small mammals) were found in 5 samples of Herring Gulls from Kelderhuispolder. While sample contamination might be expected in these cases (droppings from mammals scavenging regurgitated prey remains), it was the embedding of droppings within pellets that led us to believe that indeed the droppings were part of the regurgitated material.

Mammalian prey and breeding phase - For the Kelderhuispolder colonies, prey samples could be arranged according to breeding stage. The predators, Herring Gulls and Lesser Black-backed Gulls, produced a mirror image in frequency of occurrence of mammalian prey (Fig. 14.9), with high frequencies prior to egg laying in Herring Gulls, but rather few mammals in food samples in Lesser Black-backed Gulls in that period. Relatively high frequencies of mammalian prey were found during incubation and hatching in Herring Gulls, whereas Lesser Black-backed Gulls did not produce a single pellet with mammals during egg-laying and had relatively high frequencies during chick-care (hatching – fledging).

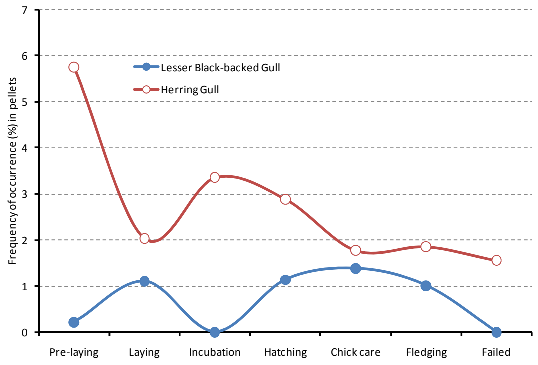


Fig. 14.9. Frequency of occurrence (%) of mammalian prey through the breeding season in pellets collected from Lesser Black-backed Gulls and Herring Gulls, Kelderhuispolder, Texel, 2005-2009.

Discussion

The importance of mammalian prey - The proportion of mammals in prey samples obtained in different colonies was strikingly different. The colony in Wormer- & Jisperveld, where 45% of the collected prey samples were found to contain mammalian prey, is situated at c. 15 km from the North Sea coast. Lesser black-backed gulls colonised the area in 2000 and the breeding population is rapidly increasing (Camphuysen *et al.* 2006). With a 40km foraging range around the breeding locality (not measured by anyone, but assumed from the feeding range in other colonies; Fig. 14.4), a large part of agricultural land in Noord-Holland is within reach as a potential feeding area. The large numbers of meadow birds, moles and voles indicate that the birds forage frequently on land, possibly in the immediate surroundings of the colony. The presence of marine fish and freshwater fish, however, shows that other habitats, including the open sea, are exploited simultaneously.

For gulls nesting in coastal colonies, the level of utilisation of inland foraging opportunities was until now much less clear. In an earlier study, Spaans (1971) demonstrated the abundant use of (uncovered) refuse dump sites in the provinces Friesland and Drenthe by Herring Gulls nesting at Terschelling, but found little evidence for other abundant terrestrial prey items, apart from insects. European Mole, Wood Mouse, and voles (*Microtus arvalis* or *M. agrestis* and *M. oeconomus*) were listed as rare, incidental prey species on Terschelling, while juvenile Rabbits were frequently encountered in years that Rabbits were abundant on the island. It was unclear whether most mammalian prey was locally obtained prey or prey flown in from the mainland. New data, including information derived from colour-ringed individuals and in particular the GPS logger data have demonstrated that some particular individuals from coastal colonies do in fact forage deep inland, at least occasionally. The data obtained at Texel, where the mole does not naturally occur, provide further evidence that at least some of the mammalian prey is flown into the colonies from abroad (in this case most likely from the Noord-Holland mainland). GPS logger data (Lesser Black-backed Gulls from Texel) and Argos satellite tracking data (both gull species from Vlieland) seemingly confirm (further analysis is required) that individual birds are highly faithful to particular foraging-sites or feeding habitats. Mammalian prey in coastal breeding lesser black backed gulls is currently rather rare, while it is slightly more frequent in Herring Gulls from Texel. The Herring Gulls from Vlieland (note small sample size) were near-completely focussed on intertidal, marine prey.

The food samples provide information on the prey species and also to some extent on the age composition of mammalian prey. The underlying data are evidently biased, because swallowed whole prey are more likely to be retrieved from pellets (compact assemblages of indigestible remains) than for example fleshy bits scavenged from a road-kill. By using frequencies of occurrence and a similar methodological approach between colonies and different predator species, even although actual levels of predation may be incorrect (likely too low), apparent patterns in the utilisation of mammalian prey can still be evaluated.

Where and how would mammalian prey be obtained - One could often only speculate as to where and how these prey were obtained. One important question would be: are they actively hunted, or is mammalian prey mostly taken by scavengers utilising carcasses found during foraging. In fact, (1) the prey may have been dead when utilised (scavenging behaviour), (2) it may have been sick or otherwise immobilised or slow and therefore more readily available, (3) the prey may have been (suddenly) uncovered and made available by for example human action (during ploughing fields or otherwise; aerial or ground pursuit behaviour), or (4) the prey could be captured alive by actively hunting gulls (active pursuit). Finally, mammalian prey could be stolen from or found as leftovers from other predators (for example from raptors or crows). Stealing from other, more specialised predators is a common phenomenon in such areas (Barnard & Thompson 1985). Very few actual field observations exist, except the frequent occurrence of scavenging gulls along roads (road-kill utilisation). Most actively foraging gulls in agricultural areas (including meadows) are birds trampling for worms, birds competing for prey behind machines working these areas, or birds searching for prey while walking in recently worked or fertilised fields. It is difficult, certainly in the absence of direct observations, to speculate about the actual origin of the retrieved mammalian prey items. Herring and Lesser Black-backed Gulls are powerful animals, known to attack and kill surprisingly large prey at times (e.g. Camphuysen *et al.* 2009). Gut-feelings would suggest that mature and healthy Brown Hares and Rabbits are far too large and strong to be attacked, but for young or sick or weakened animals, this might be very different.

Some prey may be identified as “local prey”, including animals that may be available within the colony or within the immediate surroundings of the breeding site, other prey may require more travel to obtain. Rabbits as prey at Texel tended to fluctuate in accordance with presence (from sightings) within the colony area, even though exact data were not kept. While scavenging at roadkills around the colony did occur (photo), most Rabbits found at the territory of the specialised prey were expected to be targeted within the dune area, possibly within the colony even. Hares at Wormer- & Jisperveld are abundant within that entire nature area and these could also be considered local prey. The fact that most Rabbits at Texel and most Brown Hares at the mainland colony were seemingly rather young animals might indicate that these were often actually captured prey rather than carcass finds.

Hedgehogs are common as roadkills and these nocturnal animals are likely to be plentiful available as carcasses along roadsides (Texel and Vlieland included), but difficult to hunt and kill for gulls. One partly eaten carcass of an adult Hedgehog found within the colony at Texel would suggest, however, that these animals are occasionally exploited otherwise.

With respect to the presence of species in the immediate surroundings or even within the study colonies, it is clear that the strong representation of Root Voles at Texel and at Wormer & Jisperveld is in accordance with their endemic occurrence in either area. Voles, shrews and mice attract immediate attention of gulls standing in colonies when they briefly rush from one covered place to another over the open after disturbance (*pers. observ.*). This behavioural response (alertness) is so immediate, that active chases of gulls towards these smaller mammals could be expected as soon as they leave cover for whatever reason. These animals could just as well be captured within colonies, in the immediate surroundings of breeding places, or in distant feeding areas. Only species composition within each of these areas would be indicative for the possible origin of certain prey. Unfortunately, the resolution of data on the occurrence and distribution of mammals within The Netherlands is not very high (Broekhuizen *et al.* 1992) and for that reason, within the context of this contribution, we did not explore this issue any further.

Moles at Texel (or Vlieland for that matter) could only originate from the mainland so that these prey items must have been flown in from distant feeding areas. Moles in the Wormer & Jisperveld area could just as well have been local prey. How does a gull capture moles, however? It is not entirely unlikely that gulls would monitor active mole runs and respond when moles push up the turf during one of their frequent checks of the run. There are some accounts of moles swallowed alive at least by Herring Gulls (Lyster 1972), which would suggest that such or a similar a technique has been developed among gulls. Lyster (1972), incidentally, showed that such a strategy would not be without risk for the predator. Jansen (2007) described a form of symbiosis between moles and gulls, where Herring Gulls were seen to associate with moles pushing up turf, because the escaping response of earthworms triggered by the activity of the mole would make these worms an easy prey for the gulls. Possibly the mole would be targeted as soon as it became visible under these conditions. Alternatively, moles could be captured swiftly when they became uncovered during ploughing or other activities by farmers on their land.

Forecasting an increase in utilisation of mammalian prey - Populations of herring and Lesser Black-backed Gulls have increased spectacularly in The Netherlands in recent decades, following phases of plundering, protection, persecution, and again (partial) protection during the 19th and 20th centuries (Spaans 1998ab, Spaans 2007). Mainland coast colonies, however, became under pressure in the mid-1980s when Red Foxes re-colonised the dune areas (Bouman *et al.* 1991, Spaans 1998ab).Many mainland colonies collapsed and inland breeding became more frequent. An aspect that would forecast a further change in breeding locations and foraging habits is the apparent decline in the availability of marine (fish) prey for coastal breeding Lesser Black-backed Gull populations (Camphuysen *et al.* 2008a). While facing food shortages during chick-rearing, the attention of certainly Lesser Black-backed Gulls is likely to shift from marine foraging habitats towards terrestrial areas. Given the importance of mammalian prey in these areas, increased predation pressure and a stronger impact on mammal populations could then be expected.

Conclusions and implications - Evidence is provided that mammalian prey is a significant prey for gulls nesting inland and for some specialised gulls in coastal colonies. Predation has usually been interpreted as being a compensatory mortality factor, removing only the doomed surplus (Trout & Tittensor 2008). However, the number of mammals taken by gulls can be substantial (represented in up to 45% of all prey samples within some colonies). For a number of reasons mentioned earlier, the tendency to forage on inland locations by gulls will likely increase and as a result, predation pressure on various mammal species will be higher. In case of predation by gulls, however, for which scavenging is a common technique and where active hunts may be the exception rather than the rule, predatory levels are unlikely to quickly pose a major threat to mammal populations.

Avoiding predators spatially or selecting safer habitats does improve survival prospects of potential prey animals. However, in the case of a new predator arriving on the scene (as with introduced alien predators), prey populations might lack the behavioural traits to escape predation efficiently. Fey *et al.* (2006) provided evidence for a microhabitat shift of native prey animals (voles) caused by an alien predator, the American Mink *Mustela vision* and similar shifts are likely to occur when large gulls increase substantially as potential predators. As generalist predators, gulls may be expected to switch to alternative prey when more usual resources decline below a certain point or when they enter new habitats. At the same time, they are likely to respond swiftly to population oscillations of mammalian prey (rodents for example) and may have a stabilising effect on vole or mice population dynamics (Andersson & Erlinge 1977, Hanski *et al.* 1991, Sundell 2002).

15. Synthesis and conclusions

Lesser Black-backed Gull chicks, Kelderhuispolder, 27 June 2011 (CJ Camphuysen)

Many of the ecosystem studies conducted in the Wadden Sea with birds involved currently focus on relationships between migratory species (waders, seaduck) and their resources (often benthic prey; Piersma *et al.* 1993, 1994, Van de Kam *et al.* 1999, Nebel *et al.* 2000, Van der Meer *et al.* 2001, Piersma *et al.* 2001, Van Gils *et al.* 2003, 2005, 2006, Piersma 2007, Kraan *et al.* 2009). Detailed ecological studies of (pisci- or omnivorous) gulls and terns that breed in the Wadden Sea have been discontinued in recent decades (Spaans 1971-1998, Stienen 2006). It was the ambition to resume demographical and ecological studies of avian top-predators that not only forage but also breed in the (Dutch) Wadden Sea coastal ecosystem.

The studies reported in this thesis aimed at understanding the contrasting population trends of Herring Gulls and Lesser Black-backed Gulls breeding in the western Wadden Sea. The studies were conducted at and around the island Texel, where a large and accessible mixed colony was selected. It was assumed that the results would be representative for a larger segment of the Southern North Sea population and the international Wadden Sea, where similar trends have been reported (Spaans 1998abc, Garthe *et al.* 2000, Stienen *et al.* 2002, Hornman *et al.* 2011, 2012).

The interest in population dynamics led to comprehensive measurements of fecundity and an evaluation of the key demographic processes (birth, death and migration), assessments of breeding densities, an detailed analysis of the diet of both species and a study of the foraging activities, including assessments of the distribution of individuals at sea and in other foraging habitats. The studies provided insight in the ways in which demographic processes are influenced by environmental factors (Begon *et al.* 1990) and will help forecast future population developments.

History of colonisations

In the introduction of this thesis (Chapter 1, Appendices 1-2), a historical context is provided. A long history of colonisation, hybridisation, and range expansion under the influence of long-term climatic oscillations (including glacial cycles) underlies the present day distribution patterns and abundances. The complexity of phylogenetic relationships with numerous gull taxa throughout the Northern Hemisphere has been hotly debated, mostly in the second half of the 20th century. Voous (1960) suggested that along the north-western coast of Europe, the Lesser Black-backed rather than the Herring Gull originally was the autochthonous form of a circumpolarly distributed group of large gulls: Lesser Black-backed Gulls were "driven away" by a Nearctic invader (the Herring Gull) and the recent colonisations of Lesser Black-backed Gulls in Denmark (1920) and The Netherlands (1926) were recoveries of once lost territory. According to Voous (1960), that "invasion" by Herring Gulls took place during or shortly after the great glaciations.

More recent work, based on mitochondrial DNA variation among 21 gull taxa (Liebers *et al.* 2004) and on models of gene flow relationships among 10 Lesser Black-backed Gull populations (Liebers & Helbig 2002), led to different conclusions. There was no genetic evidence for the colonisation of Europe by North American Herring Gulls. The Lesser Black-backed Gull (*Larus fuscus* group) was derived from a *cachinnans*-like ancestral population, probably in the Aralo-Caspian basin, and spread from east (NW Siberia) to west within the Palearctic: a recent westward and southward expansion along with considerable population growth. The differentiation of *Larus fuscus* into the subspecies *intermedius* and *graellsii* happened only recently (genetic uniformity and lack of population structure among the forms; Liebers & Helbig 2002).

A final century of change

Numerous factors may have influenced the population trends of gulls in The Netherlands over the last century (Appendix 2). Four major episodes of change were identified, and these have been summarised in Chapter 1. There is little doubt that the historical exploitation of colonial seabirds around the world had a devastating effect on breeding populations (Croxall *et al.* 1984, Feare 1984).

> *"During the latter half of the nineteenth century man was exploiting birds on a scale never seen before or since. Armed with the new breech loading shotgun he killed excessively for sport, for the pot, to fill a glass case with mounted specimens, or to adorn his womanfolk in egret and ostrich plumes and grebe furs. There was little chance for any species to be regarded as a serious pest for, even if some were harmful to agricultural production, a surfeit of cheap agricultural labour and means and willingness to kill gave sufficient psychological relief to the farmer's frustrations"*
>
> (Murton & Wright 1968).

The relaxation of the Victorian exploitation with its ruthless destruction of wildlife is one of the main factors explaining the rapid growth of many populations of (sea-)birds in the 20th century, large gulls included. Worldwide, many gull populations increased markedly in the 20th century (Del Hoyo *et al.* 1992). Range expansions and population increases are often attributed to the increased availability of (novel) anthropogenic resources (Fisher & Lockley 1954, Voous 1960, Cramp *et al.* 1974). Humans have evidently influenced the trends in numbers of breeding gulls in Europe. Several commoner species became closely associated with man and his activities and became more or less dependent on anthropogenic food sources (Thearle 1968, Spaans 1971, Auman 2008).

Multiple causal factors have been at work simultaneously to effectuate population changes in each of these four episodes (Table 1.1, Appendix 2). Interactions of these causal factors make observed changes difficult to interpret. Following protective measures implemented in 1907 and 1912 in The Netherlands, however, the existing breeding population of Herring Gulls increased immediately (Mörzer Bruijns 1956, Spaans 1971, Spaans 1998ac). The prompt effect of these conservation measures can be seen as evidence that human exploitation and persecution were important negative factors affecting gull populations in an environment with sufficient foraging opportunities for these birds. This suggests that populations were *unnaturally low* (suppressed) at the time.

The population expansions and the new colonisations in the 20th century (^{App}Figs 2.5-6, Box 2.3) occurred when the human population increased markedly, when industrialisation progressed, fisheries and agriculture modernised, and when marine pollution and euthrophication became significant issues. The increase in numbers of breeding birds, whenever given the chance to breed undisturbed, will somehow have been related to that variety of changes in the natural environment, most of which with a clear anthropogenic background. Not all colonising species were equally successful. The ecologically more specialised Little Gulls and Black-legged Kittiwakes have only fragile breeding populations. Gull breeding populations reached unprecedented levels in the late 20th/early 21st century (^{App}Fig. 2.2; Herring Gulls peaked in the 1980s, Lesser Black-backed Gulls around 2005). Given the anthropogenic background of many environmental changes from which gulls have profited, it could be argued that populations levels became *unnaturally* high.

Species-specific responses – Herring Gulls and Lesser Black-backed Gulls are phylogenetically related, sympatric species (Liebers *et al.* 2004). One way in which history is recorded in contemporary species is through similar adaptive responses to selective pressures (instances of parallel or convergent evolutionary change; Harvey & Pagel 1991). Animals of similar phenotype are likely to evolve similar responses to the same selective force, whereas different phenotypes may respond differently (Piersma & Van Gils 2011). In order to understand how phenotypically (dis-)similar the two study species actually are, some understanding of their species-specific adaptive responses was required. Comparative studies are inevitably based on correlational evidence and correlation is not causation. The problem of confounding variables can be reduced (not necessarily eliminated) by searching for the same relationships by different lineages (Clutton-Brock & Harvey 1979, Harvey & Pagel 1991).

Herring Gulls have been the prime subject of campaigns of destruction between the 1930s and 1960s (Spaans 2007; Appendix 2), but populations increased immediately, whenever persecution relaxed. Lesser Black-backed Gulls first bred in the late 1920s, but numbers remained small until the late 1960s (^{App}Table 2.2). Their population was either held down as a side-effect of the destruction of nests in Herring Gull colonies, or their resources (translated into fecundity and survival) may not have been large enough to stimulate a marked population growth. The recent spectacular population increase in Lesser Black-backed Gulls, when Herring Gull numbers reached peak population levels and subsequently declined, is therefore of particular interest.

Hypothesis reminder - The recently contrasting population trends led to three hypotheses that were listed earlier in this thesis:

1. Herring Gulls have changed their resource exploitation patterns as a consequence of inter-specific competition with Lesser Black-backed Gulls. Herring Gulls have been forced to focus on less profitable prey (Noordhuis & Spaans 1992).
2. Lesser Black-backed Gulls have filled an empty niche rather than outcompeted Herring Gulls. The population trends are unrelated. (Camphuysen 1995a, Garthe *et al.* 1999).
3. Differences in foraging behaviour and food availability outside breeding season are responsible for the marked differences in demographic trends in the two species (Kim & Monaghan 2006).

Considering hypothesis (1), from the population reconstruction (Appendix 2) we learned that Lesser Black-backed Gulls outnumbered Herring Gulls for the first time around 2000. Hence, this hypothesis is less likely to be true for most of the 20th century (certainly <1970). For decades, Lesser Black-backed Gulls were either absent or simply too rare to be able to outcompete Herring Gulls. In the mid-1980s, when the competitive exclusion principle was assumed to explain differences in fecundity between the two species (Noordhuis & Spaans 1992), Herring Gulls still outnumbered Lesser Black-backed Gulls by 3.7 : 1. If hypothesis (1) is to hold for that period, differences in competitive strength while feeding must have been considerable and easy to demonstrate in a simple experimental set-up.

To support hypothesis (2), a previously untapped or otherwise unavailable resource had to be identified that could be utilised solely or predominantly by Lesser Black-backed Gulls. With a population of Lesser Black-backed Gulls that remained low for more than 40 years after initial colonisations and a 75 fold population explosion since 1970 within the Wadden Sea, there is at least a temporal component that could provide clues. This sudden success of Lesser Black-backed Gulls may still have (negatively) affected Herring Gulls, even if the two species would not compete for this novel resource, simply because they are generalist seabirds with overlapping dietary preferences.

Support for hypothesis (3) should be derived from differences in "wintering success" between the two species: differences in adult winter survival and recruitment rates (juvenile and immature survival; Kim & Monaghan 2006). An increasing population would require high levels of annual survival, while a decline could result from a relatively high winter mortality.

Density dependent population regulation – In populations that are kept in check by density-dependent factors, reproductive rates vary inversely with population density (Lack 1954, Newton 1998). Coulson *et al.* (1982) hypothesized for Herring Gulls that parameters such as breeding success, the size of breeding birds and eggs, the age of recruitment, and the proportion of young returning to the colony to breed were all affected by the size of the population. Herring Gulls on the Isle of May (Scotland) decreased considerably in numbers from 1972 to 1981, as a result of culling. While the density of breeding birds decreased, the proportion of young returning to the colony to breed, body weight of breeding gulls, and the volume of eggs increased, while the age of recruitment decreased. Spaans *et al.* (1987) found the expected opposite when the effects of a markedly increased population size in Herring Gulls breeding at Terschelling were discussed: declines in breeding success and other parameters, as evidence for density-dependent population regulation.

The two best known forms of population regulation are (1) competition for resources, and (2) natural enemies (Lack 1954). If resources were plentiful, competition may take effect only at high densities, imposing a 'ceiling' on population size, but the situation is more complex because density-dependence operates against a continually changing resource base (Newton 1998). Resource competition is expected to be absent or less important at low densities, but to take effect at high densities, imposing a ceiling on population size. Large gulls breeding on the Wadden Sea islands have few natural predators now that the human kind has given up exploitation and persecution. There is little information on the adverse effects of parasites on gulls (but see Van den Broek & Jansen 1970). Given the marked population increase and the relative absence of predators, the form of population regulation that is expected to be most important in Lesser Black-backed Gulls and Herring Gulls in the Wadden Sea area is (intra- and/or inter-specific) competition for resources. Competition for resources, within and/or between species, is the issue that will return most frequently in the discussions below.

Colony life → comparisons of reproductive success

The study of the breeding biology in the Kelderhuispolder colony at Texel started in 2006, when in The Netherlands as a whole persecution and exploitation were much less severe or localised factors. Breeding densities were close to (HG) or at (LBBG) and all time high. The Kelderhuispolder colony itself is situated in a nature reserve and is strictly protected, inaccessible for the general public, and has no apparent problems with mammalian predators other than some feral cats. Natural disasters such as flooding (common elsewhere within the Wadden Sea) do not occur in this colony, shortening the list of factors that can contribute to breeding failures. Part of the dune reserve is grazed by horses and cattle (trampling an unknown proportion of nests of ground nesting birds), but the Kelderhuispolder itself is fenced off. The Herring Gull colony is fairly old and well-established (albeit declining in recent years); Lesser Black-backed Gulls colonised the area in the early 1960s and increased spectacularly in the late 1980s and 1990s (Dijksen 1996).

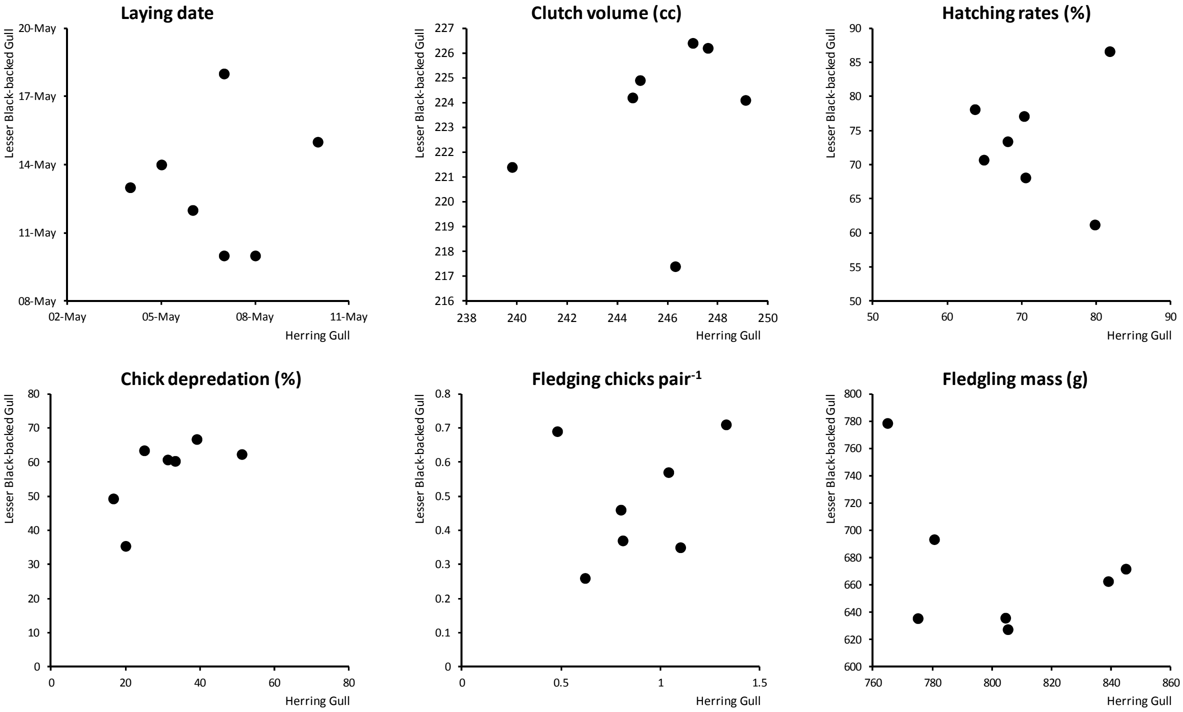


Fig. 15.1. Comparisons of vital rates describing the breeding success of sympatric Herring Gulls (horizontal axes) and Lesser Black-backed Gulls (vertical axis) in the Kelderhuispolder, 2006-2012: mean laying date, 3-egg clutch volumes (cc), the proportion of eggs laid that hatched (%), the proportion of chicks lost as a result of depredation, numbers of fledglings per pair and annual variations in body mass developments of fledglings (40d old) estimated with the 3 parameter logistic growth model (all data from Appendix 3).

During our studies (2006-2012), the breeding success of Herring Gulls appeared to be consistently higher than that of Lesser Black-backed Gulls (Table 2.1, ^{App}Tables 3.3-3.4). This was contrary to the expectations given the most recent population trends. Between seasons, the breeding success varied considerably in both species. Within seasons, even in the worst of years, at least some pairs of both species managed to fledge three chicks (the maximum score), but many pairs failed to raise chicks in any year. All relevant parameters describing the breeding success of either species are summarised in Appendix 3. Assuming that fluctuations in resources during breeding would affect fecundity, the fact that reproductive success varied independently can be interpreted as a first indication that key resources were different for either species. In fact none of the key parameters expressing breeding success, perhaps with the exception of chick depredation, were somehow correlated between the two gulls (Fig. 15.1)

Cannibalism - The reproductive success of Lesser Black-backed Gulls at Texel was strongly influenced by high rates of chick depredation (>60% in most seasons). Cannibalism (as a short for either intra- or inter-specific chick depredation) is a well known phenomenon in gull colonies (Moreau 1923, Brown 1967, Kadlec *et al.* 1969, Parsons 1971, Hunt & Hunt 1976, Fetterolf 1983, Spaans 1987, Watanuki 1988, Velarde 1992). Losses among eggs and young are often heavy (Lack 1954). In Paludan's (1951) comparative study in Denmark, only *c.* 20% of the Herring Gull hatchlings and 5% of the Lesser Black-backed Gull chicks survived and fledged. Other examples are provided in Appendix 3. Intra-specific chick depredation is generally considered to be one of the apparent disadvantages of coloniality (Paynter 1949, Emlen 1956, Parsons 1971, Hunt & Hunt 1975, Davis & Dunn 1976, Montevecchi 1977).

At Texel, there were differences between the two species in the proportion of chicks lost through cannibalism, but also with regard to the timing of chick depredation. The difference in timing meant that mostly young chicks were lost in Herring Gulls but that also notably older and certainly more mobile chicks were depredated in Lesser Black-backed Gulls. Based on Paludan's work published in 1951, Lack (1954) observed that chick losses were most serious during the first six days of life, but that two-thirds of the Herring Gulls and half of the Lesser Black-backed Gulls that survived at least 8 days "completed their development" (fledged, in other words). Pooled data from Texel suggest that initial losses are similar: 29% of Herring Gull hatchlings (n= 298) and 29% of Lesser Black-backed Gull hatchlings (n= 679), died within six days from hatching (a combination of birds that simply died and birds that were killed by conspecifics). Subsequent chick mortality, however, calculated over chicks that reached at least six days of age, amounted to 38% in Herring Gulls (n= 213) and 66% in Lesser Black-backed Gulls (n= 484). Chick losses within the colony are only one aspect of potential recruitment (fledglings have to survive at least another 4-5 years), but the observed differences in depredation rates between the two species called for an explanation.

Individual cannibalism or a collective stress response - At Texel, egg stealing as a widespread phenomenon, but usually with few, specialised individual birds involved. Chick attacks were most profound in the higher density parts of the colony dominated by Lesser Black-backed Gulls and in the most dramatic cases, numerous adults were involved.

In an experimental set-up in 2008, the issue of chick depredation was studied in Lesser Black-backed Gulls (Chapter 4). Food supplements were provided that were assumed to lead to a more effective defence of the offspring, enhanced chick growth, and reduced chick mortality. The treatment did not lead to significant results, but chick depredation levels tended to be higher in control nests than in food supplemented nests. Referees commented on the sample size in the experimental set-up as an explanation for non-significant results. While this may certainly have been a factor of concern, earlier experiments with similar set-ups and sample sizes yielded crisp results (Bukaciński *et al.* 1998, Verboven *et al.* 2003). Camphuysen & Gronert (2010a) pointed at considerable differences in reproductive success between the two study plots involved in the experiments. A rapid spread of affected areas of chick losses from one territory to the next was observed during the most serious outbreaks of cannibalism in 2006-2008, notably in the Foot Sea dunes study plot (^{App}Fig. 3.15). During the experiments in 2008, some clusters of supplemented pairs and controls were situated together at the heart of a cannibalism outbreak. Other clusters, again supplemented and control pairs, were at the periphery of the most affected area and survived when the collective aggression halted. After such outbreaks of collective aggression, large parts of the colony were entirely cleared of chicks, while otherwise apparently similar parts of the colony still had chicks under care.

These "co-ordinated" cannibalistic outbreaks occurred relatively late in the breeding season, when chicks were mobile and when the energetic demands were high. We therefore proposed that autocatalytic interactions between members of the animals in either plot may have been important in the organisation of their collective activity (*cf.* Deneubourg & Goss 1989). The idea was inspired by field observations, but backed up by hide observations in another colony of Lesser Black-backed Gulls with high levels of egg and chick depredation (Davis & Dunn 1976). The observations at Skokholm (Pembrokeshire, UK) indicated that the bulk of the egg losses arose through predation by nesting adult Lesser Black-backed Gulls on their nearest neighbours. Not infrequently the protagonist had lost its own clutch shortly before turning predator, and such a chain-sequence led to a steady build-up of aggressive failed breeders and accounted for the observed seasonal increase in egg losses.

Interactions between individuals and their environment would allow different collective patterns and decisions to appear (Deneubourg & Goss 1989). This could lead to situations where the same stress factors have a different outcome. A consideration of social dynamics and an analysis of apparently collective decisions in breeding seabirds may enhance our understanding of the observed behaviour. What remained to be explained, however, was *what* exactly triggered a cannibalistic outbreak of the scale witnessed almost annually in the Texel colonies.

Cyclic fluctuations in chick growth and chick mortality – During nest controls in the phase of chick care, developing chicks were weighed (g) and measured in order to monitor growth from hatching to fledging. Growth rates could be related to egg size (pre-hatch factors), but were primarily thought to provide information on provisioning rates during chick care (post-hatch factors). Annual variations in growth rates were small (Box 3.4) and annual fluctuations in mean growth rates between the two species were not related (R_S= -0.21, n= 7, n.s.). Variations in body mass gained at 40d of age in Lesser Black-backed Gulls varied *c.* 150g between the year with the most favourable chick growth (2010, 778 ± 15g) and the season with rather modest growth (2011, 627 ± 12g). In Herring Gulls the modelled differences between years were smaller: an 80g difference between the most favourable season (2007, 845 ± 13g) and the worst (2010, 765 ± 13g). The body mass at fledging was not or negatively correlated between the two species (R_S= -0.43, n= 7, n.s.).

Within seasons, cyclic fluctuations in chick growth were found: similar drops and gains in body mass in chicks from numerous monitored nests during subsequent visits, indicating alternating periods of low and more favourable provisioning (Chapter 3). Body mass increments of chicks were significantly reduced in weekends (Table 3.2), while remarkable spurts in growth occurred primarily on Tuesdays, Wednesdays and Thursdays (Table 3.3). These collective mass drops and gains occurred in both species and often simultaneously, but were most profound in older chicks (>15d of age), when the energetic demands are higher (Fig. 3.2). When Lesser Black-backed Gulls were nesting much later than Herring Gulls (a 9-11d difference in the onset of laying between Herring Gulls and Lesser Black-backed Gulls in 2010-2012), the chicks of this species were initially too young to be affected by starvation events that were already experienced by the larger and older chicks of Herring Gulls. While levels of chick growth tended to be lower in weekends, chick depredation rates formed a mirror image, suggesting that the cannibalistic attacks by adults were related to the low provisioning rates (periods of food stress). Note that while cannibalism (now defined as killing conspecifics for food) commonly occurred (Box 3.7), most chicks were often simply stabbed to death and their carcasses were left behind (and sometimes scavenged later) during the most violent outbreaks.

Assuming that the cyclic fluctuations in chick growth reflected cycles in provisioning rates, the fact that chick growth fluctuated simultaneously in both species suggests that some (key) resource was shared between the two or that different resources fluctuated in concert. The weekly rhythm in commercial fishing effort around Texel matched the fluctuations in chick provisioning best, even though starvation events did not occur every week. A weekly rhythm in fishing effort is characteristic for inshore and offshore bottom trawl fleets operated from The Netherlands (black box data; Chapter 3).

Intermittent breeding and a pool of floaters – A striking feature at Texel were numerous well-constructed, but empty nests in areas where Lesser Black-backed Gulls were breeding in high densities. In other words: everything according to plan (territoriality, nest construction), except egg-laying. Many colour-ringed adults (ringed in earlier years a breeding birds) returned to the colony in April ("in time") as prospectors, but only part of these birds subsequently commenced laying. Intermittent breeding (non-breeding in "established adults", birds that have bred before at Texel) was in fact common in both species at Texel. Adult Lesser Blacked-backed Gulls were more frequently found to skip breeding seasons than Herring Gulls (22%, against 15%, ^{App}Table 6.3). Skipping two or more seasons was rare in Herring Gulls (1%) but not uncommon in Lesser Black-backed Gulls (6%). Up to 75% of the prospecting adults did forego laying in some seasons.

Seabirds (large gulls included) are typically long-lived species, with delayed maturation and low annual reproductive rates. Most seabirds live in stochastic environments where in some years the difficulties in producing offspring may be particularly great (Erikstad *et al.* 1998). Calladine & Harris (1997) suggested that if resources become limited, established breeders that have returned to the breeding grounds may give up before laying and skip a season. Life history theory predicts that long-lived species should be restrictive in any increase of their current reproductive investment and adjust their effort in raising young according to their own body condition. With multiple breeding opportunities, in poor environmental conditions, maximum fitness is achieved either by not breeding at all, or by abandoning the brood (Stearns 1992).

The body condition of an individual may influence the decision to breed (Drent & Daan 1980), but multiple factors will contribute. Common factors include breeding performance in the previous season (Calladine & Harris 1997), food availability in the previous winter, resources around the breeding colony in spring, breeding experience (Wooller & Coulson 1977, Wooller *et al.* 1990) and social aspects. Colour-ring readings suggested that Lesser Black-backed Gulls at Texel breed on average once every 2.1 years, those in the mainland colony IJmuiden once every 1.8 yrs. For Herring Gulls, breeding frequencies of once every 1.5 (Texel) to 1.6 years (IJmuiden) were estimated (Appendix 6). The colony filled up nevertheless in such years, albeit sometimes delayed. A pool of non-breeding adult birds (*floaters*) may buffer density fluctuations within an established breeding population (Calladine & Harris 1997). With an intermittent breeding strategy of colour-ringed adults and more or less constant breeding densities from year to year (as on Texel and in IJmuiden), floaters must have filled in vacancies. At Texel, these floater "replacements" typically involved adult birds (no immature plumage characteristics). Colour-ringing commenced in 2006 at Texel (in 2008 in IJmuiden), and a longer series of years is required to obtain better data on breeding frequencies. A longer time-series is also required to evaluate the tendency to breed in any given year relative to the reproductive success in the year before.

In most years, part of the established breeders did forego breeding while vacancies were filled by floaters. It is quite likely that individual condition rather than general environmental conditions has influenced the breeding incentive of returning, prospecting adults in most years. Nevertheless, a particularly high tendency to forego breeding in anyone season could point at a common underlying problem, affecting a large proportion of the prospecting adult birds (established breeders *and* floaters). In 2012, when only a quarter of the (earlier established breeding) Lesser Black-backed Gulls that had returned commenced breeding, clutch volumes were significantly smaller than in other years. In other particularly late years (2010 and 2011) egg volumes were 'normal' Appendix 3). This could indicate that in 2012, when non-breeding was grotesque (75%), a relatively large proportion of relatively inexperienced or lower quality breeders participated (Thomas 1983, Bolton 1991). Intermittent breeding has been documented in a number of seabirds (Hémery *et al.* 1968, Wooller *et al.* 1992, Calladine & Harris 1997, Mougin *et al.* 1997, Bradley *et al.* 2000). The decision to forego breeding (or abandon a breeding attempt) in anyone season is more likely to occur in a long-lived than in a short-lived species. "Sabbatical" periods lasted up to 7 years (mean 1.7yrs) in a well-studied population of Cory's Shearwaters (Mougin *et al.* 1997). In Short-tailed Shearwaters *Puffinus tenuirostris* in Bass Strait (Australia) over 50 years of study, among individuals known to be alive and to have bred before, on average 14% of each sex were not present at their breeding colony in any one year (Bradley *et al.* 2000).

Field experiments, intensified colour-ringing effort, and non-invasive body condition assessments in the prospecting phase are required to further explore the issue of non-breeding or intermittent breeding in Lesser Black-backed Gulls nesting at Texel. That so many seemingly adult floaters are available to fill in vacancies (empty territories or territories next to empty sites), leading to similar nesting densities in subsequent seasons, has consequences for our expectations regarding the actual population size based on simple colony counts.

The avian calendar

Each stage in the annual cycle is assumed to have evolved to occur at the optimum time (McNamara & Houston 2008). Adaptation to an environment implies adaptation to its, usually periodic, temporal variations (Gwinner 1975). This emphasizes the need to know how events throughout the annual cycle interact (Sillett *et al.* 2000, Leyrer 2011). Migratory birds will be affected by seasonal changes in resources and changes therein as a result from climate change (Both *et al.* 2005, 2006).

Breeding on time - There is selective pressure to restrict breeding attempts to the time of year when food on which young are dependent is sufficiently abundant (Lack 1968, Daan *et al.* 1988, Dawson 2008). Avian breeding generally coincides with seasonal peaks in food supplies (Lack 1968), even though detailed studies suggest that birds may breed on either the rising or the declining slopes of food availability (Daan *et al.* 1988, Daan 2006). If food peaks are important, early and late-nesting pairs would leave fewer offspring than birds laying on the average date. Perrins (1970) observed that many birds laid too late for the offspring to profit fully from seasonal peaks of food abundance, and suggested that the proximate cause was a shortage of food for the female when forming the eggs (the *food constraint hypothesis*).

There were distinct differences between the two species in the timing of breeding at Texel and laying dates fluctuated seemingly independently (Appendix 4). Colour-ring re-sightings confirmed that the two species arrive at roughly the same date at breeding latitudes, and start visiting the colony apparently simultaneously in late March and early April (often in response to "fine weather"). Herring Gulls laid always earlier than Lesser Black-backed Gulls. Barth (1968) reviewed laying dates for both species in a number of colonies, ranging from Troms (N, 70°N) to Græsholm (DK, 55°N) and Skomer (Wales, 51°44'N) and found a consistently earlier start of Herring Gulls in comparison with Lesser Black-backed Gulls. The difference in the onset of laying between the species generally increased from south to north and could be as much as 3 weeks to one month apart. At Texel, between 2006 and 2012 the two species were increasingly out of sync, with respect to the peaks of laying ($^{\text{App}}$Figs. 4.4-5), but with Herring Gulls consistently earlier than Lesser Black-backed Gulls.

In birds, the most powerful '*Zeitgeber*'[1] of circadian rhythms is the daily variation in light intensity (Gwinner 1973). In the prospecting phase (late March and the entire month of April),

---

[1] Exogenous (external) cue that synchronizes an organism's endogenous time-keeping system (internal clock) to the earth's 24-hour light/dark cycle (http://en.wikipedia.org/wiki/Zeitgeber)

both gulls were under the same photoperiodic regime, so that species-specific variability in the timing of laying would point at different mechanisms of synchronisation. Temperature cycles seem to be of little importance as non-photic *Zeitgebers* in homoiotherms, birds included (Gwinner 1975), but cold-blooded (poikilotherm) benthic invertebrate prey may respond strongly on fluctuations therein (Honkoop & Beukema 1997, Honkoop 1998).

Herring Gulls and Lesser Black-backed Gull on Texel relied on strikingly different resources during the prospecting and incubation phase (Appendix 7). Hard substrate mussels on breakwaters along the mainland coast are an important resource for Herring Gulls breeding at Texel. These feeding grounds are abandoned by them in winter when the quality of mussels reaches its annual low (Chapter 6, Appendix 9). A rapid increase in mussel BMI is recorded in March and April (from 3.7 to 6.8 gAFDM mm^{-3} 10^{6}) and mussel quality peaks around 8 gAFDM mm^{-3} 10^{6} from May through July (^{App}Table 9.4). Mussels are particularly important in the egg phase (Appendix 7), and a laying peak in early May coincides with top quality molluscs. These observations could be seen as support for Perrins' food constraint hypothesis.

Lesser Black-backed Gulls at Texel do not feed on bivalves or any other intertidal invertebrates in the prospecting phase or during egg-laying. Pre- and post-hatching prey samples were in fact quite similar, with marine fish as the dominant prey items in either phase of breeding. Their laying date has been rather variable in the years of study and the reason for these differences in timing remain unclear. Adult Lesser Black-backed Gulls breeding on Texel have somewhat delayed their return to breeding latitudes in recent years (Chapter 5). There is no evidence for a seasonal shortage of food from fisheries discards in spring, but an overall decline in fishing effort (^{App}Fig. 2.9) may put pressure on that population throughout the breeding season. Adults also appear to swiftly abandon the breeding area after the breeding season (Fig. 5.4 and GPS logger data). A late return to and an early departure from Texel could be a consequence of the overall more limited resources in recent years. When early breeding would be advantageous, long-distance migrants could be time stressed in spring (Drent *et al.* 2006). Klaassen *et al.* (2011) found that migrating Lesser Black-backed Gulls (tagged on Vlieland) used frequent and long migratory stopovers, resulting in a low overall migration speed. Female Lesser Black-backed Gulls may thus rely on foraging opportunities while under way in spring or on food in their wintering areas (*capital* breeders; Drent & Daan 1980, Drent 2006) rather than on foraging conditions at breeding latitudes to reach breeding condition.

Moult of flight feathers – Moult requires a variety of adjustments in the physiology, energetics, and nutrition of birds (Murphy 1996). Temporal overlap between breeding and primary moult is uncommon in bird species because of the great energy demands of each process (Payne 1972, Ricklefs 1974). Variation in patterns and timing of moult among groups of birds have been reviewed by Stresemann & Stresemann (1966), Payne (1972), King (1974) and others. Overlap of breeding and wing moult has been found in some seabird species (Carrick & Dunnet 1954, Furness 1988, Barbraud & Chastel 1998). Most seabirds begin their annual post-nuptial moults in the final stages of breeding or shortly thereafter, when their body masses and lipid stores are low (Murphy 1996 and references therein). In that final phase of chick care, endogenous nutrient reserves are minimal, and a low body mass during the period of moult may allow birds to (partly) offset impediments to flight resulting from the replacement of flight feathers (Coulson *et al.* 1983b, Hedenström & Sunada 1999). Birds that fail during a breeding season often start primary moult within a week of egg or chick loss. The selective advantage of delayed primary moult in breeding birds is to retain maximum wing efficiency while feeding young (Beck 1970).

At Texel, wing moult was recorded during ringing (adult birds incubating eggs; Appendix 4), but so far, primary moult has been neglected as a constraint on breeding individuals. That Herring Gulls commenced primary moult during incubation, 1.5 - 2 months earlier than Lesser Black-backed Gulls (Chapter 2), is consistent with conclusions by Bridge (2006), that non-migratory species are more likely to overlap breeding and primary moult. Monitoring the progress of primary moult is difficult, certainly in the later stages of breeding (post-hatching), when birds cannot easily be captured and examined. With observations at distance, the absence or growth of primaries can easily be monitored, but fine details, such as particular stages of arrested moult (cf. Muusse *et al.* 2011), are easily overlooked.

Migratory movements and wintering conditions

Dutch Herring Gulls are dispersive (Chapter 6), while Lesser Black-backed Gulls are essentially migratory using the westerly flyway towards the Iberian Peninsula and NW Africa (Appendix 5). Both species abandon the breeding grounds and do not visit the colony between September and mid-March. Some Herring Gulls remain at Texel or in nearby Noord-Holland, but generally speaking, alternative foraging grounds are utilised in winter by both species.

Spaans (1971) reported that Dutch Herring Gulls in the 1950s and 1960s overwintered closer to the breeding areas than earlier in the 20th century (significant results only for juveniles). The results obtained for the 1950s and 1960s show broad similarities with the colour-ring re-sightings analysed for the 1980s and 1990s (Chapter 6): dispersal in a more or less SW direction with higher numbers in coastal areas, along large rivers, in cities and south to the northern parts of France. More recent colour-ring re-sightings (birds colour ringed during 2006-2012 at Texel), indicate a westward and northward contraction of the wintering areas (Appendices 5, 9; $^{\mathrm{App}}$Fig. 5.4). Nearly all recent sightings were in coastal provinces, probably because most inland landfill areas have disappeared ($^{\mathrm{App}}$Fig. 9.10), and adults return earlier to breeding latitudes. These findings are backed up by satellite tracks of birds breeding at Vlieland. The Herring Gulls from the Wadden Sea islands must have encountered increased competition on their wintering grounds from more or less resident birds breeding in Zeeland, Maasvlakte and Europoort, where the population peaked nearly 20 years later than in the Wadden Sea area ($^{\mathrm{App}}$Table 2.2). The sites chosen in recent years were cities and coastal resorts in Noord-Holland and Zuid-Holland ($^{\mathrm{App}}$Fig. 9.11). It is unknown how important marine resources are in winter for Herring Gulls that breed on the Wadden Sea islands (no sea trips were recorded in several years of satellite tagging). With a wintering range contraction, substantially reduced opportunities to feed at landfill sites, and increased intra-specific competition, the wintering conditions for Herring Gulls from the Wadden Sea must have deteriorated over the past decades. This finding would provide support for the hypothesis formulated by Kim & Monaghan (2006; Hypothesis #3).

Alerstam (1990) stated *"Gulls lead a fairly mobile life in winter and change their place of residence if the climate or the food supply deteriorates"*. The saying "As free as a bird" does not apply to dispersive or migratory gulls - if it applies at all to any migratory birds (Piersma 1994) -, and this comment is certainly challenged with data provided in the present study. The Argos satellite PTTs, GPS loggers and the colour-ring re-sightings have all demonstrated that Lesser Black-backed Gulls and Herring Gulls are rather conservative and site-faithful individuals that tend to use the same stop-overs and wintering areas over and over again. Lesser Black-backed Gulls wintering in the UK suddenly moved towards a Mediterranean wintering area during particularly cold spells in winter, but there is no evidence that the birds are particularly mobile and "adventurous" when they have arrived at favourite stopovers or wintering areas. The colour-ring data suggest that immatures spend some 3-4 years exploring a somewhat larger area between wintering and breeding grounds, gradually moving further to the north in subsequent summers (Chapter 5-6). Once a "decision" is made, preferred sites are used over and over again indicating that intimate knowledge of the foraging and roosting conditions at stop-overs and in winter areas is advantageous. Levels of individual specialisation deserve particular attention in future studies, but the diversity and the spread of individual birds over a large range could minimise population level effects of localised declines in resources (the closure of individual dump sites or fisheries) or environmental disasters (e.g. major oil spills).

Wintering habitats of Lesser Black-backed Gulls were rather diverse, ranging from open sea via harbours and coastal resorts to rice-fields, inland rivers, lakes and landfills (Appendix 5).

Certainly the large dumps in Portugal and Spain attract many thousands of scavenging gulls every winter. Portugal and Spain, until today, have low rates of domestic waste recycling and rely heavily on landfills. The low (human) population density and lower waste generation rate, as well as poor investments in waste management in the past, have resulted in this reliance on landfill use (Anon 2001). The wintering conditions for Lesser Black-backed Gulls do require attention in the near future, now that plans to close major landfill sites in these countries become effectuated (following EU regulations, within the framework of the Fifth European Union Action Programme, "Towards a sustainable development"; see also Appendix 9). Of the major landfill sites commonly used by Dutch Lesser Black-backed Gulls, Taboeira (Aveiro, PT) is one of the first to be closed down (T. van Nus *pers. comm.*).

Fecundity, annual survival and recruitment (BPA)

In calculating the population turnover for any species, it is important to know the rate at which new adults of breeding age are reproduced (Lack 1954). Fecundity is one aspect, but survival from one year to the next and recruitment rates are equally important (Chabrzyk & Coulson 1976, Begon *et al.* 1990, Bolton 1991, Stearns 1992, Skalski *et al.* 2005). Young birds have to survive at least the first 4-6 years of life to reach sexual maturity (Vercruijsse 1999, Schreiber & Burger 2002). Stable populations of large gulls are expected to lay clutches of approximately three eggs per pair, fledge about one chick per pair of which one fifth or a quarter survives long enough to reach sexual maturity and recruits, and with annual adult survival rates around 90% or better (Kadlec & Drury 1968, Harris 1970, Glutz von Blotzheim & Bauer 1982, Cramp & Simmons 1983, Perrins & Smith 2000). Few of these figures were met at Texel.

Lesser Black-backed Gulls in the Kelderhuispolder fledged rather few offspring each season (~0.49 pair^{-1}), but their apparent adult annual survival rate (~0.91) was favourable. About 20% of the fledglings reached sexual maturity (0.10 pair^{-1}), but the low fecundity led to a negative BPA (Chapter 2). More or less the opposite was found in Herring Gulls: comparatively favourable breeding results (~0.88 pair^{-1}), but a low annual survival of adults *and* immatures (Chapter 7, Appendix 6), leading to a strongly negative BPA (Chapter 2). Estimates of adult annual survival rates for Herring Gulls in other studies ranged from 88% to 94% (Chabrzyk & Coulson 1976. Coulson & Butterfield 1986, Migot 1992, Calladine & Harris 1997). Survival rates at Texel were notably lower, not only in adult Herring Gulls, but also in sub-adults. Only 13% of Herring Gull fledglings reached sexually maturity (0.10 pair^{-1} annum^{-1}), against *c.* 20% in an earlier study in Schouwen (Vercruijsse 1999). If higher levels of reproductive success would relate to more energy spent by parents to the raising of young, adult survival would be compromised in actively breeding birds, but not in (immature) non-breeders. That also first year and immature survival were consistently lower in Herring Gulls points at common problems in the wintering areas affecting all cohorts. The low annual survival of Herring Gulls is thus likely a winter problem. If the deterioration of wintering conditions discussed earlier may had consequences for the annual survival Herring Gulls, it would have affected all age groups. Immature survival rates in Lesser Black-backed Gulls from Texel (14% of all fledglings) were at least twice higher than in Herring Gulls. This is in agreement with the relatively larger number of recruits in Lesser Black-backed Gulls recorded so far. The results indicate that overwinter survival is more favourable in Lesser Black-backed Gulls than in Herring Gulls.

Negative relationships between fecundity and adult survival indicate that the energy per individual parent devoted to the raising of young comes at the expense of adult survival (^{App}Fig. 6.1; Cody 1966, Weimerskirch 2002). In Lesser Black-backed Gulls, models fitted to assess structure in the apparent survival process that included additive year effects provided highest model support (Chapter 7). A negative relationship between apparent survival and fecundity could not be demonstrated, due to a small sample size, but the apparent survival tended to be higher following seasons with lower numbers of fledglings and vice versa (Fig. 7.3, Table 7.4). We have little concrete information on the wintering conditions of Lesser Black-backed Gulls and the effect on (apparent) adult survival. However, a strongly reduced breeding success seems the more important negative factor in this species.

Forecasting population change - In species such as large gulls that may live over 35 years and that first breed between 4 and 7 years of age, a balanced and realistic picture of life, death and recruitment can only emerge from many years data (Begon *et al.* 1990, Lande et al. 2002, Skalski *et al.* 2005, Bijlsma *et al.* 2012). Adequate information comes from standardized population monitoring spanning decades rather than just a few years. For the colony at Texel, the data series is steadily growing, so that within a few years time properly parameterised population models can be constructed, perhaps even forecasting future population developments (see Conclusions). For now however, this was considered premature.

It is obvious that the breeding populations of both species are currently not flourishing (Appendices 3-6). Even in Herring Gulls, where the reproductive success is often reasonably high, the rather high annual adult (apparent) mortality, the low survival of fledglings and the low recruitment rates (according to visual observations) lead to a strongly negative Balance Per Annum (BPA; Chapter 2). It is a small sample size, but the near-absence of even only prospecting "recruits" (colour-ringed visitors fledged in earlier years) and any nesting birds in immature plumage at Texel fed the suspicion that these colonies are "ageing".

If the negative BPAs are realistic (Chapter 2, note that many parameters have a slender factual basis as a result of small sample size), the population of Lesser Black-backed Gulls would be expected to half over a period of approximately ten years. However, density assessments for Lesser Black-backed Gulls in the Kelderhuispolder colony indicated a positive trend rather than a 8% decline per annum (Appendix 3). An 8% decline is also not in accordance with the currently available population trends (Appendix 2). A 23% per annum decline in Herring Gulls would rather swiftly lead to (near-) local extinction! The density assessments for Herring Gulls within the study area (Appendix 3, ^{App}Table 3.8) did suggest marked declines in breeding numbers (a 21% decline from 2009 to 2010, a further 13% decline in 2010-2011), and recent population counts indicated a continuing decline, at least at Texel (Appendix 2). Future monitoring and more solid (longer-term) estimates of annual mortality rates are required to confirm these findings.

The calculations of apparent annual adult survival, and certainly those of immature survival and recruitment rates in this thesis must be regarded as preliminary results. Longer time-series are required to obtain more robust values. In recent years there has been a great public demand for demographical data and in the absence of reliable estimates of annual survival, recruitment, and breeding success, models have too often been fed with parameters taken from literature (e.g. Maclean *et al.* 2007, Boon *et al.* 2010, Dirksen *et al.* 2012). While for some research questions a population model based on vital rates from another colony (or from more than one study) may yield useful results, in most case the outcomes will be misleading.

What's on the menu?

As stressed earlier, at Texel and probably on all other Wadden Sea islands, resource competition is the most likely prime driver of current population trends. The spectacular increase in numbers of Herring Gulls in the 1970s-1980s and the continuing increase in Lesser-black-backed Gulls in the 1990s, would not have happened in the absence of abundant food supplies. An accelerating population increase (when resources are plentiful) levels off when the carrying capacity of an area is approached. When resources are exploited to the limits, density dependent regulation will lead to changes in demographic variables. The poor reproductive success in the late 1980s and 1990s in Herring Gulls and in more recent years in Lesser Black-backed Gulls were indications that essential resources became scarce (perhaps overexploited). In order to shed more light on the current foraging opportunities of both species in the western Wadden Sea, the composition of their diet during breeding had to be analysed. These sympatric birds may share a breeding ground but not necessarily also their feeding grounds (Tasker *et al.* 1999). Inter-specific resource competition is more likely to occur with overlapping foraging habitats. A detailed examination of their diets at Texel was a first but crucial step towards the identification of these feeding grounds.

Composition of the diets -A bewildering variety of prey items was found in both species, but staple foods could be identified. From the dietary information presented in Appendix 7 it is obvious that both gull species are genuine generalists, but with clear preferences for certain prey types. The more marine orientation of the Lesser Black-backed Gull was evident, while Herring Gulls switched from almost entirely intertidal prey in the early breeding season to more diverse and mixed diets including more marine fish during chick care. Individual pairs often adjusted their prey spectra during chick care, obviously in an attempt to meet the energetic requirements of the offspring. The dietary spectrum of Lesser Black-backed Gulls narrowed (^{App}Fig. 7.2; towards higher quality fish prey?), whereas that of Herring Gulls widened (Chapter 9). As a result, the dietary overlap and the likelihood of exploitative competition between the two species was more substantial during chick care than during prospecting, egg-laying and incubation (Table 2.3).

Foraging distributions, foraging techniques and digestion - Foraging theory suggests that birds should concentrate their foraging efforts where there is abundant, easily obtained, high quality food (Schoener 1971, Stephens & Krebs 1986, Wanless *et al.* 2005). For most seabirds, food is patchily distributed, difficult to find, sometimes distant, and ephemeral (Ashmole 1963, Diamond 1984). Animals that are foraging in groups might do better when exploiting patchy, ephemeral food, because individuals might learn about temporary local abundances of food, either by going to sites where others are already foraging, or by learning about new foraging techniques (Krebs *et al.* 1972).

The natural foraging techniques are varied and gulls forage in flocks as well as solitary. If individuals prefer to avoid variation in searching time while exploiting a patchy environment, flocking should be favoured (Caraco 1981). Different prey require different foraging techniques or even physiological adaptations and it is therefore quite understandable that individual birds tend to specialise on particular resources. The consumption of mussels and most other bivalves requires a well-developed muscular stomach (Herring Gulls crush shellfish in their gizzards; Cadée 1995); shellfish that need to be crushed internally simply cannot be taken opportunistically (Piersma *et al.* 2002, Van Gils *et al.* 2005a). Specialised individuals manage to open Pacific Oysters or large Common Shorecrabs, but a majority of the birds is unable to do that and will have to move on in search of more suitable prey. Foraging for earthworms (rainy weather) and non-swarming insects (sunny summer weather) is more or less individualistic (interference nor exploitation competition), but the opportunities are seasonal and weather dependent.

Competing for discards – A high proportion of the fish brought ashore were demersal fish species that without doubt were obtained while scavenging at trawlers (notably beam-trawler and shrimpers; the dominant fisheries in the Southern and German Bights). Successfully competing for fisheries discards requires physical strength or extreme manoeuvrability (two different options; Strann & Vader 1992, Camphuysen *et al.* 1995). An analysis of the competitive interactions of foraging gulls while scavenging for discards at trawlers has been provided in Appendix 7, based on earlier studies conducted at sea. The at-sea studies gave an important insight in the foraging behaviour and prey choices in a competitive setting: both species were confronted with the same prey in experiments with different numbers of competitors, around the North Sea and through the year. If the foraging areas would overlap, Herring Gulls were expected to be more successful foragers. Based on these and other at-sea studies, it was concluded that:

(1) discards are a prime source of food for both species when they are at sea,

(2) the slightly larger Herring Gulls are dominant over Lesser Black-backed Gulls in direct confrontations (more wins than losses in direct combat and vice versa),

(3) in mixed flocks, Herring Gulls take slightly larger prey than Lesser Black-backed Gulls in accordance with species-specific differences in body size, and

(4) prey choice (or better, the actual consumption) in mixed groups is slightly different between the two species, either as a result of different preferences, or resulting from interference competition (Garthe 1992, Camphuysen 1993, 1995, Camphuysen *et al.* 1993, 1995, Appendix 7).

With this information, some of the most important results of the diet study could be interpreted. From the at-sea discarding experiments, it could be predicted that from a shared resource, Herring Gulls would bring in slightly larger fish prey than Lesser Black-backed Gulls.

Herring Gulls delivered smaller individuals of the same fish species than Lesser Black-backed Gulls (^{App}Table 7.5) and have a different prey species composition (Appendix 7). The size of some flatfish (small 0-group) and the frequent occurrence of Brown Shrimps *Crangon crangon* indicated that Herring Gulls commonly foraged behind (nearshore/Wadden Sea) shrimpers. Fish brought in by Lesser Black-backed Gulls, and some of the common secondary prey (*Polinices polianus*) found in prey samples, showed that Lesser Black-backed Gulls mostly scavenged around (large) offshore beamtrawlers. Simple dietary information from regurgitated boluses in the colony, coupled with information from competitive strength and size selection during sessions of experimental discarding, suggests resource partitioning rather than resource sharing. This issue will be explored below, after a brief discussion on marine distribution patterns, seasonality, and species composition in different habitats.

Catching fish (natural feeding) - Fish shoals near the surface have to be found first. The behaviour of gulls at sea (with predominantly white plumages, signalling presence at substantial distances) is quite similar to that of many other seabirds that profit from ephemeral foraging opportunities (gannets, boobies, tropicbirds, gulls, terns): a behavioural change of a conspecific, seen at distance, triggers an immediate response by birds within sight (Frings *et al.* 1955, Simmons 1972, Camphuysen 2011d). When one forager finds a patch, others immediately join the finder to share the food. To get the fish, particular skills are required, depending on the exact situation (Camphuysen & Webb 1999). Flocks of seabirds that develops over a large fish school will have the same or similar characteristics and dominance hierarchies as a flock of birds following a trawler. Such feeding opportunities are typically short-lived, and Lesser Black-backed Gulls together with Herring Gulls, in the area where this system is most extensively studied generally profited from producers and are often categorised as joiners or suppressors in multi-species feeding frenzies (MSFAs; Camphuysen & Webb 1999). Herring Gulls and Lesser Black-backed Gulls off the Scottish east coast were clearly aiming for MSFAs while foraging (>80% of recorded offshore feeding activities in summer within MSFAs), indicating how important these relatively short-lived foraging opportunities can be. It is these (natural) fishing techniques that give access to energy rich, fatty prey species.

MSFA formation in Dutch waters is a much less studied phenomenon, but during ship-based surveys in summers 2002-2009, only 3% Lesser Black-backed Gulls and just below 1% of all Herring Gulls were seen to join MSFAs (^{App}Table 8.5). The representation of fatty fish in the diets studied at Texel was low, suggesting that natural feeding frenzies over schooling fish as described above were uncommon.

Food quality – Birds have to provide adequate food for themselves throughout the year, and for developing chicks in the second half of the breeding season. Several studies have shown that adults select prey with a higher calorific value for their chicks than for themselves (Tasker *et al.* 1999).

Most Herring Gulls focus on mussels during prospecting and incubation, while a shift towards more energy rich prey (more fish) occurred during chick care. Most successful Herring Gulls, with on average more rapidly developing chicks, added substantial amounts of fish to the prey loads for their offspring. Pairs that continued to feed mussels were less successful and pairs that specialised on crustaceans (Common Shore Crabs) during chick care generally failed to fledge young (Chapter 9). Similar results were presented by Spaans (1971) and various other authors studying Herring Gulls around the North Sea (Ehlert 1961, Glutz von Blotzheim & Bauer 1982).

Lesser Black-backed Gulls were expected to focus more on fatty fish during chick care (clupeids, sandeels), but also in the second half of breeding, mostly low quality (discarded) fish species were used for chick provisioning. Perrins & Smith (2000) investigated prey choice in Lesser Black-backed Gulls breeding on Skomer during a period of population decline. Earthworms *Lumbricus terrestris* were important food items early in the season with a dietary shift to proportionally more fish (discards) during the chick rearing period. In later years, with fisheries discards apparently less and less available, birds continued to forage on mainland agricultural land during the chick rearing period. The years of worst breeding failure were exceptionally dry summers when also worms were difficult to find. When breeding success declined, the majority of chicks died within a week of hatching and most were clearly underweight. Their food, as judged by regurgitates, was mostly earthworms. While parents themselves were apparently able to survive on a diet of earthworms, they were unable to collect sufficient earthworms for a rapidly growing brood.

Sexual segregation while foraging – An important finding in Chapter 10 was that male and female Lesser Black-backed Gulls focused on different foraging habitats and with that also on different prey types. Sexual segregation in foraging behaviour is widespread among sexually dimorphic marine vertebrates (Stauss *et al.* 2012) and these are often thought to be mediated via differences in dominance, foraging behaviour, flight efficiency and competitive ability (Wearmouth & Sims 2008, see discussion in Chapter 10). Sex-related differences in foraging behaviour have also been described for monomorphic species, such as Northern Gannets *Morus bassanus* (Lewis *et al.* 2002), and the underlying mechanisms are in fact poorly understood. The habitat use by 34 tracked individuals of Lesser Black-backed Gulls from Texel, ranged from almost completely terrestrial to completely marine (Fig. 10.1), suggesting a tendency of individuals to specialise on particular foraging areas, at least during the breeding season. Males spent considerably more time foraging on the North Sea than females. Stauss *et al.* (2012) suggested that differences during the breeding season can be attributed to sex-specific provisioning behaviour and differential parental roles, inter-sexual competition, or sex-specific habitat specialisation. A further suggestion was that nutritional investments by female into developing eggs could lead to sex-specific differences in prey choice (Carey 1996), but this option is put aside here, given that these sexual differences persisted throughout the breeding season (Chapter 10). It turned out to be impossible to link particular prey items to individual birds, and hence to the 'appropriate sex', but the parameters summarized on Table 10.2 strongly suggest that sex-specific provisioning behaviour and differential parental roles could be of importance. The net result, however, sexual habitat/resource partitioning will be discussed below.

Risk sensitive foraging - Foraging animals select resources in response to the probability distributions of rewards obtained and costs expended, rather than the expected energetic values alone (Caraco 1981). In Appendix 7, the most important prey types were categorised according to their availability, the expected competition while exploited, and the foraging techniques or skills required. The variety in prey items and foraging habitats is large and there is no need to repeat that information here. Further aspects that could have been added, however, are: physiological adaptations required (such as a muscular stomach for crushing), the expected reward (expected intake rates, calorific value, and the costs involved to find and handle prey), and the risk of failure. Bateson (2002) observed that individual birds (European Starlings *Sturnus vulgarus*) that were offered a choice of a constant or a variable feeding option in an experimental setting, were either risk-averse or risk-prone. Whether animals were risk-averse or risk-prone appeared to depend for example on the energetic status of the forager, and the type of variance associated with the feeding options.

The common prey types taken by large gulls breeding at Texel have an availability that is either cyclic (tidal rhythm, fisheries effort, seasonal), weather dependent, or unpredictable. The most predictable resources that require less competitive skills could be ranked as "risk adverse". We could expect individual gulls, depending on their nutritional status or competitive strength, to select a resource with the most appropriate energetic return (cost/benefit). The choice will likely be different with a nest full of hungry chicks to care for. If we revisit the list of important prey items (Appendices 7-9), the following scenarios are seemingly relevant for our two sympatric predators:

(1) Intertidal prey (molluscs, crustaceans) → risk adverse, predictable resource, calorific value peaks May-July but fairly low (<3.5 kJ g^{-1} fresh mass), physiological adaptation required (muscular stomach), exploitation and interference competition (Herring Gulls only).

(2) Pelagic fish shoals (herring, sprat, mackerel, horse mackerel, sandeels) → risk prone, unpredictable resources, weather dependent, calorific value high (6.5 or >10 kJ g^{-1}), facilitation may be required (sub-surface predators), flock feeding, dominance hierarchies, interference competition (most obvious in Lesser Black-backed Gulls).

(3) Discards (gadoids, flatfish) → risk prone, fairly predictable resource with weekly cycle in availability, weather dependent, calorific value moderate (3.5-5 kJ g^{-1}), flock feeding, dominance hierarchies, interference competition, potentially high rewards (Lesser Black-backed Gulls entire breeding season, Herring Gull during chick care, Herring Gull potentially more successful).

(4) Discards (offal) → risk prone, fairly predictable resource with weekly cycle in availability, weather dependent, calorific value high (>10 kJ g^{-1}), flock feeding, dominance hierarchies, interference competition (Lesser Black-backed Gulls entire breeding season, Herring Gull during chick care, Herring Gull more successful).

(5) Crustaceans (swimming crabs) → unpredictable resource, weather dependent?, calorific value moderate (3.5 kJ g^{-1}), exploitation competition, low rewards (both species opportunistically)

(6) Nereid worms (polychaetes) → unpredictable resource, weather dependent?, calorific value low (<3 kJ g^{-1}), exploitation competition, high rewards in dense swarms only (opportunistically, most obvious in Lesser Black-backed Gulls)

(7) Insecta → unpredictable resource, weather dependent, exploitation competition, high rewards in dense swarms only (opportunistically, most obvious in Lesser Black-backed Gulls)

(8) Oligochaetes (earthworms) → unpredictable resource, weather dependent, high rewards (opportunistically, most obvious in Lesser Black-backed Gulls, in winter seemingly more prominent in Herring Gulls)

(9) Domestic refuse → risk adverse?, fairly predictable resource, calorific value variable but potentially high, exploitation competition & dominance hierarchies (most obvious in Herring Gulls)

The data collected so far suggest that most Herring Gulls on Texel "played safe" during prospecting, laying and incubation, but diversified (broader diet) and utilised more risk prone, energetically more profitable resources during chick care. Some individuals (or pairs rather) were found to choose different, "non-mainstream" prey, with different, positive or negative, demographic consequences (Chapter 9). In Lesser Black-backed Gulls, males apparently focussed on risk-prone, offshore resources while female conspecifics travelled shorter, towards areas with more predictable and more diverse foraging options and prey types within short distances (risk averse behaviour; Chapter 10). There is currently no information about sex-specific foraging strategies in Herring Gulls.

A summary of principal resources (or main prey types) is provided in Appendix 10. As could be seen throughout this thesis, these two generalists are quite different in their dietary preferences and specialisations. Their diets are supposed to be a reflection of their foraging habitats, and this aspect is discussed below, primarily from data presented in Chapters 10-14 and

Appendices 5-9. In this part of the work, the birds were joined and observed within their foraging habitats, notably at sea.

Genuine "seagulls" ?

Seasonal patterns and breeding origin of gulls at sea - From ship-based studies, it was concluded that nearly one million Herring Gulls occurred dispersed throughout the North Sea in winter (November-February; Appendix 8). In summer and autumn (May-October) numbers of Herring Gulls at sea dropped markedly. Seawatching data indicated a small nearshore peak in abundance of adult Herring Gulls in July (during chick care; Box 4.2); an aspect that was entirely missed by ship-based surveys in the area. More or less an opposite picture was sketched for Lesser Black-backed Gulls. These birds returned in March from wintering areas far to the south and dispersed over the European Continental shelf coasts, utilising virtually the entire North Sea. Numbers were highest March-August, when some 95% of all Lesser Black-backed Gulls were found in the eastern half of the North Sea, mostly within *c.* 50km of the nearest coast. In autumn and winter, the North Sea was largely abandoned by Lesser Black-backed Gulls. These opposite trends in abundance at sea (translated into proportions of relative abundance) are sketched in Fig. 15.2.

In seasons when numbers of gulls were high at sea, both species had a strong tendency to gather around commercial trawlers. Schwemmer & Garthe (2005) discussed the at-sea distribution and behaviour of Lesser Black-backed Gulls in the German Bight. Most were associated with fishing vessels (25%; strongly aggregated), with high numbers in coastal waters associated with shrimp trawlers and at 40 to 60 km distance from the shore with beam trawlers. Birds actively searching for natural food (14%) were more evenly distributed and occurred widespread over the study area. Most prey items observed were crustaceans (85) and marine fish (39), which was in accordance to expectation based on prey samples collected at Amrum and Juist (Garthe *et al.* 1999, Kubetzki & Garthe 2003). Around Texel, the most substantial groups of foraging seabirds in natural feeding frenzies with Lesser Black-backed Gulls occurred in rather discrete water masses: a fairly narrow strip of nearshore waters off the mainland coast within the 20m depth contour and at the transition zone between Southern Bight waters and the more saline, clear central North Sea water around the Frisian Front (Chapters 11, 13). The exact marine habitat characteristics (one of the objectives of the entire research project) still require further attention.

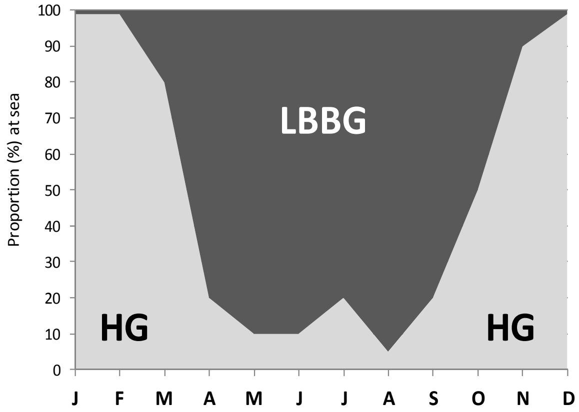


Fig. 15.2. Simplified species composition of Herring Gulls and Lesser Black-backed Gulls at sea, from ship-based surveys in the southern North Sea

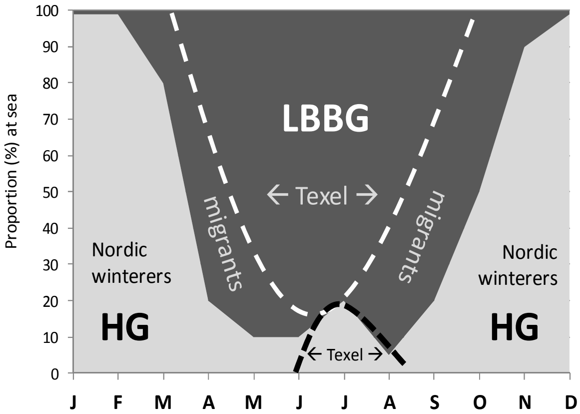


Fig. 15.3. Hypothetical contributions of birds from Texel and "foreign" birds (passage migrants and wintering gulls from Scandinavia) to the at sea populations.

Who are all these birds and how do these temporal and spatial trends fit our hypotheses? The competitive scenario (hypothesis #1) suggested that Herring Gulls were forced to leave the sea and moved towards intertidal and inland resources instead (Noordhuis & Spaans 1992). Herring Gulls were presumably assumed to return to the North Sea as soon as the Lesser Black-backed Gulls had left for their wintering areas, but this is not specifically mentioned. The empty niche scenario (hypothesis #2) implied that Lesser Black-backed Gulls invaded an area or exploited a resource without any significant competition. Why would Herring Gulls give way for Lesser Black-backed Gulls prior to breeding, if marine resources are so important? How would they have been outcompeted at sea in the mid-1980s when Herring Gulls still outnumbered Lesser Black-backed Gulls?

From the material presented in this thesis, we have in fact no evidence that Herring Gulls breeding in the western Wadden Sea utilise marine resources, apart from a brief phase during chick care, and they rarely venture out to sea beyond *c.* 10km (Chapter 10). One could wonder how correct the assumption is that Herring Gulls breeding on the Wadden Sea islands disperse into the open sea after breeding. Colour-ring re-sightings may be seen as useless to provide the evidence, but there is an overall wintering dispersal to the south (Chapter 6). Spaans (1971) reported that Herring Gulls dispersed non-directionally in winter over a limited area, and that birds from Dutch colonies occur regularly on the south and east coasts of England. Non-directional movements would include flights to the north and west (open sea). Stanley *et al.* 1981 confirmed that some birds from Dutch colonies were found in southeast England, but an analysis of >86,000 colour-ring sightings in later years indicated that flights to and from the UK were in fact quite rare (Chapter 6). Moreover, Herring Gulls from Vlieland that carried satellite PTTs for a number of years have provided no evidence that these birds utilised marine resources for any significant length of time ($^{\text{App}}$Fig. 5.3 ; Appendix 8).

From an analysis of ringing recoveries, body measurements, timing of primary moult and of arrival and departure, it is suggested that most Herring Gulls wintering inland in south-east England originate from breeding colonies in Arctic Norway and Russia (Stanley *et al.* 1981, Coulson *et al.* 1984). A move from Nordic countries towards the south-eastern parts of the UK involves a crossing of the North Sea and the timing sketched by Coulson *et al.* (1984) would fit the seasonal pattern found in ship-based surveys covering the North Sea at large very well (Stone *et al.* 1995). The seasonal return of (wintering) populations of “Nordic” Herring Gulls, together with Great Black-backed Gulls breeding in that same general area, leads almost certainly to the annual increase in high densities of Herring Gulls offshore in the North Sea. Scandinavian Herring Gulls arrive in Britain in September and October, the proportion peaks in Dec-Jan and the birds depart abruptly in late Jan-early Feb.

A third scenario, therefore, would be that Nordic gulls, not our birds, occupy the same offshore areas in winter that our breeding Lesser Black-backed Gulls can occupy only in summer (Fig. 10.3). The nearshore peak in abundance of Lesser Black-backed Gulls in Aug-Sep and even most of the spring peak in April recorded during seawatches ($^{\text{Box}}$4.2) would involve passage migrants from German, Danish and Norwegian colonies (Fig. 10.3; Kylin *et al.* 2011). In this scenario, Herring Gulls breeding in the western Wadden Sea briefly touch upon marine resources in mid-summer (to provision their chicks with high caloric value prey), but spend their winters mostly inland and in coastal areas south to Belgium and France (in line with colour-ring data and tracking results). Scandinavian and Russian Herring Gulls not so much leave the North Sea when they return to their colonies, but they abandon a large wintering range that *includes* the North Sea. When Lesser Black-backed Gulls return in spring, they find a more or less empty sea: wintering Nordic Herring Gulls have just left. But a vacant niche? An answer on the question why Lesser Black-backed Gulls would have been so successful *after* the 1960s and early 1970s is provided below.

A vacant niche? - From the historical overview in Appendix 2, it appeared that the severely persecuted Herring Gulls increased promptly, whenever or wherever the levels of destruction declined. Apparently, resources to facilitate population growth were present. Lesser Black-backed Gulls did not increase much during all these years, but started to increase in the late 1960s and the population exploded, some 40 years after the birds colonised The Netherlands. What marine resource could have been underexplored by birds, or what *new* resource could have been responsible for the imminent success of these seabirds?

The introduction of "beamtrawlers" (quickly replacing otter-trawlers) may have been just that factor (Jennings & Kaiser 1998, Rijnsdorp *et al.* 2008). Double beam trawling, introduced in the early 1960s, proved a successful fishing method to catch deep burying flatfish, in particular Sole *Solea solea* (Rijnsdorp *et al.* 2008). In less than 10 years, the otter trawl fleet was replaced by a highly specialised beam trawling fleet, despite an initial doubling of the loss rate of vessels due to stability problems. Engine power, size of the beam trawl, number of tickler chains and fishing speed rapidly increased and fishing activities expanded into previously lightly fished grounds and seasons. Beamtrawl fisheries became widespread in the south-eastern half of the North Sea, in an area bordering 'suddenly' flourishing populations of Lesser Black-backed Gulls in Denmark, Germany, The Netherlands and Belgium. Double beamtrawlers produced unbelievable quantities of discards, more than most other fisheries (Van Beek *et al.* 1990, Camphuysen 1994b, Fonds 1994a, Jennings & Kaiser 1998, Lindeboom & De Groot 1998) and discards from large beamtrawlers formed the main component of Lesser Black-backed Gulls breeding at the Wadden Sea islands in recent decades (Noordhuis & Spaans 1992, this thesis). Assuming a 5 year delay in population response (for fledglings to survive and return to breed), the expansion of the beamtrawl fleet and the increase in fisheries effort fits the population increase of Lesser Black-backed Gulls through the 1960s, 1970s, and 1980s (Fig. 15.4). As concluded by Tasker *et al.* (2003): *"Perhaps the most important fishery induced impact on gull populations has been caused by the production of discards from commercial fisheries."*. Numerous examples were provided. The success story of Lesser Black-backed Gulls in the southern North Sea is just another example.

The substantial decline in fisheries effort in more recent years could explain why current breeding success in Lesser Black-backed Gulls is low, why chick depredation rates are high, that cyclic starvation events and growth spurts run in concert with a weekly rhythm in fishing effort, why Lesser Black-backed Gulls increasingly forage inland (an unconfirmed proposition of numerous bird watchers in The Netherlands), and even why Lesser Black-backed Gulls in recent years could have a greater tendency to delay their return to the north and advance their move south to their wintering grounds. Herring Gulls, in the 1970s and 1980s still much more abundant than Lesser Black-backed Gulls, must have been unable to profit from the offshore fisheries. Over the years, the nearshore fleet composition changed: a "Plaice Box" became established in 1989 (Pastoors *et al.* 2000), essentially excluding fisheries with large bottom trawlers from fishing nearshore, and the main fishery off Terschelling became shrimp rather than flatfish orientated. Discards from shrimpers is currently more typical for Herring Gulls (Appendix 7, ^{App}Table 7.5).

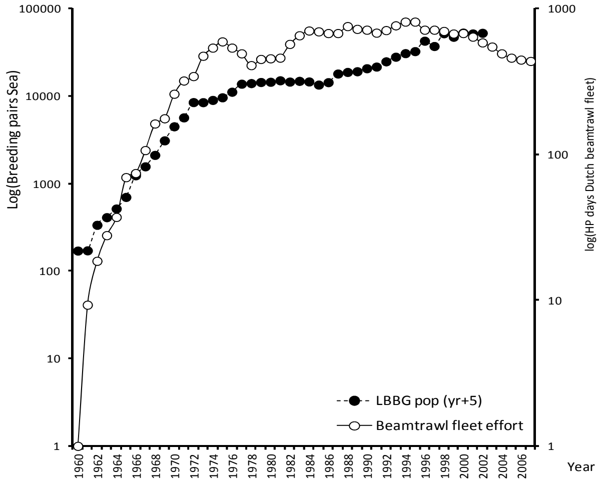


Fig. 15.4. Changes in the Dutch beamtrawl fleet effort (log-transformed horse power days), from 1960 to 2008 (open circles; from Rijnsdorp *et al.* 2008, updated by A. Rijnsdorp) and changes in the Wadden Sea breeding population of Lesser Black-backed Gulls 5 years later (the population plot is shifted 5 positions to the left; black circles).

The high price of fuel and the relatively low biomass of sole and plaice jeopardised the survival of the large beam trawl fleet in recent decades. The prospects of this fleet are further threatened EU directives to minimise the production of discards and other impacts of this fishery on the ecosystem.

Competitive exclusion? - Part of the argument to propose "competitive exclusion" as a factor to explain the decline in breeding success of Herring Gulls in the 1980s, was an observed decline in the frequency of occurrence of fish prey in Herring Gulls at Terschelling where Lesser Black-backed Gull numbers were increasing. The study by Noordhuis & Spaans (1992) in the 1980s, in which the diet was compared with that in the 1960s, showed that in the earlier period:

Herring Gulls ate much more marine fish

Proportionally more fish originated from the North Sea (more from the Wadden Sea in the 1980s)

Marine fish taken by Lesser Black-backed Gulls on Terschelling in the 1980s were of the same species and size classes as those eaten by Herring Gulls in the 1960s, suggesting that marine fish was still available. Moreover, they observed that the size of the fish eaten (gadoids and Horse Mackerel) taken by Herring Gulls in the 1960s were of similar length as those consumed by Lesser Black-backed Gulls in the 1980s. Hence the conclusions that Herring Gulls were outcompeted.

It was explicitly stated that Herring Gulls were forced to forage at inshore shrimpers rather than at offshore fishing vessels. This argument fails to correct for changes in fleet size, shifts in fisheries effort and discards production: all of which changed markedly since the 1960s. There are no reasons to expect that discarded fish size within the various fleets remained the same, however. That Lesser Black-backed Gulls provisioned their chicks with the same species and size classes of fish in the 1980s as Herring Gulls in the 1960s does not in itself prove that the former has been replaced by the latter in an area. In Chapter 11, the suggestion was put forward that the larger beamtrawlers were increasingly out of reach for the more inshore orientated Herring Gulls.

Given that in the mid-1980s Herring Gulls still outnumbered Lesser Black-backed Gulls, the species-specific differences in competitive strength at the trawl must have been considerable to allow for competitive exclusion. Sessions of experimental discarding (summarised in Appendix 7) did not reveal a subordinate role of Herring Gulls compared with Lesser Black-backed Gulls. The opposite was demonstrated to be true behind trawlers, time and time again (Garthe 1992, Camphuysen *et al.* 1995, Walter & Becker 1997). Also, there was no evidence for Herring Gulls being "outmanoeuvred" by the smaller and more agile Lesser Black-backed Gulls during these sessions of experimental discarding, as reported from Norway for the more slender nominate *L. f. fuscus* (Strann & Vader 1992).

Between March 1993 and August 1994, the number and species composition of birds following shrimp trawlers were determined in the (German) Wadden Sea (Walter & Becker 1997). Most numerous as scavengers were Herring and Black-headed Gulls. Mew, Lesser Black-backed, Great Black-backed Gull, and commic terns *Sterna hirundo/paradisaea* were represented in much smaller numbers. Herring gulls were the most successful scavengers: although representing only 45% of all birds associated with the trawlers, they took 82% of all discards taken by scavengers. In this light, the sexual segregation in foraging Lesser Black-backed Gulls referred to earlier, is paricularly interesting. Apparently, mostly female Lesser Black-backed Gulls from Texel are attracted to resources in deeper waters of the western Wadden Sea (^{App}Fig. 9.4). There is little else but shrimpers (dominated by Herring Gulls) in these waterways. Hence, while avoiding intra-specific competition with the larger (more powerful) males behind beamtrawlers on the North Sea, these females run into inter-specific competition with on average even larger Herring Gulls behind shrimpers. Their foraging success behind shrimpers is an urgent study subject that will be picked up in the same season as a (GPS) tracking study of Herring Gulls breeding on Texel (to be continued).

Inland and intertidal foraging opportunities

Both species utilise other foraging areas, both in winter and during breeding, details of which have been provided in Chapters 6, 8, 9, 10, and 14 and in Appendices 2, 5, 7, and 9. Evidence is provided that Herring Gulls utilise the intertidal zone to a much greater extent than Lesser Black-backed Gulls, where they capture rather different prey. On land, Lesser Black-backed Gulls and Herring Gulls utilise slightly different resources, or co-occur in different constellations (one or the other species normally more numerous), which is clearly reflected in their dietary preferences. Two aspects require further attention and both refer to Herring Gulls in winter.

Abandoning an intertidal resource in winter – Within the Wadden Sea, Herring Gulls are important bivalve and crustacean consumers and high numbers occur year-round. Again, it is quite possible that breeding and wintering populations refer to different areas of origin; rather few colour-ringed individuals remain on Texel and Vlieland in winter (NIOZ colour-ring database), but the number of Herring Gulls utilising these areas in the non-breeding season are huge. Colour-ring reading is well possible at onshore roosts, but difficult on the mudflats themselves. Satellite tracking data (using birds from Vlieland) confirmed that most birds leave the Wadden Sea in winter and stay on the Continental mainland. A follow-up logger study, to quantify habitat use throughout the year, will be required to update and significantly improve existing information on the utilisation of resources within the Wadden Sea and other major estuaries.

One of the most important feeding areas for Herring Gulls from Texel, the breakwaters along the mainland coast of Noord-Holland (mussels) are mainly utilised by colour-ringed birds from Dutch colonies in (late) summer, suggesting that this resource is abandoned in winter. A seasonal peak in mussel quality might explain this seasonal pattern. However, there are still large numbers of Herring Gulls foraging along the tideline and on breakwaters in that area in winter and the near-absence "local" colour-rings suggests that these birds predominantly come from other breeding areas. Possibly, the poor quality mussels are supplemented by other prey types by these gulls, including nearshore fisheries. Any trawler hauling a net within sight of the Dutch coast is immediately approached by hundreds, sometimes thousands of Herring Gulls, together with Great Black-backed Gulls, Mew Gulls and Black-headed Gulls.

The exact wintering whereabouts of Herring Gulls breeding in the western Wadden Sea are an issue of importance given the recent population declines and the strong suspicion that wintering environments rather than resources during breeding are an important factor. Colour-ring data and the sparse satellite tracking data both suggest that mainland resources are of prime importance for these birds (Appendix 9). The intertidal Wadden Sea is largely abandoned.

Declines in the access to domestic refuse – The increase in numbers of Herring Gulls and the expansion of their breeding range in Europe and in North America has generally been attributed to garbage dumps, which provided a dependable food supply throughout the year, but particularly in winter (Drury 1965, Kadlec & Drury 1968, Spaans 1971, Drury & Kadlec 1974, Kihlman & Larsson 1974, Burger 1977, Monaghan 1978). The results presented in this thesis suggest a contraction of the main wintering area of Herring Gulls breeding on Texel and Vlieland away from the favoured (and now mostly defunct) domestic refuse dumps in Brabant and Zeeland. Higher intra-specific competition for the available resources within a smaller wintering area may have been a consequence. Intra-specific competition at the traditional wintering grounds will also have increased as a result of the higher numbers of gulls breeding in the Dutch Delta area, many of which move only short distances away from their breeding sites in winter (Chapter 6). In line with findings of Belant *et al.* (1989) and Pons (1994), female (smaller, subordinate) Herring Gulls may have suffered disproportionally from this situation, which could explain the lower annual survival found in this sex (Chapter 7). For the moment, the available data seemingly support Hypothesis #3; a reduction in food availability in winter compromising the (overwinter) survival of all age classes of Herring Gulls breeding at Texel.

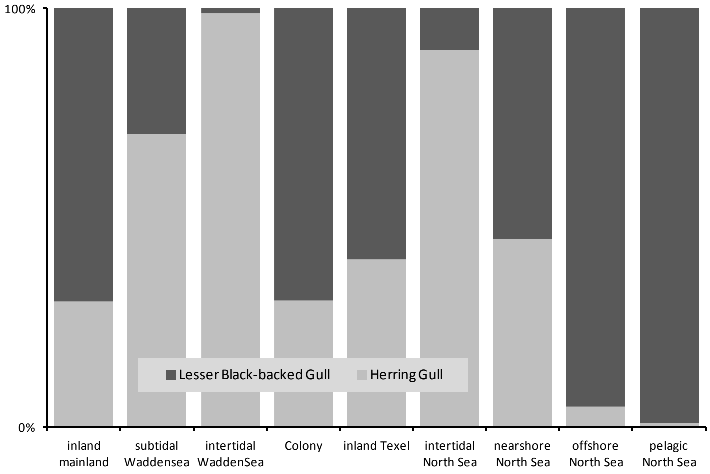


Fig. 15.5. Resource partitioning by Herring Gulls (HG) and Lesser Black-backed Gulls (LBBG) breeding at Texel. The relative abundance within the colony amounts to 30% HG versus 70% LBBG. Intertidal mudflats are rarely visited by LBBG, commonly by HG, whereas the North Sea intertidal is utilised somewhat by LBBGs in the chick care phase. LBBGs outnumber HGs with increasing distances away from the coast, but close to the shore and in deeper parts of the Wadden Sea, HGs are more abundant.

Resource partitioning

According to niche theory, ecologically similar species coexist by virtue of niche differences (Wiens 1989). When wrapping up the abundant material discussed above, the following generalisations could be made:

- Lesser Black-backed Gulls were numerically dominating in continental mainland foraging sites, within the colony, inland at Texel, and offshore on the North Sea.
- Despite their lower overall numbers as breeding birds, Herring Gulls numerically dominated over Lesser Black-backed Gulls in all intertidal areas, including the deeper gullies (subtidal areas) of the Wadden Sea.
- At sea, with increasing distance to the North Sea shoreline Herring Gulls were increasingly outnumbered by Lesser Black-backed Gulls (cf. Camphuysen 1995).

If the key habitats are seen as resources linearly ordered along a single dimension, the utilisation functions of each species can be portrayed as frequency distributions on this dimension, indicating the proportion of resource use (Fig. 15.5; MacArthur & Levins 1967). In this graph the bars represent numerical abundance of each species, which could be taken as a proxy for resource use in ecologically similar and closely related species of roughly the same body size and energetic requirements. What actually *is* shared will be different in each of the resources. The species' exploitation strategies are apparently discretely segregated rather than opportunistic. The graph could even be amended by implementing the sexual segregation reported for Lesser Black-backed Gulls.

Inter-specific competition and resource limitation is more often inferred than measured. If resources are abundant, overlap may be high without fostering competition (Pianka 1981, Wiens 1989). In offshore multi-species foraging associations, the presence or absence of certain "competitors" (*producers*) can make the difference between a foraging opportunity or a waste of time for surface feeding species (commensal interactions; Camphuysen & Webb 1999). If food (or any resource) is an important limiting resource, communities or foraging assemblages should be structured on the basis of how food is partitioned among species within the assemblage (Zwarts & Wanink 1984, 1993). Within the colony, both species compete for nesting space, but the exact micro-habitat requirements differ slightly (Appendix 3). Herring Gulls and Lesser Black-backed Gulls foraging along the North Sea coastline, in the intertidal zone and on land share areas, but generally target different prey (Appendix 7) and have different skills and a different physiology (a muscular stomach is characteristic for Herring Gulls).

Each of the habitats (or resources), linearly ordered in Fig. 15.5, are shared with different assemblages of competitors targeting the same or similar prey (guilds). Within these guilds dominance hierarchies become established and in most of the scenarios sketched below, Herring and Lesser Black-backed Gulls are among the largest (most powerful) species. The enormous variety of prey items require highly different skills and in each of these resources more specialised and efficient competitors may be encountered.

- The inland resource is a mix of opportunities (cities, meadows, arable land, sewage plants, refuse processing facilities) shared with different species assemblages, including two species of gulls (Black-headed Gull and Mew Gull), various meadow birds, corvids, and Starlings
- The subtidal Wadden Sea resource is an area where shrimpers are targeted (4 species of gulls, Common Terns). Herring Gulls and Black-headed Gulls are normally most abundant, female Lesser Black-backed Gulls were found to utilise this resource extensively (this thesis).
- The intertidal of the Wadden Sea has mussel- and cocklebeds (Oystercatcher, Common Eider), but also mudflat invertebrates including crustaceans and small bivalves (waders). Shell crushing behaviour (by dumping prey items such as bivalves and crabs from mid-air) is only known from Herring Gulls.
- Inland Texel is another mix of opportunities with tourist resorts, meadows and other grasslands, arable land, sheep-feeders, and natural dune areas as most characteristic habitats. Competing species are basically the same groups as mentioned for the continental mainland.
- Another foraging opportunity, not restricted to a particular area, but originating from land, are swarming insects (aerial pursuit). Competing species include Black-headed and Mew Gulls, Starlings, swallows, swifts and some other birds.
- The intertidal North Sea includes hard-substrate mussel beds on breakwaters (fully dominated by Herring Gulls, some Oystercatchers and Common Eiders as competing species) or the tideline and surf. Competing species on the tideline include some waders, Black-headed and Mew Gulls. In the surf, Common Eiders, at least four species of terns and summering Great Black-backed Gulls can be added.
- Off the coast, 4-5 species of gulls compete for natural foraging opportunities (marine fish, swimming crabs and invertebrates near the surface) and discards (bottom trawlers). Herring Gulls, but often also Black-headed and Mew Gulls outnumber Lesser Black-backed Gulls in the first kms from the shoreline, but the proportions reverse at greater distances. Far offshore, some further competing, scavenging species include Northern Fulmar *Fulmarus glacialis*, Northern Gannet *Morus bassanus*, and Black-legged Kittiwake (even in summer), but here Lesser Black-backed Gull tend to be the numerically dominating species.

It is unlikely that any individual gull would be equally successful in all these situations. A tendency to specialise on a subset of foraging opportunities is quite likely. Some resources are more distant than others and for gulls breeding at the south tip of Texel, the largest *variety* of foraging opportunities (based on the number of habitats nearby) would be within a 10km radius around the colony. To complicate things, within each of these areas the two gull species negotiate a bewildering variety of predictable and less predictable (ephemeral) resources. Based on all available data presented in this thesis, the intra- and inter-specific resource partitioning of marine areas can be sketched as in Fig. 15.6.

Much less known is the use of resources at the Continental mainland by Herring Gulls and Lesser Black-backed Gulls nesting at Texel. Both species were found to regurgitate prey items that were typical the mainland, because the availability on Texel was unlikely (Appendix 7). Herring Gulls produced more domestic refuse that may have originated from cities. Lesser Black-backed Gulls were demonstrated to extensively forage in land (GPS logger data and probably outnumber Herring Gulls at most grasslands and areas with arable land (see also Camphuysen *et al.* 2006, Chapter 14). In future studies, GPS loggers will need to be used on Herring Gulls to be able to evaluate the relative importance of different foraging areas inland.

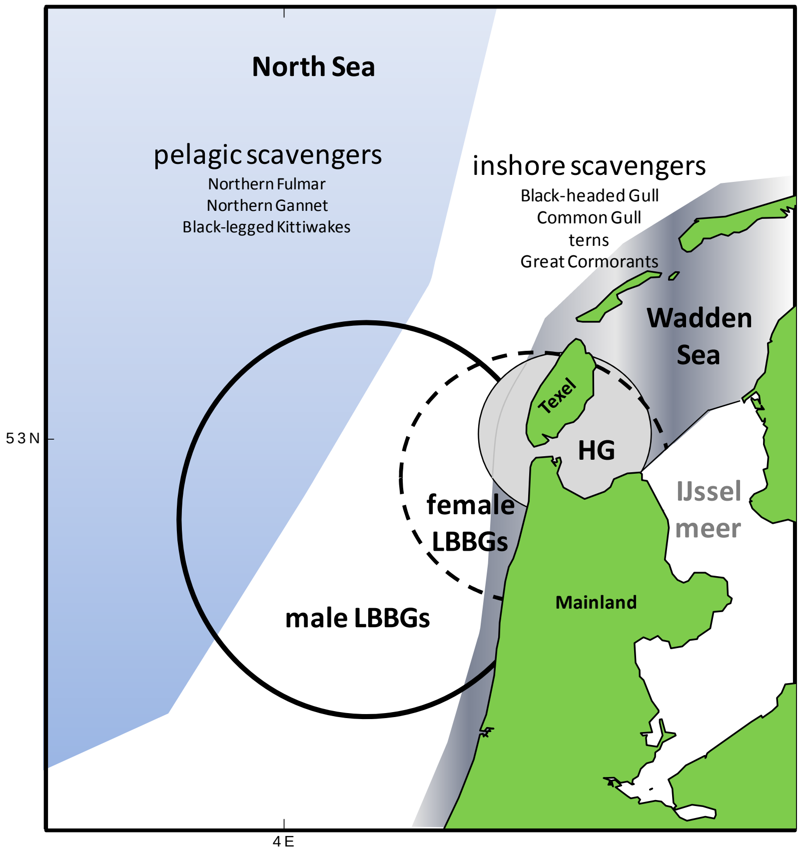


Fig. 15.6. Schematic representation of resource partitioning during breeding in Herring Gulls (HG) and Lesser Black-backed Gulls (LBBGs) from Texel as scavengers behind fishing vessels. The most numerous other seabird species in feeding assemblages in each area are provided. Sources: ship-based surveys, seawatching data, GPS logger data, and dietary studies at Texel.

Overpopulations?

Considerations by conservationists regarding a desired population size are remarkably inconsistent between taxa: all animals are equal but some are more equal than others (Orwell 1945). Liked and disliked animals are treated differently and many species of gulls (not all!) are black-listed for reasons that are not always easy to grasp. Throughout the 20th century, but even today, gull populations have been considered as being ”too large” (see specifically Mörzer Bruijns 1956; Appendix 2). Obviously, animals are more likely to come to be disliked when they interfere with the way in which we utilize our environment, compete with us for resources, damage our constructions or spread disease (Furness & Monaghan 1987). But how *serious* is the actual damage or the discomfort inflicted by Herring Gulls and Lesser Black-backed Gulls in a country like The Netherlands? Exactly why gulls are generally disliked is not clear. Some education could help to reduce the most silly “problems” that people have with these birds.

Nature conservation is too often translated into management terms. *“What can we do?”* is a common response if certain less-desirable population trends are presented. It is a reflex phrase if one disliked species feeds occasionally on (chicks or eggs of) a more appreciated one, even if the make-up of a natural ecosystem is basically just eat or be eaten (Forbes 1887, Paine 1966). *“What have we done”* is a phrase heard less often, except when positive population trends in popular species are believed to be a direct result of our interferences (see Chase 1986 and Bijlsma 2012 for further thoughts on this issue).

Extensive culling took place in the UK (Coulson 1991), in Germany (Goethe 1964, Vauk & Prüter 1987) and in The Netherlands (Spaans 2007). Culling, justified on the grounds of a bewildering variety of reasons, including nature conservation (to protect vegetation, other wild birds), human properties (by protecting poultry or damage on houses), to reduce the risk of bird strikes on aircraft, to reduce water pollution, to reduce the nuisance caused by gulls nesting in towns (vocalisations, nest defence behaviour), droppings on laundry, tearing up plastic rubbish bags or food remains on street sides; Tinbergen 1939, Blaak 1957, Goethe 1964, Thomas 1972, Coulson 1991, Harris & Wanless 1997, Perrins & Smith 2000, Spaans 2007). Between 1972 and 1987 in Britain, nearly 100,000 Herring and Lesser Black-backed Gulls have been killed (Coulson 1991). Slightly earlier, in The Netherlands, from 1947-1966, some 90,000 adult Herring Gulls were either shot or poisoned and some 500,000 eggs were destroyed (Spaans 2007). Culling is a pretty pointless approach if the *reason* for a large population (the carrying capacity in a system) is either not understood or not taken into consideration. A population increase levels off when the carrying capacity of an area is approached. When numbers are artificially reduced by culling but while the resources remain intact, density dependent regulation is expected to lead to changes in demographic variables: higher breeding success, higher recruitment rates, high survival. Unwanted side-effects of culling are commonly reported in the literature spanning at least one century: colonies disintegrated, while new settlements occurred, often in locations that were foreseen nor appreciated (Appendix 2 and references therein). Populations usually bounced back as soon as the persecution was halted.

Roof-nesting gulls, notably in large cities but also in industrial areas, are now commonly seen as a nuisance. The phenomenon commenced in Europe somewhere half-way the 20th century (Strijbos 1942ab, Goethe 1958, Monaghan & Coulson 1977, Monaghan 1982, Rock 2005), but is currently widespread. The "city-phenotype", after numerous generations of successful nesting, would probably not even recognise dune reserves as suitable nesting habitat anymore (Rock 2005). If a problem with some gull population exists, it is wise to research relationships between breeders (fecundity, age composition, recruitment rate, population trends) and their foraging opportunities. City nesting gulls do not necessarily forage in cities. Gulls nesting on a small uninhabited island in IJmuiden commonly forage in Amsterdam (*unpubl.* colour-ring data). Persistent disturbances may simply spread a concentrated breeding population to various new locations. With regard to "gull problems" in cities and other areas, sorting out what the problem exactly is, which birds are involved and what the *long-term* effect of a particular measure should would be a useful first step.

Within The Netherlands we have the rather bizarre situation that not particularly well performing populations of Lesser Black-backed Gulls in the Wadden Sea area are currently strictly protected (Aarts *et al.* 2008, Janssen & Schaminée 2009), while large colonies that are doing rather well in the industrial area of Maasvlakte, Europoort, and Moerdijk risk total destruction because they "hinder us" (Lensink & Van Horssen 2009, Van Swelm 2011). The rationale behind this is not completely clear, but the environmental conditions and the carrying capacity of the respective areas are certainly not taken into account. It is highly likely, therefore, that both the consolidation of a large population in the Wadden Sea islands and the elimination of colonies in the Europoort region will fail. Nothing new…there have been numerous examples of ineffective countermeasures to keep gulls within arbitrary limits in the (recent) past (Appendix 2).

Prospects

As suggested in Chapter 2 of this thesis, a meta-population analysis is required to clarify why on a pan-European scale many populations have fluctuated or changed in concert. While the foraging ecology (or dietary 'preferences'; a risky word) or even the reproductive success of the same species in two neighbouring colonies can be quite different, there are more or less similar population trends spanning much of the (NW) European population simultaneously. At least for the moment, this was considered an overambitious and potentially confusing sidetrack.

With regard to the utilisation of the Wadden Sea and inland resources, additional data are required. Colour-ring data are just not good enough and although the satellite PTTs yielded highly useful information (still awaiting proper analysis), it is evident that for a successful analysis of the foraging energetic and habitat utilisations higher resolution data are needed. GPS loggers will need to be deployed on Herring Gulls to fill in some gaps in our current understanding.

The step from "frequency of occurrence" towards actual intake rates (in energetic terms) has to be made in the studies of the foraging ecology of both species. The data must subsequently be linked to each of the key foraging habitats of the study species. This may require a different set-up of the dietary work, and it certainly means that studies should focus on the 3-4 most important feeding areas for each species. The results should provide more insight in the relative importance of the open sea, the intertidal zone, the Wadden Sea and particular inland resources in energetic terms: costs and benefits. The modern data loggers currently used will provide the essential information on foraging costs (amount of time in flight, soaring, resting, and actively foraging in each habitat). This part of the study should pinpoint which areas are of ecological significance for each species.

The outbreaks of cannibalism require further attention and carefully designed experiments to disentangle the responsible factors that play a role in colonies with high breeding densities. Field work (perhaps including field experiments) and additional colour-ringing is also required to answer some questions regarding the non-breeding of part of the population.

A continuation of detailed demographical studies is required to establish firmer estimates of annual survival rates, recruitment rates, the age of first breeding and levels of intermittent breeding. Population models can then be fed with solid data. Data series of only 7 years in a long-lived seabird, no matter how rare such datasets are, are in fact too short and many of the calculations and modelling must be regarded as "preliminary estimates". As inspiring examples showing the possibilities of analysis now due (including seasonal patterns in the likelihood of survival), are recent studies on Red Knots (Leyrer 2011) and European Spoonbills (Lok *et al.* 2011, 2012).

Conclusions

The results suggest that the recent population trends of Herring Gulls and Lesser Black-backed Gulls breeding in the Western Wadden Sea are more or less independent, even though the birds do compete for certain resources (no support for hypothesis #1). Herring Gulls currently have more favourable breeding results, but relatively poor winter survival and recruitment rates. Following the decommissioning of numerous open landfill areas in the southern and central parts of The Netherlands and intensified intra-specific competition within their wintering range, winter mortality has increased and recruitment rates are subsequently lower than historically (supporting hypothesis #3).

Lesser Black-backed Gulls have profited from a fishing fleet modernisation in the 1960s: a rather unsustainable type of fisheries that has generated vast amounts of discards, and that peaked in the late 1980s and early 1990s. This resource must have been the expected "vacant niche" (supporting hypothesis #2). Winter conditions for this long-distance migrant are (so far) excellent. The problems that Lesser Black-backed Gulls currently face at Texel, low breeding success and high levels of cannibalism, are signs of food stress during breeding. The recent reduction in fishing effort leads to reductions in the amount of discards produced at sea; a key resource for this species. Further declines in discards as a resource can be foreseen because the European Commission proposed a complete ban on discarding, to be effectuated sometime between now and 2019.

Herring Gulls breeding at Texel also showed signs of reductions in provisioning rates during chick care, with cyclic reductions in chick growth alternating with growth spurts, suggesting that this species is under the same "weekend regime" as the Lesser Black-backed Gull. This weekly rhythm follows that in bottom trawl fishing effort. The structurally higher reproductive success in Herring Gulls than in Lesser Black-backed Gulls is probably the result of a wider dietary spectrum (more options) in the former species than in the latter.

The availability of domestic refuse at dumps has been in decline for decades, influencing overwinter survival of Herring Gulls. The availability of fisheries discards will follow the same trajectory if EU directives become fully implemented in national legislation (Price 2001, Penas 2007, Schou 2011). Summering Lesser Black-backed Gulls, can be foreseen to increasingly focus on alternative resources in years to come, which could even lead to increased inter-specific competition with Herring Gulls. If the EU demanded changes in waste management on the Iberian Peninsula, in France and within the UK would become implemented, wintering Lesser Black-backed Gulls will lose another important resource. Marked population changes, declines most likely, can be foreseen. Noordhuis & Spaans (1992) reviewed population trends in the 1980s and 1990s and called "*The situation ...[that]… has developed over only 20 or 30 years …to be rather unstable*." A similar remark could be made today.

That commercial fisheries around the North Sea produce *c.* 789,000 t of discards and offal annum^{-1}, supporting nearly six million seabirds, was highlighted in a paper published in 1996:

Garthe S.[1,2*], C.J. Camphuysen[3] & R.W. Furness[4] 1996. **Amounts of discards in commercial fisheries and their significance as food for seabirds in the North Sea**. Mar. Ecol. Progr. Ser. 136: 1-11.

[1]Institut für Vogelforschung 'Vogelwarte Helgoland', Inselstation, PO Box 1220, D-27494 Helgoland, Germany; [2]Institut für Meereskunde, Abt. Meereszoologie, Düsternbrooker Weg 20, D-24105 Kiel, Germany, ***Correspondence author**, e-mail: sgarthe@ifm.uni-kiel.d400.de; [3]Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands; [4]Applied Ornithology Unit, University of Glasgow, Glasgow G12 8QQ, U.K.

Most types of fishery produce discards and offal in considerable quantities which are fed upon by seabirds. This paper demonstrates the importance to seabirds of fishery waste in the North Sea. The total amount of fishery waste in the North Sea region is estimated at 62,800 t of offal, 262,200 t of roundfish, 299,300 t of flatfish, 15,000 t of elasmobranchs and 149,700 t of benthic invertebrates annum^{-1}, representing 4 % of the total biomass of fish and 22% of the total landings This equals an energy value of about 3.4 X 10^{12} kJ. Beam trawl fisheries discharge discards at the highest rates of all fishing fleets. Their discard fraction is dominated by flatfish which are less favoured by seabirds because of their shape. In contrast, the amounts of discards from pelagic and gadoid fisheries are less, but fish species and lengths are more appropriate as food for seabirds. The number of seabirds potentially supported by fishery waste in the North Sea is estimated to be roughly 5.9 million individuals in an average scavenger community (composition in proportion to the seasonal abundance of scavenging species). During experimental discard studies, the proportions of fishery waste consumed by seabirds was calculated. We estimated that the mass of discards and offal consumed by birds during our study amounted to 55,000 t of offal (88%), 206,000 t of roundfish (79%), 38,000 t of flatfish (13%), 2000 t of elasmobranchs (13%) and 9000 t of benthic invertebrates (6%).

References

Aarts B., L. van den Bremer, E. van Winden & D. Zoetebier 2008. Trendinformatie en referentiewaarden voor Nederlandse kustvogels. WOt-rapport 79 & SOVON-informatierapport 2008/06. Wettelijke Onderzoekstaken Natuur & Milieu, Wageningen.

Adema J.P.H.M. 1991. De krabben van Nederland en België (Crustacea, Decapoda, Brachyura). Nationaal Natuurhistorisch Museum, Leiden.

Adriaens P., H.J.P. Vercruijsse & E.W.M. Stienen 2012. Hybrid gulls in Belgium-an update. Brit. Birds 105: 530-542.

Aebischer N.J. & Coulson J.E. 1990. Survival of the Kittiwake in relation to sex, year, breeding experience and position in the colony. J. Anim. Ecol. 59: 1063-1071.

Aebischer N.J. & S. Wanless 1992. Relationships between colony size, adult non-breeding and environmental conditions for Shags *Phalacrocorax aristotelis* on the Isle of May, Scotland. Bird Study 39: 43-52.

Agardy M.T. 1994. Advances in marine conservation: the role of marine protected areas. TREE9: 267-270.

Aken H.M. van 2008. Variability of the water temperature in the western Wadden Sea on tidal to centennial time scales. J. Sea Res. 60: 227-234.

Aken H.M. van 2010. Meteorological forcing of long-term temperature variations of the Dutch coastal waters. J. Sea Res. 63: 143-151.

Albarda H. 1897. Aves Neerlandicae-Naamlijst van Nederlandsche Vogels. Coöp. Handelsdr., Leeuwarden.

Alerstam T. 1990. Bird migration. Cambridge Univ. Press, Cambridge.

Alerstam T., A. Hedenström & S. Åkesson 2003. Long-distance migration: evolution and determinants. Oikos 103: 247-260.

Alerstam T., M. Rosén, J. Bäckman, P.G.P. Ericson & O. Hellgren. 2007. Flight Speeds among Bird Species: Allometric and Phylogenetic Effects. PLoS Biology 5: 1656-1662.

Alexander W.B. 1928. Birds of the Ocean. A Handbook for Voyagers. G.P. Putnam's Sons, New York.

Allaby M. 2010. Oxford dictionary of ecology. Fourth edition. Oxford Univ. Press, Oxford.

Allard K.A., A.R. Breton, H.G. Gilchrist & A. Diamond 2006. Adult survival of Herring Gulls breeding in the Canadian arctic. Waterbirds 29: 163-168.

Allard K.A., H.G. Gilchrist, A.R. Breton, C.D. Gilbert & M.L. Mallory 2010. Apparent survival of adult Thayer's and Glaucous Gulls nesting sympatrically in the Canadian high Arctic. Ardea 98: 43-50.

Altenburg R. & M. Muusse 2004. Herkenning en voorkomen van Eerste kalenderjaar grote meeuwen in Amsterdam. De Gierzwaluw 42(2): 7-31.

Ambrose W.G. 1986. Estimate of removal rate of Nereis virens (Polychaeta: Nereidae) from an intertidal mudflat by gulls (Larus spp.). Mar. Biol. 90: 243-247.

Amlaner C.J. & N.J. Ball 1983. A synthesis of sleep in wild birds. Behaviour 87: 85-119.

Anderson A. 1980. Band wear in the Fulmar. J. Field Orn. 51: 101-109.

Anderson D.R. & K.P. Burnham 1999. Understanding information criteria for selection among capture-recapture or ring recovery models. Bird Study 46, S1: S14-S21.

Anderson D.R., K.P. Burnham & G.C. White 1994. AIC Model selection in overdispersed capture-recapture data. Ecology 75: 1780-1793.

Anderson D.R., K. P. Burnham & G.C. White 1998. Comparison of Akaike information criterion and consistent Akaike information criterion for model selection and statistical inference from capture-recapture studies. J. Appl. Statistics 25: 263-282.

Anderson O., Small C., Croxall J.P., Dunn E., Sullivan B., Yates O. & Black, A 2011. Global seabird bycatch in longline fisheries. Endang. Species Res. 14: 91-106.

Anderson W. 1965. Waterfowl production in the vicinity of gull colonies. Calif. Fish and Game 51: 5-15.

Andersson A. 1970. Food habits and predation of an inland-breeding population of the Herring Gull *Larus argentatus* in southern Sweden. Ornis Scand. 1: 75-81.

Andersson M. & S. Erlinge 1977. Influence of predation on rodent populations. Oikos 29: 591-597.

Anker-Nilssen T. & Nygård T. 1989. Notes on the food choice of adult and young guillemots Uria aalge during post-breeding migration in central Norway. Fauna Norv. Ser.C, Cinclus 10: 53–56.

Anker-Nilssen T. & Øyan H.S. 1995. Hekkebiologiske langtidsstudier av lunder på Røst. NINA Fagrapport, 15. 48 pp.

Annett C. & Pierotti R. 1989. Chick hatching as a trigger for dietary switching in the western gull. Col. Waterb. 12: 4–11.

Annett C.A. & R. Pierotti 1999. Long-term reproductive output in Western Gulls: Consequences of alternate tactics in diet choice. Ecology 80: 288-297.

Anonymous 1880. Binnenland. Nieuwe Tilburgsche Courant 12 Sep 1880, Vol. 2(75), Tilburg.

Anonymous 1892. De nadere bepaling, bij Kon. besluit vastgesteld, tot bescherming van diersoorten, nuttig voor landbouw of houtteelt. Tilburgsche Courant, 13 Nov 1892.

Anonymous 1893. Nuttige diersoorten. Het nieuws van den dag : kleine courant, 28 June 1893, Nr 7181.

Anonymous 1902. Binnenland. Texelse Courant 9 Nov 1902.

Anonymous 1912. Tweede kamer. Vergadering van Dinsdag 19 Maart-De vogelwet. Rotterdamsche Courant 69, nr. 79, 20 March 1912.

Anonymous 1918. In een tuin bij Den Haag. DLN 23: 280-282.

Anonymous 1994a. Britse Kleine mantelmeeuw broedt op daken. Het Vogeljaar 42: 275.

Anonymous 1994b. Report of the study group on seabird/fish interactions. ICES C.M. 1994/L: 3, pp 1-119.

Anonymous 1995. Kleine Mantelmeeuwen broeden op daken. Het Vogeljaar 43: 30.

Anonymous 2001. The impact of Community environmental waste policies on economic and cosial cohesion. http://ec.europa.eu/regional_policy/sources/docgener/studies/pdf/enviwas.pdf.

Arcos J., D. Oro & D. Sol 2001. Competition between the yellow-legged gull *Larus cachinnans* and Audouin's gull *Larus audouinii* associated with commercial fishing vessels: the influence of season and fishing fleet. Mar. Biol. 139: 807-816.

Arnett R.T.P. & Whelan J. 2001. Comparing the diet of cod (*Gadus morhua*) and grey seals (*Halichoerus grypus*): an investigation of secondary ingestion. J. Mar. Biol. Ass. UK 81: 365–366.

Arroyo G.M. & D. Cuenca 2004. The migration of seabirds through the Straits of Gibraltar: the Migres Seabird project. Abstracts poster presentations 8th Intern. Seabird Group Conference "North Atlantic Seabird Populations: 11. King's College Conference Centre, Aberdeen University, 2-4 April 2004, Aberdeen.

Aschoff J. & Pohl H. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergroße. J. Orn. 11: 38-47.

Ashmole N.P. 1971. Sea bird ecology and the marine environment. In: Farner D.S. & King J.R. (eds). Avian Biology, 1: 224-286. Acad. Press, New York.

Auman H.J. 2008. Effects of anthropogenic food on the body condition, biochemistry, stable isotopes and egg quality in Silver Gulls *Larus novaehollandiae* in Tasmania. Ph.D.-thesis, School of Zoology, University of Tasmania.

Baerends G.P. & R.H. Drent 1970. The herring gull and its egg. Part I. Behaviour, Suppl. 17: 1-312.

Baerends G.P. & R.H. Drent 1982. The herring gull and its egg. Part II. Behaviour 82: 1-415.

Bailey E.E., Woolfenden G.E. & Robertsen W.B. 1987. Abrasion and loss of bands from Dry Tortugas Sooty Terns. J.Field Orn. 58: 413-424.

Bailey R.S. & Hislop J.R.G. 1978. The effects of fisheries on seabirds in the northeast Atlantic. Ibis 120: 104-105.

Bairlein F. 2001. Results of bird ringing in the study of migration routes. In: Jenni L. & C.J. Camphuysen (eds) Bird ringing 100 years. Proc. int. conf. Helgoland, 29 Sep-3 Oct 1999. Ardea 89 (special issue): 7-19.

Baker R.R. 1980. The significance of the Lesser Black-backed Gull to models of bird migration. Bird Study 27: 41-50.

Bakker H.C. 1937. Geen gevaar. Texelse Courant 15 May 1937: 6.

Bakker M. de , W. Bouten, J. Shamoun-Baranes & C.J. Camphuysen 2012. Semi-automatic construction of a classifier for bird behaviour from accelerometer data. BeneLearn and PMLS submitted.

Baptist H.J.M. & Wolf P.A. 1993. Atlas van de vogels van het Nederlands Continentaal Plat. Rapport DGW-93.013, Dienst Getijdewateren, Rijkswaterstaat, Middelburg.

Barbraud C. & Chastel O. 1998. Southern Fulmars molt their primary feathers while incubating. Condor 100: 563-566.

Baretta-Bekker J.G., Duursma E.K. & Kuipers B.R. (eds) 1998. Encyclopedia of Marine Sciences. Second, corrected and enlarged edition, Springer-Verlag, Berlin.

Barnard C.J. & D.B.A. Thompson 1985. Gulls and plovers: the ecology and behaviour of mixed-species feeding groups. Columbia Univ. Press, New York.

Barnes J.A.G. 1953. The migrations of the Lesser Black-backed Gull. Brit. Birds 46: 238-252.

Barrett R.T., C.J. Camphuysen, T. Anker-Nilssen, J.W. Chardine, R.W. Furness, S. Garthe, O. Hüppop, M.F. Leopold, W.A. Montevecchi, R.R. Veit 2007. Diet studies of seabirds: a review and recommendations. ICES J. Mar. Sc. 64: 1675-1691.

Barrett R.T., Røv N., Loen J. & Montevecchi W.A. 1990. Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and implications for gadoid stock recruitment. Mar. Ecol. Progr. Ser. 66: 205–218.

Barth E.K. 1953. Calculation of egg volume based on loss of weight during incubation. Auk 70: 151-159.

Barth E.K. 1968. Egg dimensions and laying dates of *Larus marinus*, *L. argentatus*, *L. fuscus*, and *L. canus*. Nytt Mag. Zool. 15: 5-34.

Barth E.K. 1975. Moult and taxonomy of the Herring Gull *Larus argentatus* and the Lesser Black-backed Gull *L. fuscus* in northwestern Europe. Ibis 117: 384-387.

Baudinette R.V. & Schmidt-Nielsen K. 1974. Energy cost of gliding flight in herring gulls. Nature (London) 248: 83-84.

Bearhop S., R.A. Phillips, R. McGill, Y. Cherel, D.A. Dawson & J.P. Croxall. 2006. Stable isotopes indicate sex-specific and long-term individual foraging specialization in diving seabirds. Mar. Ecol. Progr. Ser. 311: 157-164.

Beaugrand G., Brander K.M., Lindley J.A., Souissi S. & Reid P.C. 2003. Plankton effect on cod recruitment in the North Sea. Nature 426: 661-664.

Beaugrand G., Reid P.C., Ibanez F., Lindley J.A. & Edwards M. 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296: 1692-1694.

Beck J.R. 1970. Breeding seasons and moult in some smaller Antarctic petrels. In: Holdgate M.W. (ed.) Antarctic ecology 1: 542-550. Acad. Press, London.

Becker P.H. & M. Erdelen 1986. Egg size in Herring Gulls (*Larus argentatus*) on Mellum Island, North Sea, West Germany: the influence of nest vegetation, nest density, and colony development. Col. Waterb. 9: 68-80.

Becker P.H. & M. Erdelen 1987. Die Bestandsentwicklung von Brutvögeln der Deutschen Nordseeküste 1950–1979. J. Orn. 128: 1–32.

Becker P.H. & H. Wendeln 1997. A new application for transponders in population ecology of the Common Tern. Condor 99: 534-538.

Beek F.A. van 1990. Discard sampling programme for the North Sea. Dutch participation. Internal RIVO-report, Demvis 90-303.

Beek F.A. van, P.I. van Leeuwen & A.D. Rijnsdorp. 1990. On the survival of plaice and sole discards in the otter trawl and beamtrawl fisheries in the North Sea. Neth. J. Sea Res. 26: 151-160.

Beers P.W.M. van & Habraken J.M.P.M. 1993. De invloed van getij, wind en leeftijd van de kuikens op de voedselaanvoer van de grote stern *Sterna sandvicensis*. M.Sc.-thesis KU Nijmegen/Instituut voor Bos- en Natuuronderzoek, Arnhem.

Begon M., Harper J.L. & Townsend C.R. 1990. Ecology - Individuals, populations and communities. Blackwell Scientific Publ., Boston.

Behm-Berkelmann K. & H. Heckenroth 1991. Übersicht der Brutbestandsentwicklung ausgewählter Vogelarten 1900–1990 an der niedersächsischen Nordseeküste. Natursch. Landschaftspfl. Nieders. 27: 1–97.

Belant J.L., Seamans T.W., Gabrey T.W. & Ickes S.K. 1993. Importance of landfills to nesting Herring Gulls. The Condor 95: 817-830.

Bellebaum J. 2005. Between the Herring Gull *Larus argentatus* and the bulldozer: Black-headed Gull *Larus ridibundus* feeding sites on a refuse dump. Orn. Fenn. 82: 166-171.

Bellebaum J., Buchheim A., Nowakowski J. & Sell M. 2000. Was tun, wenn der Müll knapp wird? 25 Jahre überwinternde Möwen (Laridae) im Ruhrgebiet. In: Helbig A.J. & Flade M. (eds) Vogelmonitoring 2. Zweiter Bericht zur Lage der Vögel in Deutschland. Vogelwelt 121: 165-172.

Belopol'skii L.O. 1957. Ecology of sea colony birds of the Barents Sea. Israel Program of Scientific Translation 1961, 346 pp.

Bennekom A.J. van & S.B. Tijssen 1976. Lage zuurstofgehaltes in het water op het Balgzand. $H_2$0 9(2) : 28-31.

Bennett P.M. & P.F. Owens. 2002. Evolutionary ecology of birds. Life histories, mating systems and extinction. Oxford Univ. Press, Oxford.

Bent A.C. 1921. Life histories of North American gulls and terns. U.S. Natl. Mus. Bull. 113, Reprint 1963, Dover Publ., New York.

Benvenuti S., F. Bonadonna, L. Dall'Antonia & G.A. Gudmundsson 1998. Foraging flights of breeding Thick-billed Murres (*Uria lomvia*) as revealed by bird-borne direction recorders. Auk 115:57-66.

Berg A.B. van den & Bosman C.A.W. 1999. Zeldzame vogels van Nederland. Avifauna van Nederland, 1. KNNV Uitgeverij Utrecht en GMB Uitgeverij, Haarlem.

Berghahn R. & Rösner H.-U 1992. A method to quantify feeding of seabirds on discards from the shrimp fishery in the North Sea. Neth. J. Sea Res. 28: 347-350.

Bergman G. 1957. Zum Problem der gemischten Kolonien: Die Reiherente (*Aythya fuligula*) und die Lariden. Vogelwarte 19: 15-25.

Bergman G. 1982. Population dynamics, colony formation and competition in *Larus argentatus*, *fuscus* and *marinus* in the archipelago of Finland. Ann. Zool. Fenn. 19: 143-164.

Bergman G., Fabricius E. & Haartman L. von 1940. En preliminär undersökning över silltrutens, *Larus f. fuscus* L., och gråtrutens, *Larus a. argentatus* Pontopp., näringsbiologie, särskilt ur jaktvårdssynpunkt. Orn. Fenn. 17: 33-41.

Bernstein C., J.R. Krebs, A. Kacelnik 1991. Distribution of birds amongst habitats: theory and relevance to conservation. In: Perrins C.M., J-D. Lebreton & G.J.M. Hirons (eds), Bird population studies: 317-345. Oxford Univ. Press, Oxford.

Berthold P. 2001. Bird Migration: a general survey. Oxford Ornithology Series, Oxford Univ. Press, Oxford.

Beukema J.J. 2002. Expected changes in the Wadden Sea benthos in a warmer world: lessons from periods with mild winters. J. Sea Res. 30:73-79.

Beukema J.J. & G.C. Cadée 1986. Zoobenthos responses to eutrophication in the Dutch Wadden Sea. Ophelia 26: 55-64.

Beukema J.J. & G.C. Cadée 1987. De eutrofiëring van ons kustwater: genoeg of al te veel? Vakbl. Biol. 67(9): 153-157.

Beukema J.J. & G.C. Cadée 1996. Consequences of the sudden removal on nearly all mussels and and cockles from the Dutch Wadden Sea. Mar. Ecol. 17: 279-289.

Beukema J.J. & R. Dekker 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. Mar. Ecol. Progr. Ser. 287: 149–167.

Bewick T. 1826. A History of British Birds. Edw. Walker, Newcastle.

Bijlsma R.G. 2012. Mijn roofvogels. Atlas, Amsterdam.

Bijlsma R.G., Hustings F. & Camphuysen C.J. 2001. Schaarse en algemene vogels van Nederland. Avifauna van Nederland, 2. KNNV Uitgeverij Utrecht en GMB Uitgeverij, Haarlem.

Bijlsma R.G., M. Vermeulen, L. Hemerik & C. Klok 2012. Demography of European Honey Buzzards *Pernis apivorus*. Ardea 100: 163-177.

Binsbergen N. 1935. De schuilhut op de belt. De Lev. Nat. 39: 297-302.

Birdlife International 2004. Tracking ocean wanderers: the global distribution of albatrosses and petrels. Results from the Global Procelariiform Tracking workshop, 1-5 September 2003, Gordon's Bay, South Africa, Birdlife International, Cambridge.

Birt V.L., T.P. Birt, D. Goulet, D.K. Cairns & W.A. Montevecchi 1987. Ashmole's halo: direct evidence for prey depletion by a seabird. Mar. Ecol. Progr. Ser. 40:205-208.

Birt-Friesen V.L. Montevecchi W.A. Cairns D.K. & Macko S.A. 1989. Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. Ecology 70: 357-367.

Blaak H. 1957. Vogelleven in Wassenaars duinen. De Lev. Nat. 60: 217-222.

Blake B.F. 1984. Diet and fish stock availability as possible factors in the mass death of auks in the North Sea. J. Exp. Mar. Biol. Ecol. 76: 89-103.

Blake B.F., T.J. Dixon, P.H. Jones & M.L. Tasker 1985. Seasonal changes in the feeding ecology of guillemots (*Uria aalge*) off north and east Scotland. Est., Coast. Shelf Sc. 20: 559–568.

Blake B.F., M.L. Tasker, P.H. Jones, T.J. Dixon, R. Mitchell & D.R. Langslow 1984. Seabird Distribution in the North Sea. Nature Conservancy Council, Huntingdon.

Blanco G. & J. Marchamalo 1999. Post-breeding inland movements and use of refuse dumps by Audouin's and other gulls in Spain. Waterbirds 22: 307-309.

Blokpoel H. & A.L. Spaans 1991. Superabundance in gulls: causes and consequences. In: Acta XX Congressus Internationalis Ornithologici. New Zealand Ornithological Congress: 2360-2364. Trust Board, Wellington, New Zealand.

Boag P.T. & A.J. van Noordwijk 1987. Quantitative genetics. In: Cooke F. & P.A. Buckley (eds) Avian genetics: 45-78. Acad. Press, New York.

Boele A. 2012. Zeldzame broedvogels in 2012: veel Witwangsterns en Kleinst Waterhoentjes en de eerste Pontische Meeuw. Sovon Nieuws 5(4): 3-5.

Boer P., Brenkelen W. van, Monsees G.R., Mulder T. & Vlies K. van der 1970. Het Balgzand, bedreigd gebied. Wet. meded. KNNV No. 86, Hoogwoud.

Boersema J.J., J.W. Copius Peereboom & W.T. de Groot 1984. Basisboek milieukunde. Boom Meppel, Amsterdam.

Boersma P.D., D.L. Stokes, I.J. Strange 2002. Applying ecology to conservation: tracking breeding penguins at New Island South reserve, Falkland Islands. Aquatic Conserv. Mar. Freshw. Ecosyst. 12:63-74.

Bogdanova M.I., F. Daunt, M. Newell, R.A. Phillips, M.P. Harris & S. Wanless 2011. Seasonal interactions in the black-legged kittiwake, *Rissa tridactyla*: links between breeding performance and winter distribution. Proc. R. Soc. B doi:10.1098/rspb.2010.2601.

Bolnick D.I., R. Svanbäck, J.A. Fordyce, L.H. Yang, J.M. Davis, C.D. Hulsey & M.L. Forister 2003. The Ecology of Individuals: Incidence and Implications of Individual Specialization. Am. Nat. 161: 1-28.

Bolnick D.I., L.H. Yang, J.A. Fordyce, J.M. Davis & R. Svanbäck 2002. Measuring individual-level resource specialisation. Ecology 83: 2936-2941.

Bolton M. 1991. Determinants of chick survival in the Lesser Black-backed Gull: relative contributions of egg size and parental quality. J. Anim. Ecol. 60: 949-960.

Boon A.R., R. ter Hofstede, C. Klok, M.F. Leopold, G. Blacquiere, M.J.M. Poot, R.A. Kastelein & C.J. Camphuysen 2010. Monitoring and researching ecological effects of Dutch offshore wind farms, Masterplan. Deltares, Utrecht/Delft.

Booy H.L. & N. Tinbergen 1937. Nieuwe feiten over de sociologie van de Zilvermeeuwen. De Lev. Nat. 41: 325-334.

Bosman D.S., H.J.P. Vercruijsse, E.W.M. Stienen, M. Vincx, L. DeNeve & L. Lens 2012. Effects of body size on sex-related migration vary between two closely related gull species with similar size dimorphism. Ibis 154: 52-60.

Bost C.A., A. Jaeger, W. Huin, P. Koubbi, L.G. Halsey, N. Hanuise & Y. Handrich 2008. Monitoring prey availability via data loggers deployed on seabirds: advances and present limitations. In: Tsukamoto K., T. Kawamura, T. Takeuchi, T.D. Beard Jr & M.J.Kaiser (eds) Fisheries for Global Welfare and Environment: . 121-137. Memorial book of the 5th World Fisheries Congress 2008. Terrapub, Tokyo.

Boswall J. 1960. Observations on the use by sea-birds of human fishing activities. Brit. Birds 53: 12-215.

Boswall J. 1977. The use by seabirds of human fishing activities. Brit. Birds 70: 79-81.

Both C., S. Bouwhuis, C.M. Lessells & M.E. Visser 2006. Climate change and population declines in a long-distance migratory bird. Nature 441: doi:10.1038/nature04539.

Both C., T. Piersma & S.P. Roodbergen 2005. Climate change explains much of the 20th century advance in laying date of Northern Lapwing *Vanellus vanellus* in the Netherlands. Ardea 93: 79-88.

Boulinier T., E. Danchin, J-V. Monnat, C. Doutrelant & B. Cadiou 1996. Timing of prospecting and the value of information in a colonial breeding bird. J. Avian Biol. 27: 252-256.

Bouma J.P. 1929. In en om de schuilhut I. Om de schuilhut. De Lev. Nat. 33: 273-279.

Bouman A.E., Bruijn G.J. de, Hinsberg A. van, Sevenster P., Wanders E.A.J. & Wanders R.M. 1991. Meeuwen-opkomst en ondergang van een meeuwenkolonie. Wet. Med. KNNV nr. 204: 1-68.

Bourget A.A. 1973. Relation of Eiders and gulls nesting in mixed colonies in Penobscot Bay, Maine. Auk 90: 809-820.

Bourne W.R.P. 1968. Oil pollution and bird populations. In: Carthy J.D. & Arthur D.R. (eds) The biological effects of oil pollution on littoral communities. Proc. symp. Pembroke Wales 17-19 February 1968. Field Studies Suppl. 2: 99-121.

Bourne W.R.P. 1970. Oil pollution and bird conservation. Biol. Conserv. 2: 300-302.

Bourne W.R.P. 1976. Seabirds & pollution. In: Johnston R. (ed.) Marine Pollution: 403-502. Acad. Press, London.

Bouten B., E.W. Baaij, J. Shamoun-Baranes & C.J. Camphuysen 2013. A flexible GPS tracking system for studying bird behaviour at multiple scales. J. Orn. 154: 571-580.

Bowen S.H., E.V. Lutz & M.O. Ahlgren 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. Ecology 76: 899-907.

Bradley J.S., I.J. Skira & R.D. Wooller 1990. A long-term study of Short-tailed Shearwaters *Puffinus tenuirostris* on Fisher Island, Australia. Ibis 133 suppl. I: 55-61.

Bradley J.S. & R.D. Wooller 1991. Philopatry and age of first-breeding in long-lived birds. Acta XX Congr. Intern. Ornith. 1657-1665.

Bradley J.S., R.D. Wooller & I.J. Skira 2000. Intermittent Breeding in the Short-Tailed Shearwater *Puffinus tenuirostris*. J. Anim. Ecol. 69: 639-650.

Bradley J.S., R.D. Wooller, I.J. Skira & D.L. Serventy, D.L. 1989. Age-dependent survival of breeding Short-tailed Shearwaters *Puffinus tenuirostris*. J. Anim. Ecol. 58: 175-188.

Brandl R. & M. Gorke 1988. How to live in colonies: foraging range and patterns of density around a colony of Black-headed Gulls Larus ridibundus in relation to the gulls' energy budget. Om. scand. 19: 305-308.

Breiby A. 1985. Otolitter fra Saltvannsfisker i Nord-Norge. Naturvit. nr. 45, Univ. Tromsø, Tromsø.

Brenninkmeijer A. & E.W.M. Stienen 1992. Ecologisch profiel van de Grote Stern (Sterna sandvicensis). RIN-rapport 92/17, DLO-Instituut voor Bos- en Natuuronderzoek, Wageningen.

Breton A.R., G.A. Fox & J.W. Chardine 2008. Survival of Adult Herring Gulls (*Larus argentatus*) from a Lake Ontario Colony Over Two Decades of Environmental Change. Waterbirds 31: 15-23.

Breton G., M. Faasse, P. Noël & T. Vincent 2002. A new alien crab in Europe: *Hemigrapsus sanguineus* (Decapoda: Brachyura: Grapsidae). J. Crust. Biol. 22: 184-189.

Bridge E.S. 2003. Effects of simulated primary moult on pigeon flight. Orn. Fenn. 80: 121–129.

Bridge E.S. 2006. Influences of morphology and behavior on wing-molt strategies in seabirds. Mar. Orn. 34: 7-19.

Briggs D.R., Prince P.A. & Croxall J. P. 1993. Movements and interactions of wandering albatrosses: the roles of satellite tracking and direct observations. Sea Swallow 42: 41–44.

Brinkman A.G. & Smaal A.C. 2003. EVA II project F7: Onttrekking en natuurlijke productie van schelpdieren in de Nederlandse Waddenzee in de period 1976-1999. Alterra report 888, 1-243. Alterra,Wageningen.

Brockmann U.H., R.W.P.M. Laane & H. Postma 1990. Cycling of nutrient elements in the North Sea. Neth. J. Sea Res. 26: 239-264.

Broek E. van den & Jansen J. 1970. Parasites of animals in The Netherlands, suppl. V: Endoparasites of wild birds. Ardea 59: 28-33.

Broekhuizen S., Hoekstra B., Laar V. van, Smeenk C. & Thissen J.B.M. 1992. Atlas van de Nederlandse Zoogdieren. Kon. Ned. Natuurhist. Ver., Utrecht.

Brooke M. de L. 1986. Manx Shearwater chicks: seasonal, parental, and genetic influences on the chick's age and weight at fledging. Condor 88: 324-327.

Brooke M. de L. 1990. The Manx Shearwater. Poyser, London.

Brouwer A., A.L. Spaans. & A.A.N de Wit 1995. Survival of Herring Gull *Larus argentatus* chicks: an experimental analysis of the need for early breeding. Ibis 137: 272-278.

Brouwer G.A. 1927. *Falco peregrinus* Tunst. en *Larus fuscus affinis* Reinh. broedvogel in Nederland. Ardea 16: 4-10.

Brouwer G.A. & F. Haverschmidt 1928. Waarnemingen in 1926 en 1927, I. Broedvogels. Ardea 17: 5-46.

Brouwer G.A. & F. Haverschmidt 1942. Een kleine broedkolonie van *Larus minutus* Pall. in Nederland in 1942. Ardea 31: 157-174.

Brouwer G.A. & G.C.A. Junge 1945. Waarnemingen van broedvogels en trekvogels in 1943. Ardea 33: 136.

Brouwer G.A. & G.C.A. Junge 1946. Waarnemingen van broedvogels en trekvogels in 1944 en 1945. Ardea 34: 315-314.

Brown K.M. & A.S. Lang 1996. Cannibalism by color-banded Ring-billed Gulls. Col. Waterb. 19: 121-123.

Brown M.E. 1995. The effect of experience on parental feeding investment by male and female Western Gulls breeding on Alcatraz Island. Abstracts of the Joint Conference of the Colonial Waterbird Society and the Pacific Seabird Group, 8-12 November 1995: 34-35. Victoria, B.C.

Brown R.G.B. 1967. Breeding success and population growth in a colony of Herring and Lesser Black-backed Gulls. Ibis 109: 502-515.

Brugger K.E. 1993. Digestibility of three fish species by double crested cormorants. Condor 95: 25–32.

Bruyne R.H. de, R.A. Bank, J.P.H.M. Adema & F.A. Perk 1994. Nederlandse naamlijst van de weekdieren (Mollusca) van Nederland en België. Uitg. Nederl. Malacol. Vereniging, Backhuys, Leiden.

Bryant D.M. & Furness R.W. 1995. Basal metabolic rates of North Atl. Seabirds. Ibis 137: 219-226.

Buchholz R. 2007. Behavioural biology: an effective and relevant conservation tool. TREE 22: 401-407.

Buckland S.T., B.J. Turnock 1992. A robust line transect method. Biometrics 48: 901-909.

Bugoni L. & Vooren C.M. 2004. Feeding ecology of the common tern Sterna hirundo in a wintering area in southern Brazil. Ibis 146: 438–453.

Bukacińska M. & Bukaciński D. 1993. The effect of habitat structure and density of nests on territory size and territorial behaviour in the black-headed gull (*Larus ridibundus* L.). Ethol. 94: 306-316.

Bukacińska M., Bukaciński D. & Spaans A.L. 1996. Attendance and diet in relation to breeding success in Herring Gulls (*Larus argentatus*). Auk 113: 300-309.

Bukaciński D., M. Bukacińska & A.L. Spaans 1998. Experimental evidence for the relationship between food-supply, parental effort and chick survival in the Lesser Black-backed Gull *Larus fuscus*. Ibis 140: 422-430.

Burger A.E. & Wilson R. P. 1988. Capillary-tube depth gauges for diving animals: an assessment of their accuracy and applicability. J. Fld Ornith. 59: 345–354.

Burger J. 1974. Breeding biology and ecology of the Brown-hooded Gull in Argentina. Auk 91: 601-613.

Burger J. 1980. The transition to independence and postfledging parental care in seabirds. In: Burger J., B.L. Olla & H.E. Winn (eds) Behavior of marine animals 4; Marine birds: 367-447. Plenum Press, New York.

Burger J. 1981a. Feeding competition between Laughing Gulls and Herring Gulls at a sanitary landfill. Condor 83: 328-335.

Burger J. 1981b. Effects of human disturbance on colonial species, particularly gulls. Col. Waterb. 4: 28-36.

Burger J. 1984. Pattern, mechanism, and adaptive significance of territoriality in Herring Gulls (*Larus argentatus*). Orn. Monogr. 34, American Ornithological Union, Washington.

Burger J. & J. Shisler 1978. Nest site selection and competitive interactions of Herring and Laughing Gulls in New Jersey. Auk 95: 252-266.

Burnham K.P. & D.R. Anderson 2002. Model selection and multi-model inference: a practical information-theroretic approach. Second edition. Springer, New York.

Burnham K.P., D.R. Anderson, G.C. White, C. Brownie & K.H. Pollock 1987. Design and analysis of fish survival experiments based on release-recapture data. American Fisheries Society Monogr. 5, Bethesda, Maryland.

Burt W.H. 1943. Territoriality and Home Range Concepts as Applied to Mammals. J. Mamm. 24:346-352.

Butler R.G. & Janes-Butler S. 1982. Territoriality and behavioral correlates of reproductive success of Great Black-backed Gulls. Auk 99: 58-66.

Bustnes J.O., R.T. Barrett & M. Helberg 2010. Northern Lesser Black-backed Gulls: what do they eat? Waterbirds 33: 534-540.

Butterfield J., Coulson J.C., Kearsey S.V., Monaghan P., McCoy J.H. & Spain G.E. 1983. The herring gull *Larus argentatus* as a carrier of salmonella. J. Hyg. (Lond.) 91: 429-36.

BWP*i* 2004. The birds of the western Palearctic interactive. DVD Birdguides, Shrewsbury.

Cadée G.C. 1986. Increased phytoplankton primary production in the Marsdiep area (western Dutch Wadden Sea). Neth J. Sea Res. 20: 285-290.

Cadée G.C. 1995. Birds as producers of shell fragments in the Wadden Sea, in particular the role of the Herring Gull. GEOBIOS M.S. 18: 77-85.

Cadée G.C. 2000. Japanse Oester (*Crassostrea gigas*) populaties tussen Oudeschild en Mok, Texel. Het Zeepaard 60: 260-269.

Cadée G.C. 2001. Herring gulls learn to feed on a recent invader in the Dutch Wadden Sea, the Pacific oyster *Crassistrea gigas*. Basteria 65: 33-42.

Cadée G.C. 2007. Zilvermeeuwen en strandkrabben. Natura 104: 150-153.

Cadee G.C. 2008a. Zilvermeeuwen gooien met Japanse oesters en stenen. De Skor, manuscript.

Cadée G.C. 2008b. Herring gulls feeding again on Pacific oysters *Crassostrea gigas* in the Dutch Wadden Sea near Texel. Basteria 72: 33-36.

Cadiou B. 1999. Attendance of breeders and prospectors reflects the quality of colonies in the Kittiwake *Rissa tridactyla*. Ibis 141: 321-326.

Cairns D.K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5: 261-271.

Cairns D.K. 1998. Diet of cormorants, mergansers and kingfishers in northeastern North America. Can. Techn. Rep. Fish. Aq. Sc. 2225, 29 pp.

Cairns D.K., Montevecchi W.A., Birt-Friesen V.L. & Macko S.A. 1990. Energy expenditure, activity budgets, and prey harvest of breeding Common Murres. In: Sealy S.G. (ed.). Auks At Sea. Stud. Av. Biol. 14: 84-92.

Calladine J. 1997a. A comparison of Herring Gull *Larus argentatus* and Lesser Black-backed Gull *Larus fuscus* nest sites: their characteristics and relationships with breeding success. Bird Study 44: 318-326(9).

Calladine J. 1997b. The efficiency of detecting color-banded Herring Gulls (*Larus argentatus*) and lesser Black-backed Gulls (*Larus fuscus*) at the breeding colony: Practical implications for the determination of adult survival rates. Col. Waterb. 20: 41-46.

Calladine J. 2002. Herring Gull *Larus argentatus*. In: Wernham C., M. Toms, J. Marchant, J. Clark, G. Siriwardena & S. Baillie (eds). The migration atlas: movements of the birds of Britain and Ireland: 369-372. T. & A.D. Poyser, London.

Calladine J. & Harris M.P. 1997. Intermittent breeding in the Herring Gull *Larus argentatus* and the Lesser Black-backed Gull *Larus fuscus*. Ibis 139: 259-263.

Calvino-Cancela M. 2011. Gulls (Laridae) as frugivores and seed dispersers. Plant. Ecol. DOI 10.1007/s11258-011-9894-2.

Cam E., J.E. Hines, J-Y. Monnat, J.D. Nichols & E. Danchin 1998. Are adult nonbreeders prudent parents? The Kittiwake model. Ecology 79: 2917-2930.

Camphuysen C.J. 1985. Zeetrektellingen. In: Hustings M.F.H., Kwak R.G.M., Opdam P.F.M. & Reijnen M.J.S.M. (eds). Vogelinventarisatie: 215-219. Pudoc, Wageningen.

Camphuysen C.J. 1989a. Beached Bird Surveys in the Netherlands 1915-1988; Seabird Mortality in the southern North Sea since the early days of Oil Pollution. Techn. Rapport Vogelbescherming 1, Werkgroep Noordzee, Amsterdam.

Camphuysen C.J. 1989b. Crash van pas uitgevlogen Drieteenmeeuwen (*Rissa tridactyla*) op de Nederlandse kust augustus 1987. Graspieper 9: 11-17.

Camphuysen C.J. 1989c. Massale sterfte van Zeekoeten *Uria aalge* voor de Nederlandse kust, winter 1988/89. Sula 3: 22-25.

Camphuysen C.J. 1990a. Verstrikking van zeevogels in plastics: een probleem van toenemende omvang? Sula 4: 12-18.

Camphuysen C.J. 1990b. Fish stocks, fisheries and seabirds in the North Sea. Technisch Rapport Vogelbescherming, 5. Vogelbescherming Nederland, Zeist.

Camphuysen C.J. 1992a. Auk wrecks in the southern North Sea, 1981-1991: oil pollution or food shortage? In: Tasker M.L. (ed). Proc. Seabird Group Conference 'European Seabirds', Glasgow 27-29 March 1992: 23.

Camphuysen C.J. 1992b. Karakteristieken van in 1985 in Nederland gestrande Middelste Jagers *Stercorarius pomarinus*. Sula 6: 139-147.

Camphuysen C.J. 1993a. Scavenging seabirds behind fishing vessels in the northeast Atlantic, with emphasis on the southern North Sea. NIOZ report 1993-1, BEON report 20, Netherlands Institute for Sea Research, Texel.

Camphuysen C.J. 1993b. Fourageermogelijkheden voor zeevogels in de boomkorvisserij: een verkennend onderzoek. Sula 7: 81-104.

Camphuysen C.J. 1993c. Een verkennend onderzoek: De exploitatie van op zee overboord geworpen vis en snijafval door zeevogels. Het Vogeljaar 41: 106-114.

Camphuysen C.J. 1994a. Scavenging seabirds at beamtrawlers in the southern North Sea: distribution, relative abundance, behaviour, prey selection, feeding efficiency, kleptoparasitism, and the possible effects of the establishment of 'protected areas'. BEON Report 1994-14, Netherlands Institute for Sea Research, Texel.

Camphuysen C.J. 1994b. Flatfish selection by Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus* scavenging at commercial beamtrawlers in the southern North Sea. Neth. J. Sea Res. 32: 91-98.

Camphuysen C.J. 1994c. Verstrikkingen van zeevogels in plastics en vistuig aan de Nederlandse kust, 1990-93. Sula 8: 226-229.

Camphuysen C.J. 1995a. Herring Gull *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus* feeding at fishing vessels in the breeding season: competitive scavenging versus efficient flying. Ardea 83: 365-380.

Camphuysen C.J. 1995b. Olieslachtoffers langs de Nederlandse kust als indicatoren van de vervuiling van de zee met olie. Sula 9(special issue): 1-90, I-XX.

Camphuysen C.J. 1996. De verspreiding van zeevogels in de Noordzee: naar een beter begrip van patronen en verbanden. Sula 10: 41–88.

Camphuysen C.J. 1997. Olievervuiling en olieslachtoffers langs de Nederlandse kust, 1969-97: signalen van een schonere zee. Sula 11(special issue): 41-156.

Camphuysen C.J. 1998. Beached bird surveys indicate decline in chronic oil pollution in the North Sea. Mar. Poll. Bull. 36: 519-526.

Camphuysen C.J. 2001a. Northern Gannets *Morus bassanus* found dead in The Netherlands, 1970-2000. Atl. Seabirds 3: 15-30.

Camphuysen C.J. 2001b. Seabirds and fisheries interactions. In: Steele J.H., Thorpe S.A. & Turekian K.K. (eds) Encyclopedia of Ocean Sciences: 2677-2686. Acad. Press, London.

Camphuysen C.J. 2003. Characteristics of Atlantic Puffins *Fratercula arctica* wrecked in The Netherlands, January-February 2003. Atl. Seabirds 5: 21-30.

Camphuysen C.J. (ed.) 2005. Understanding marine foodweb processes: an ecosystem approach to sustainable sandeel fisheries in the North Sea. IMPRESS Final Report, EU Project #Q5RS-2000-30864, Royal Netherlands Institute for Sea Research, Texel.

Camphuysen C.J. 2008. Aflezingen van gekleurringde Zilvermeeuwen *Larus argentatus* en Kleine Mantelmeeuwen *Larus fuscus* in Nederland. Sula 21: 3-32.

Camphuysen C.J. 2008a. Het regent soms kleine alken in november. Natura 53(2): 52-54.

Camphuysen C.J. 2008b. Verstrikkingen van zeevogels in zwerfvuil en vistuig, 1970-2007. Sula 21: 88-92.

Camphuysen C.J. 2008c. Aflezingen van gekleurringde Zilvermeeuwen *Larus argentatus* en Kleine Mantelmeeuwen *Larus fuscus* in Nederland. Sula 21: 3-32.

Camphuysen C.J. 2010. Declines in oil-rates of stranded birds in the North Sea highlight spatial patterns in reductions of chronic oil pollution. Mar. Poll. Bull. 60: 1299-1306.

Camphuysen C.J. 2011a. Seabirds and chronic oil pollution: self-cleaning properties of gulls, Laridae, as revealed from colour-ring sightings. Mar. Poll. Bull. 62: 514-519.

Camphuysen C.J. 2011b. Lesser Black-backed Gulls nesting at Texel: foraging distribution, diet, survival, recruitment and breeding biology of birds carrying advanced GPS loggers. NIOZ Report 2011-05, Royal Netherlands Institute for Sea Research, Texel.

Camphuysen C.J. 2011c. Recent trends and spatial patterns in nearshore sightings of harbour porpoises (*Phocoena phocoena*) in the Netherlands (Southern Bight, North Sea), 1990-2010. Lutra 54: 37-44.

Camphuysen C.J. 2011d. Northern gannets *Morus bassanus* in the North Sea: foraging distribution and feeding techniques around the Bass Rock. Brit. Birds 104: 60-76.

Camphuysen C.J. in press. Het tellen van grote, gemengde kolonies Zilvermeeuwen en Kleine Mantelmeeuwen in het Waddengebied (2) determinatie van nesten. Limosa.

Camphuysen C.J., Barreveld H., Dahlmann G. & Franeker J.A. van 1999. Seabirds in the North Sea demobilised and killed by polyisobutylene $(C_4H_8)_n$. Mar. Poll. Bull. 38: 1171-1176.

Camphuysen C.J., C.M. Berrevoets, H.J.W.M. Cremers, A. Dekinga, R. Dekker, B.J. Ens, T.M. van der Have, R.K.H. Kats, T. Kuiken, M.F. Leopold, J. van der Meer & T. Piersma 2002. Mass mortality of common eiders (*Somateria mollissima*) in the Dutch Wadden Sea, winter 1999/2000: starvation in a commercially exploited wetland of international importance. Biol. Conserv.106: 303-317.

Camphuysen C.J., S. Boekhout, A. Gronert, V. Hunt, T. van Nus & J. Ouwehand 2008. Bizarre prooien: vreemd voedsel opgepikt door Zilvermeeuwen en Kleine Mantelmeeuwen. Sula 21: 49-61.

Camphuysen C.J., P. de Boer, W. Bouten, A. Gronert & J. Shamoun-Baranes 2010. Mammalian prey in Laridae: increased predation pressure on mammal populations expected. Lutra 53: 5-20.

Camphuysen C.J., J. van den Bruggen, K. Koffijberg & H. Schekkerman in press. Het tellen van grote, gemengde kolonies Zilvermeeuwen en Kleine Mantelmeeuwen in het Waddengebied I: methodieken om koloniegrootte te bepalen. Limosa.

Camphuysen C.J., **.** Calvo, J. Durinck, K. Ensor, A. Follestad, R.W. Furness, S. Garthe, G. Leaper, H. Skov, M.L. Tasker & C.J.N. Winter 1995. Consumption of discards by seabirds in the North Sea. Final report to the European Commission, study contract BIOECO/93/10, NIOZ–Report 1995–5, Netherlands Institute for Sea Research, Texel.

Camphuysen C.J., D.C. Camphuijsen & T.M. van Spanje 2006. Het voedsel van de Kleine Mantelmeeuwen van het Wormer- en Jisperveld. Limosa 78: 145-154.

Camphuysen C.J. & P.J.T. Derks 1989. Voorkomen en sterfte van de Fuut *Podiceps cristatus* voor de Nederlandse kust, 1974-86. Limosa 62: 57-62.

Camphuysen C.J. & J. van Dijk 1983. Zee- en kustvogels langs de Nederlandse kust, 1974-79. Limosa 56: 81-230 (*special issue*).

Camphuysen C.J., J. van Dijk, H. Witte & N. Spaans 2008a. De voedselkeuze van Kleine Mantelmeeuwen en Zilvermeeuwen en andere indicaties die aanwijzingen geven over het ruimtegebruik van deze vogelsoorten in de Noord-Hollandse kustwateren. NIOZ Rapport 2008-12, Koninklijk Nederlands Instituut voor Zeeonderzoek, Texel.

Camphuysen C.J., B.J. Ens, D. Heg, J. Hulscher, J. van der Meer & C.J. Smit 1996. Oystercatcher winter mortality in The Netherlands: the effect of severe weather and food supply. Ardea 84a: 469-492.

Camphuysen C.J., K. Ensor, R.W.Furness, S. Garthe, O. Hüppop, G. Leaper, H. Offringa & M.L. Tasker 1993. Seabirds feeding on discards in winter in the North Sea. Final report to the European Comm., study contr. 92/3505, NIOZ-Report 1993-8, Netherlands Institute for Sea Research, Texel.

Camphuysen C.J., A.D. Fox, M.F. Leopold & I.K. Petersen 2004. Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K. Report commissioned by COWRIE for the Crown Estate, London. Royal Netherlands Institute for Sea Research, Texel.

Camphuysen C.J. & Garthe S. 1997. An evaluation of the distribution and scavenging habits of northern fulmars (*Fulmarus glacialis*) in the North Sea. ICES J. Mar. Sc.54: 654–683.

Camphuysen C.J. & Garthe S. 2000. Seabirds and commercial fisheries: population trends of piscivorous seabirds explained? Chapter 11 In: Kaiser M.J. & Groot S.J. de (eds). Effects of fishing on non-target species and habitats: Biological, Conservation and Socio-Economic Issues: 163-184. Blackwell Science, Oxford.

Camphuysen C.J. & S. Garthe 2004. Recording foraging seabirds at sea: standardised recording and coding of foraging behaviour and multi-species foraging associations. Atl. Seabirds 6: 1-32.

Camphuysen C.J. & A. Gronert 2010a. De broedbiologie van Zilver- en Kleine Mantelmeeuwen op Texel, 2006-2010. Limosa 83: 145-159.

Camphuysen C.J. & A. Gronert 2010b. On the brink of collapse: prospects for a seabird population relying on fisheries in the light of a new European policy for sustainable fisheries. [subtitle: “*Killing the kids on Sunday*”] Oral presentation Symposium "Seabird-fisheries interactions: a global perspective", World Seabird Conference, 7-11 Sep 2010, Victoria, Canada BC.

Camphuysen C.J. & A. Gronert 2010c. `Self-cleaning' en broedsucces van een zwaar met olie besmeurde Kleine Mantelmeeuw *Larus fuscus* op Texel. Sula 23: 49-68.

Camphuysen C.J. & A. Gronert 2012. Apparent survival and fecundity of sympatric Lesser Black-backed Gulls and Herring Gulls with contrasting population trends. Ardea 100: 113-122.

Camphuysen C.J. & M. Heubeck 2001. Marine oil pollution and beached bird surveys: the development of a sensitive monitoring instrument. Env. Poll. 112: 443-461.

Camphuysen C.J. & E.J. van IJzendoorn 1988a. Invasie van Middelste Jagers in Nederland in november 1985. Dutch Birding 10: 54-65.

Camphuysen C.J. & E.J. van IJzendoorn 1988b. Influx of Pomarine Skua in northwestern Europe in autumn 1985. Dutch Birding 10: 66-70.

Camphuysen C.J. & M.F. Leopold 1994. Atlas of seabirds in the southern North Sea. IBN Research report 94/6, NIOZ-Report 1994-8, Institute for Forestry and Nature Research, Netherlands Institute for Sea Research and Dutch Seabird Group, Texel.

Camphuysen C.J. & M.F. Leopold 1996. Invasies van de Kleine Alk *Alle alle*: voorkomen en achtergronden. Sula 10: 169-182.

Camphuysen C.J. & M.F. Leopold 2008. Drieteenmeeuw vestigt zich op meerdere platforms in Nederlandse wateren. Limosa 80: 153-156.

Camphuysen C.J. & J. van der Meer 1996. Recent trends in oiled seabirds. Ad Hoc working group on Monitoring, Oslo and Paris Convention for the Prevention of Marine Pollution, Environmental Assessment and Monitoring Committee (ASMO) . MON 1995 summary record: 20-48, Copenhagen.

Camphuysen C.J., J. Ouwehand, A. Gronert & N. Gallego Garcia 2008b. Over de top: van exponentiële groei naar ineenstorting of stabilisatie: onderzoek naar factoren die contrasterende populatietrends bij Kleine Mantelmeeuw en Zilvermeeuw kunnen verklaren. Interne rapportage Koninklijk Nederlands Instituut voor Zeeonderzoek, Texel.

Camphuysen C.J., C.D. Romay & A. Gronert 2009. Wing development in large gulls in the chick phase: a manual. Sula 22: 67-76.

Camphuysen C.J., A. Schrimpf & C.D. Romay 2010. Kauwtjes *Corvus monedula* als prooi van Zilvermeeuwen *Larus argentatus* en Kleine Mantelmeeuwen *L. fuscus*. Sula 23: 15-20.

Camphuysen C.J., B. Scott & S. Wanless 2006. Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multi-species foraging assemblages and habitat-specific feeding strategies. In: Boyd I.J., S. Wanless & C.J. Camphuysen (eds) Top predators in Marine Ecosystems: monitoring change in upper trophic levels: 82-97. Cambridge Univ. Press, Cambridge.

Camphuysen C.J., J. Shamoun-Baranes, W. Bouten, S. Garthe 2012. Identifying ecologically important marine areas for seabirds using behavioural information in combination with distribution patterns. Biol. Conserv. 156: 22-29.

Camphuysen C.J. & Spaans A.L. 2005. Beobachtungen und Wiederfunde in Deutschland von farbberingten Silbermöwen *Larus argentatus* aus den Niederlanden, 1986-2005. Seevögel 26: 20-24.

Camphuysen C.J., A. Talamelli, R-J. Buijs, P. de Boer, K. Oosterbeek & A. Gronert 2009. Nederlandse Kleine Mantelmeeuwen *Larus fuscus* in Italië. Sula 22: 77-82.

Camphuysen C.J., H.J.P. Vercruijsse & A.L. Spaans 2011. Colony- and age-specific seasonal dispersal of Herring Gulls *Larus argentatus* breeding in The Netherlands. J. Orn. 152: 849-868.

Camphuysen C.J. & F. de Vreeze 2005. De Drieteenmeeuw *Rissa tridactyla* als broedvogel in Nederland. Limosa 78: 65-74.

Camphuysen C.J. & A. Webb 1999. Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. Ardea 87: 177-198.

Carey C. 1996. Female reproductive energetics. In: Carey C. (ed.) Avian Energetics and Nutritional Ecology: 324-374. Chapman & Hall, New York.

Carrick R. & G. Dunnet 1954. Breeding of the Fulmar *Fulmarus glacialis*. Ibis 96: 356-370.

Carson R. 1962. Silent spring. Houghton Mifflin, Boston.

Carss D.N., R.M. Bevan, A. Bonetti, G. Cherubini, J. Davies, D. Doherty, A. El Hili 1997. Techniques for assessing cormorant diet and food intake: towards a consensus review. Suppl. Ric. Biol. Selvaggina 26: 197–230.

Carter I.C., J.M. Williams, A. Webb, M.L. Tasker 1993. Seabird concentrations in the North Sea: an atlas of vulnerability to surface pollutants. Joint Nature Conservation Committee, Aberdeen.

Casaux R.J., Favero M., Barrera-Oro E.R. & Silva P. 1999. Feeding trial on an imperial cormorant *Phalacrocorax atriceps*: preliminary results on fish intake and otolith digestion. Mar. Orn. 23: 101–106.

Casaux R.J., Favero M., Coria N. & Silva P. 1997. Diet of the imperial cormorant *Phalacrocorax atriceps*: comparison of pellets and stomach contents. Mar. Orn. 25: 1–4.

Casey M. 2005. Mother bird makes 2,500-mile journey: in the skies over Indonesia, a search for food for her baby. Associated Press http://www.philly.com/mld/philly/news/nation/13469931.htm.

Catard A., H. Weimerskirch & Y. Cherel 2000. Exploitation of distant Antarctic waters and close shelf-break waters by white-chinned petrels rearing chicks. Mar. Ecol. Prog. Ser. 194:249-261.

CBS 2012. Bevolking van Nederland. http://nl.wikipedia.org/wiki/Bevolking_van_Nederland, accessed 4 May 2012.

CBS, PBL, Wageningen UR 2011. Stortplaatsen, aantal en capaciteit, 1991-2009. Indicator 0393, versie 10, 2 maart 2011; www.compendiumvoordeleefomgeving.nl. CBS, Den Haag; Planbureau voor de Leefomgeving, Den Haag/Bilthoven en Wageningen UR, Wageningen.

Certain G., E. Bellier, B. Planque & V. Bretagnolle 2007. Characterising the temporal variability of the spatial distribution of animals: an application to seabirds at sea. Ecography 30: 695–708

Chabrzyk G. & Coulson J.C. 1976. Survival and recruitment in the Herring Gull *Larus argentatus*. J. Anim. Ecol. 45: 187-203.

Chapman J.W., R.H.G. Klaassen, V.A. Drake, S. Fossette, G.C. Hays, J.D. Metcalfe, A.M. Reynolds, D.R. Reynolds & T. Alerstam. 2011. Animal Orientation Strategies for Movement in Flows. Current Biol. 21: R861-R870.

Chardine J.W. & R.D. Morris 1983. Herring Gull mates eat their own eggs. Wilson Bull. 95(3).

Cherel Y., H. Weimerskirch & C. Trouvé 2000. Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. Mar. Ecol. Progr. Ser. 207:183-199.

Chinsamy A., L.D. Martin & P. Dobson 1998. "Bone microstructure of the diving Hesperornis and the volant Ichthyornis from the Niobrara Chalk of western Kansas." Cretaceous Res. 19: 225-235.

Choquet R., J-D. Lebreton, O. Gimenez, A-M. Reboulet & R. Pradel 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating Capture-Recapture data. Ecography 32: 1071-1074.

Christensen V., S. Guénette, J.J. Heymans, C.J. Walters, R. Watson, D. Zeller & D. Pauly 2003. Hundred year decline of North Atlantic predatory fishes. Fish and Fisheries 4: 1-24.

Clark R.B. 2001. Marine Pollution. Fifth Edition, Oxford Univ. Press, Oxford.

Clarke J., B. Manly, K. Kerry, H. Gardner, E. Franchi, S. Corsolini & S. Focardi. 1998. Sex differences in Adélie penguin foraging strategies. Polar Biol. 20: 248-258.

Clarke J.A. 2004. Morphology, phylogenetic taxonomy, and systematics of Ichthyornis and Apatornis (Avialae: Ornithurae). Bull. Am. Mus. Nat. Hist. 286: 1-179 .

Clobert J. & J-D. Lebreton 1991. Estimation of demographic parameters in bird populations. In: Perrins C.M., J-D. Lebreton & G.J.M. Hirons (eds). Bird population studies: 75-104. Oxford Univ. press, Oxford.

Clover C. 2004. The end of the line: how overfishing is changing the world and what we eat. Ebury Press, London.

Clutton-Brock T.H. 1988. Reproductive success. Univ. Chicago Press, Chicago.

Clutton-Brock T.H. 1991. The evolution of parental care. Princeton Univ. Press, Princeton.

Clutton-Brock T.H. & P.H. Harvey 1979. Comparison and Adaptation. Proc. R. Soc. Lond. B 205: 547-565.

Cobley N.D., J.P. Croxall & P.A. Prince 1998. Individual quality and reproductive performance in the Grey-headed Albatross *Diomedea chrysostoma*. Ibis 140: 315-322.

Cody M.L. 1966. A general theory of clutch size. Evolution 20: 174-184.

Coleridge S.T. 1854. The rime of the ancient mariner.

Commissie Nederlandse Avifauna (CNA) 1970. Avifauna van Nederland. E.J.Brill, Leiden.

Compton T.J., S. Holthuijsen, A. Koolhaas, A. Dekinga, J. ten Horn, J. Smith, Y. Galama, M. Brugge, J. van der Meer, H.W. van der Veer & T. Piersma 2012. Synoptic intertidal benthic survey across the Dutch Wadden Sea. Report on data collected from 2008 to 2010, Royal Netherlands Institute for Sea Research, Texel.

Conradt L. 2005. Definitions, hypotheses, models and measures in the study of animal segregation. In: Ruckstuhl K.E. & P. Neuhaus (eds) Sexual segregation in vertebrates: ecology of the two sexes: 11-32. Cambridge Univ. Press, Cambridge.

Cook M.I. & K.C. Hamer 1997. Effects of supplementary feeding on provisioning and growth rates of nestling Puffins *Fratercula arctica*: evidence for regulation of growth. J. Avian Biol. 28: 56-62.

Cooke F., R.F. Rockwell & D.B. Lank 1991. Recruitment in long-lived birds: genetic considerations. Acta XX Congr. Intern. Ornith. 1666-1677.

Corten A. 2001. Herring and climate: changes in the distribution of North Sea herring due to climatic fluctuations. Ph.D.-thesis, Univ. Groningen, Groningen.

Costers R. 1992. Zilvermeeuwen met kleurringen deel 10: broedend in De Putten. Windbreker 53: 8-11.

Costers R. & A. Gronert 1989. Zilvermeeuwen met kleurringen deel 5: individuele voorkeur voor een bepaald kustgedeelte. Windbreker 14: 7-9.

Cottaar F. 1994. Broedende Kleine Mantelmeeuwen *Larus fuscus* op daken in IJmuiden. Sula 8: 272-274.

Cottaar F. 2002. Bald Eagles moesten op daken broedende meeuwen in IJmuiden verdrijven. Nieuwsbr. NZG 4: 1-2.

Cottaar F. 2004. Stormmeeuwen zoeken het hogerop bij CORUS. Nieuwsbr. NZG 6: 3-4.

Cottaar F. & Maassen E. 1989. Meeuwenkolonies in Zuid-Kennemerland in 1988. Fitis 25: 132-139.

Coulson J.C. 1991. The population dynamics of culling Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus*. In: Perrins C.M., J.-D. Lebreton & G.J.M. Hirons (eds) Bird population studies: 479-497. Oxford Univ. Press, Oxford.

Coulson J.C. 2002. Colonial breeding in seabirds. In: Schreiber E.A. & J. Burger (eds) Biology of Marine Birds: 87-113. CRC Press, Boca Raton.

Coulson J.C. & M.G. Brazendale 1968. Movements of Cormorants ringed in the British Isles and evidence of colonyspecific dispersal. Brit. Birds 61: 1-21.

Coulson J.C. & J. Butterfield 1985. Movements of British Herring Gulls. Bird Study 32: 91-103.

Coulson J.C. & J. Butterfield J. 1986. Studies on a colony of colour-ringed Herring Gulls *Larus argentatus*: I. Adult survival rates. Bird Study 33: 51-54.

Coulson J.C., Butterfield J., Duncan N. & Thomas C. 1987. Use of refuse tips by adult British Herring Gulls *Larus argentatus* during the week. J. Appl. Ecol. 24: 789-800.

Coulson J.C., J. Butterfield & C. Thomas 1983a. The herring gull *Larus argentatus* as a likely transmitting agent of Salmonella montevideo to sheep and cattle. J. Hygiene 91: 437-443.

Coulson J.C. & B.A. Coulson 2008. Lesser Black-backed Gulls *Larus fuscus* nesting in an inland urban colony: the importance of earthworms (Lumbricidae) in their diet. Bird Study 55: 297-303.

Coulson J.C., N. Duncan & C. Thomas 1982. Changes in the breeding biology of the Herring Gull (*Larus argentatus*) induced by reduction in the size and density of the colony. J. Anim. Ecol. 51: 739-756.

Coulson J.C., P. Monaghan, J.E.L. Butterfield, N. Duncan, K. Ensor, C. Shedden & C.S. Thomas 1984. Scandinavian Herring Gulls wintering in Britain. Orn. Scand. 15: 79-88.

Coulson J.C., Monaghan P., Butterfield J.E.L., Duncan N., Thomas C.S. & Shedden C. 1983b. Seasonal changes in the Herring Gull in Britain: weight, moult and mortality. Ardea 71: 235-244.

Coulson J.C. & J.M. Porter 1985. Reproductive success of the Kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. Ibis 127: 450-466.

Coulson J.C. & C. Thomas 1985. Differences in the breeding performance of individual Kittiwake Gulls, *Rissa tridactyla*. In: Sibly R.M. & Smith R.H. (eds): Behav. Ecol. Blackwell, Oxford.

Coulson J.C., C.S. Thomas, J.E.L. Butterfield, N. Duncan & P.C. Monaghan 1983c. The use of head and bill length to sex live gulls Laridae. Ibis 125: 549-557.

Coulson J.C. & E. White 1960. The effect of age and density of breeding birds on the time of breeding of the Kittiwake *Rissa tridactyla*. Ibis 102: 71-86.

Coveney P.V. & M.P. Atkinson 2009. Crossing boundaries: computational science, e-Science and global e-Infrastructure. Phil. Trans. Royal Soc., A: Math., Phys. & Eng. Sc. 367: 2425-2427.

Cramp S. & K.E.L. Simmons (eds) 1983. The Birds of the Western Palearctic, 3. Oxford Univ. Press, Oxford.

Cramp S., Bourne W.R.P. & Saunders D. 1974. The Seabirds of Britain and Ireland. Collins, London.

Crawley M.J. 2007. The R book. John Wiley & Sons, England.

Creutzberg F. 1989. Het Friese Front. Waddenbull. 24(1): 4-8.

Croxall J.P., P.G.H. Evans & R.W. Schreiber 1984. Status and Conservation of the World's Seabirds. Techn Publ. No. 2, ICBP, Cambridge.

Croxall J.P., P. Rothery & A. Crisp 1992. The effect of maternal age and experience on egg-size and hatching success in Wandering Albatrosses *Diomedea exulans*. Ibis 134: 219-228.

CSG 2010. Conservation of Arctic Flora and Fauna, CBird XVI. Circumpolar Seabird Group Meeting Report, Tofino, British Columbia, Canada, 13 September - 16 September 2010, CBird XVI, Tofino, British Columbia, Canada.

Daan N., PJ. Bromley, J.R.G. Hislop & N.A. Nielsen 1990. Ecology of North Sea fish. In: P. de Wolf, H.J. Lindeboom & R.W.P.M. Laane (eds). Proc. int. symp. Ecol. North Sea, May 1988. Neth. J. Sea Res. 26:343-386.

Daan S., C. Dijkstra R. Drent & T. Meijer 1988. Food supply and the annual timing of avian reproduction. In: Ouellet H. (ed.) Acta XIX: Congr.Intern. Orn. Ottawa: 392-407. University of Ottawa Press, Ottawa.

Dahlmann G., Timm D., Averbeck C., Camphuysen C.J. & Skov H. 1994. Oiled seabirds-Comparative investigations on oiled seabirds and oiled beaches in the Netherlands, Denmark and Germany (1990-1993). Mar. Poll. Bull. 28: 305-310.

Danchin E. 1992. The incidence of the tick parasite *Ixodes uriae* in kittiwake *Rissa tridactyla* colonies in relation to the age of the colony, and a mechanism of infecting new colonies. Ibis 134: 134-141.

Danchin E., B. Cadiou, J-Y. Monnat & R.R. Estrella 1991. Recruitment in long-lived birds: conceptual framework and behavioural mechanisms. Acta XX Congr. Intern. Ornith. 1641-1655.

Danchin E., G. González-Dávila & J.D. Lebreton 1995. Estimating bird fitness correctly by using demographic models. J. Avian Biol. 26: 67-75.

Dändliker G. & Mülhauser G. 1988. L'exploitation des dechets de chalutage par les oiseaux de mer au large des Orcades et des Shetland (Nord-Est Atlantique). Nos Oiseaux 39: 257-288.

Dann P. & J.M. Cullen 1990. Survival, patterns of reproduction, and lifetime reproductive output in Little Blue Penguins (*Eudyptula minor*) on Phillip Island, Victoria, Australia. In: Davis L.S. & J.T. Darby (eds): Penguin Biology: 63-84. Acad. Press, New York.

Dankers N., A. Meijboom, M. De Jong, E. Dijkman, J. Cremer, F. Fey, A. Smaal, J. Craeymeesch, E. Brummelhuis, J. Steenbergen & D. Baars 2006. De ontwikkeling van de Japanse oester in Nederland (Waddenzee en Oosterschelde). IMARES Rapport C040/06, Wageningen.

Dare P.J. 1982. Notes on seabirds attending a commercial trawler fishing in shelf waters off Ireland. Seabird 6: 110-114.

Darling F.F. 1938. Bird flocks and the breeding cycle: A contribution to avian sociality. Cambridge Univ. Press, London.

Davidson N. & Rothwell P. (eds) 1993. Disturbance to waterfowl on estuaries. Wader Study Group Bulletin, 68 (special issue): 1-106.

Davis J.W.F. 1975. Age, egg-size and breeding success in the Herring Gull. Ibis 117: 460-473.

Davis J.W.F. & E.K. Dunn 1976. Intraspecific predation and colonial breeding in Lesser Black-backed Gulls *Larus fuscus*. Ibis 118: 65-77.

Dawson A. 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. Phil. Trans. R. Soc. B 363: 1621-1633.

Dean D. 1978. Migration of the sandworm Nereis virens during winter nights. Mar. Biol. 45: 165-173.

Deflorenne P. & F. Carion Ellis 2012. Statut du Goéland brun *Larus fuscus* dans l'Entre-Sambre-et-Meuse: déplacements, origine, effectifs... Importance du site des barrages de l'Eau d'Heure. Aves 49: 205-224.

Dekker R. 2011. Macrozoobenthosonderzoek MWTL, voor- en najaar 2009, Waterlichaam: Waddenzee (Balgzand en sublitorale westelijke Waddenzee). NIOZ Report 2011-1, Koninklijk Nederlands Instituut voor Onderzoek der Zee, Texel.

Dekker R. & J.J. Beukema 2012. Long-term dynamics and productivity of a successful invader: the first three decades of the bivalve *Ensis directus* in the western Wadden Sea. J. Sea Res. 71: 31-40.

Delany S. & D. Scott 2002. Waterbird population estimates. Wetlands International Global Series 12, Wageningen.

Delany S. & D. Scott 2006. Waterbird population estimates. Fourth Edition, Wetlands International, Wageningen.

Demuth M. 1983. Untersuchungen zur Nahrung der Silbermöwe (*Larus argentatus*) in einer Binnenlandkolonie Schleswig-Holsteins zur Brutzeit. Seevögel 4: 19-23.

Deneubourg J.L. & S. Goss 1989. Collective patterns and decision-making. Ethol. Ecol. & Evolution 1: 295-311.

Densing M. 1939. The Herring Gulls of Hat island, Wisconsin. Wilson Bull. 51: 170-175.

Derby C.E. & Lovvorn J.R. 1997. Comparison of pellets versus collected birds for sampling diets of double-crested cormorants. Condor 99: 549–553.

Derian G. 2007. Paramètres reproducteurs du Goéland Argenté *Larus argentatus argenteus* en milieu Urbain. Alauda 75: 353-372.

Dernedde T. 1994. Foraging overlap of three gull species (*Larus* spp.) on tidal flats in the Wadden Sea. Ophelia Suppl. 6: 225-238.

Diederich S., G. Nehls, J.E.E. van Beusekom & K. Reise 2005. Introduced Pacific oysters (*Crassostrea gigas*) in the northern Wadden Sea: invasion accelerated by warm summers? Helgol. Mar. Res. 59:97-106.

Dierschke A-K. & O. Hüppop 2003. Langfristige Veränderungen in der Ernährung von Silbermöwen (*Larus argentatus*) auf Helgoland unter dem Einfluss der Fischerei mit Vergleichen zur Heringsmöwe (*Larus fuscus*). Seevögel 24: 3-15.

Dijk A.J. van 1998. Breeding Black-headed Gulls *Larus ridibundus* along the coast of The Netherlands during the 20th century. Sula 12: 147-158.

Dijk A.J. van, F. Hustings, A. Boele, K. Koffijberg, D. Zoetebier & C. Plate 2010. Kolonievogels en zeldzame broedvogels in Nederland in 2006 en 2007. Limosa 83: 1-20.

Dijk A.J. van, F. Hustings, K. Koffijberg, C. van Turnhout, M. van der Weide, D. Zoetebier & C. Plate 2007. Kolonievogels en zeldzame broedvogels in Nederland in 2003-05. Limosa 80: 49-67.

Dijk A.J. van, F. Hustings & T. Verstrael 1994. SOVON broedvogelverslag 1992. SOVON-monitoringrapport 1994/03. SOVON, Beek-Ubbergen.

Dijk B. van 1986. The breeding biology of eiders at Ile aux Pommes, Quebec. In: Reed A. (ed.). Eider Ducks in Canada: 119-126. Can. Wildl. Rep. Series no. 47, Canadian Wildlife Service, Ottawa.

Dijk J. van, H. van der Kooij, M. Lok, P. Meininger, J. van der Straaten & J. Vink (eds) 1981. Randstad en broedvogels. VWG Avif. West-Nederland. Tilburg.

Dijk K. van., R. Oosterhuis, B. Middendorp & F. Majoor 2012. New longevity records of Black-headed Gull, with comments on wear and loss of aluminium rings. Dutch Birding 34: 20-31.

Dijken K. van 1999. Vogels en beheer op Rottumeroog. De Grauwe Gors 27(1): 15-26.

Dijksen A.J. 1996a. Vogels op het Gouwe Boltje-Een volledig overzicht van de avifauna van Texel. Langeveld & De Rooy, Den Burg.

Dijksen A.J. 1996b. Een kolonie 'Groote (Mantel?)meeuwen' op Texel. Sula 10: 98-100.

Dijksen A.J. & L.J. Dijksen 1977. Texel-vogeleiland. Kon. Ned. Nat. Ver. Uitgave nr. 25, Thieme & Cie, Zutphen.

Dijksen A.J., A. Wassink & M. Witte (eds) 1999. Ornithologisch Jaarverslag Texel 1998. Vogelwerkgroep Texel, Den Burg.

Dijksen L. 2006. Een Texelse Kleine Mantelmeeuw in Finland. De Skor 25: 154-156.

Dijkstra C., A. Bult, S. Bijlsma, S. Daan, T. Meijer & M. Zijlstra M. 1990. Brood size manipulations in the Kestrel (*Falco tinnunculus*) – effects on offspring and parent survival. J. Anim. Ecol. 59: 269–285.

Dirksen S., M. Japink & J.C. Hartman 2012. Kleine mantelmeeuwen en offshore windparken: nieuwe informatie voor schatting aantal aanvaringsslachtoffers. 23 mei 2012 rapport nr. 12-087, Bureau Waardenburg, Culemborg.

Dixon D. 2007. The complete illustrated encyclopedia of dinosaurs & prehistoric creatures. Anness Publ. Ltd, London.

Dobben W.H. van 1931. Einzelheiten über Farbe und Brutbiologie der auf Terschelling nistenden Heringsmöwen (*Larus fuscus* subspec.). Ardea 20: 143-147.

Dobben W.H. van 1934. Bijdrage tot het meeuwenvraagstuk. Org. Club Ned. Vogelk. 7(2): 63-78.

Doornbos G. 1979. Winter food habits of smew (Mergus albellus) on lake IJssel, The Netherlands: species and size selection in relation to fish stocks. Ardea 67: 42–48.

Dornheim H. & G. Wegner 1998. Unterschiedliche Trends beim Fischnachwuchs der Nordsee. Inf. Fischwirtsch. 45: 103–108.

Drent R.H. 1967. Functional aspects of incubation in the Herring Gull (*Larus argentatus* Pont.). Ph.D.-thesis Univ. Groningen, Groningen.

Drent R.H. 2006. The timing of birds' breeding seasons: the Perrins hypothesis revisited especially for migrants. Ardea 94: 305-322.

Drent R. & Daan S. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68: 225-252.

Drent R.H., A.D. Fox & J. Stahl 2006. Travelling to breed. J. Orn. 147: 122-134.

Drent R.H., M. Klaassen & B. Zwaan 1992. Predictive growth budgets in terns and gulls. In: Spaans A.L. (ed.). Population dynamics of Lari in relation to food resources. Ardea 80: 5-17.

Drijver J. 1920. Een nieuwe zilvermeeuwenkolonie. De Lev. Nat. 25: 128.

Drijver J. 1934. Texel, het vogeleiland. 1e druk, De Spieghel, Amsterdam.

Drijver J. 1957. Texel, het vogeleiland. 2e druk, L.J. Veen Uitg., Amsterdam.

Drinkwater K.F., A. Belgrano, A. Borja, A. Conversi, M. Edwards, C.H. Greene, G. Ottersen, A.J. Pershing & H. Walker 2003. The response of marine ecosystems to climate variability associated with the North Atlantic Oscillation. In: Hurrell J.W., Y. Kushnir, G. Ottersen & M. Visbeck (eds) The North Atlantic Oscillation: Climatic Significance and Environmental Impact: 211-234. Geophysical Monograph 134, American Geophysical Union Washington, DC.

Drost R., E. Frocke & G. Freytag 1961. Entwicklung und Aufbau einer Population der Silbermöwen, *Larus argentatus* argentatus. J. Orn. 404-429.

Drost R. & L. Schilling 1940. Über den Lebensraum deutscher Silbermöwen, *Larus a. argentatus* Pontopp., auf Grund von Beringungsergebnisse. Vogelzug 11: 1-22.

Duffy D.C. & S. Jackson 1986. Diet studies of seabirds: a review of methods. Col. Waterb. 9: 1–17.

Duhem C., E. Vidal, J. Legrand & T. Tatoni 2003. Opportunistic feeding responses of the Yellow-legged Gull *Larus michahellis* to accessibility of refuse dumps: The gulls adjust their diet composition and diversity according to refuse dump accessibility. Bird Study 50: 61-67.

Duhem C., E. Vidal, P. Roche & J. Legrand 2005. How is the diet of Yellow-legged Gull chicks influenced by parents' access to landfills. Waterbirds 28: 46-52.

Duinker J.C. & J.H. Koeman 1978. Summary report on the distribution and effects of toxic pollutants (metals and chlorinated hydrocarbons) in the Wadden Sea. In: K. Essink & W J. Wolff.(eds) Pollution of the Wadden Sea area: 45-54. Report 8. Wadden Sea Working Group, Balkema, Rotterdam.

Duncan N. 1978. The effects of culling Herring Gulls (*L. argentatus*) on recruitment and population dynamics. J. Appl. Ecol. 15: 697-713.

Dunnet G.M. 1982. Oil pollution and seabird populations. Phil. Trans. R. Soc. London (B) 297(1087): 413-427.

Dunnet G.M. 1987. Seabirds and North Sea oil. In: Hartley J.P. & Clark R.B.(eds). Environmental effects of North Sea oil and gas developments Proc. R. Soc. Disc. Meet. London Phil. Trans. R. Soc. Lond. B 316: 513-524.

Dunnet G.M., Anderson A. & Cormack R.M. 1963. A study of survival of adult fulmars with observations on the pre-laying exodus. Brit. Birds 56: 2-18.

Durant J.M., T. Anker-Nlssen & N.C. Stenseth 2003. Trophic interactions under climate fluctuations: the Atlantic puffin as an example. Proc. R. Soc. Lond., B. 270: 1461-1466.

Durinck J., H. Skov, F.P. Jensen & S. Pihl 1994. Important marine areas for wintering birds in the Baltic Sea. EU DG XI research contract no. 224/90-09-01, Ornis Consult Report 1994: 1-110, Copenhagen.

Dwight J. 1922. Description of a new race of the Lesser Black-backed Gull from the Azores. Am. Mus. Novit. 44: 1-2.

Dwight J. 1925. The gulls (Laridae) of the world; their plumages, molts, variations relationships and distribution. Bull. Am. Mus. Nat. Hist. 52: 63-401.

Eaton M.A., A.F. Brown, D.G. Noble, A.J. Musgrove, R.D. Hearn, N.J. Aebischer, D.W. Gibbons, A. Evans & R.D. Gregory 2009. Birds of Conservation Concern 3: The population status of birds in the United Kingdom, Channel Islands and Isle of Man. Brit. Birds 102: 296-341.

Eaton R.J. 1933. The migratory movements of certain colonies of Herring Gulls (*Larus argentatus smithsonianus* Coues) in eastern North America. J. Fld Ornithol. 4: 165-176.

Ebels E.B. 2002. Transatlantic vagrancy of Palearctic species to the Caribbean region. Dutch Birding 24: 202-209.

Ebels E.B., Koffijberg K., Lindenburg P., Krijger J-P. de, Schoppers E. & Woets B. 2006. Spectaculaire influx van Dunbekmeeuwen. Dutch Birding 28: 195-198.

Eberhardt L.L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83: 2841-2854.

Edwards M. & A.J. Richardson 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430: 881-884.

Eecke R. van 1912. De Vogelfauna van Texel. Ardea 1: 63-68.

Ehlert W. 1961. Weitere untersuchungen über die Nahrungswelt der Silbermöwe (*Larus argentatus*) auf Mellum. Vogelwarte 21: 48-50.

Eigenhuis K.J. 1996. Mantelmeeuwen *Larus marinus/fuscus* reeds in vroegere eeuwen broedvogel in Nederland? Sula 10: 95-98.

Elliot R.D., Ryan P.C. & Lidtser W.W. 1990. The winter diet of thick-billed murres in coastal Newfoundland waters. In: Sealy S.G. (ed.) Auks at sea. Stud. Av. Biol 14: 125–138.

Elliott K.H., A.J. Gaston & D. Crump. 2010. Sex-specific behavior by a monomorphic seabird represents risk partitioning. Behav. Ecol. 21: 1024-1032.

Ellis H.I. 1984. Energetics offree-ranging seabirds. In: Whittow G.C. & H. Rahn (eds). Seabird Energetics: 203-234. Plenum Press, New York.

Ellis H.I. & G.W. Gabrielsen 2002. Energetics of free-ranging seabirds. In: Schreiber E.A. & J. Burger (eds) Biology of Marine Birds: 359-407. CRC Press, Boca Raton.

Emlen Jr. J.T. 1956. Juvenile mortality in a ring-billed gull colony. Wilson Bull. 68: 232-238.

Engelen A.F.V. van , J. Buisman & F. IJnsen 2001. A millenium of weather, winds and water in the Low Countries. In: Jones, P.D., A.E.J. Ogilvie, T.D. Davies and K.R. Briffa (eds). History and Climate; Memories of the Future?: 101-124. Plenum Publ., New York.

Enoksson B. 1988. Age- and sex-related differences in dominance and foraging behaviour of nuthatches Sitta europaea. Anim. Behav. 36: 231-238.

Ens B.J. 1992. The social prisoner: causes of natural variation in reproductive success of the Oystercatcher. Ph.D.-Thesis, Univ. Groningen, Groningen.

Ens B.J., F. Bairlein, C.J. Camphuysen, P. de Boer, K-M. Exo, N. Gallego, R. Klaassen, K. Oosterbeek & J. Shamoun-Baranes 2009. Onderzoek aan meeuwen met satellietzenders. Limosa 82: 33-42.

Erikstad K.E., Fauchald P., Tveraa T. & Steen H. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. Ecology 79: 1781-1788.

Esselink P. & Zwarts L. 1989. Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. Mar. Ecol. Progr. Ser. 56: 243-254.

Etkin D.S. 1999. Historical overview of oil spills from all sources (1960-1998). http://www.environmental-research.com/publications/pdf/spill_costs/paper1.pdf. GESAMP Working Group 32 Project. Proc. 1999 Intern. Oil Spill Conf.: 1097-1102.

Eulderink J.H.M., R.M. Wanders, G.J. de Bruyn & W.J. ter Keurs 1990. De invloed van de nestplaatskeuze van Zilvermeeuwen en Kleine Mantelmeeuwen op eipredatie door Vossen *Vulpes vulpes*. Huid & Haar 9: 97-110.

Euring 2010. European Longevity Records. Generated on: Friday, 26 Nov 2010, http://www.euring.org/

Falk K. & S. Møller 1995. Satellite tracking of higharctic northern fulmars. Polar Biology, 15: 495–502.

Favero M., R.M.P. Silva & L. Mauco 2000. Diet of Royal (*Thalasseus maximus*) and sandwich (*T. sandvicensis*) terns during the austral winter in the Buenos Aires Province, Argentina. Orn. Neotrop. 11: 259–262.

Feare C.J. 1984. Human exploitation. In: Croxall J.P., P.G.H. Evans & R.W. Schreiber (eds). Status and Conservation of the World's Seabirds: 691-699. Techn Publ. No. 2, ICBP, Cambridge.

Fetterolf P.M. 1983. Infanticide and non-fatal attacks on chicks by ring-billed gulls. Anim. behave. 31:1018-1028.

Fey K., P.B. Banks & E. Korpimäki 2006. Different microhabitat preferences of field and bank voles under manipulated predation risk from an alien predator. Ann. Zool. Fennici 43: 9-16.

Fisher H. 1972. The nutrition of birds. In: Farner D.S. & King J.R. (eds). Avian Biology, 2: 431-469. Acad. Press, New York.

Fisher J. 1952. The Fulmar. Collins New Naturalist Series, Facsimile 1984, Collins, London.

Fisher J. & R.M. Lockley 1954. Seabirds. Collins New Naturalist Series, Facsimile 1989, Bloomsbury Books, London.

Fleet D.M., J. Frikke, P. Südbeck & R.L. Vogel 1994. Breeding birds in the Wadden Sea 1991. Wadden Sea Ecosystem No. 1, Common Wadden Sea Secr., Wilhelmshaven.

Flisik T. & M. Horn 2010. Effects of a partial diet of pipefish, a low quality prey, on the growth of captive Elegant Tern chicks. Poster presentation Symposium Interactions between seabirds and fisheries: a global perspective V8-1, World Seabird Conference, Victoria, Canada, 10 Sep 2010.

Folland C.K. & T.R. Karl (eds) 2001. Observed Climate Variability and Change. In: Houghton J.T., Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden, X. Dai, K. Maskell & C.A. Johnson (eds) Climate Change 2001: The Scientific Basis: 99-182. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change Published for the Intergovernmental Panel on Climate Change. Cambridge Univ. Press, Cambridge.

Fonds M. 1994a. Catch composition of 12-m beam trawl and 4-m beam trawl for Sole fishing. In: Groot S.J. de & Lindeboom H.J. (eds). Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. EC Research contract MA 2-549, Netherlands Institute for Fisheries Research, IJmuiden and Netherlands Institute for Sea Research, Texel.

Fonds M. 1994b. Mortality of fish and invertebrates in beam trawl catches and the survival changes of discards. In: Groot S.J. de & Lindeboom H.J. (eds). Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. EC Research contract MA 2-549, Netherlands Institute for Fisheries Research, IJmuiden & Netherlands Institute for Sea Research, Texel.

Forbes S.A. 1887. The lake as a microcosm. Bull. Peoria Sc. Ass. (1887): 77-87 *[reprinted in Illinois State Natural History Survey 15 (1925): 537-550]*.

Forslund P. & T. Pärt 1995. Age and reproduction in birds-hypotheses and tests. TREE 10: 374-378.

Fowler C.W. 1981. Density Dependence as Related to Life History Strategy. Ecology 62: 602-610.

François R. 2003. Aantalsevolutie en gedrag van dakbroedende Zilvermeeuwen *Larus argentatus* en Kleine Mantelmeeuwen *Larus fuscus* in België. Natuur.oriolus 68(3): 123-126.

Frederiksen M., Wanless S., Harris M.P., Rothery P. & Wilson L.J. 2004. The role of industrial fisheries and oceanographic change in the decline of North Sea black-legged kittiwakes. J. Appl. Ecol. 41: 1129-1139.

Freeman A.N.D., D.G. Nicholls, K-J. Wilson & J.A. Bartle 1997. Radio- and satellite tracking Westland Petrels Procellaria westlandica. Mar. Ornithol. 25: 31-36.

Friend M. & J.C. Franson (eds) 1999. Field manual of wildlife disease: General field procedures and diseases of birds. USGS Biological Resources Division, Madison.

Frieswijk J.J. & Bresser H. 1965. Het trappelen van voedselzoekende meeuwen. De Lev. Nat. 68: 201-205.

Frings H., M. Frings, B. Cox & L. Peissner 1955. Auditory and visual mechanisms in food-finding behavior of the Herring Gull. Wilson Bull. 67: 155-170.

Fromentin J-M. & Planque B. 1996. Calanus and environment in the eastern North Atlantic, II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Mar. Ecol. Progr. Ser. 134: 111-118.

Fuellhaas U., Strobel U., Bergmann H.-H. & Düttmann H. 1997. Herring gulls, *Larus argentatus*, preying upon Shelduck *Tadorna tadorna* ducklings on unfavourable habitat. Seevögel 18: 26-28.

Furness R.W. 1978. Energy requirements of seabird communities: a bioenergetics model. J. Anim. Ecol. 47: 39-53.

Furness R.W. 1988. Influences of status and recent breeding experience on the moult strategy of the Yellow-nosed Albatross *Diomedea chlororhynchos*. J. Zool. 215: 719-727.

Furness R.W. 1989. Changes in diet and breeding ecology of seabirds on Foula, 1971-88. In: Heubeck M. (ed.) Seabirds and sandeels: proceedings of a seminar held in Lerwick, Shetland, 15-16th October 1988. Shetland Bird Club, Lerwick.

Furness R.W. 1992. Implications of changes in net mesh size, fishing effort and minimum landing size regulations in the North Sea for seabird populations. JNCC Report 133, Joint Nature Conservation Committee, Peterborough.

Furness R.W. 1997. The impact of predation by great skuas on other seabird species, with particular reference to Special Protection Areas in Shetland. Northern Isles Area Report, Scottish Natural Heritage, Lerwick.

Furness R.W. & Barrett R.T. 1985. The food requirements and ecological relationships of a seabird community in North Norway. Ornis Scandinavica 16: 305–313.

Furness R.W. & T.R. Birkhead 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature (London) 311 :655-656.

Furness R.W. & C.J. Camphuysen 1997. Seabirds as monitors of the marine environment. ICES J Mar Sc 54: 726-737.

Furness R.W. & Cooper J. 1982. Interactions between breeding seabird and pelagic fish populations in the southern Benguela region. Mar. Ecol. Progr. Ser. 8: 243-250.

Furness R.W., K. Ensor & A.V. Hudson 1992. The use of fishery waste by gull populations around the British Isles. Ardea 80: 105-113.

Furness R.W. & J.R.G. Hislop 1981. Diets and feeding ecology of the Great Skua Catharacta skua during the breeding season in Shetland. J. Zool., London 195: 1–23.

Furness R.W., A.V. Hudson & K. Ensor 1988. Interactions between scavenging seabirds and commercial fisheries around the British Isles. In: Burger J. (ed.). Seabirds & Other Vertebrates: Competition, Predation and Other Interactions: 240-268. Columbia Univ. Press, New York.

Furness R.W. & P. Monaghan 1987. Seabird Ecology. Blackie Glasgow, London.

Futuyma D.J. & G. Moreno. 1988. The evolution of ecological specialization. Ann. Rev. Ecol., Evol., and System. 19: 207-233.

Gabrey S.W. 1996. Migration and dispersal in Great Lakes Ring-billed and Herring Gulls. J. Fld Orn. 67: 327-339.

Gagliardi A., Martinoli A., Wauters L. & Tosi G. 2003. A floating platform: a solution to collecting pellets when cormorants roost over water. Waterbirds 26: 54–55.

Gaines S.D., S.E. Lester, K. Grorud-Colvert, C. Costello & R. Pollnac 2010a. Evolving science of marine reserves: new developments and emerging research frontiers. PNAS 107: 18251-18255.

Gaines S.D., C. White, M.H. Carr & S.R. Palumbi 2010b. Designing marine reserve networks for both conservation and fisheries management. PNAS 107: 18286-18293.

Galbraith H. & Furness R.W. 1983. Wear and legibility of Shag rings. Ringing & Migr. 4: 145-147.

Gallego Garcia N. 2008. Growth in chicks of Lesser Black-backed Gulls *Larus fuscus* and Herring Gulls *Larus argentatus* in the Kelderhuispolder colony, Texel. M.Sc.-thesis, Univ. of Amsterdam, Amsterdam.

Garcia-Barcelona S., J.C. Baezi, A. Luz Marquez, A Estratda, R. Real & D. Macias 2010. Differential age-related phenology in Lesser Black-backed Gull *Larus fuscus* wintering in the Malaga area. Ardeola 57: 127-132.

Garthe S. 1992. Quantifizierung von Abfall und Beifang der Fischerei in der südöstlichen Nordsee und deren Nutzung durch Seevögel. Diplomarb. Math.-Naturw. Fakult., Inst. Meeresk., Christian-Albr. University, Kiel.

Garthe S. 1993. Quantifizierung von Abfall und Beifang der Fischerei in der südöstlichen Nordsee und deren Nutzung durch Seevögel. Hamburger avifaun. Beitr. 25: 125-237.

Garthe S. 1996. Distribution and abundance of North Sea seabirds and their feeding ecology in relation to fisheries and hydrography. Ph.D.-thesis, Christian-Albr. University, Kiel.

Garthe S. 1997. Influence of hydrography, fishing activity and colony location on summer seabird distribution in the southeastern North Sea. ICES J. Mar. Sc 54: 566–577.

Garthe S., Camphuysen C.J. & Furness R.W. 1996. Amounts of discards in commercial fisheries and their significance as food for seabirds in the North Sea. Mar. Ecol Progr. Ser. 136: 1-11.

Garthe S. & Damm U. 1997. Discards in beam trawl fisheries in the German Bight. Arch. Fish. Mar. Res. 45: 223–242.

Garthe S., Flore B-O., Hälterlein B., Hüppop O., Kubetzki U. & Südbeck P. 2000. Die Brutbestandsentwicklung der Möwen (Laridae) an der deutschen Nordseeküste in der zweiten Hälfte des 20. Jahrhunderts. Vogelwelt 121: 1–13.

Garthe S., Freyer T., Hüppop O. & Wolke D. 1999a. Lesser Black-Backed Gulls *Larus graellsii* and Herring Gulls *Larus argentatus*: Coexistence or competition? Ardea 87: 227-236.

Garthe S., N. Guse & N. Sonntag 2008. Spatio-temporal patterns of inshore and offshore foraging by Great Cormorants in the southwestern Baltic Sea. In: Wollny-Goerke K. & K. Eskildsen (eds) Marine mammals and seabirds in front of offshore wind energy. MINOS - Marine warm-blooded animals in North and Baltic Seas: 317-345. Teubner, Wiesbaden.

Garthe S. & Hüppop O. 1993. Gulls and Fulmars following ships and feeding on discards at night. Ornis Svecica 3: 159-161.

Garthe S. & Hüppop O. 1994. Distribution of ship-following seabirds and their utilization of discards in the North Sea in summer. Mar. Ecol. Progr. Ser. 106: 1-9.

Garthe S. & Kubetzki U. 1998. Diet of Sandwich terns Sterna sandvicensis on Juist (Germany). Sula 12: 13–19.

Garthe S., Kubetzki U., Hüppop O. & Freyer T. 1999b. Zur Ernährungsökologie von Herings-, Silber- und Sturmmöwe (*Larus fuscus*, *L. argentatus* und *L. canus*) auf der Nordseeinsel Amrum während der Brutzeit. Seevögel 20: 52-58.

Garthe S., N. Markones, O. Hüppop, S. Adler 2009. Effects of hydrographic and meteorological factors on seasonal seabird abundance in the southern North Sea. Mar. Ecol. Progr. Ser. 391: 243-255.

Garthe S., W.A. Montevecchi & G. Davoren 2007. Flight destinations and foraging behaviour of northern gannets (Sula bassana) preying on a small foraging fish in a Low Arctic ecosystem. Deep-Sea Res. II 54: 311-320.

Garthe S., W.A. Montevecchi & G.K. Davoren 2011. Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. Limnol. Oceanogr. 56: 802-812.

Garthe S., Walter U., Tasker M.L., Becker P.H., Chapdelaine G. & Furness R.W. 1999. Evaluation of the role of discards in supporting bird populations and their effects on the species composition of seabirds in the North Sea. ICES Coop. Res. Rep. 232: 29–41.

Gasparini J., T. Tveraa & T. Boulinier 2004. Variation in parental quality and the correlation between egg size, clutch size and the ability to produce a replacement clutch in Black-legged Kittiwakes. Poster presentation 8th Intern. Seabird Group Conference "North Atlantic Seabird Populations: 24. King's College Conference Centre, Aberdeen University, 2-4 April 2004, Aberdeen.

Gaston A.J. 1985. Development of the young in the Atlantic Alcidae. In: Nettleship D.N. & T.R. Birkhead (eds) The Atlantic Alcidae. Acad. Press, London.

Gaston A.J., B.L. Collins & A.W. Diamond 1987. The 'Snapshot' Count for Estimating Densities of Flying Seabirds During Boat Transects: A Cautionary Comment. Auk 104: 336-338.

Gaston A.J., D.F. Bertram, A.W. Boyne, J.W. Chardine, G. Davoren, A.W. Diamond, A. Hedd, W.A. Montevecchi, J.M. Hipfner, M.J.F. Lemon, M.L. Mallory, J-F. Rail & G.J. Robertson 2009. Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs. Environ. Rev. 17: 267-286.

Gause G.F. 1934. The struggle for existence. Williams & Wilkins, Baltimore, MD.

Geelhoed S., Groot H., Huijssteeden E. van, Leeuwen G. van & Nobel P. de 1998. Vogels in het landschap van Zuid-Kennemerland en de Haarlemmermeer. Vogelwerkgroep Zuid-Kennemerland en KNNV Uitgeverij, Utrecht.

Gelderblom PG. 2012. Eerste broedgeval Pontische Meeuw voor Nederland, maart-augustus 2012. http://www.birdingwageningen.blogspot.nl dinsdag 7 augustus 2012.

Georges J.-Y., Guinet C., Jouventin P. & Weimerskirch H. 1997. Satellite tracking of seabirds: interpretation of activity pattern from the frequency of satellite locations. Ibis 139: 403-405.

Gerritsen H., H. de Vries & M. Philippart 1995. The Dutch Continental Shelf Model. In: Lynch D.R. & A.M. Davies (eds) Quantitative Skill Assessment for Coastal Ocean Models, 47: 425-467. American Geophysical Union, Washington, DC.

Geyr von Schweppenburg H. 1938. Zur Systematik der *fuscus-argentatus*-Möwen. J. Orn. 86: 345-365.

Ghalambor C.K.& T.E. Martin 2001. Fecundity-Survival trade-offs and parental risk-taking in birds. Science 292: 494-497.

Gieskes W.W.C. & Kraay G.W. 1977. Continuous plankton records: changes in the plankton of the North Sea and its eutrophic Southern Bight from 1948 to 1975. Neth J. Sea Res. 11(3/4): 334-364.

Gijsbertsen M. 2011. Meeuwen teisteren 'Petten'. Schager Courant 9 november 2011.

Gill F. & D. Donsker (eds) 2010. IOC World Bird Names (version 2.4). http://www.worldbirdnames.org/ [Accessed 30 March 2010].

Gill F. & M. Wright 2006. Birds of the World: Recommended English Names. Princeton Univ. Press, Princeton NJ, Version 2.9.13 generated on 10 July 2011 [Accessed 25 July 2011].

Gill Jr R.E., T.L. Tibbitts, D.C. Douglas, C.M. Handel, D.M. Mulcahy, J.C. Gottschalck, N. Warnock, B.J. McCaffery, P.F. Battley & T. Piersma 2008. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proc. R. Soc. B doi:10.1098/rspb.2008.1142.

Gill V.A. & S.A. Hatch 2002. Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. J. Avian Biol. 33: 113-126.

Gillett W.H., Hayward Jr J.L. & Stout J.F. 1975. Effects of human activity on egg and chick mortality in a Glaucous-winged Gull colony. Condor 77: 492-495.

Gilman E.L., P. Dalzell & S. Martin 2006. Fleet communication to abate fisheries bycatch. Marine Policy 30: 360-366.

Gils J.A. van, Rooij S.R. de, Belle J. van, Meer J. van der, Dekinga A., Piersma T. & Drent R. 2005a. Digestive bottleneckaffects foraging decisions in red kots Calidris canutus, I. Prey choice. J. Anim. Ecology 74: 105-119.

Gils J.A. van, A. Dekinga, B. Spaans, W.K. Vahl & T. Piersma 2005b. Digestive bottleneck affects foraging decisions in red kots Calidris canutus, II. Patch choice and length of working day. J. Anim. Ecology 74: 120-130.

Gils J.A. van, T. Piersma, A. Dekinga & M.W. Dietz 2003. Cost-benefit analysis of mollusc eating in a shorebird I. Optimizing gizzard size in the face of seasonal demands. J. Exp. Biol. 206: 3369-3380.

Gils J.A. van, T. Piersma, A.Dekinga, B. Spaans & C. Kraan 2006. Shellfish dredging pushes a flexible avian top predator out of a marine protected area. PLoS Biology 4(12): e376.

Ginn H.B. & D.S. Melville 1983. Moult in Birds. BTO Guide 19, BTO, Tring.

Girdwood R.W.A., C.R. Fricker, D. Munro, C.B. Shedden & P. Monaghan 1985. The incidence and significance of salmonella carriage by gulls (*Larus* spp.) in Scotland. J. Hyg., Camb. 95: 229-241.

Gjerde K.M., & C. Breide 2003. Towards a Strategy for High Seas Marine Protected Areas. Proceedings of the IUCN, WCPA and WWF Experts Workshop on High Seas Marine Protected Areas, 15-17 January 2003, Malaga, Spain. IUCN, Gland, Switzerland.

Gjerdrum C. 2004. Parental provisioning and nestling departure decisions: a supplementary feeding experiment in Tufted Puffins (*Fratercula cirrhata*) on Triangle Island. British Columbia. Auk 121: 463-472.

Gjertz I., K.M. Kovacs, C. Lydersen & Ø. Wiig2000. Movements and diving of adult ringed seals (Phoca hispida) in Svalbard. Polar Biology 23:651-656.

Glass G.E., R.D. Holt & N.A. Slade 1985. Infanticide as an evolutionarily stable strategy. Anim. Behav. 33: 384-391.

Glutz von Blotzheim U.N. & K.M. Bauer 1982. Handbuch der Vögel Mitteleuropas, 8/I-II. Akad. Verl., Wiesbaden.

Gmelig Meyling A. & A. Gittenberger 2006. Exoten en andere nieuwkomers in onze zoute wateren. De Levende Natuur 107: 242-246.

Gochfeld M. 1985. Predation and coloniality in seabirds. Proc. Int. Orn. Congr. 18: 882-891.

Goes D. van der & L. Hartog 2011. Drinkputten of kolken op Texel. Tussen Duin en Dijk 10(3): 12-13.

Goethe F. 1937. Beobachtungen und Untersuchungen zur Biologie der Silbermöwe (*Larus argentatus* Pontopp.) auf der Vogelinsel Memmertsand. J. Orn. 85: 1-119.

Goethe F. 1955. Vergleichende Untersuchungen über die Nahrung der Silbermöwe (*Larus argentatus*) und der Heringsmöwe (*L. fuscus*). Acta XI Congr. Intern. Orn. 1954, Basel: 577-582.

Goethe F. 1956. Die Silbermöwe. Neue Brehm-Bücherei nr. 182, A. Ziemsen Verlag, Wittenberg Lutherstadt.

Goethe F. 1958. Felsbrütertum und weitere beachtenswerte Tendenzen bei der Silbermöwe. Proc. 12th Int. Orn. Congr.: 252-258.

Goethe F. 1964. Lenkung der Möwenbestande an der deutschen Nordseekuste mit Hilfe der Einschläferung erwachsener Möwen durch Glukochloralose? Mt. Rat Vogelschutz Deutsche Sektion 4: 1-6.

Goethe F. 1975. Zur Biologie der Heringsmöwe *Larus fuscus* unter besonderer Berücksichtigung ethologischer Aspekte. I. Nahrung und Nahrungserwerb. Ornis Fennica 52: 5-12.

Goldbach R. & Hansen K. 1979. De Zilvermeeuw. Kosmos Vogelmonografieën, Amsterdam/Antwerpen.

González-Solís J., J.P. Croxall, D. Oro & X. Ruiz 2007. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. Front. Ecol. Environ. 5:297-301.

González-Solís J., J.P. Croxall & A.G. Wood. 2000. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. Oikos 90: 390-398.

Gonzalez-Solis J., Oro D., Jover L., Ruiz X. & Pedrocchi V. 1997. Trophic niche width and overlap of two sympatric gulls in the south western Mediterranean. Oecologia 112: 75-80.

Goodman D. 1974. Natural selection and a cost ceiling on reproductive effort. Am. Nat. 108: 247–268.

Götmark F. & Åhlund M. 1988. Nest predation and nest site selection among Eiders *Somateria mollissima*: the influence of gulls. Ibis 130: 111-123.

Götmark F. 1984. Food and foraging in five species of Larus gulls in the breeding season: a comparative review. Orn. Fenn. 61: 9-18.

Granadeiro J.P., Monteiro L.R., Silva M.C. & Furness R.W. 2002. Diet of common terns in the Azores, Northeast Atlantic. Waterbirds 25: 149–155.

Granadeiro J.P. & Silva M.A. 2000. The use of otoliths and vertebrae in the identification and size-estimation of fish in predator-prey studies. Cybium 24: 383-393.

Grant G.S. 1992. Opportunistic Foraging on Swarming Ants by Gulls, Shorebirds, and Grackles. The Chat 56: 80-82.

Grecian W.J., M.J. Witt, M.J. Attrill, S. Bearhop, B.J. Godley, D. Grémillet, K.C. Hamer & S.C. Votier S.C. 2012. A novel technique to identify important at-sea areas for seabird conservation . Biol. Conserv. 156: 43-52.

Green R.E. & M.G.J. Hirons 1988. Effects of nest failure and spread of laying on counts of breeding birds. Ornis Scand. 19: 76-78.

Greenstreet S.P.R., Becker P.H., Barrett R.T., Fossum P. & Leopold M. F. 1999. Consumption of pre-recruit fish by seabirds and the possible use of this as an indicator of fish stock recruitment. In Diets of seabirds and consequences of changes in food supply, pp. 6–17. Ed. by R. W. Furness & M. L. Tasker. ICES Cooperative Research Report No. 232.

Greig S., Coulson J.C. & Monaghan P. 1983. Age-related differences in foraging success in the Herring Gull (*Larus argentatus*). Anim. Behav. 31: 1237-1243.

Greig S., Coulson J.C. & Monaghan P. 1985. Feeding strategies of male and female adult Herring Gulls (*Larus argentatus*). Behaviour 94: 41-59.

Grémillet D. & Argentin G. 1998. Cormorans et pêcheries autour des Iles Chausey. Le Cormoran 10: 196–202.

Groenewold S. 1996. The effects of discard materials from beam trawl fisheries on the food uptake and population dynamics of selected marine scavengers in the North Sea. Final report EU fellowship ERB 4001 GT 930098, Netherlands Institute for Sea Research, Texel.

Gronert A. 1994. Broedende meeuwen blijven verrassen. De Windbreker 69: 22-23.

Groot C. 1921. De Zilvermeeuwen van Wassenaar. De Lev. Nat. 26: 176-185.

Groot S.J. de, Dijkema R. & Redant F. 1988. Vis-, schelp- en schaaldieren. Het Spectrum, Utrecht.

Guicking D., D. Ristow, P.H. Becker, R. Schlatter, P. Berthold & U. Querner 2001. Satellite tracking of the pink-footed shearwater in Chile. Waterbirds 24:8-15.

Guilford T.C., J. Meade, R. Freeman, D. Biro, T. Evans, F. Bonadonna, D. Boyle, S. Roberts & C.M. Perrins 2008. GPS tracking of the foraging movements of Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. Ibis 150:462-47.

Gwinner E. 1975. Circadian and circannual rhythms in birds. In: Farner D.S. & King J.R. (eds). Avian Biology, vol. 5: 221-285. Acad. Press, New York.

Gwinner E. 1996. Circannual clocks in avian reproduction and migration. Ibis 138: 47-63.

Hagemeijer E.J.M. & Blair M.J. (eds) 1997. The EBCC Atlas of European breeding birds, their distribution and abundance. T. & A.D. Poyser, London.

Hald-Mortensen P. 1995. Danske skarvers (*Phalacrocorax carbo sinensis*) fødevalg i 1992–1994 baseret på analyser af gylp fra 23 forskjellige kolonier samt 2 overnattingspladser. Report from Skov og Naturstyrelsen, Miljøministeriet. 418 pp.

Halley D.J., M.P. Harris & S. Wanless 1995. Colony attendance patterns and recruitment in immature Common Murres (*Uria aalge*). Auk 112: 947-957.

Hallgrimsson G.T., H. Gunnarsson, O. Torfason, R-J. Buijs & C.J. Camphuysen 2012. Migration pattern of Icelandic Lesser Black-backed Gulls *Larus fuscus graellsii*: indications of a leap-frog system. Journal of Ornithology DOI 10.1007/s10336-012-0816-4.

Halpern B.S., S.E. Lester & K.L. McLeod 2010. Placing marine protected areas onto the ecosystem-based management seascape. PNAS 107: 18312-18317.

Halpin P.N., A.J. Read, B.D. Best, K.D. Hyrenbach, E. Fujioka, M.S. Coyne, L.B. Crowder, S.A. Freeman & C. Spoerri 2006. OBIS-SEAMAP: developing a biogeographic research data commons for the ecological studies of marine mammals, seabirds, and sea turtles. Mar. Ecol. Prog. Ser. 316: 239-246.

Hälterlein B. 1996. Brutvogelbestände im Schleswig-Holsteinischen Wattenmeer. Teilprojekt A2.7. Ökosystemforschung Schleswig-Holsteinisches Wattenmeer, Tönning.

Hälterlein B. 1998. Brutvögel-Bestände im Schleswig-Holsteinischen Wattenmeer. Teilbericht zum Forschungsvorhaben 108 02 085/01, Umweltbundesamt, Berlin.

Hamer K.C., Furness R.W. & Caldow R.W.G. 1991. The effects of changes in food availability on the breeding ecology of great skuas Catharacta skua in Shetland. J. Zool., London 223: 175–188.

Hamer K.C., E.M. Humphreys, S. Garthe, J. Hennicke, G. Peters, D. Grémillet, R.A. Phillips, M.P. Harris & S. Wanless 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. Mar. Ecol. Progr. Ser. 338: 295-305.

Hamer K.C., E.M. Humphreys, M.C. Magalhães, S. Garthe, J. Hennicke, G. Peters, D. Grémillet, H. Skov & S. Wanless 2009. Fine-scale foraging behaviour of a medium-ranging marine predator. J. Anim. Ecol. 78: 880-889.

Hamer K.C., P. Monaghan, J.D. Uttley, P. Walton & M.D. Burns 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. Ibis 135: 255–263.

Hamer K.C., R.A. Phillips, S. Wanless, M.P. Harris & A.G. Wood 2000. Foraging ranges, diets and feeding locations of gannets in the North Sea: evidence from satellite telemetry. Mar. Ecol. Progr. Ser. 200, 257-264.

Hamer K.C., E.A. Schreiber & J. Burger 2002. Breeding biology, life histories, and life-history-environment interactions in seabirds. In: Schreiber E.A. & J. Burger (eds) Biology of Marine Birds: 217-261. CRC Press, Boca Raton.

Hammen van der 1978. Meijendel mededelingen 6(2): 44-134 .

Hanski I., I. Hansson & H. Henttonen 1991. Specialist predators, generalist predators, and the microtine rodent cycle. Journal of Animal Ecology 60: 353-367.

Hanssen S.A., D. Hasselquist, I. Folstad, K-E. Erikstad 2005. Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. Proc. Royal Soc. Biol. Sc. B. 272: 1039–1046.

Hardege J.D., H.D. Bartels-Hardege, E. Zeeck & F.T. Grimm 1990. Induction of swarming of *Nereis succinea*. Mar. Biol. 104: 291-295.

Hardin G. 1960. The Competitive Exclusion Principle. Science 131: 1292-1297.

Hario M. 1994. Reproductive performance of the nominate Lesser Black-backed Gull under the pressure of Herring Gull predation. Ornis Fennica 71(1): 1-10.

Harris M.P. 1962. Migration of British Lesser Black-backed Gulls as shown by ringing data. Bird Study 9: 174-182.

Harris M.P. 1964a. Aspects of the breeding biology of the gulls *Larus argentatus*, *L. fuscus* and L. marinus. Ibis 106: 432-455.

Harris M.P. 1964b. Recoveries of ringed Herring Gulls. Bird Study 11: 183-191.

Harris M.P. 1965. The food of some Larus gulls. Ibis 107: 43-53.

Harris M.P. 1970. Rates and causes of increase of some British gull populations. Bird Study 17: 325-335.

Harris M.P. 1971. Ecological adaptations of moult in some British gulls. Bird Study 18: 113-118.

Harris M.P., D.J. Halley & S. Wanless 1992. The post-fledging survival of young Guillemots *Uria aalge* in relation to hatching date and growth. Ibis 134: 335-339.

Harris M.P. & Hislop J.R.G. 1978. The food of young puffins *Fratercula arctica*. J.Zool., Lond. 185:213-236.

Harris M.P. & Jones P.H. 1969. Sexual differences in measurements of Herring and Lesser Black-backed Gulls. Brit. Birds 62: 129-133.

Harris M.P. & P. Rothery 1985. The post-fledging survival of young Puffins *Fratercula arctica* in relation to hatching date and growth. Ibis 127: 243-250.

Harris M.P. & S. Wanless 1986. The food of young razorbills on the Isle of May and a comparison with that of young guillemots and puffins. Ornis Scandinavica 17: 41–46.

Harris M.P. & S. Wanless 1993. The diet of shags *Phalacrocorax aristotelis* during the chick-rearing period assessed by three methods. Bird Study 40: 135–139.

Harris M.P. & S. Wanless 1997. The effect of removing large numbers of gulls Larus spp. on an island population of oystercatchers *Haematopus ostralegus*: Implications for management. Biol. Conserv.82: 167-171.

Hartung R. 1976. The impact of environmental pollutants on wildlife-an overview. *In:* Page L.A. (ed.) Wildlife diseases: 317-332. Plenum Press, New York.

Harvey P.H. & M.D. Pagel 1991. The comparative method in evolutionary biology. 1998 reprint, Oxford Univ. Press, Oxford.

Hatch S.A. 1990. Individual variation in behavior and breeding success of Northern fulmars. Auk 107: 750-755.

Hausmann K. 1969: Beobachtungen an der Westlichen Heringsmöwe auf der Insel Memmert. Orn. Mitt. 21: 119–126.

Haverschmidt F. 1942. Faunistisch overzicht van de Nederlandse broedvogels. Brill, Leiden.

Hayes F.E., G.L. White, M. Kenefick & H. Kilpatrick 2002. Status of the Lesser Black-backed Gull Larus [fuscus] graellsii in Trinidad and Tobago. Atl. Seabirds 4: 91-100.

Hayward P.J. & Ryland J.S. 1995. Handbook of the Marine Fauna of North-West Europe. Oxford University Press, Oxford.

Hazelwood A. & J.M. Harrison 1953. A note on Larus "capistratus" Temminck. Bull. Brit. Orn. Club 73: 98-100.

Hebblewhite M. & D.T. Haydon 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Phil. Trans. R. Soc. B 365: 2303-2312.

Hébert P.N. & R.M.R. Barclay 1986. Asynchronous and synchronous hatching: effect on early growth and survivorship of Herring Gull, *Larus argentatus*, chicks. Can. J. Zool. 64: 2357-2362.

Hébert P.N. & McNeil R. 1999. Nocturnal activity of Ring-billed Gulls at and away from the colony. Waterbirds 22: 445-451.

Hedd A. & Montevecchi W.A. 2006. Diet and trophic position of Leach's storm-petrel during breeding and molt, inferred from stable isotope analysis of feathers. Mar. Ecol. Progr. Ser. 322: 291–301.

Hedenström A. & S. Sunada 1999. On the aerodynamics of moult gaps in birds. J. Exp. Biol. 202: 67–76.

Hedgren S. 1981. Effects of fledging weight and time of fledging on surval of Guillemots *Uria aalge* chicks. Ornis Scand. 12: 51-54.

Heffeman O. 2009. No more fish in the sea. Nature 460: 956

Helberg M., G.H. Systad, I. Birkeland, N.H. Lorentzen & J.O. Bustnes 2009. Migration patterns of adult and juvenile Lesser Black-backed Gulls *Larus fuscus* from northern Norway. Ardea 97: 281-286.

Helm F. van der 1992. De vos jaagt meeuwen het dak op. Vogels 12(4): 34-35.

Hémery G., d'Elbee E. & Terrasse J.-F. 1968. Régulation d'une population de pétrels-tempête *Hydrobates pelagicus* par reproduction intermittente. C.R. Acad. Sci. Ser. III Sci. Vie 303: 353-356.

Henson S.M., B. Dennis, J.L. Hayward, J.M. Cushing & J.G. Galusha 2007. Predicting the dynamics of animal behaviour in field populations. Anim. Behav. 74: 103-110.

Henson S.M. & J. Hayward 2010. Effects of climate, habitat, and predation on hatching success in Glaucous-winged Gulls. Poster presentation Symposium Interactions between seabirds and fisheries: a global perspective V8-1, World Seabird Conference, Victoria, Canada, 10 Sep 2010.

Henzi S.P., Graves J. & Whiten A. 1990. Interactions between parents and non-residential intruders at a breeding colony of Herring Gulls *Larus argentatus*. Bird Study 37: 53-60.

Herklots J.A. 1853. Bouwstoffen voor eene Fauna van Nederland, onder medewerking van onderscheidene Geleerden en Beoefenaars der Dierkunde. Eerste Deel. E.J. Brill, Leiden.

Heubeck M., Camphuysen C.J., Bao R., Humple D., Sandoval A., Cadiou B., Bräger S. & Thomas T. 2003. Assessing the impact of major oil spills on seabird populations. Mar. Poll. Bull. 46: 900-902.

Hey T. & A. Trefethen 2003, The Data Deluge: An e-Science Perspective. In: Berman F., G. Fox & T. Hey (eds) Grid computing: Making the global infrastructure a reality: 317-345. John Wiley & Sons, London.

Hill J.K. & Hamer K.C. 1994. Do great skuas Catharacta skua respond to changes in the nutritional needs of their chicks? Seabird 16: 3–7.

Hillis J.P. 1971. Seabirds scavenging at trawlers in Irish waters. Irish Nat. J. 17: 129-132.

Hiom L., Bolton M., Monaghan P. & Worrall D. 1991. Experimental evidence for food limitation of egg production in gulls. Ornis Scand. 22: 94-97.

Hislop J.G. & Harris M.P. 1985. Recent changes in the food of young puffins Fratercula arctica on the Isle of May in relation to fish stocks. Ibis 127: 234–239.

Hislop J.R.G., Harris M.P. & J.G.M. Smith 1991. Variation in the calorific value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. J.Zool., Lond. 224: 501-517.

Hoagland P., U.R. Sumaila, S. Farrow, H.S. John, K.T. Karl & A.T. Steve 2001. Marine Protected Areas. Encyclopedia of Ocean Sciences: 672-677. Acad. Press, Oxford.

Holgersen H. 1938. Vom Zuge der norwegischen Heringsmöwen (*Larus fuscus* intermedius Schiöl.). Der Vogelzug 9: 22-27.

Holley A.J.F. 1986. Post-fledging parental care of a Lesser Black-backed Gull *Larus fuscus* brood. Seabird 9: 24-25.

Honkoop P.J.C. 1998. Bivalve reproduction in the Wadden Sea-Effects of winter conditions on reproductive effort and recruitment. Ph.D.-thesis, Univ. of Groningen, Groningen.

Honkoop P.J.C. & Beukema J.J. 1997. Loss of body mass in three intertidal bivalve species: an experimental and observational study of the interacting effects between water temperature, feeding time and feeding behaviour. J. Exp. Mar. Biol. & Ecol. 212: 277-297.

Hoogerwerf A. 1973. Vragen rond de geringe aanwas van Eiders (*Somateria mollissima*) en Bergeenden (*Tadorna tadorna*) op Vlieland. Pieper 12: 41-51.

Hoogerwerf A. 1974. Het geringe broedsucces van eiders en bergeenden op Vlieland. Waddenbull. 8(4): 34-35.

Hornman M., Hustings F., Koffijberg K., Kleefstra R., Klaassen O., Winden E. van, SOVON Ganzen- en Zwanenwerkgroep & Soldaat L. 2012. Watervogels in Nederland 2009/2010. Waterdienst-rapport BM 12.06, SOVON-monitoringrapport 2012/02, SOVON Vogelonderzoek Nederland, Nijmegen.

Hornman M., Hustings F., Koffijberg K., Winden E. van, SOVON Ganzen- en Zwanenwerkgroep & Soldaat L. 2011. Watervogels in Nederland 2008/2009. Waterdienst-rapport BM 10.24, SOVON-monitoringrapport 2011/03, SOVON Vogelonderzoek Nederland, Nijmegen.

Horton N., Brough T. & Rochard J.B.A. 1983. The importance of refuse tips to gulls wintering in an inland area of south-east England. J. Appl. Ecol. 20: 751-765.

Houghton J.D.R., A. Cedras, A.E. Myers, N. Liebsch, J.D. Metcalfe, J.A. Mortimer & G.C. Hays 2008b. Measuring the state of consciousness in a free-living diving sea turtle. J. Exp. Mar. Biol. Ecol. 356: 115-120.

Houghton J.D.R., T.K. Doyle, J. Davenport, R.P. Wilson & G.C. Hays 2008a. The role of infrequent and extraordinary deep dives in leatherback turtles (*Dermochelys coriacea*). J. Exp. Biol. 211: 2566-2575.

Houghton J.T., G.J. Jenkins & J.J. Ephraums 1990. Climate change, the IPCC Scientific Assessment. Cambridge Univ. Press, Cambridge.

Houston A.I. 1993. The importance of state. In: Hughes R.N. (ed.) Diet selection: 10-31. Blackwell Scientific Publ., London.

Houttuyn F. 1763. Natuurlijke historie of uitvoerige beschrijving der dieren, planten en mineraalen, eerste deels, vijfde stuk: Vervolg der vogelen. F. Houttuyn, Amsterdam.

Howell S.N.G. & J. Dunn 2007. Gulls of the Americas. Peterson Reference Guides, Houghton Mifflin Harcourt Publ., New York.

Howes L.A. & W.A. Montevecchi 1993. Longterm population trends of gulls and terns in Gros Morne National Park, Newfoundland. Can. J. Zool. 71: 1516–1520.

Hoyo J. del, A. Elliott & J. Sargatal (eds) 1996. Handbook of the birds of the world, 3. Lynx edition, Barcelona.

Hoyt D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96: 73-77.

Hudson A.V. 1989. Interspecific and age-related differences in the handling time of discarded fish by scavenging seabirds. Seabird 12: 40–44.

Hudson A.V. & R.W. Furness 1988. Utilization of discarded fish by scavenging seabirds behind white fish trawlers in Shetland. J. Zool., Lond. 215:151166.

Hudson A.V. & R.W. Furness 1989. The behaviour of seabirds foraging at fishing boats around Shetland. Ibis 131: 225–237.

Hüppop O. & A. Fründt 2002. Zur Speiballen-Produktion freilebender Kormorane (*Phalacrocorax carbo*) im Winter. Jahresber. Inst. Vogelforsch 5: 11.

Hüppop O. & Hüppop K. 1999. The food of breeding Herring Gulls *Larus argentatus* at the lower river Elbe: does fish availability limit inland colonisation?. Atl. Seabirds 1(1): 27-42.

Hüppop O. & S. Garthe 1993. Seabirds and fisheries in the southeastern North Sea. Sula 7: 9-14.

Hüppop O., S. Garthe, E. Hartwig & U. Walter 1994. Fischerei und Schiffsverkehr: Vorteil oder Problem für See- und Küstenvögel? In: Lozán J.L., E. Rachor, K. Reise, H. von Westernhagen & W. Lenz (eds) Warnsignale aus dem Wattenmeer: 278-285. Blackwell Wissenschafts-Verlag, Berlin.

Hüppop O. & S. Wurm 2000. Effects of winter fishery activities on resting numbers, food and body condition of large gulls *Larus argentatus* and *L. marinus* in the southeastern North Sea. Mar. Ecol. Progr. Ser. 194: 241–247.

Hughes R.N. 1993. Diet selection: an interdisciplinary approach to foraging behaviour. Blackwell, London. 232 pp.

Hugueney M., D. Berthet, A-M. Bodergat, F. Escuillié, C. Mourer-Chauviré & A. Wattinne 2003. La limite Oligocène-Miocène en Limagne: changements fauniques chez les mammifères, oiseaux et ostracodes des different niveaux de Billy-Créchy (Allier, France). Geobios 36: 719-731.

HuntJr. G.L. & M.W. Hunt 1973. Habitat partitioning by foraging gulls in Maine and Northwestern Europe. Auk 90: 827-839.

Hunt Jr. G.L. & M.W. Hunt 1976. Gull chick survival: the significance of growth rates timing of breeding and territory size. Ecology 57: 62-75.

Hunt Jr. G.L. & S.C. McLoon 1975. Activity patterns of gull chicks in relation to feeding by parents: their potential significance for density-dependent mortality. Auk 92: 523-527.

Hunt Jr. G.L., F. Mehlum, R.R. Russell, D. Irons, M.B. Decker & P.H. Becker 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams N.J. & R.H. Slotow (eds) Proc. 22 Int. Ornithol. Congr., Durban: 2040-2056. BirdLife South Africa, Johannesburg.

Hunt V. 2006. *Larus fuscus* and *Larus argentatus*: pellet and bolus analysis guide. Unpubl. report Royal Netherlands Institute for Sea Research, Texel.

Hunt W.G. 1998. Raptor floaters at Moffat's equilibrium. Oikos 82: 191-197.

Hurrell J.W. 1995. Decadal trends in the the North Atlantic Oscillation: regional temperatures and precipitation. Science 269: 676-679.

Husson A.M. 1962. Het determineren van schedelresten van zoogdieren in braakballen van uilen. Zoölogische Bijdragen No 5., Rijksmuseum van Natuurlijke Historie, uitgeverij E.J. Brill, Leiden.

Hustings F., K. Koffijberg, E. van Winden, M. van Roomen, SOVON Ganzen- en Zwanenwerkgroep & L. Soldaat 2009. Watervogels in Nederland 2007/2008. Waterdienst-rapport 2009.020, SOVON-monitoringrapport 2009/02, SOVON Vogelonderzoek Nederland, Beek-Ubbergen.

Hustings F. & J-W. Vergeer (eds) 2002. Atlas van de Nederlandse broedvogels, 1998-2000. Nederlandse Fauna 5, Sovon Vogelonderzoek Nederland, Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & European Invertebrate Survey, Leiden.

Hutton T., S. Mardle, S. Pascoe & R.A. Clark 2004. Modelling fishing location choice within mixed fisheries: English North Sea beam trawlers in 2000 and 2001. ICES Journal of Marine Science, 61: 1443-1452.

Hyrenbach K.D., K.A. Forney & P.K. Dayton 2000. Marine protected areas and ocean basin management. Aq. Conserv.: MAr. Freshw. Ecosys. 10: 437-458.

IJsseling M.A. & A. Scheygrond 1943. De Zoogdieren van Nederland, 2. Thieme, Zutphen.

IJzendoorn A.L.J. van 1950. The Breeding-birds of the Netherlands. Brill, Leiden.

IJzendoorn E.J. van 1968. De broedvogels van Duin en Kruidberg. De Lev. Nat. 71: 201-212.

Innes J.P. & S. Pascoe 2010. A multi-criteria assessment of fishing gear impacts in demersal fisheries. J. Environm. Manage 91: 932-939.

Irons D.B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. Ecology 79: 647-655.

Jansen G. 2007. Een tekort aan regenwormen. De Gelderlander 13 December 2007

Janssen J.A.M. & J.H.J. Schaminée (eds) 2009. Europese Natuur in Nederland: Zee en kust-Natura 2000-gebieden. KNNV Uitgeverij, Zeist.

Jarvis M.J.F. 1974. The ecological significance of clutch size in the South African Gannet (*Sula capensis* [Lichtenstein]). J. Anim. Ecol. 43: 302-352.

Jehl J.R. Jr. 1994. Absence of nest density effects in a growing colony of California Gulls. Avian Biol. 25: 224-230.

Jenni L. & C.J. Camphuysen (eds) 2001. Bird ringing 100 years. Ardea 89 (special issue): 1-252.

Jennings S. & M.J. Kaiser 1998. The effects of fishing on marine ecosystems. Adv. Mar. Biol. 34: 201-352.

Jennings S., M.J. Kaiser & J.D. Reynolds 2001. Marine fisheries ecology. Blackwell Science, Oxford.

Jickells T. 2005. External inputs as a contributor to eutrophication problems. J. Sea Res. 54: 58-69.

Jobling M. & A. Breiby 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. Sarsia 71: 265–274.

Johansen R., R.T. Barrett & T. Pedersen 2001. Foraging strategies of great cormorants *Phalacrocorax carbo carbo* wintering north of the Arctic Circle. Bird Study 48: 59–67.

Johnson J.H., R.M. Ross & D.R. Smith 1997. Evidence of secondary consumption of invertebrate prey by double-crested cormorants. Col. Waterb. 20: 547–551.

Jones I.L., F.M. Hunter & G.J. Robertson 2002. Annual adult survival of Least Auklets (Aves, Alcidae) varies with large-scale climatic conditions of the North Pacific Ocean. Oecologia 133: 38-44.

Jones K.M., G.D. Ruxton & P. Monaghan 2002. Model parents: is full compensation for reduced partner nest attendance compatible with stable biparental care? Behav. Ecol. 13:838-843.

Jones P.D., T. Jonsson & D. Wheeler 1997. Extension to the North Atlantic Oscillation using early instrumental pressure observations from Gibraltar and South-West Iceland. Int. J. Climatol. 17: 1433-1450.

Jones P.D., T.J. Osborn, K.R. Briffa, C.K. Folland, E.B. Horton, L.V. Alexander, D.E. Parker & N.A. Rayner 2001: Adjusting for sampling density in grid box land and ocean surface temperature time series. J. Geophys. Res. 106: 3371-3380.

Jones R.D. & Byrd G.V. 1979. Interrelations between seabirds and introduced animals. In: Bartonek J.C. & D.N. Nettleship (eds). Conservation of Marine Birds of Northern North America: 221-226. Wildlife Research Report 11, Fish and Wildl. Service, Washington DC.

Jong P.H. de 1984. Korte mededelingen. Broedgeval Zilvermeeuw op dak. Het Vogeljaar 32: 87.

Jonge V.N. de 1990. Response of the Dutch Wadden Sea ecosystem to phosphorus discharges from the River Rhine. Hydrobiologia 195: 49-62.

Jonge V.N. de, J. F. Bakker & M. Van Stralen 1996. Recent changes in the contributions of river Rhine and North Sea to the eutrophication of the western Dutch Wadden Sea. Aquatic Ecology 30: 27-39.

Jonge V.N. de & K. Essink 1991. Long-term changes in nutrient loads and primary and secondary producers in the Dutch Wadden Sea. In: M Elliott & J.-P. Ducrotoy (eds) Estuaries and coasts spatial and temporal intercomparisons. Estuarine and coastal Sciences Association Symposium 19: 307-316. Olsen & Olsen, Fredensborg.

Jongejan W. 1991. Korte mededelingen. Kleine Mantelmeeuw, nieuwe predator van weidevogels in Alblasserwaard en De Vijfheerenlanden. Het Vogeljaar 39: 219.

Jorge P.E., D. Sowter & P.A.M. Marques 2011. Differential annual movement patterns in a migratory species: effects of experience and sexual maturation. PLoS ONE 6(7): e22433. doi:10.1371/journal.pone.0022433.

Jørgensen O.M. 1973. Some results of Herring Gull ringing in Denmark, 1958-1969. Dansk Orn. Foren. Tiddskr. 67: 53-63.

Jost O. 1975. Fisch-Otolithen in Speiballen der Wasseramsel. Natur und Museum 105: 283–286.

Jouventin P. & H. Weimerskirch 1991. Changes in the population size and demography of southern seabirds: management implications. In: Perrins C.M., Lebreton J.-D. & Hirons G.J.M. (eds). Bird population studies: 297-314. Oxford Univ. press, Oxford.

Kadlec J.A. 1975. Recovery rates and loss of aluminium, titanium, and incoloy bands on Herring Gulls. Bird-Banding 46: 230-235.

Kadlec J.A. 1976. A re-evaluation of mortality rates in adult Herring Gulls. Bird-Banding 47: 8-12.

Kadlec J.A. & W.H. Drury 1968. New-England Herring Gull population. Ecology 49: 644-676.

Kadlec J.A., W.H. Drury & D.K. Onion 1969. Growth and mortality of Herring Gull chicks. Bird Banding 40: 222-233.

Källander H. & L. Rosenkvist 2000. Differential daytime distribution by age in Black-headed Gulls *Larus ridibundus*: adult physical dominance or competitive superiority? Ibis 142: 491-494.

Kam J. van de, B.Ens, T. Piersma & L. Zwarts 1999. Ecologische Atlas van de Nederlandse Wadvogels. Schuyt & Co., Haarlem.

Kapteyn K. (ed.) 1999. Braakballen pluizen. Noord-Hollandse Zoogdierstudiegroep, KNNV Uitgeverij, Utrecht.

Kate C.G.B. ten 1959. Ornithologie van Nederland, 1956-II en 1957. Limosa 32: 37-69.

Kawasaki T. 1985. Fisheries. In: Kates R.W., J.H. Ausubel & M. Berberian (eds) Climate impact assessment: 131-153. Scope 27, Scientific Committee on problems of the Environment, John Wiley & Sons, Chichester.

Keijl G.O. & F.A. Arts 1998. Breeding Common Gulls *Larus canus* in The Netherlands, 1900-1996. Sula 12: 159-171.

Kelcey J.G. & G. Rheinwald 2005. Birds in European cities. Ginster Verlag, St Katharinen.

Kennedy G.J.A. & J.E. Greer 1988. Predation by cormorants, *Phalacrocorax carbo* L., on the salmonid populations of an Irish river. Aquacult. Fish. Manage.19: 159–170.

Kie J.G., J. Matthiopoulos, J. Fieberg, R.A. Powell, F. Cagnacci, M>S. Mitchell, J.M. Gaillard & P.R. Moorcroft 2010. The home-range concept: are traditional estimators still relevant with modern telemetry technology? Phil. Trans. Royal Soc., B: 365:2221-2231.

Kihlman J. & L. Larsson 1974. On the importance of refuse dump as a food resource of wintering Herring Gulls. Orn. Scand. 5: 53-65.

Kilpi M. & M. Oest 1998. Reduced availability of refuse and breeding output in a herring gull (*Larus argentatus*) colony. Ann. Zool. Fennici 35: 37-42.

Kilpi M. & P. Saurola 1983a. Geographic distribution of breeding season recoveries of adult and immature *Larus marinus*, *L. argentatus* and *L. fuscus* ringed in Finland. Ornis Fennica 60: 117-125.

Kilpi M. & P. Saurola 1983b. Pre-migration movements of coastal Finnish Herring Gulls (*Larus argentatus*) in autumn. Ann. Zool. Fenn. 20: 245-254.

Kilpi M. & P. Saurola 1984. Migration and wintering strategies of juvenile and adult *Larus marinus*, *L. argentatus* and *L. fuscus* ringed from Finland. Ornis Fennica 61: 1-8.

Kim S.Y. & Monaghan P. 2005b. Effects of vegetation on nest microclimate and breeding performance of Lesser Black-backed Gulls (*Larus fuscus*). J. Ornithol. 146: 176-183.

Kim S.-Y. & P. Monaghan 2005a. Interacting effects of nest shelter and breeder quality on behaviour and breeding performance of herring gulls. Anim. Behav. 69: 301-306.

Kim S-Y. & P. Monaghan 2006. Interspecific differences in foraging preferences, breeding performance and demography in herring (*Larus argentatus*) and lesser black-backed gulls (*Larus fuscus*) at a mixed colony. J. Zool. 270: 664-671.

King J.R. 1974. Seasonal allocation of time and energy resources in birds. In: R.A. Paynter (ed.) Avian energetics: 152-297. Publ. Nuttall Ornithol. Club No. 15: 4-85, Cambridge, Massachusetts.

Klaassen R., B.J. Ens, J. Shamoun-Baranes, K-M. Exo & F. Bairlein 2011. Migration strategy of a flight generalist, the Lesser Black-backed Gull *Larus fuscus*. Behavioral Ecology doi: 10.1093/beheco/arr150.

Kleijn D., J. van der Hout, H. Jansman, D. Lammertsma & D. Melman 2012. Brandganzen en Kleine Mantelmeeuwen in het Wormer- en Jisperveld: Effecten op weidevogels. Alterra-rapport 2293, Alterra Wageningen UR, Wageningen.

Klein A.W.O. & J.T. van Buuren 1992. Eutrophication of the North Sea in the Dutch coastal zone, 1976-1990. Report WS-92.003, Tidal Waters Division, Ministry of Transport and Public Works, Den Haag.

Klein R. 2001. Raum-Zeit-Strategien der Silbermöwe *Larus argentatus* und verwandter Taxa im westlichen Ostseeraum. Dissertation Universität Rostock; http://www.greengull.de/img/dissertation_rklein.pdf, accessed 27 August 2009

Kleinwee M. van & C.J. Camphuysen 2010. Rui en plaatstrouw van Zilvermeeuw *Larus argentatus* ZDGA op grond van kleurringaflezingen. Sula 23: 69-86.

Kleunen A. van, K. Koffijberg, P. de Boer, J. Nienhuis, C.J. Camphuysen, H. Schekkerman, K. Oosterbeek, M. de Jong, B.J. Ens & C. Smit 2010. Broedsucces van kustbroedvogels in de Waddenzee in 2007 en 2008. SOVON-monitoringrapport 2010/04, SOVON Vogelonderzoek Nederland, Nijmegen.

Klinken A. van 1992. The impact of additional food provisioning on chick growth and breeding output in the Herring Gull *Larus argentatus*: a pilot experiment. In: Spaans A.L. (ed.). Population dynamics of Lari in relation to food resources. Ardea 80: 151-155.

KNMI 2012. Daggegevens van het weer in Nederland. http://www.knmi.nl/klimatologie/daggegevens/download.cgi.

Knopf F.L. & J.L. Kennedy 1981. Differential predation by two species of piscivorous birds. Wilson Bulletin 93: 554–556.

Koeman J.H. 1971. Het voorkomen en de toxicologische betekenis van enkele chloorkoolwaterstoffen aan de Nederlandse kust in de periode 1965 tot 1970. Ph.D.-thesis, University of Utrecht, Utrecht.

Koeman J.H., T. Bothof, R. de Vries, H. van Velzen-Blad & J.G. Vos 1972. The impact of persistent pollutants on piscivorous and molluscivorous birds. TNO-nieuws 12: 561-569.

Koeman J.H. & H. van Genderen 1972. Tissue levels in animals and effects caused by chlorinated hydrocarbon insectides, chlorinated biphenyls and mercury in the marine environment along the Netherlands coast. In: Ruivo M. (ed.) Marine pollution and sea life: 428-435. Fishing News books, London.

Koeman J.H., M.C. ten Noever de Brauw & R.H. de Vos 1969. Chlorinated Biphenyls in fish, mussels and birds from the River Rhine and the Netherlands Coastal Area. Nature 221 (5186): 1126-1128.

Koeman J.H., W.H.M. Peters, C.J. Smit, P.S. Tsjioe & J.J.M. de Goeij 1972. Persistent chemicals in marine mammals. TNO-nieuws 12: 570-578.

Koeman J.H., J. Veen, E.Brouwer, L. Huisman-de Brouwer & J.L. Koolen 1968. Residues of chlorinated hydrocarbon insecticides in the North Sea environment. Helgol. wiss. Meeresunters. 17: 375-380.

Koffijberg K., L.Dijksen, B. Hälterlein, K.Laursen, P. Potel & P. Südbeck 2006. Breeding birds in the Wadden Sea in 2001: results of the total survey in 2001 and trends in numbers between 1991 and 2001. Wadden Sea Ecosystem No. 22, Common Wadden Sea Secr., Wilhelmshaven.

Koks B.J. 1994. Broedvogelmonitoring in het Nederlandse Wadden-gebied in 1993. SOVON-monitoringrapport 94-02. SOVON, Beek-Ubbergen.

Koks B.J. 1998. The Little Gull *Larus minutus* as a breeding bird in The Netherlands. Sula 12: 139–148.

Koks B.J. & M.G.M. Jongenelen 1998. Great Black-backed Gull *Larus marinus*: latest newcomer as breeding bird in The Netherlands. Sula 12: 201-205.

Kooistra H. 1985. Stormmeeuwen *Larus canus* broedend op en tegen gebouwen. Limosa 58: 73-74.

Korpimäki E. & J. Wiehn 1998. Clutch size of kestrels: seasonal decline and experimental evidence for food limitation under fluctuating food conditions. Oikos 83: 259–272.

Korringa P. 1947. Relations between the moon and periodicity in the breeding of marine animals. Ecological Monogr. 17: 347-381.

Kraan C., J.A. van Gils, B. Spaans, A. Dekinga, A.I. Bijleveld, M. van Roomen, R. Kleefstra & T. Piersma 2009. Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. J. Anim. Ecol. 78: 1259-1268.

Krebs C.J. 1989. Ecological Methodology. Harper Collins Publ., New York.

Kube J., A.J. Helbig, R. Juvaste, K. Pedersen, C. Rahbek & P. Saurola . Hop or jump: Autumn migration strategies of Lesser Black-backed Gulls *Larus fuscus* as revealed by satellite tracking. http://www.cls.fr/documents/argos/ wildlife/gulls_poster.pdf.

Kubetzki U. 1997. Ernährungsökologie von Sturmmöwen (*Larus canus* L., 1758) verschiedener Kolonien an der deutschen Nordseeküste. Diplomarbeit Inselstation Helgoland des Instituts für Vogelforschung "Vogelwarte Helgoland" & Institut für Angewandte Zoologie der Rheinischen Friedr.-Wilhelms-Universität Bonn.

Kubetzki U. & S. Garthe 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Mar. Biol. 143: 199-207.

Kubetzki U., S. Garthe & O. Hüppop 1999. The diet of common gulls *Larus canus* breeding on the German North Sea coast. Atl. Seabirds 1: 57–70.

Kuhlman T., N. Polman, B. Smit, G. Venema, J. Buurma, A. van Duijn, J. van Dijk, Y. Dijkxhoorn, J. Helming, J. Jager, B. Janssens, G. Jukema, H. Prins & R. Stokkers 2009. Landbouwperspectieven in Noord-Holland tot 2040: Bouwstenen voor de structuurvisie van de provincie. Rapport 2009-043, Juni 2009, Projectcode 21161, LEI Wageningen UR, Den Haag.

Kylin H., H. Bouwman & M. Louette 2011. Distributions of the subspecies of Lesser Black-backed Gulls *Larus fuscus* in sub-Saharan Africa. Bird Study 58: 186-192.

Lack D. 1943 The age of the Blackbird. Brit Birds 36: 166-175.

Lack D. 1954. The Natural Regulation of Animal Numbers. Clarendon Press, Oxford.

Lack D. 1968. Ecological adaptations for breeding in birds. Methuen & Co., London.

Lamb J.P. Jr. 1997. Marsh was right: Ichthyornis had a beak. J. Vertebr.Paleont. 17: 59A.

Landsborough Thomson A. 1924. The migrations of the Herring Gull and Lesser Black-backed Gull: results of the marking method. Brit. Birds 18: 34-44

Larsen L.J., J. Durinck & H. Skov 2007. Trends in chronic marine oil pollution in Danish waters assessed using 22 years of beached bird surveys. Mar. Poll. Bull. 54: 1333-1340.

Lasiewski R.C. & W.R. Dawson 1967. A re-examination of the relation between metabolic rate and body weight in birds. Condor 69: 13-23.

Laursen K., J. Blew J., K. Eskildsen, K. Günther, B. Hälterlein, R. Kleefstra, G. Lüerßen, P. Potel & S. Chrader 2010. Migratory waterbirds in the Wadden Sea 1987-2008. Wadden Sea Ecosystem No. 30, Common Wadden Sea Secr., Wilhelmshaven.

Lebreton J.D., K.P. Burnham, J. Clobert & D.R. Anderson 1992. Modeling survival and testing biological hypotheses using marked animals - A unified approach with case-studies. Ecol. Monogr. 62: 67-118.

Lebreton J.-D. & J. Clobert 1991. Bird population dynamics, management, and conservation: the role of mathematical modelling. In: Perrins C.M., J.-D. Lebreton & G.J.M. Hirons (eds). Bird population studies: 105-125. Oxford Univ. press, Oxford.

Leege O. 1907. Ein Besuch bei den Brutvögeln der holländischen Nordseeinseln. Orn. Monatsschr. 32: 334-353, 357-379, 389-398, 419-432.

Leege O. 1911. Brutergebnis 1909-1910 der Vogelkolonie Memmert. Orn. Monatsschrift 36: 37-61.

Leege O. 1912. Brutergebnis 1911 der Vogelkolonie Memmert. Orn. Monatsschrift 37: 98-112.

Leege O. 1913. Brutergebnis der Vogelkolonie Memmert für 1912. Orn. Monatsschrift 38: 5-28.

Leege O. 1914. Brutergebnis der Vogelkolonie Memmert für 1913 nebst Bemerkungen über die anderen Vogelfreistätten auf den ostfriesischen Inseln. Orn. Monatsschrift 39: 33-59.

Leege O. 1915. Brutergebnis der Vogelkolonie Memmert für 1914. Orn. Monatsschrift 40: 19-49.

Leege O. 1917. Die Nahrung der Silbermöwen an der ostfriesischen Küste. Orn. Monatsschr. 2: 110-116 und 123-134.

Leege O. 1928. 20 Jahre Vogelinsel Memmert. Orn. Monatsschrift 53: 2-24.

Leege O. 1943. Nahrung der Silbermöwen während des harten Winters 1941/42 auf den Ostfriesischen Inseln. Dt. Vogelwelt 68: 60-62.

Legendre L. & P. Legendre 1983. Measures of ecological resemblance. Elsevier, New York.

Lensink L. & P.W. van Horssen 2009. Faunabeheerplan meeuwen havengebied Rotterdam 2010-2015. Rapport nr. 09-083, Bureau Waardenburg, Culemborg.

Lensink R. 2002. Zilvermeeuw (*Larus argentatus*). In: Lensink R., H. van Gasteren, F. Hustings, L. Buurma, G. van Duin, L. Linnartz, F. Vogelzang & C. Witkamp (eds) Vogeltrek over Nederland, 1976-1993: 154-155. Schuyt & Co, Haarlem

Leopold M.F. 1991. Toppredatoren op het Friese Front: zeevogels en zeezoogdieren. In: A. de Gee, M.A. Baars & H.W. van der Veer (eds). De ecologie van het Friese Front: 79-89. NIOZ- Rapport 1991-2, Netherlands Institute for Sea Research, Texel.

Leopold M.F. & C.J.G. van Damme 2003. Great cormorants *Phalacrocorax carbo* and polychaetes: can worms sometimes be a major prey of a piscivorous seabird? Mar. Orn. 31: 75–79.

Leopold M.F., C.J.G. van Damme, C.J.M. Philippart & C.J.N. Winter 2001. Otoliths of North Sea fish-Fish identification key by means of otoliths and other hard parts, version 1.0. World Biodiversity Database, CD Rom Series, ETI/NIOZ/Alterra, Biodiversity Center of ETI, Univ. of Amsterdam, Amsterdam.

Leopold M.F., C.J.G. van Damme & H.W. van der Veer 1998. Diet of cormorants and the impact of cormorant predation on juvenile flatfish in the Dutch Wadden Sea. J. Sea Res. 40: 93–107.

Leopold M.F., B. Grunsky, O. Hüppop, A.M. Maul & J. van der Meer 2005. How large an area of sea do Helgoland seabirds use for foraging during the breeding season? Helgoländer Meeresunters. 49: 603-604.

Levitus S., J.I. Antonov, T.P. Boyer & C. Stephens 2000. Warming of the World Ocean. Science 287: 2225-2229.

Lewis S., S. Benvenuti, L. Dall-Antonia, R. Griffiths, L. Money, T.N. Sherratt, S. Wanless & K.C. Hamer. 2002. Sex-specific foraging behaviour in a monomorphic seabird. Proc. Royal Soc. Lond., B. 269: 1687-1693.

Lewis S., S. Benvenuti, F. Daunt, S. Wanless, L. Dall'Antonia, P. Luschi, D.A. Elston, K.C. Hamer & T.N. Sherratt 2004. Partitioning of diving effort in foraging trips of northern gannets. Can. J. Zool. 82: 1910-1916.

Lewis S., K. Hamer, L. Money, R. Griffiths, S. Wanless & T. Sherratt 2004. Brood neglect and contingent foraging behavior in a pelagic seabird. Behav. Ecol. Sociobiol. 56: 81-88.

Leyrer J. 2011. Being at the right time at the right place: interpreting the annual life cycle of Afro-Siberian red knots. Ph.D.-thesis Univ. Groningen, Groningen.

Liebers D. & A.J. Helbig 2002. Phylogeography and colonization history of Lesser Black-backed Gulls (*Larus fuscus*) as revealed by mtDNA sequences. J. Evol. Biol. 15: 1021-1033.

Liebers D., P. de Knijff & A.J. Helbig 2004. The herring gull complex is not a ring species. Proc. R. Soc. Lond. B (2004) 271, 893-901.

Lilliendahl K. & J. Solmundsson 1997. An estimate of summer food consumption of six seabird species in Iceland. ICES J. Mar. Sc.54: 624–630.

Lima S.L. & N.C. Rattenborg 2007. A behavioural shutdown can make sleeping safer: a strategic perspective on the function of sleep. Anim. Behav. 74: 189-197.

Lima S.L., N.C. Rattenborg, J.A. Lesku & C.J. Amlaner 2005. Sleeping under the risk of predation. Anim. Behav. 70: 723-736.

Linden M. & A.P. Møller 1989. Cost of reproduction and covariation of life-history traits in birds. Trends Ecol. Evol 4: 367-371.

Lloyd C.S. 1979. Factors affecting breeding of Razorbills *Alca torda* on Skokholm. Ibis 121: 165-176.

Lloyd C.S., Tasker M.L. & Partridge K. 1991. The Status of Seabirds in Britain and Ireland. T. & A.D. Poyser, London.

Lok T., O. Overdijk & T. Piersma 2012. Migration tendency delays distributional response to differential survival prospects along a flyway. Am. Nat. *in press*.

Lok T., O. Overdijk, M. Tinbergen & T. Piersma 2011. The paradox of spoonbill migration: most birds travel to where survival rates are lowest. Anim. Behav. 82: 837-844.

Lopez Sepulcre A. & H. Kokko 2005. Territorial defense, territory size, and population regulation. Am. Nat. 166: 317-325.

Louzao M., J. Becares, B. Rodriguez, K.D. Hyrenbach, A. Ruiz & J.M. Arcos 2009. Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. Mar. Ecol. Progr. Ser. 391, 183-197.

Louzao M., K.D. Hyrenbach, J.M. Arcos, P. Abello, L.G. de Sola & D. Oro 2006. Oceanographic habitat of an endangered Mediterranean procellariiform: Implications for marine protected areas. Ecol. Appl. 16: 1683-1695.

Love R.M. 1970. The chemical biology of fishes. Acad. Press, London.

Luczak C., G. Beaugrand, J.A. Lindley, J-M. Dewarumez, P.J. Dubois & R.R. Kirby 2012. North Sea ecosystem change from swimming crabs to seagulls. Biol. Lett. doi:10.1098/rsbl.2012.0474.

Lüttringhaus C. & Vauk-Hentzelt E. 1983. Ein Beitrag zur Ernährung auf Müllplatzen gesammelter Silber-, Sturm- und Lachmöwen (*Larus argentatus, L. canus, L. ridibundus*) von Emden und Leer. Vogelwelt 104: 95-107.

Lyster I.H.J. 1972. Mole kills Herring Gull. Scottish Birds 7: 207.

Lytle M.H. 2007. The Gentle Subversive: Rachel Carson, Silent Spring, and the Rise of the Environmental Movement (New Narratives in American History). Oxford University Press, New York.

MacArthur R. & Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101: 377-385.

MacArthur R.H. & E.O. Wilson 1967. The theory of Island Biogeography. Monographs in Population Biology 1: 1-203

Maclean I.M.D., M. Frederiksen & M.M. Rehfisch 2007. Potential use of population viability analysis to assess the impact of offshore windfarms on bird populations. COWRIE PVA-03-07, BTO Research Report No. 480, British Trust for Ornithology, The Nunnery, Thetford, Norfolk.

MacRoberts B.R. & M.H. MacRoberts 1972. Social stimulation of reproduction in Herring and Lesser Black-backed Gulls. Ibis 114: 495-506.

Makkink G.F. 1935. Korte mededeelingen. British Lesser Black-backed Gull x Herring Gull in Texel. Ardea 24: 208-209.

Marincola F.M. 2007. In support of descriptive studies; relevance to translational research. J. Trans. Medicine 5:21 doi:10.1186/1479-5876-5-21.

Markones N. &N. Guse 2007. Räumlich-zeitliche Verteilung und Nahrungserwerbsstrategien von Silbermöwen *Larus argentatus* der westlichen Ostsee:Erkenntnisse einer Ringfundanalyse. Vogelwarte 45: 1-13.

Markones N., S. Garthe, V. Dierschke & S. Adler 2008. Small scale temporal variability of seabird distribution patterns in the south-eastern North Sea. In: Wollny-Goerke K, Eskildsen K (eds): Marine mammals and seabirds in front of offshore wind energy, 115-140. MINOS-Marine warm-blooded animals in North and Baltic Seas. Teubner, Wiesbaden.

Marle J.G. van & K.H. Voous 1943. Geografische vormen van *Larus argentatus* en *Larus fuscus* in Nederland. Limosa 16: 146-149.

Marques P.A.M., D. Sowter & P.E. Jorge 2009. Gulls can change their migratory behavior during lifetime. Oikos doi: 10.1111/j.1600-0706.2009.18192.x.

Marsh O.C. 1872a. Notice of a new and remarkable fossil bird. American Journal of Science, Series 3, 4(22): 344.

Marsh O.C. 1872b. Notice of a new reptile from the Cretaceous. American Journal of Science, Series 3, 4(23): 406.

Martin A.R. 1989. The diet of the Atlantic puffin Fratercula arctica and northern gannet Sula bassana chicks at a Shetland colony during a period of changing prey availability. Bird Study 36:170–180.

Martin T.E. 1987. Food as a limit on breeding birds - A life-history perspective. Ann. Rev. Ecol. Syst. 18: 453-487.

Martin T.E. 1995. Avian life-history evolution in relation to nest sites, nest predation, and food. Ecol. Monogr. 65: 101-127.

Massal L-P. 1929. Recherche sur la formation du calcaire dans les glandes de Morren des Lombriciens. Bull. Soc. Zool. France, 54: 46-61.

Mauco L. & Favero M. 2005. The food and feeding biology of common terns wintering in Argentina: influence of environmental conditions. Waterbirds 28: 450–457.

Maurer B.A. 1996. Energetics of avian foraging. In: Carey C. (ed.) Avian Energetics and Nutritional Ecology: 250-279. Chapman & Hall, New York

Mayfield H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73: 255-261.

Mayfield H. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456-466.

Mayr E. 1940. Speciation phenomena in birds. Am. Nat. 74: 249–278.

Mayr E. 1942. Systematics and the origin of species. Columbia University Press, New York.

Mayr G. 2009. Paleogene fossil birds. Springer-Verlag, Berlin.

McChesney G.J. & Tershy B.R. 1998. History and status of introduced mammals and impacts to breeding seabirds on the California Channel and northwestern Baja California islands. Col. Waterb. 21: 335-347.

McCleery R.H. & R.M. Sibly 1986. Feeding specialization and preference in Herring Gulls. J. Anim. Ecol. 55: 245-259.

McLeay L.J., B. Page, S.D. Goldsworthy, D.C. Paton, C. Teixeira, P. Burch & T. Ward 2010. Foraging behaviour and habitat use of a short-ranging seabird, the crested tern. Mar. Ecol. Progr. Ser. 411:271-283.

McNamara J.M. & A.I. Houston 1996. State-dependent life histories. Nature 380: 215-221.

McNamara J.M. & A.I. Houston 2008. Optimal annual routines: behaviour in the context of physiology and ecology. Phil. Trans. R. Soc. B 363: 301-319.

Meer J. van der, T. Piersma & J.J. Beukema 2001. Population dynamics of benthic species on tidal flats: the possible roles of shorebird predation. In: Reise K. (ed.) Ecological comparisons of sedimentary shores. Ecological studies 151: 317-335, Springer-Verlag, Berlin.

Mehner T. 1990. Zur Bestimmung der Beutefischearten aus Fragmenten der Wirbelsäule bei der Nahrungsanalyse (Osteichthyes, Teleostei). Zool. Anz. 225: 210-222.

Meijering M.P.D. 1954. Zur Frage der Variationen in der Ernährung der Silbermöwe, *Larus argentatus* Pont. Ardea 42: 163–175.

Meinertzhagen R.M. 1935. The races of *Larus argentatus* and *Larus fuscus*; with special reference to Herr. B. Stegmann's recent paper on the subject. Ibis (London), p. 762-773.

Meininger P.L. & R. Flamant 1998. Breeding populations of Mediterranean Gull *Larus melanocephalus* in The Netherlands and Belgium. Sula 12: 127-136.

Meininger P.L. 1999. The history of colour-ringing Mediterranean Gulls *Larus melanocephalus*. In: Meininger P.L., Hoogendoorn W., Flamant R. & Raevel P. (eds) Proceedings of the 1st International Mediterranean Gull Meeting, Le Portel, Pas-de-Calais, France, 4-7 September 1998: 61-68. Econom, Bailleul.

Meininger P.L., F.A. Arts & N.D. van Swelm 2000. Kustbroedvogels in het Noordelijk Deltagebied: ontwikkelingen,knelpunten en potenties. Rapport RIKZ/2000.052. Rijksinstituut voor Kust en Zee, Middelburg/Stiching Ornithologisch Station Voorne, Oostvoorne.

Meltofte H., J. Blew, J. Frikke, H.-U. Rösner & C.J. Smit 1994. Numbers and distribution of waterbirds in the Wadden Sea. IWRB Publ. 34, Wader Study Group Bull. 74 (special issue), Comm. Secr. Coop. Prot. Wadden Sea, Wilhelmshaven.

Meltofte H. & J. Faldborg 1987. Forekomsten af måger og terner på Blåvandshuk 1963-1977. Dansk Orn. Foren. Tidsskr. 81: 137-166.

Meynier L., C. Pusineri, J. Spitz, M.B. Santos, G.J. Pierce & V. Ridoux 2008. Intraspecific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: importance of fat fish. Mar. Ecol. Progr. Ser. 354: 277-287.

Michel P. & Thompson P.M. 2003. A simple photogrammetric technique for estimating egg volume from field measurements. Atl. Seabirds 5: 31-34.

Mierauskas P. & Buzun V. 1991. Competetive interactions between the Herring Gull *L. a. cachinnans* and the Great Black-headed Gull *L. ichthyaetus* at Sivash Lake (South Ukraine). Seevögel 12: 34-35.

Migot P. 1992. Demographic changes in French Herring Gull *Larus argentatus* populations: a modelling approach and hypothesis concerning regulation of numbers. In: Spaans A.L. (ed.). Population dynamics of Lari in relation to food resources. Ardea 80: 161-169.

Miller P.J.O., K. Aoki, L.E. Rendell & M. Amano 2008. Stereotypical resting behavior of the sperm whale. Curr. Biol. 18: R21-R23.

Mills J.A. 1989. Red-billed Gull. In: Newton I. (ed.) Lifetime reproduction in birds: 387-404. Acad. Press, London.

Mitani Y., R.D. Andrews, K. Sato, A. Kato, Y. Naito & D.P. Costa 2010. Three-dimensional resting behaviour of northern elephant seals: drifting like a falling leaf. Biol. Lett. 6: 163-166.

Mitchell P.I., S.F. Newton, N. Ratcliffe & T.E. Dunn 2004. Seabird populations in Britain and Ireland. T. & A.D. Poyser, London.

Moerke M. 2008. Kenmerken van locatieontwikkeling ter plaatse van voormalige vuilstortplaatsen in Nederland. BK Groep, Velserbroek, Stern Milieutechniek & Faculteit Construerende Wetenschappen, Univ. Twente.

Møller A.P. 1981. Problems with Danish Herring Gulls *Larus argentatus*. Proc. 2nd Nordic Congr. Orn. 1979: 127-135.

Møller A.P. 2011. Climate change and birds. In: Hoyo J. del, A. Elliott & D. Christie (eds). Handbook of the birds of the world, 16: 13-39.

Møller A.P., E. Flensted-Jensen & W. Mardal 2009. Adjustment of the annual cycle to climatic change in a long-lived migratory bird species. Current Zoology 55: 92-101.

Monaghan P. 1980. Dominance and dispersal between feeding sites in the Herring Gull (*Larus argentatus*). Anim. Behav. 28: 521-527.

Monaghan P. 1982. The breeding ecology of urban nesting gulls. In: Bornkamm R., J.A. Lee & M.R.D. Seaward (eds) Urban ecology: 111-121. Blackwell Sc. Publ., Oxford.

Monaghan P. 1993. Lesser Black-backed Gull *Larus fuscus*. In: Gibbons D.W., J.B. Reid & R.A. Chapman (eds) The New Atlas of Breeding Birds in Britain and Ireland: 1988-1991. T. & A.D. Poyser, London.

Monaghan P. & J.C. Coulson 1977. Status of large gulls nesting on buildings. Bird Study 24: 89-104.

Monaghan P. & R.G. Nager 1997. Why don't birds lay more eggs? Trends in Ecology and Evolution 12: 270–274.

Monaghan P., R.G. Nager & D.C. Houston 1998. The price of eggs: increased investment in egg production reduces the offspring rearing capacity of parents. Proc. Royal Soc. Lond., B. 265: 1731–1735.

Monaghan P., Uttley J.D., Burns M.D., Thaine C. & Blackwood J. 1989. The relationship between food supply, reproductive effort and breeding success in arctic terns Sterna paradisaea. J. Animal Ecology 58: 261–274.

Montevecchi W.A. 1993. Birds as indicators of change in marine prey stocks. Furness R.W. & J.J.D. Greenwood (eds). Birds as Monitors of Environmental Change. Chapman & Hall, London: 217-266.

Montevecchi W.A., V.L. Birt-Friesen & D.K. Cairns 1992. Reproductive energetics and prey harvest by Leach's storm-petrels in the northwest Atlantic. Ecology 73: 823–832.

Montevecchi W.A., A. Hedd, L.M. Tranquilla, D.A. Fifield, C.M. Burke, P.M. Regular, G.K. Davoren, S. Garthe, A.J. Gaston, G.J. Robertson & R.A. Phillips 2012. Tracking seabirds to identify ecologically important and high risk marine areas in the western North Atlantic. Biological Conserv. 156: 62-71

Montevecchi W.A. & R.A. Myers 1996. Dietary changes of seabirds indicate shifts in pelagic food webs. Sarsia 80: 313–322.

Montevecchi W.A. & J. Piatt 1984. Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. Comparative Biochemistry and Physiology A. 78: 15–20.

Montevecchi W.A. & J.M. Porter 1980. Parental investments by seabirds at the breeding area with emphasis on northern gannets, *Morus bassanus*. In: Burger J., B.L. Olla & H.E. Winn (eds) Behavior of marine animals. 4: 323–365. Plenum, London.

Montevecchi W.A., R.E. Ricklefs, I.R. Kirkham & D. Gabaldon 1984. Growth energetics of nestling Northern Gannets (*Sula bassanus*). Auk 101: 334-341.

Moreau R.E. 1923. Herring Gull eating its own chick. Brit. Birds 16: 221-222.

Mörzer Bruijns M.F. 1958. Gulls which are a menace to other species, The Herring problem in The Netherlands. Bull. Int. Comm. Bird Preserv. 7: 103-107.

Mörzer Bruijns M.F. 1972. Nature preservation and chemical pollution: Historical survey (review). TNO-nieuws 12: 528-31.

Mougin J.-L., Joaunin C. & Roux F. 1997. Intermittent breeding of Cory's Shearwater *Calonectris diomedea* of Selvagen Grande, North Atlantic. Ibis 139: 40-44.

Mourer-Chauviré C., D. Berthet & M. Hugueney 2004. The late Oligocene birds of the Créchy quarry (Allier, France), with a description of two new genera (Aves: Pelecaniformes: Phalacrocoracidae, and Anseriformes: Anseranatidae). Senckenberg Lethaea 84: 303-315.

Mudge G.P. & Ferns P.N. 1982. The feeding ecology of five species of gulls (Aves: Larini) in the inner Bristol Channel. J. Zool., Lond. 197: 497-510.

Mulder J. 1996. Vossen op de Waddeneilanden? Zoogdier 7: 23-25.

Mulder J. 2011. De vossen van Vlieland. http://www.mulder-natuurlijk.nl/de_vossen_van_vlieland.htm Accessed 30 May 2012.

Murphy M.E. 1996. Energetics and nutrition of molt. In: Carey C. (ed.) Avian Energetics and Nutritional Ecology: 158-198. Chapman & Hall, New York.

Murton R.K. & E.N. Wright (eds) 1968. The problems of birds as pests. Symposia of the Institute of Biology No. 17, Proc. Royal Geogr. Soc., London, 28-29 Sep 1967, Acad. Press, London.

Muusse M., T. Muusse, R.-J. Buijs, R. Altenburg, C. Gibbins & B.-J. Luijendijk 2011. Phenotypic characteristics and moult commencement in breeding Dutch Herring Gulls *Larus argentatus* & Lesser Black-Backed Gulls *L. fuscus*. Seabird 24: 42-59.

Nager R.G., P. Monaghan & D.C. Houston 2001. The cost of egg production: increased egg production reduces future fitness in gulls. J. Avian Biol. 32: 159-166.

Nagy K.A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57: 111-128.

Naves L.C. & Vooren C.M. 2006. Diet of black skimmers in southern Brazil. Waterbirds 29: 335–344.

Nebel S., T. Piersma, J. van Gils, A. Dekinga & B. Spaans 2000. Length of stopover, fuel storage and a sex-bias in the occurrence of two subspecies of Red Knots (Calidris c. canutus and islandica) in the Dutch Wadden Sea during southward migration. Ardea 88(2): 165-176.

Nehls G. 2001. Food selection by Eiders - why quality matters. Wadden Sea Newsl. 2001-1: 39-41.

Nelissen P.H.M. & Stefels J. 1988. Eutrophication in the North Sea. NIOZ-Report 1988-4, Netherlands Institute for Sea Research, Texel.

Nerheim M. 2004. The New Common Fisheries Policy (CFP): Towards Sustainable Management and a Profitable Fisheries Sector? Eipascope 2004/1: 30-35.

Newton I. 1989. Lifetime reproductive success in birds. London, Acad. Press.

Newton I. 1998. Population limitation in birds. Acad. Press, San Diego.

Niedernostheide N. 1996. Vergleichende nahrungsökologische Untersuchungen an Fluß- und Küstenseeschwalben (Sterna hirundo und S. paradisaea) auf Nigehörn und Scharhörn (Elbmündung). Seevögel 17: 40–45.

Niermann U., E. Bauerfeind, W. Hickel & H.V. Westernhagen 1990. The recovery of benthos following the impact of low oxygen content in the German Bight. Neth. J. Sea Res. 25: 215-226.

Nijland R. & J. Beekman 2002. *Hemigrapsus pencillatus* Haan 1835 waargenomen in Nederland. Zeepaard 60: 169-171.

Nijssen H. & De Groot S.J. 1987. De Vissen van Nederland. Stichting Uitg. KNNV, Utrecht

Nisbet I.C.T. 1973. Courtship-feeding, egg size and breeding success in Common Terns *Sterna hirundo*. Nature 241: 169-178.

Nisbet I.C.T. 1996. Post-fledging survival in Common Terns in relation to brood order, hatching date and parental age. Col. Waterb. 19: 253-255.

Nisbet I.C.T. & W.H. Drury 1972. Post-fledging survival in Herring Gulls in relation to brood-size and date of hatching. Bird-Banding 43: 161-240.

Nisbet I.C.T., J.A. Spendelow& J.S. Hatfield 1995. Variation in growth of Roseate Tern chicks. Condor 97: 335-344.

Nisbet I.C.T., J.M. Winchell & A.E. Heise 1984. Influence of age on the breeding biology of Common Terns. Col. Waterb. 7: 117-126.

Nocera J.J. & Kress S.W. 1996. Nocturnal predation on Common Terns by Great Black-backed Gulls. Col. Waterb. 19: 277-279.

Nogales M., Zonfillo B. & Monaghan P. 1995. Diets of adult and chick Herring Gulls *Larus argentatus argenteus* on Ailsa Craig, south-west Scotland. Seabird 17: 56-63.

Noordhuis R. 1987. Voedseloecologie van zilver- en kleine mantelmeeuw op Terschelling: een geval van het 'competitive exclusion principle'. Intern rapport, Rijksinstituut voor Natuurbeheer, Arnhem.

Noordhuis R. 1989. De relatie tussen zilvermeeuwen op vuilstortplaatsen en de schade op mosselpercelen en in weidevogelgebieden in Zuidwest-Nederland. RIN-rapport 89/4, Rijksinstituut voor Natuurbeheer, Arnhem

Noordhuis R. & A.L. Spaans 1992. Interspecific competition for food between Herring *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus* in the Dutch Wadden Sea area. Ardea 80: 115-132.

Norberg U.M. 1990. Vertebrate flight: mechanics, physiology, morphology, ecology and evolution. Springer-Verlag, Berlin.

Norris D.R. & B.J.M. Stutchbury 2001. Extraterritorial Movements of a Forest Songbird in a Fragmented Landscape. Conserv. Biol. 15:729-736.

Nozeman C. & M. Houttuyn 1797. Nederlandsche Vogelen; volgens hunne huishouding, aert, en Eigenschappen beschreeven. Derde deel. J.C. Sepp en Zoon, Amsterdam.

Nur N. 1984. The consequences of brood size for breeding Blue Tits I. Adult survival, weight change and the cost of reproduction. J. Anim. Ecol. 53: 479-496.

Nus T.M.C. van 2007. Inter- & intraspecific predation within a mixed colony of Herring gulls (*Larus argentatus*) and Lesser Black-backed gulls (*Larus graellsii*). B.Sc.-thesis Van Hall Larenstein University, Velp & Royal Netherlands Institute for Sea Research, Texel.

O'Connell M.J., Coulson J.C., Raven S. & Joyce S. 1997. Non-breeding and nests without eggs in the Lesser Black-backed Gull *Larus fuscus*. Ibis 139: 252-258.

O'Connor R.J. 1978. Brood reduction in birds: Selection for fratricide, infanticide and suicide? Anim. Behav. 26: 79-96.

Oka N., Akinori T., Kohji I. & Yutaka W. 1999. The past and present impact of oil pollution on seabird mortality world-wide. J. Yamashina Inst. Ornithol.: 31: 108-133.

Ollason J.C. & G.M. Dunnet 1978. Age, experience and other factors affecting the breeding success of the Fulmar, *Fulmarus glacialis*, in Orkney. J. Anim. Ecol. 47: 961-976.

Ollason J.C. & G.M. Dunnet 1988. Variation in breeding success in Fulmars. In: Clutton-Brock T.H. (ed.) Reproductive success: Studies of individual variation in contrasting breeding systems: 263-278. The Univ. Chicago Press, Chicago, London.

Olmos V., Aragoneses J., Echevarrias J.L. & Oltra R. 2000. Composición de la dieta e impacto del Cormorán grande (*Phalacrocorax carbo sinensis*) durante la invernada en las Salinas de Santa Pola, Alicante, este de España. Ardeola 47: 227–236.

Olsen K.M. 1992. Danmarks fugle-en oversigt. Dansk Orn. Forening, København.

Olsen K.M. & H. Larsson 2003. Gulls of Europe, Asia and North America. C. Helm, London.

Ommering G. van & J.N.C. van der Salm 1990. Ontwikkelingen in de broedvogelbevolking van Meijendel. Meded. Meijendel Comité, Nieuwe Serie no. 115: 1-86.

Oordt G.J. van 1941. Korte mededeelingen. Een Zilvermeeuw (*Larus argentatus* Pont.) broedend in het polderland. Ardea 30: 269-270.

Oordt G.J. van & J. Verwey 1925. Voorkomen en trek der in Nederland in het wild waargenomen vogelsoorten. Brill, Leiden.

Oort E.D. van 1912. Over in Nederland waargenomen voorwerpen van de Kleine mantelmeeuw. Ardea 1: 61-62.

Orden C. van & C. Ooyevaar 1971. Korte mededelingen. Interessante broedgevallen in Schoorl in 1970. Limosa 44: 61.

Orden C. van, A.J. Dijksen & L.J. Dijksen 1967. De vogels van Texel. Texelse Museumvereniging, Den Burg.

Oro D., L. Jover & X. Ruiz 1996. Influence of trawling activity on breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii*. Mar. Ecol. Progr. Ser. 139: 19-29.

Oro D. & A. Martínez-Abraín 2007. Deconstructing myths on large gulls and their impact on threatened sympatric waterbirds. Animal Conservation 10: 117-126.

Oro D. & X. Ruiz 1997. Exploitation of trawler discards by breeding seabirds in the north-western Mediterranean: differences between the Ebro Delta and the Balearic Islands areas. ICES J Mar Sc 54: 695-707.

Orwell G. 1945. Animal Farm: A Fairy Story. Secker & Warburg, London.

Paine R.T. 1966. Food web complexity and species diversity. Am. Nat. 100(910): 65-75.

Paitz R.T., H.K. Harms, R.M. Bowden & F.J. Janzen 2007. Experience pays: offspring survival increases with female age. Biol. Lett. 3: 44-46.

Paiva V.H., J.A. Ramos, Machado D., Penha-Lopes G., Bouslama M.F., Dias N., Nielsen S. 2006. Importance of marine prey to growth of estuarine tern chicks: evidence from an energetic balance model. Ardea 94: 241-255.

Paiva V.H., J.A. Ramos, J. Martins, A. Almeida & A. Carvalho. 2008. Foraging habitat selection by Little Terns *Sternula albifrons* in an estuarine lagoon system of southern Portugal. Ibis 150: 18-31.

Paludan K. 1951. Contributions to the breeding biology of *Larus argentatus* and *Larus fuscus*. Meddelelser frå Naturfredningsraadet Reservatudvalg 38: 1-142.

Parsons J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). Nature 228: 1221-1222.

Parsons J. 1971. Cannibalism in herring gulls. Brit. Birds 64: 528-537.

Parsons J. 1975. Asynchronous hatching and chick mortality in the Herring Gull *Larus argentatus*. Ibis 117: 517-520.

Parsons J. 1976. Nesting density and breeding success in the Herring Gull *Larus argentatus*. Ibis 118: 537-546.

Parsons J., G. Chabrzyk & N. Duncan 1976. Effects of hatching date on post-fledging survival in Herring Gulls. J. Anim. Ecol. 45: 667-675.

Parsons J. & N. Duncan 1978. Recoveries and dispersal of Herring Gulls from the Isle of May. J. Anim. Ecol. 47: 993-1005.

Pascoe S., Wilcox C. & Donlan C.J. 2011. Biodiversity Offsets: A Cost-Effective Interim Solution to Seabird Bycatch in Fisheries? PLoS ONE 6(10): e25762. doi:10.1371/journal.pone.0025762.

Pastoors M.A., A.D. Rijnsdorp & F.A. van Beek 2000. Effects of a partially closed area in the North Sea (“plaice box'') on stock development of plaice. ICES J. Mar. Sc. 57: 1014-1022.

Patton S.R. 1988. Abundance of gulls at Tampa Bay landfills. Wilson Bulletin 100: 431-442.

Payne R.B. 1972. Mechanism and control of molt. In: Farmer D.S. & J.R. King (eds) Avian biology 11: 103-155. Acad. Press, New York.

Paynter R.A. 1949. Clutch size and egg and chick survival of Kent Island herring gulls. Ecology 30: 146-166.

Pearson T.H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37: 521-552.

Pelt Lechner A.A. van 1900. Een en ander over de vogelwereld van Rottum en Schouwen. De Lev. Nat. 6: 239-241.

Pelt Lechner A.A. van 1908. De Kleine Zeemeeuw (*Larus canus* L.) broedvogel op Rottum. Jaarboekje der NOV 5: 034.

Penas E. 2007. The fishery conservation policy of the European Union after 2002: towards long-term sustainability. ICES J. Mar. Sc. 64: 588-595.

Penniman T.M., Coulter M.C., Spear L.B. & Boekelheide R.J. 1990. Western Gull. In: Ainley D.G. & Boekelheide R.J. (eds) Seabirds of the Farallon Islands: 218-244. Stanford Univ. Press, California.

Pennycuick C.J. 1989. Bird flight performance. A practical calculation manual. Oxford University Press, Oxford.

Pennycuick C.J. 2008. Modelling the flying bird. Academic Pres, Amsterdam.

Perdeck A.C. & Speek B.J. 1963. Hoge leeftijden bij meeuwen. Limosa 36: 117-118.

Perrins C.M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

Perrins C.M. 1979. British Tits. Collins New Naturalist Series, Collins, London.

Perrins C.M. 1991. Constraints on the demographic parameters of bird populations. In: Perrins C.M., Lebreton J.-D. & Hirons G.J.M (eds) Bird Population Studies: Relevance to Conservation and Management: 190-206. Oxford University Press, Oxford.

Perrins C.M., J-D. Lebreton & G.J.M Hirons (eds) 1991. Bird Population Studies: Relevance to Conservation and Management. Oxford University Press, Oxford.

Perrins C.M., M.P. Harris & C.K. Britton1973. Survival of Manx Shearwaters Puffinus puffinus. Ibis 115: 535-548.

Perrins C.M. & S.B. Smith 2000. The breeding Larus gulls on Skomer Island National Nature Reserve, Pembrokeshire. Atl. Seabirds 2: 195-210.

Philippart C.J.M. & E. Epping 2009. Climate change and Ecology. Thematic Report No. 4.2, In: Marencic H. & J. de Vlas (eds) Quality Status Report 2009. Wadden Sea Ecosystem No. 25. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.

Phillips R.A., J.R.D. Silk, B. Phalan, P. Catry & J.P. Croxall. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? Proc. Royal Soc. Lond.,B. 271: 1283-1291.

Phillips R.A., J.C. Xavier & J.P. Croxall JP. 2003. Effects of satellite transmitters on albatrosses and petrels. The Auk 120:1082-1090.

Pianka E.R. 1970. On “r” and “K” selection. Am Nat 104: 592-597.

Pianka E.R. 1981. Competition and niche theory. In May R.M. (ed.) Theoretical ecology: 167-196. Sinauer ass., Sunderland.

Pianka E.R. 1994. Evolutionary ecology. Fifth edition, HarperCollins College Publ., New York.

Pierotti R. 1991. Infanticide versus adoption: an intergenerational conflict. Am. Nat 138: 1140-1158.

Pierotti R. & Annett C. 1987. Reproductive consequences of dietary specialization and switching in an ecological generalist. In: Kamil A.C., Krebs J. & Pulliam H.R. (eds). Foraging behaviour: 417-442. Plenum Publ. Corp.

Pierotti R.J. & Good T.P. 1994. Herring Gull *Larus argentatus*. In: Poole A. & Gill F. (eds) The Birds of North America No. 124. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington D.C.

Piersma T. 1994. Close to the edge: energetic bottlenecks and the evolution of migratory pathways in Knots. Ph.D.-thesis Univ. of Groningen, Groningen.

Piersma T. 1997. Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? Forum, Oikos 80: 623-631.

Piersma T. 2007. Why do molluscivorous shorebirds have such a hard time in the Wadden Sea by now? In: Reineking B. & P. Sⁿdbeck (eds) Seriously declining trends in migratory waterbirds: causes-concerns-consequences. Proc. Int. Workshop 31 August 2006, Wilhelmshaven, Germany. Wadden Sea Ecosystem No. 23, Common Wadden Sea Secretariat, Wilhelmshaven, Germany.

Piersma T. & J. van Gils 2011. The flexible phenotype. Oxford Univ. Press, Oxford.

Piersma T., Gessaman J.A., Dekinga A. & Visser G.H. 2004. Gizzard and other lean mass components increase, yet Basal Metabolic Rates decrease when red knots *Calidris canutus* are shifted from soft to hard-shelled food. J. Avian Biol. 35: 99-104.

Piersma T., Goeij P. de & Tulp I. 1993. An evaluation of intertidal feeding habitats from a shorebird perspective: towards relevant comparisons between temperate and tropical mudflats. Neth. J. Sea Res. 31: 503-512.

Piersma T., Koolhaas A., Dekinga A., Beukema J.J., Dekker R. & Essink K. 2001. Long-term indirect effects of cockle-dredging on intertidal bivalve stocks: is mechanical shellfishing in the Wadden Sea sustainable? J. Appl. Ecol. 38: 976-990.

Piersma T., Verkuil Y. & Tulp I. 1994. Resources for long-distance migration of knots Calidris canutus islandica and C. c. canutus: how broad is the temporal exploitation window of benthic prey in the western and eastern Wadden Sea? Oikos 71: 393-407.

Pingree R.D. & Griffiths D.K. 1978. Tidal fronts on the shelf seas around the British Isles. J. Geoph. Res. 83 C9: 4615-4622.

Pingree R.D. & Griffiths D.K. 1980. Currents driven by a steady uniform wind on the shelf seas around the British Isles. Oceanologica acta 3: 227-236.

Pinheiro J.C. & D.M. Bates. 2000. Mixed-effects models in S and S-PLUS. Springer, New York.

Pinheiro J.C., D.M. Bates, S. DebRoy & D. Sarkar. R Development Core Team 2012. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-103.

Platteeuw M., N.F. van der Ham & J.E. den Ouden 1994. Zeetrektellingen in Nederland in de jaren tachtig. Sula 8: 1-203.

Pol M. van de & J. Wright 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. Anim. Behav. 77: 753-758.

Pons J.-M. 1992. Effects of changes in the availability of human refuse on breeding parameters in a Herring Gull *Larus argentatus* population in Brittany, France. In: Spaans A.L. (ed.). Population dynamics of Lari in relation to food resources. Ardea 80: 143-150.

Pons J.M. 1994. Feeding strategies of male and female herring gulls during the breeding season under various feeding conditions. Ethology Ecology & Evolution 6: 1-12.

Pons J-M. & Migot P. 1995. Life-history strategy of the herring gull: changes in survival and fecundity in a population subjected to various feeding conditions. J. Anim. Ecol. 64: 592-599.

Poos J-J. 2010. Effort allocation of the Dutch beam trawl fleet. Ph.D.-thesis, Rijksuniversiteit Groningen, Groningen.

Poot M. 2008. De eerste Kleine Mantelmeeuwen *Larus fuscus* broedend op een dak in Utrecht in 2007 en 2008. Sula 21: 36-37.

Porter J.M. 1988. Prerequisites for recruitment of Kittiwakes *Rissa tridactyla*. Ibis 130: 204-215.

Porter J.M. & J.C. Coulson 1997. Long-term changes in recruitment to the breeding group, and the quality of recruits at a Kittiwake *Rissa tridactyla* colony. J. Anim. Ecol. 56: 675-690.

Postma H. 1985. Eutrophication of Dutch coastal waters. Neth. J. Zool. 35: 348-359.

Price J.L. 2001. The landfill directive and the challenge ahead: demands and pressures on the UK householder. Resources, Conservation and Recycling 32: 333-348.

Price T.D. & P.T. Boag 1987. Selection in natural bird populations. In: Cooke, F. and Buckley, P.A. (eds.) Avian genetics: 257-287. New York: Acad. Press.

Prince P.A., J.P. Croxall, P.N. Trathan & A.G. Wood 1998. The pelagic distribution of South Georgia albatrosses and their relationships with fisheries: 137-167. In: Robertson G. & R. Gales (eds) Albatross biology and conservation. Surrey Beatty & Sons, Chipping Norton.

Prüter J. 1984. Methoden und vorläufige Ergebnisse der Großmöwenberingung auf Helgoland. Seevögel 5 (Sonderband): 61-65.

Pütz K., A.J. Helbig, K.T. Pedersen, C. Rahbek, P. Saurola & R. Juvaste 2008. From fledging to breeding: long-term satellite tracking of the migratory behaviour of a Lesser Black-backed Gull *Larus fuscus intermedius*. Ring. & Migr.24: 7-10.

Pugesek B.H. 1993. Chick growth in the California Gull: relationships with hatching asynchrony and parental age. Col. Waterb. 16: 183-189.

Pyle P., N. Nur, W.J. Sydeman & S.D. Emslie 1997. Cost of reproduction and the evolution of deferred breeding in the Western Gull. Behav. Ecol. 8: 140-147.

Quinn G. & M. Keough 2002. Experimental design and data analysis for biologists. Cambridge Univ. Press, Cambridge.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Raevel P. & C. Duponcheel 1993. First results of colour-ringing non-breeding Mediterranean Gulls *Larus melanocephalus* in NW France. Sula 7: 145-148.

Ramenofsky M. & J.C. Wingfield 2007. Regulation of migration. Bioscience 57: 135–143.

Ramos R., F. Ramirez, C. Sanpera, L. Jover & X. Ruiz 2009. Diet of Yellow-legged Gull (*Larus michahellis*) chicks along the Spanish Western Mediterranean coast: the relevance of refuse dumps. J. Ornithol. 150: 265-272.

Ratcliffe N. 2004. Cause of seabird population change. In: Mitchell P.I., S.F. Newton, N. Ratcliffe & T.E. Dunn (eds) Seabird populations in Britain and Ireland: 407-437. T. & A.D. Poyser, London.

Ratnieks F.L.W. 1996. Evolution of unstable and stable biparental care. Behav. Ecol. 7:490–493.

Rattenborg N.C., D. Martinez-Gonzalez & J.A. Lesku 2009. Avian sleep homeostasis: Convergent evolution of complex brains, cognition and sleep functions in mammals and birds. Neurosci. Biobehav. R. 33: 253-270.

Rattenborg N.C., B. Voirin, A.L. Vyssotski, R.W. Kays, K. Spoelstra, F. Kuemmeth, W. Heidrich & M. Wikelski 2008. Sleeping outside the box: electroencephalographic measures of sleep in sloths inhabiting a rainforest. Biol. Lett. 4: 402-405.

Rattiste K. & V. Lilleleht 1986. Some aspects of the demography of the Common Gull Larus canus in Estonia. Vår Fägelv. Suppl. II: 179-186.

Raymont J.E.G. 1963. Plankton and productivity in the oceans. Pergamon Press, Oxford.

Reid J.B., Becker P.H. & Furness R.W. 1999. Evidence for decadal scale variations in seabird population ecology and links with the North Atlantic Oscillation. In: Furness R.W. & Tasker M.L. (eds) Diets of seabirds and consequences of changes in food supply: 47-50. ICES Coop. Res. Report No. 232, International Council for the Exploration of the Sea, Copenhagen.

Reid J.B. & Camphuysen C.J. 1998. The European Seabirds at Sea database. In: Spina S. & A. Grattarola (eds). Proceedings of the 1st meeting of the European Orn. Union. Biol. Cons. Fauna 102: 291.

Reid P.C., Holliday N.P. & Smyth T.J. 2001. Pulses in the eastern margin current and warmer water off the north west European shelf linked to North Sea ecosystem changes. Mar. Ecol. Progr. Ser. 215: 283-287.

Reijnders R. 1997. Opmerkelijk herstel van een olieslachtoffer: Grote Mantelmeeuw *Larus marinus*. Sula 11: 203-204.

Remis M.J. 1999. Tree structure and sex differences in arboreality among western lowland gorillas (Gorilla gorilla gorilla) at Bai Hokou, Central African Republic. Primates 40: 383-396.

Ricklefs R.E. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978-983.

Rickleffs R.E. 1974. Energetics of reproduction in birds. In: R.A. Paynter (ed.) Avian energetics. Publ. Nuttall Ornithol. Club No. 15: 152-297, Cambridge, Massachusetts.

Rijkswaterstaat. Stroomatlas Zuidelijk Noordzee model. http://www.meetadviesdienst.nl/nl/dossiers/stroomatlas-noordzee.htm (last accessed: 9 August 2010)

Rijnsdorp, A. D., Buys, A. M., Storbeck, F., and Visser, E. G. 1998. Micro-scale distribution of beam trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the sea bed and the impact on benthic organisms. ICES J. Mar. Sc. 55: 403–419.

Rijnsdorp A.D., J.J. Poos & F.J. Quirijns 2011. Spatial dimension and exploitation dynamics of local fishing grounds by fishers targeting several flatfish species. Can. J. Fish. Aquat. Sci. 68: 1064-1076.

Rijnsdorp A.D., J.J. Poos, F.J. Quirijns, R. HilleRisLambers, J.W. de Wilde & W.M. den Heijer 2008. The arms race between fishers. J. Sea Res. 60: 126-138.

Rijsdijk K. 1968a. Eerste bekende broedgeval van *Larus fuscus intermedius* in Nederland. Limosa 41: 72.

Rijsdijk K. 1968b. Tweede bekende broedgeval van *Larus fuscus intermedius* in Nederland. Limosa 41: 153.

Ristow D., P. Berthold, D. Hashmi & U. Querner 2000. Satellite tracking of Cory's Shearwater migration. Condor 102:696-699.

Ritz M.S., S. Hahn & H.U. Peter 2005. Factors affecting chick growth in the South Polar Skua (*Catharacta maccormicki*): food supply, weather and hatching date. Polar Biology 29: 53-60.

Robinson T.P. & G. Metternicht 2006. Testing the performance of spatial interpolation techniques for mapping soil properties. Comp. Electr. in Agricult. 50: 97-108

Robinson W.D., M.S. Bowlin, I. Bisson, J. Shamoun-Baranes, K. Thorup, R.H. Diehl, T.H. Kunz, S. Mabey& D.W. Winkler 2010. Integrating concepts and technologies to advance the study of bird migration. Front. Ecol. Environ. 8: 354-361.

Rock P. 1999. The efficacy of the colour-ringing system used for Herring Gulls (*Larus argentatus*) and Lesser Black-backed Gulls (*Larus fuscus*). Ring. & Migr.19: 306-310.

Rock P. 2002. Lesser Black-backed Gull *Larus fuscus*. In: Wernham C., M. Toms, J. Marchant, J. Clark, G. Siriwardena & S. Baillie (eds). The migration atlas: movements of the birds of Britain and Ireland: 365-368. T. & A.D. Poyser, London.

Rock P. 2003. Birds of a feather flock together. Environmental Health Journal May 2003, pages 132-135.

Rock P. 2005. Urban gulls: problems and solutions. Brit. Birds 98: 338-355.

Roff D.A. 2002. Life history evolution. Sinauer Associates Inc., Sunderland, Massachusetts, USA.

Rogers D.I., P.F. Battley, T. Piersma, J.A. van Gils & K.G. Rogers 2006. High-tide habitat choice: insights from modelling roost selection by shorebirds around a tropical bay. Anim. Behav. 72: 563-575.

Romano M.D., Piatt J.F. & Roby D.D. 2006. Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. Waterbirds 29: 407-524.

Roobeek K. 2010. Meeuweninventarisatie in het stedelijke gebied van Alkmaar in 2009. Tussen Duin en Dijk 9(1): 14-17.

Rooth J. & Jonkers D.A. 1972. The status of some piscivorous birds in The Netherlands. TNO-Nieuws (1972): 551-555.

Ropert-Coudert Y., D. Grémillet, A. Kato, P.G. Ryan, Y. Naito & Y. Le Maho 2004. A fine-scale time budget of Cape gannets provides insights into the foraging strategies of coastal seabirds. Anim. Behav. 67: 985-992.

Ropert-Coudert Y. & R.P. Wilson 2005. Trends and perspectives in animal-attached remote sensing. Front. Ecol. Environ. 3: 437-444.

Rose L.M. 1994. Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). Int. J. Primatol. 15: 95-114.

Rose P.M. & Scott D.A. 1994. Waterfowl population estimates. IWRB Publ. 29, Int. Waterf. Wetl. Res. Bureau, Slimbridge.

Royle N. 2000. Overproduction in the Lesser Black-backed Gull - can marginal chicks overcome the initial handicap of hatching asynchrony? J. Avian Biol. 31: 335-344.

Royle N.J. & K.C. Hamer 1998. Hatching asynchrony and sibling size hierarchies in gulls: effects on parental investment decisions, brood reduction and reproductive success. J. Avian Biol. 29: 266-272.

Royle N.J., I.R. Hartley & G.A. Parker. 2004. Parental investment and family dynamics: interactions between theory and empirical tests. Pop. Ecol. 46: 231-241.

Ruitenbeek W. & F. Cottaar 2010a. Kleine Mantelmeeuw. In: Scharringa C.J.G., W. Ruitenbeek & P.J. Zomerdijk (eds) Atlas van de Noord-Hollandse broedvogels, 2005-2009: 180-181. Samenwerkende Vogelwerkgroepen Noord-Holland (SVN), Landschap Noord-Holland, Castricum/Heiloo, Assendelft.

Ruitenbeek W. & F. Cottaar 2010b. Zilvermeeuw. In: Scharringa C.J.G., W. Ruitenbeek & P.J. Zomerdijk (eds) Atlas van de Noord-Hollandse broedvogels, 2005-2009: 182-183. Samenwerkende Vogelwerkgroepen Noord-Holland (SVN), Landschap Noord-Holland, Castricum/Heiloo, Assendelft.

Russell A.F., Wanless S. & Harris M.P. 1995. Factors affecting the production of pellets by shags *Phalacrocorax aristotelis*. Seabird 17: 44–4.

Rutten M. 1929. De mantelmeeuwen. De Lev. Nat. 34: 265-271.

Rutz C. & G.C. Hays 2009. New frontiers in biologging science. Biol. Lett. 5: 289-292.

Sæther B-E., S. Engen, A.P. Moller, H. Weimerskirch, M.E. Visser, W. Fiedler, E. Matthysen, M.M. Lambrechts, A. Badyaev, P.H. Becker, J.E. Brommer, D. Bukaciński, M. Bukacińska, H. Christensen, J. Dickinson, C. du Feu, F.R. Gehlbach, D. Heg, H. Hötker, J. Merilä, J. Tottrup Nielsen, W. Rendell, R.J. Robertson, D.L. Thomson, J. Török & P. van Hecke 2004. Life-history variation predicts the effects of demographic stochasticity on avian population dynamics. Am. Nat. 164: 793-802.

Safina C., J. Burger, M. Gochfeld & R.H. Wagner 1988 Evidence for prey limitation of common and roseate tern reproduction. Condor 90: 852–859.

Sahrhage D. 1958. Untersuchungen über die Vernichtung untermaßiger Schellfische durch die deutsche Heringsschleppnetzfischerei in der Nordsee. Ber. Dtsch. Wiss. Komm. Meeresforsch. 15: 105-131.

Sahrhage D. 1959. Untersuchungen über den Anteil untermaßiger Wittlinge in den Fängen der deutschen Heringsschleppnetzfischerei in der Nordsee. Ber. Dtsch. Wiss. Komm. Meeresforsch. 15: 335-356.

Salsbury C.M. & K.B. Armitage 1994. Home-Range Size and Exploratory Excursions of Adult, Male Yellow-Bellied Marmots. J. Mammal. 75:648-656.

Sandvik H., K.E. Erikstad, R.T. Barrett & N.G. Yoccoz 2005. The effect of climate on adult survival in five species of North Atl. Seabirds. J. Anim. Ecol. 74: 817-831.

Sanger G.A. & Ainley D.G. 1988. Review of the distribution and feeding ecology of seabirds in the oceanic subarctic North Pacific Ocean. Bulletin of Ocean Research Institute, University of Tokyo, 26: 161–186.

Sangster G., A.B. van den Berg, A.J. van Loon & C.S. Roselaar 2003. Dutch avifaunal list: taxonomic changes in 1999-2003. Ardea 91: 279-285.

Sangster G., C.J. Hazevoet, A.B. van den Berg, C.S. Roselaar & R. Sluys 1999. Dutch avifaunal list: species concepts, taxonomic instability, and taxonomic changes in 1977-1998. Ardea 87: 139-165.

Saris F. 2007. Een eeuw vogels beschermen. KNNV Uitgeverij, Zeist.

Schaefer K.E. 1970. The Environmental Crisis. Commentary on the 1970 European Conservation Year. Experientia 26: 672-676.

Schaub B.E.M. & W.W.C. Gieskes 1991. Trends in eutrophication of Dutch coastal waters: the relation between Rhine river discharge and chlorophyll-a concentrations. In: M Elliott & J.-P. Ducrotoy (eds) Estuaries and coasts spatial and temporal intercomparisons. Estuarine and coastal Sciences Association Symposium 19: 85-90. Olsen & Olsen, Fredensborg.

Scheel D. & C. Packer. 1991. Group hunting behaviour of lions: a search for cooperation. Anim. Behav. 41: 697-709.

Schierbeek 1926. Het Meyendel onderzoek. Natura 1926: 145-152.

Schlegel H. 1852. Naamlijst der tot heden in de Nederlanden in den wilden staat waargenomen vogels. In: Herklots J.A. (ed.). Bouwstoffen voor eene fauna van Nederland, 1: 58-103. Leiden.

Schlegel H. 1854-58. De vogels van Nederland. P.W.M. Trap, Leiden.

Schlegel H. 1860a. Natuurlijke Historie van Nederland. De Dieren van Nederland, Gewervelde dieren, 1. Vogels. A.C. Kruseman, Haarlem.

Schlegel H. 1860b. De Vogels van Nederland, 1-6. D. Noothoven van Goor, Leiden.

Schlegel H. 1878. De vogels van Nederland, 2. Tweede druk, Amsterdam.

Schmaljohann H., F. Liechti & B. Bruderer 2006. First records of Lesser Black-backed Gulls (*Larus fuscus*) crossing the Sahara non-stop. In: Schmaljohann H. (2006) The relative importance and biological significance of non-stop and intermittent flight strategies in bird migrants crossing the Sahara. Ph.D.-thesis University Basel, Sempach.

Schmaljohann H., F. Liechti & B. Bruderer 2008. First records of lesser black-backed gulls *Larus fuscus* crossing the Sahara non-stop. J. Avian Biol. 39(2): 233-237.

Schoener T.W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2: 369-404.

Schofield G., V.J. Hobson, M.K.S. Lilley, K.A. Katselidis, C.M. Bishop, P. Brown & G.C. Hays 2010. Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management. Biol. Conserv. 143:722-730.

Schou M. 2011. A new Common Fisheries Policy-incentives for eliminating discards. El Anzuelo 23: 4.

Schreiber E.A. & J. Burger 2002. Biology of Marine Birds. CRC Press, Boca Raton.

Schüz E. 1933. Von den Wanderungen der Eismeer- und Ostsee-Silbermöwen (*Larus a. argentatus*). Orn. Fenn. 10(2): 17-19.

Schüz E. 1934. Vom Zug Schwarzrückigen Heringsmöwe (*Larus f. fuscus*). Vogelzug 5: 123-134.

Schulz H. 1947. Die Welt der Seevögel. Anton Lettenbauer, Hamburg.

Schwemmer P. & S. Garthe 2005. At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull *Larus fuscus*, and its association with different prey. Mar. Ecol. Progr. Ser. 285: 245-258.

Schwemmer P., S. Garthe & R. Mundry 2008. Area utilization of gulls in a coastal farmland landscape: habitat mosaic supports niche segregation of opportunistic species. Landscape Ecol. 23: 355-367.

Schwilch R., T. Piersma, N.M.A. Holmgren & L. Jenni 2002. Do migratory birds need a nap after a long non-stop flight? Ardea 90: 149-154.

Scott B.E., J. Sharples, O.N. Ross, J. Wang, G.J. Pierce & C.J. Camphuysen 2010. Sub-surface hotspots in shallow seas: fine scale limited locations of marine top-predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. Mar. Ecol. Progr. Ser. 408: 207-226.

Seymour N.R. 1972. Success of three gull species feeding on swarming ants in Antigonish County, Nova Scotia. Canadian Field-Nat. 86: 391-392.

Seys J., J. van Waeyenberge, K. DeVos & P. Meire 1998. The recent expansion of breeding gulls along the Belgian North Sea coast. Sula 12: 207-215.

Shamoun-Baranes J., R. Bom, E.E. van Loon, B.J. Ens, K. Oosterbeek & W. Bouten 2012a. From sensor data to animal behaviour: an Oystercatcher example. PLoS One 7(5): e37997. doi:10.1371/journal.pone.0037997.

Shamoun-Baranes J., W. Bouten, C.J. Camphuysen & E. Baaij 2010. Riding the tide: intriguing observations of gulls resting at sea. Ibis 153: 411-415.

Shamoun-Baranes J. & E.E. van Loon 2006. Energetic influence on gull flight strategy selection. J. Exp. Biol. 209: 3489-3498.

Shamoun-Baranes J., E.E. van Loon, R.S. Purves, B. Speckmann, D. Weiskopf & C.J. Camphuysen 2012b. Analysis and visualization of animal movement. Biol. Lett. 8: 6-9.

Shedden C.B., P. Monaghan, K. Ensor & N. B. Metcalfe 1985. The influence of colour-rings on recovery rates of Herring and Lesser Black-backed Gulls. Ring. & Migr.6: 52-54.

Shepard E.L.C., R.P. Wilson, F. Quintana, A. Gõmez Laich, N. Liebsch, D.A. Albareda, L.G. Halsey, A. Gleiss, D.T. Morgan, A.E. Myers, C. Newman, D.W. Macdonald 2008. Identification of animal movement patterns using tri-axial accelerometry. Endangered Spec. Res. 10: 47-60.

Shimada K. & M.V. Fernandes 2006. Ichthyornis sp. (Aves: Ichthyornithiformes) from the lower Turonian (Upper Cretaceous) of western Kansas. Trans. Kansas Acad. Sc. 109: 21-26.

Shugart G.W., M.A. Fitch & G.A. Fox. 1987. Female floaters and non-breeding seondary females in Herring Gulls. Condor 89: 902-906.

Sibly R.M. & R.H. McCleery 1983a. The distribution between feeding sites of Herring Gulls breeding at Walney Island, U.K. J. Anim. Ecol. 52: 51-68.

Sibly R.M. & R.H. McCleery 1983b. Increase in Weight of Herring Gulls While Feeding. J. Anim. Ecol. 52: 35-50.

Siegel J.M. 2008. Do all animals sleep? Trends Neurosci. 31: 208-213.

Siegel-Causey D. 1990. Gastroliths assist digestion in shags. Notornis 37: 70-72.

Sillett T.S., R.T. Holmes & T.W. Sherry 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288(5473): 2040-2042.

Silva M.P., Favero M., Copello S. & Bastida R. 2001. Does access to high-quality prey increase the breeding success of Kelp Gulls *Larus dominicanus* in the Antarctic Peninsula? Mar. Ornithol. 29: 85-88.

Simmons K.E.L. 1972. Some adaptive features of seabird plumage types. Brit. Birds 65: 465-479, 510-521.

Singer F.(ed.) 1968. Global effects of environmental pollution. Sympos. Am. Assn. Adv. Sci., Dallas, Texas, Dec. 1968.

Siriwardena G.M., S.R. Baillie & J.D. Wilson 1999. Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. Ibis 141: 621-636.

Skalski J.R., K.E. Ryding & J.J. Millspaugh 2005. Wildlife demography: analysis of sex, age, and count data. Elsevier, Amsterdam.

Skov H. & Durinck J. 2001. Seabird attraction to fishing vessels is a local process. Mar. Ecol. Progr. Series 214: 289-298.

Skov H., J. Durinck, M.F. Leopold & M.L. Tasker 1995. Important bird areas for seabirds in the North Sea, including the Channel and the Kattegat. Birdlife International, Cambridge.

Skov H., J. Durinck, M.F. Leopold & M.L. Tasker 2007. A quantitative method for evaluating the importance of marine areas for conservation of birds. Biol. Conserv. 136: 362-371.

Skov H., E. Humphreys, S. Garthe, K. Geitner, D. Gremillet, K.C. Hamer, J. Hennicke, H. Parner & S. Wanless 2008. Application of habitat suitability modelling to tracking data of marine animals as a means of analyzing their feeding habitats. Ecol. Modelling 212: 504-512.

Sluiters J.E. 1939. Van slapen en slaapvlucht bij verschillende vogelsoorten, II. Levende Nat 44: 112-117.

Smit C.J. & Wolff W.J. 1981. Birds of the Wadden Sea. Report no. 6, Final report of the section Birds of the Wadden Sea Working Group, Balkema, Rotterdam.

Snouckaert van Schauburg R.B. 1901. Overzicht der voornaamste waarnemingen op ornithologisch gebied van 1 Mei 1900 tot en met 30 April 1901. De Lev. Nat. 6: 160-165.

Snouckaert van Schauburg R.C.E.G.J. 1908. Avifauna Neerlandica. Meijer & Schaafsma, Leeuwarden.

Snow D. & C. Perrins (eds) 1998. The Birds of the Western Palearctic, concise edition, 1. Oxford University Press, Oxford.

Soanes L., Ratcliffe N., Booker H., Atkinson P.W. & Michel C.C. 2010. Is an increase in gull numbers responsible for limiting Atlantic Puffin *Fratercula arctica* numbers on Burhou, Channel Islands? Seabird 23: 91-103.

Sokal R.R. & F. Rohlf 1981. Biometry. Freeman, New York.

SOVON 1987. Atlas van de Nederlandse Vogels. SOVON, Arnhem.

SOVON 2012. Satellietzenders bij meeuwen en ganzen. http://s1.sovon.nl/onderzoek/esa/esa_meeuwen_en_ganzennw.asp *Last accessed* 14 Oct 2012.

Spaans A.L. 1971. On the feeding ecology of the Herring Gull *Larus argentatus* Pont. in the northern part of the Netherlands. Ardea 59: 73-188.

Spaans A.L. 1979a. Kleine Mantelmeeuw *Larus fuscus. In:* Teixeira R.M. (ed.). Atlas van de Nederlandse broedvogels: 170-171. Vereniging tot behoud van Natuurmonumenten, ‘s Graveland.

Spaans A.L. 1979b. Zilvermeeuw *Larus argentatus*. *In:* Teixeira R.M. (ed.). Atlas van de Nederlandse broedvogels: 172-173. Vereniging tot behoud van Natuurmonumenten, 's Graveland.

Spaans A.L. 1980. Gull demography in The Netherlands. Gull Study Group Bulletin 2: 4-9.

Spaans A.L. 1984. Actualiteiten. Zilver- en Kleine Mantelmeeuwen met kleurringen. Limosa 57: 73.

Spaans A.L. 1987a. Overzicht broedvogelstand Zilvermeeuw, Kleine Mantelmeeuw en Stormmeeuw in 1985. Intern rapport 87/2, Rijksinstituut voor Natuurbeheer, Arnhem.

Spaans A.L. 1987b. Stabilisatie van broedvogelaantallen bij de Zilvermeeuw. Limosa 60:99-100.

Spaans A.L. (ed.) 1992. Population dynamics of Lari in relation to food resources. IBN-DLO Special Publication, Ardea 80: 1-200.

Spaans A.L. 1998a. Booming gulls in the Low Countries during the 20th century. Sula 12: 121-126.

Spaans A.L. 1998b. Breeding Lesser Black-backed Gulls *Larus graellsii* in The Netherlands during the 20th century. Sula 12: 173-182.

Spaans A.L. 1998c. The Herring Gull *Larus argentatus* as a breeding bird in The Netherlands during the 20th century. Sula 12: 183-196.

Spaans A.L. 2002a. Kleine Mantelmeeuw. In: Hustings F. & Vergeer J-W. (eds). Atlas van de Nederlandse broedvogels, 1998-2000: 238-239. Nederlandse Fauna 5, Sovon Vogelonderzoek Nederland, Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & European Invertebrate Survey, Leiden.

Spaans A.L. 2002b. Zilvermeeuw. In: Hustings F. & Vergeer J-W. (eds). Atlas van de Nederlandse broedvogels, 1998-2000: 242-243. Nederlandse Fauna 5, Sovon Vogelonderzoek Nederland, Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij & European Invertebrate Survey, Leiden.

Spaans A.L. 2007. Meeuwenbestrijding in historisch perspectief. In: Saris F. (ed.) Een eeuw vogels beschermen: 154-163. KNNV Uitgeverij, Zeist.

Spaans A.L., M. Bukacińska, O. Bukaciński & N.D. van Swelm 1994. The relationship between food supply, reproductive parameters and population dynamics in Dutch Lesser Black-backed Gulls *Larus fuscus*: a pilot study. IBN Research Report 94/9: 1–65.

Spaans A.L. & R. Noordhuis 1989. Voedselconcurrentie tussen Kleine Mantelmeeuwen en Zilvermeeuwen. In: Spaans A.L. (ed.), Wetlands en Watervogels, p. 35-47. Pudoc, Wageningen.

Spaans M.J. & A.L. Spaans 1975. Enkele gegevens over de broedbiologie van de Zilvermeeuw *Larus argentatus* op Terschelling. Limosa 48: 1-39.

Spaans A.L., N. van Swelm & R. Vogel 1996. Wel en wee van de Zilvermeeuw door de jaren heen. De Lev. Nat. 97: 79-85.

Spaans A.L. & A.A.N. de Wit 1985. Verspreiding van Zilvermeeuwen:vogels op de voet gevolgd. Vogeljaar 33: 200-207.

Spaans A.L. & A.A.N. de Wit 1986. Plaatstrouw van Kleine Mantelmeeuwen *Larus fuscus* aan broedkolonie. Limosa 59: 38-40.

Spaans A.L., A.A.N. de Wit & M.A. van Vlaardingen 1987. Effects of increased population size in Herring Gulls on breeding success and other parameters. In: Hand J.L., Southern W.E. & Vermeer K. (eds) Ecology and Behavior of Gulls. Studies of Avian Biology 10: 57-65.

Spaans A.L., A.A.N. de Wit, M.A. van Vlaardingen & R. Noordhuis 1987a. Hoe kunnen we de Zilvermeeuw in ons land het beste beheren? De Lev. Nat. 88: 103-109.

Spear L. & N. Nur 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in Western Gulls. J. Anim. Ecol. 63: 283-298.

Spear L., N. Nur & D.G. Ainley 1992. Estimating absolute densities of flying seabirds using analysis of relative movement. Auk 109: 385-389.

Spear L.B., D.G. Ainley, B.D. Hardesty, S.N.G. Howell & S.W. Webb 2004. Reducing biases affecting at-sea surveys of seabirds: use of multiple observer teams. Mar. Ornith.32: 147-157.

Speek B.J. & Speek G. 1984. Thieme's vogeltrekatlas. Thieme, Zutphen.

Spendelow J.A. 1991. Postfledging survival and recruitment of known-origin Roseate Terns (Sterna dougallii) at Falkner Island, Connecticut. Col. Waterb. 14: 108-115.

Staav R. 2008. European Longevity Records. EURING Website http://www.vogeltrekstation.nl/resultaten/longevity-list-roland-staav.

Staav R. & Fransson T. 2006. EURING list of longevity records for European birds. Generated on: 23 Aug 2006, http://www.euring.org/data_and_codes/longevity-voous.htm.

Stanley P.I., T. Brough, M.R. Fletcher, N. Horton & J.B.A. Rochard 1981. The origins of herring gulls wintering in south-east England. Bird Study 28: 123-132.

Stauss C., S. Bearhop, T.W. Bodey, S. Garthe, C. Gunn, W.J. Grecian, R. Inger, M.E. Knight, J. Newton, S.C. Patrick, R.A. Phillips, J.J. Waggitt & S.C. Votier 2012. Sex-specific foraging behaviour in Northern Gannets *Morus bassanus*: incidence and implications. Mar. Ecol. progr. Ser. 457: 151-162.

Stearns S.C. 1992. The evolution of life histories. Oxford Univ. Press, Oxford.

Stegenga H. 2005. Veranderingen in de zeewierflora van Zuidwest-Nederland: verschil in vestiging en verspreidingspatroon tuusen inheemse en Europese soorten en exoten. Gorteria 31: 57-66.

Stegmann B. 1934. Uber die formen der grossen Möwen (subgenus Larus) und ihre gegenseitigen Beziehungen. J. Orn. 82: 340-380.

Stephens D.W. & J.R. Krebs 1986. Foraging theory. Princeton Univ. Press, Princeton.

Stephenson D.B. 1997. Impacts of the NAO. In: The North Atlantic Oscillation thematic web site http://www.met.rdg.ac.uk/cag/NAO/main.htm.

Stevick P.T., L.S. Incze, S.D. Kraus, S. Rosen, N. Wolff & C. Baukus 2008. Trophic relationships and oceanography on and around a small offshore bank. Mar. Ecol. Progr. Ser. 363: 15-28.

Stienen E.W.M. 2006. Living with gulls: trading off food and predation in the Sandwich Tern *Sterna sandvicensis*. Alterra Scientific Contributions 15, Ph-D. Theses, Univ. Groningen, Groningen.

Stienen E.W.M. & Brenninkmeijer A. 1992. Ecologisch profiel van de Visdief (*Sterna hirundo*). RIN-rapport 92/18: 1-128.

Stienen E.W.M., J. van Waeyenberge & H.J.P. Vercruijsse 2002. Zilvermeeuw *Larus argentatus* en Kleine Mantelmeeuw *Larus fuscus* als broedvogels in Vlaanderen. Natuur.oriolus 68(3): 104-110.

Stone C.J., A. Webb, C. Barton, N. Ratcliffe, T.C. Reed, M.L. Tasker, C.J. Camphuysen & M.W. Pienkowski 1995. An atlas of seabird distribution in north-west European waters. Joint Nature Conservation Committee, Peterborough.

Stone C.J., A. Webb & I.C. Carter 1992. Lesser Black-backed Gull distribution at trawlers and food availability in the Celtic Sea, 1991. JNCC Report no. 106, Joint Nature Conservation Committee, Aberdeen.

Stonehouse B. 1966. Egg volume from linear dimensions. Emu 65: 227-228.

Stork V. (ed.) 2007. Ornithologisch Jaarverslag Texel 2006. Vogelwerkgroep Texel, Den Burg, 56pp.

Stowe T.J. 1982. Recent population trends in cliff-breeding seabirds in Britain & Ireland. Ibis 124: 502–510.

Strann K.-B. & Vader W. 1992. The nominate Lesser Black-backed Gull *Larus fuscus fuscus*, a gull with a tern-like feeding biology, and its recent decrease in northern Norway. In: Spaans A.L. (ed.). Population dynamics of Lari in relation to food resources. Ardea 80: 133-142.

Stresemann E. & V. Stresemann 1966. Die Mauser der Vögel. J. Orn. 107(suppl): 1-445.

Strijbos J.P. 1941. De meeuwen in 1941. De Lev. Nat. 46: 159-160.

Strijbos J.P. 1942a. Een Zilvermeeuwennest op het dak. Vogels die van aanpassen weten. De courant Het nieuws van den dag 28 July 1942.

Strijbos J.P. 1942b. Merkwaardige nestplaats van de Zilvermeeuw. De Lev. Nat. 47: 127.

Strijbos J.P. 1977. Texel. Uniek vogelparadijs in de Waddenzee. Het Spectrum, Utrecht.

Stull R.B. 1988. An introduction to boundary layer meteorology. Kluwer, Dordrecht.

Suddaby D. & N. Ratcliffe 1997 The effects of fluctuating food availability on breeding Arctic terns (*Sterna paradisaea*). Auk 114: 524–530.

Südbeck P. & Hälterlein B. 1997. Brutvogelbestände an der deutschen Nordseeküste im Jahre 1995-Neunte Erfassung durch die Arbeitsgemeinschaft “Seevogelschutz”. Seevögel 18: 11–19.

Südbeck P. & Hälterlein B. 1999. Brutvogelbestände an der deutschen Nordseeküste im Jahre 1997-Elfte Erfassung durch die Arbeitsgemeinschaft “Seevogelschutz”. Seevögel 20: 9–16.

Südbeck P., Hälterlein B., Knief W. & Köppen U. 1998. Bestandsentwicklung von Fluß- Sterna hirundo und Küstenseeschwalbe S. paradisaea an den deutschen Küsten. Vogelwelt 119: 147–163.

Sundell J. 2002. Vole population dynamics: experiments on predation. Ph.D.-thesis, University of Helsinki, Finland.

Suter W. & Morel P. 1996. Pellet analysis in the assessment of great cormorant *Phalacrocorax carbo* diet: reducing biases from otolith wear when reconstructing fish length. Col. Waterb. 19: 280–284.

Sutherland W.J. 1996. Ecological census handbook. Cambridge Univ. Press, Cambridge.

Svensson L. & P.J. Grant 2009. Collins Bird Guide. 2nd revised and enlarged edition, HarperCollins Publishers, London.

Swaddle J.P. & M.S. Witter 1997. The effects of molt on the flight performance, body mass, and behavior of European Starlings (Sturnus vulgaris): an experimental approach. Can. J. Zool. 75: 1135–1146.

Swelm N.D. van 1998. Status of the Yellow-legged Gull *Larus michahellis* as a breeding bird in The Netherlands. Sula 12: 197-200.

Swelm N.D. van 2011. Rotterdam verjaagt grootste meeuwenkolonie van Europa. [EBNNL] Tue Mar 15, 2011 12:04 pm, http://groups.yahoo.com/group/VogelnetZH/ message/2159 Accessed 28 Oct 2012.

Swennen C. 1971. Het voedsel van de Groenpootruiter *Tringa nebularia* tijdens het verblijf in het Nederlandse Waddengebied. Limosa 44: 71–83.

Swennen C. 1972. Clorinated hydrocarbons attacked the Eider population in The Netherlands. TNO-nieuws 12: 556-560.

Swennen C. 1989. Gull predation upon Eider *Somateria mollissima* ducklings: destruction or elimination of the unfit? Ardea 77: 21-45.

Swennen C. 1990. Oystercatchers feeding on Giant Bloody Cockles on the Banc d'Arguin. Ardea 78: 21-45.

Swennen C. & Duiven P. 1977. Size of food objects of three fish-eating seabird species: *Uria aalge, Alca torda*, and *Fratercula arctica* (Aves, Alcidae). Neth. J. Sea Res. 11: 92–98.

Swennen C. & Duiven P. 1991. Diving speed and food-size selection in common guillemots *Uria aalge*. Neth. J. Sea Res. 27: 191–196.

Sydeman W.J. & J.O. Eddy 1995. Repeatability in laying date and its relationship to individual quality for Common Murres. Condor 97: 1048-1052.

Székely T., T. Lislevand & J. Figuerola. 2007. Sexual size dimorphism in birds. In: Fairbairn D.J., W.U. Blanckenhorn & T. Székely (eds). Sex, size & gender roles - evolutionary studies of sexual size dimorphism: 27-37. Oxford University Press, Oxford.

Tasker M.L. & P.H. Becker 1992. Influences of human activities on seabird populations in the North Sea. Neth. J. Aquat. Ecol. 26: 59-73.

Tasker M.L., C.J. Camphuysen, J. Cooper, S. Garthe, W.A. Montevecchi & S.J.M. Blaber 2000. The impacts of fishing on marine birds. ICES J. Mar. Sc. 57: 531-547.

Tasker M.L., Camphuysen C.J. & Fossum P. 1999. Variation in prey taken by seabirds. In: Furness R.W. & Tasker M.L. (eds) Diets of seabirds and consequences of changes in food supply: 18-28. ICES Coop. Res. Report No. 232, International Council for the Exploration of the Sea, Copenhagen.

Tasker M.L., C.J. Camphuysen, S. Garthe & T. Anker-Nilssen 2003. The alteration of the composition of seabird communities by fisheries: indirect effects on breeding *Larus* gulls and terns in the southeastern North Sea. *In:* Tasker M.L. & R.W. Furness (eds) 2003. Seabirds as monitors of the marine environment: 37-51. ICES Coop. Res. Report No. 258, International Council for the Exploration of the Sea, Copenhagen.

Tasker M.L. & R.W. Furness 1996. Estimation of food consumption by seabirds in the North Sea. In: Hunt G.L. & R.W. Furness (eds) Seabird/fish interactions, with particular reference to seabirds in the North Sea: 6–42. ICES Cooperative Research report No. 216.

Tasker M.L., P.H. Jones, B.P. Blake, T.J. Dixon & A.J. Wallis 1986. Seabirds associated with oil production platforms in the North Sea. Ringing & Migr. 7:7-14.

Tasker M.L., P.H. Jones, T.J. Dixon & B.F. Blake 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. Auk 101: 567-577.

Tasker M.L., A. Webb, A.J. Hall, M.W. Pienkowski & D.R. Langslow 1987. Seabirds in the North Sea. Nature Conserv. Council, Peterborough.

Tatum J.B. 1974. The volume of an egg. The Auk 91: 132-138.

Tatum J.B. 1975. Egg volume. Auk 92: 576-580.

Teixeira R.M. (ed.) 1979. Atlas van de Nederlandse Broedvogels. Natuurmonumenten, 's-Graveland.

Terluin A.B. 1994. Klein drama: Kleine Mantelmeeuw eet kleine Meerkoet. Het Vogeljaar 42: 226.

Tesch P. 1907. De nestbouw van onze vogels. De Lev. Nat. 12: 155-157.

Thaxter C.B., F. Daunt, K.C. Hamer, Y. Watanuki, M.P. Harris, D. Grémillet, G. Peters & S. Wanless. 2009. Sex-specific food provisioning in a monomorphic seabird, the common guillemot Uria aalge: nest defence, foraging efficiency or parental effort? J. Avian Biol. 40: 75-84.

Thearle R.J.P. 1968. Urban bird problems. In: Murton R.K. & E.N. Wright (eds) The problems of birds as pests: 181-197Symposia of the Institute of Biology No. 17, Proc. Royal Geogr. Soc., London, 28-29 Sep 1967, Acad. Press, London.

Thiele W. 1994. Baumkurrenfischerei an der Küste und in tiefen Gewässern. In: Lozán J.L., E. Rachor, K. Reise, H. von Westernhagen & W. Lenz (eds) Warnsignale aus dem Wattenmeer: 244-247. Blackwell Wissenschafts-Verlag, Berlin.

Thijsse J.P. 1909. Vogelbescherming op de Waddeneilanden. De Lev. Nat. 14: 121-124, 141-146.

Thijsse J.P. 1912a. Rottum. De Lev. Nat. 16: 213-220.

Thijsse J.P. 1912b. Het schuivend eiland. De Lev. Nat. 17: 193-198.

Thijsse J.P. 1936. De Zilvermeeuwen. De Lev. Nat. 40: 259-261.

Thomas C.S. 1983. The relationships between breeding experience, egg volume and reproductive success of the Kittiwake *Rissa tridactyla*. Ibis 125: 567-574.

Thomas C.S. & J.C. Coulson 1988. Reproductive success of Kittiwake Gulls, *Rissa tridactyla*. In: Clutton-Brock T.H. (ed.) Reproductive success: Studies of individual variation in contrasting breeding systems: 251-262. The Univ. Chicago Press, Chicago, London.

Thomas G.J. 1972. A review of gull damage and management methods at Nature Reserves. Biol. Conserv. 4: 117-127.

Thompson R.C., S.H. Swan, C.J. Moore & F.S. von Saal 2009. Our plastic age. Phil. Trans. R. Soc. B 364: 1973-1976.

Thomson A.L. 1924. The migrations of the Herring Gull and Lesser Black-backed Gull: results of the marking method. Brit. Birds 18: 34-44.

Thrane M., F. Ziegler & U. Sonesson 2009. Eco-labelling of wild-caught seafood products. J. Cleaner Prod. 17: 416-423.

Tiews K. 1978. Non-commercial fish species in the German Bight: records of by-catches of the Brown Shrimp fishery. Rapp. Proc.-verb. Réun. Cons. Int. Explor. Mer 172: 259-265.

Tinbergen N. 1929a. In en om de schuilhut. De Lev. Nat. 34: 273-284.

Tinbergen N. 1929b. In en om de schuilhut II. In de schuilhut. De Lev. Nat. 33: 279-284.

Tinbergen N. 1929c. A breeding-pair of Herring-Gull (*Larus a. argentatus* Pont.) x Lesser Black-backed Gull (*Larus fuscus subspec.*). Ardea 18: 1.

Tinbergen N. 1932a. Vergelijkende waarnemingen aan enkele Meeuwen en Sterns. Ardea 21: 1-13.

Tinbergen N. 1932b. Waarnemingen aan Zilvermeeuwen in de broedkolonie te Wassenaar. De Lev. Nat. 37: 213-219, 248-252.

Tinbergen N. 1936a. Waarnemingen en proeven over de sociologie van een Zilvermeeuwenkolonie. De Lev. Nat. 40: 262-280.

Tinbergen N. 1936b. Waarnemingen en proeven over de sociologie van een Zilvermeeuwenkolonie II. De Lev. Nat. 40: 304-308.

Tinbergen N. 1936c. Zur Soziologie der Silbermöwe, *Larus a. argentatus*. Beitr. Fortpfl. Biol. Vög. 12: 89-96.

Tinbergen N. 1937. Meeuwen en konijnen. De Lev. Nat. 41: 318.

Tinbergen N. 1939. Vogelbeschermers beschermen zich tegen hun beschermelingen. De Lev. Nat. 43: 102-108.

Tinbergen N. 1948. Dierkundeles in het Meeuwenduin. De Lev. Nat. 51: 49-56.

Tinbergen N. 1949. De functie van de rode vlek op de snavel van de Zilvermeeuw. Bijdr. Dierk. 28: 453-265.

Tinbergen N. 1952a. On the significance of territory in the Herring Gull. Ibis 94: 158-159.

Tinbergen N. 1952b. De trek van Zilvermeeuwen langs de Nederlandse kust. Ardea 40: 77-80.

Tinbergen N. 1953. The Herring Gull's world. Collins, London.

Tinbergen N. 1955. Zilvermeeuwennieuws. De Lev. Nat. 58: 21-30.

Tinbergen N. 1956. On the function of territory in gulls. Ibis 98: 401-411.

Tinbergen N. 1960a. The evolution of behavior in gulls. Scientific American 1960 (Dec): 1-11.

Tinbergen N. 1960b. Vergelijkende studies over het gedrag van meeuwen. In: Tinbergen N. 1976. Het dier in zijn wereld, 1. Veldonderzoek. Aula paperback, Het Spectrum, Utrecht/Antwerpen, pp. 20-85.

Tinbergen N. 1970. Ziende blind. De Lev. Nat. 73: 97-105.

Tinbergen N. 1971. Clever gulls and dumb ethologists. Vogelwarte 26: 232-238.

Tinbergen N. 1978. Onbehaaglijke co-existentie. De Lev. Nat. 81(1): 11-21.

Tinbergen N. & A.C. Perdeck 1950. On the stimulus situation releasing the begging response in the newly hatched Herring Gull chick (*Larus a. argentatus* Pontopp.). Behaviour 3: 1-38.

Tollitt D.J., Greenstreet S.P.R. & Thompson P.M. 1997. Prey selection by harbour seals Phoca vitulina in relation to variations in prey abundance. Can. J. Zool. 75: 1508–1518.

Townsend C.W. 1921. *Larus argentatus* Pontoppidan, Herring Gull. In: Bent A.C. (ed.) Life Histories of North American Gulls and Terns. U.S. Natl. Mus. Bull. 113. Reprint Dover Publications, 1963, New York: 102-120.

Trauttmansdorff J. & Wassermann G. 1995. Number of pellets produced by immature cormorants *Phalacrocorax carbo sinensis*. Ardea 83: 133–134.

Troost K. 2007. Hoe gevaarlijk is de Japanse Oester? Spirula 359: 158-162.

Trout R.C. & A.M. Tittensor 2008. Can predators regulate wild Rabbit *Oryctolagus cuniculus* population density in England and Wales? Mammal Review 19: 153-173.

Urrutia L.P. & H. Drummond 1990. Brood reduction and parental infanticide in Heermann's gull. Auk 107: 772-774.

Vader W., Barrett R.T., Erikstad K.E. & Strann K.B. 1990. Differential responses of common and thick-billed murres Uria spp. to a crash in the capelin stock in the southern Barents Sea. In: Sealy S.G. Auks at sea. Studies in Avian Biology 14: 175–180.

Valiela I. 2006. Global coastal change. Blackwell Publ., Malden MA.

Vauk G. & J. Prüter 1987. Möwen. Niederelbe Verlag, Jordsandbuch Nr 6. Herausgegeben vom Verein Jordsand zum Schutz der Seevögel e.V. Otterndorf.

Vauk G., Prüter J. & Hartwig E. 1989. Long-term population dynamics of breeding bird species in the German Wadden Sea area. Helgol. Meeresunters. 43: 357-365.

Veen J., O. Overdijk & H. Koning 2003. Zilvermeeuwen en andere kolonievogels op Schiermonnikoog: onderzoek in het kader van beheer 1997-2002. VEDA Consultancy, Wiesel.

Veen J., Peeters J., Leopold M.F., van Damme C.J.G. & Veen T. 2003. Les oiseaux piscivores comme indicateurs de la qualité de l’environnement marin: suivides effets de la pêche littorale en Afrique du Nord-Ouest. Alterra Report 666: 1- 190.

Veer H.W. van der, W. van Raaphorst & M.J.N. Bergman 1989. Eutrophication of the Dutch Wadden Sea: External nutrient loadings of the Marsdiep and Vliestroom basin. Helgoland Marine Research 43: 501-515.

Vegelin J.C.G. 1989. Zilvermeeuwen *Larus argentatus* en Kleine Mantelmeeuwen *L. fuscus* als broedvogel op daken in IJmuiden. Limosa 62: 154-155.

Velando A. & C. Alonso-Alvarez 2001. Effect of testosterone on the behaviour of Yellow-legged gulls (*Larus cachinnans*) in a high-density colony during the courtship period. Ethology Ecology and Evolution 13: 341-349.

Velarde E. 1992. Predation of Heermann's Gull (*Larus heermanni*) chicks by yellow-footed Gulls (*Larus livens*) in dense and scattered nesting sites. Col. Waterb. 15: 8-13.

Veld M. in 't & J.J. Krol 2005a. Advies Nazorg Voormalige Stortplaatsen (NAVOS). Unpublished report Tauw BV, Deventer.

Veld M. in 't & J.J. Krol 2005b. Achtergronden bij het Advies Nazorg Voormalige Stortplaatsen (NAVOS). Unpublished report Tauw BV, Deventer.

Verbeek N.A.M. 1977a. Comparative feeding ecology of Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus*. Ardea 65: 25-42.

Verbeek N.A.M. 1977b. Interactions between Herring Gulls and Lesser Black-backed Gulls feeding on refuse. Auk 94: 726-735.

Verbeek N.A.M. 1977c. Timing of primary moult in Herring Gulls and Lesser Black-backed Gulls. J. Orn. 117: 87-92.

Verbeek N.A.M. 1979. Some aspects of the breeding biology and behavior of the Great Black-backed Gull. Wilson Bull. 91: 575-582.

Verboven N., Monaghan P., Evans D.M., Schwabl H., Evans N., Whitelaw C. & Nager R.G. 2003. Maternal condition, yolk androgens and offspring performance: a supplemental feeding experiment in the lesser black-backed gull (*Larus fuscus*). Proc. Royal. Soc., Lond. B. 270: 2223-2232.

Vercruijsse H.J.P. 1999. Zilvermeeuwen uit de duinen van Schouwen: verspreiding, sterfte en broedbiologie. Eigen uitgave H.J.P.Vercruijsse, ISBN 90-9013167-1, Tilburg, 272pp.

Vercruijsse H.J.P. & Spaans A.L. 1994. Eerste broedgeval van de Grote Mantelmeeuw *Larus marinus* in Nederland. Limosa 67: 111-113.

Vermeer K. 1963. The breeding ecology of the glaucous-winged gull (*Larus glaucescens*) on Mandarte Island, B.C. British Columbia Provincial Museum Occ. Papers 113.

Vermeer K. 1992. Population growth of the Glaucous-winged Gull *Larus glaucescens* in the Strait of Georgia, British Columbia, Canada. In: Spaans A.L. (ed.) Population dynamics of Lari in relation to food resources. Ardea 80: 181-185.

Verwey J. 1915. Lijster en Vischdiefje. De Lev. Nat. 20: 220.

Vijverberg J. 1917. Uit het gezinsleven van meeuwen en sterns. De Lev. Nat. 21: 361-369.

Vijverberg J. 1935. *Larus melanocephalus* Temm. broedvogel in Nederland (Schouwen). Ardea 24: 260-261.

Viksne J. & M. Janaus1993. Post-fledging survival of the Black-headed Gull (Larus ridibundus) depending on hatching parameters. Ring 15: 387-389.

Villuendas E. & Sarzo B. 2003. Growth of Audouin's gull chicks: the role of prehatch and posthatch factors. Sci. Mar. 67(S2): 113-116.

Vliet G.F. van der 1918. Veldmuis en klauwier. De Lev. Nat. 23: 221.

Vogeltrekstation Heteren 2008. Longevity record for Herring Gull 5054793. Ring report Herring Gull 5054793 issued by Vogeltrekstation Heteren.

Voous K.H. 1946. Sur un cas d'hybridation naturelle entre *Larus fuscus* L. et *Larus argentatus* Pont. dans les Pays-Bas. Alauda 14: 21-32.

Voous K.H. 1960. Atlas of European Birds. Nelson and sons Ltd, London.

Voslamber B. 1991. Meeuwen in het IJsselmeergebied: voedseloecologie van zeven op het meer voorkomende soorten. Intern rapport 1991-9 liw, Directie Flevoland, Rijkswaterstaat, Lelystad.

Vossen W.J. van (ed.) 2001. Natural attenuation en voormalige stortplaatsen NA-Toetsingsmethodiek en set van kenmerkende NA-Parameters. Integraal hoofdrapport, eindrapportage DUIV-kerngroep NAVOS, IPO-publicatienummer 141, Royal Haskoning, 's-Hertogenbosch.

Votier S.C., Bearhop S., Crane J.E., Arcos J.M. & Furness R.W. 2007. Seabird predation by great skuas Stercorarius skua –intra-specific competition for food? J. Avian Biol. 38: 234–246.

Votier S.C., Bearhop S., MacCormick A., Ratcliffe N.R. & Furness R.W. 2003. Assessing the diet of great skuas, Catharacta skua, using five different techniques. Polar Biology 26: 20–26.

Votier S.C., Bearhop S., Ratcliffe N. & Furness R.W. 2001. Pellets as indicators of diet in great skuas Catharacta skua. Bird Study 48: 373–376.

Votier S.C., Crane J.E., Bearhop S., de Leon A., McSorley C., Minguez E., Mitchell I. 2007. Nocturnal foraging by great skuas Stercorarius skua: implications for conservation of stormpetrel populations. J. Orn. 147: 405–413.

Votier S.C., Furness R.W., Bearhop S., Crane J.E., Caldow R.W.G., Catry P., Ensor K. 2004. Changes in fisheries discard rates and seabird communities. Nature 427: 727–730.

Waeyenberge J. van, E.W.M. Stienen & H.J.P. Vercruijsse 2002. Kleurringproject van Zilvermeeuw *Larus argentatus* en Kleine Mantelmeeuw *Larus fuscus* aan de Belgische kust: overzicht van algemene resultaten. Natuur.oriolus 68(3): 146-157.

Wakefield E.D., R.A. Phillips & J. Matthiopoulos 2009. Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. Mar. Ecol. Progr. Ser. 391: 165-182.

Walsh P.M., Halley D.J., Harris M.P., Nevo A. del, Sim I.M.W. & Tasker M.L. 1995. Seabird monitoring handbook for Britain and Ireland. Joint Nature Conservation Committee / RSPB / ITE / Seabird Group, Peterborough.

Walsh P.M., Sears J. & Heubeck M. 1991. Seabird numbers and breeding success in 1990. NCC Chief Sc. Dir. Report No. 1235, Nature Conservancy Council, Aberdeen.

Walter U. 1997. Quantitative analysis of discards from brown shrimp trawlers in the coastal area of the East Frisian islands. Arch. Fisch. Mar. Res. 45: 61-76.

Walter U. & Becker P. 1994. The significance of discards by the Brown Shrimp fisheries for seabirds in the Wadden Sea-preliminary results. Ophelia suppl. 6: 253-262.

Walter U. & P.H. Becker 1997. Occurrence and consumption of seabirds scavenging on shrimp trawler discards in the Wadden Sea. ICES J. Mar. Sc. 54: 684-694.

Walters J. 1978. The primary moult in four gull species near Amsterdam. Ardea 66: 32-47.

Wanders R.M. 1982. Kleine Mantelmeeuwen en Zilvermeeuwen: concurrentie zonder beperkingen. Meijendel Mededelingen 23: 39-42.

Wanless S., Corfield T. & Buckland S.T. 1992. Diving behaviour of shags Phalacrocorax aristotelis in relation to habitat and prey. In: Tasker M.L. (ed.) European seabirds. Proceedings of the Seabird Group conference, Glasgow 27–29 March 1992, p. 26. Seabird Group, Sandy.

Wanless S. & M.P. Harris 1984. Effect of date on counts of nests of herring and lesser black-backed gulls. Orn. Scand. 15: 89-94.

Wanless S., M.P. Harris, J. Calladine & P. Rothery 1996. Modelling responses of Herring Gull and Lesser Black-backed Gull populations to reduction of reproductive output: implications for control measures. J. Appl. Ecol. 33: 1420-1432.

Wanless S., M.P. Harris & J.A. Morris 1985. Radio-monitoring as a method for estimating time budgets of guillemots *Uria aalge*. Bird Study 32: 170–175.

Wanless S., M.P. Harris, P. Redman & J. Speakman 2005. Low fish quality as a probable cause of a major seabird breeding failure in the North Sea. Mar. Ecol. Progr. Ser. 294: 1-8.

Wanless S., Harris M.P. & Russell A.F. 1993. Factors influencing food load sizes brought in by shags Phalocrocorax aristotelis during chick rearing. Ibis 135: 19–24.

Watanuki Y. 1988. Intraspecific predation and chick survival: comparison among colonies of Slaty-Backed Gulls. Oikos 53: 194-202.

Watanuki Y. 1992. Individual diet difference, parental care and reproductive success in Slaty-Backed Gulls. Condor 94: 159-171.

Watson P.S. 1981. Seabird observations from commercial trawlers in the Irish Sea. Brit.Birds 74: 82-90.

Watt J., Pierce G.J. & Boyle P.R. 1997. Guide to the identification of North Sea fish using premaxillae and vertebrae. ICES Coop. Res. Rep. No. 220, International Council for the Exploration of the Sea, Copenhagen.

Wearmouth V.J. & D.W. Sims 2008. Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. Adv. Mar. Biol. 54: 107-170

Weidensaul S., F. Gill, S. Conyne, B. Etter, T. Johnson & C. Rutt 2008. North American winter distribution and movement in Lesser Black-backed Gulls (*Larus fuscus*). http://www.dvoc.org/OrnithStudy/Presentations/Presentations2008/LesserBlackBacked Gull.pdf Accessed 11 April 2009.

Weidinger K. 1998. Incubation and brooding rhythm of the cape petrel *Daption capense* at Nelson Island, south Shetland Islands, Antarctica. Ibis 140: 163-170.

Weigelt C. 1891. Die Abfälle der Seefischerei. Experi-mentelle Untersuchungen über deren Natur, Menge, Verarbeitung und Verwerthung. Mitt. Sekt. Küsten- u. Hochseefisch. 1891, Sonderbeilage 2.

Weimerskirch H. 1992. Reproductive effort in long-lived birds: Age-specific patterns of condition, reproduction and survival in the Wandering Albatross. Oikos 64: 464-473.

Weimerskirch H. 1995. Regulation of foraging trips and incubation routine in male and female Wandering Albatrosses. Oecologia 102:.37-43.

Weimerskirch H. 1998. How can a pelagic seabird provision ist chick when relying on a distant food source? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. J. Anim. Ecol. 67: 99-109.

Weimerskirch H. 2002. Seabird demography and its relationship with the marine environment. In: Schreiber E.A. & J. Burger (eds) Biology of Marine Birds: 115-135. CRC Press, Boca Raton.

Weimerskirch H. & Robertson G. 1994. Satellite tracking of light-mantled sooty albatross. Polar Biology 14: 123–126.

Weimerskirch H. & T. Guionnet 2002. Comparative activity pattern during foraging of four albatross species. Ibis 144: 40-50.

Weimerskirch H., A. Ancel, M. Caloin, A. Zahariev, J. Spagiari, M. Kersten & O. Chastel 2003. Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. J. Anim. Ecol. 72:500-508.

Weimerskirch H., F. Bonadonna, F. Bailleul, G. Mabille, G. Dell'Omo & H-P. Lipp 2002. GPS tracking of foraging albatrosses. Science 295: 1259.

Weimerskirch H., O. Chastel & L. Ackermann 1995. Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the Thin-billed prion *Pachyptila belcheri*. Behav. Ecol. and Sociobiol. 36: 11-16.

Weimerskirch H., O. Chastel, L. Ackerman, T. Chaurand, F. Cuenot-Chaillet, X. Hindermeyer & J. Judas 1994. Alternate long and short foraging trips in pelagic seabird parents. Anim. Behav. 47:472-476.

Weimerskirch H., Y. Cherel, F. Cuenot-Chaille & V. Ridoux 1997. Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. Ecology 78:2051-2063.

Weimerskirch H., L. Zimmermann & P.A. Prince 2001. Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. Behav. Ecol. 12: 22-30.

Wendeln H. & P.H. Becker 1996. Body mass change in breeding Common Terns (Sterna hirundo). Bird Study 43: 85-95.

Wendeln H. & P.H. Becker 1998. Populationsbiologische Untersuchungen an einer Kolonie der Flußseeschwalbe (*Sterna hirundo*). Vogelwelt 119: 209-213.

Wendeln H. & P.H. Becker 2002. Effects of parental quality and effort on the reproduction of Common Terns *Sterna hirundo*. J. Anim. Ecol. 68: 205-214.

Wendeln H. 1997a. Body mass of female Common Terns (Sterna hirundo) during courtship: relationships to male quality, egg mass, diet, laying date and age. Col. Waterb. 20: 235-243.

Wendeln H. 1997b. Allocation of parental duties and foraging behaviour influence body condition of adult Common Terns, Sterna hirundo. Bird Behaviour 12: 47-54.

Wendeln H., P.H. Becker & M. Wagener 1997. Beziehungen zwischen Körpermasse und Körpergröße bei Paarpartnern der Flußseeschwalbe *Sterna hirundo*. Vogelwarte 39: 141-148.

Werkgroep Afvalregistratie 2007. Afvalverwerking in Nederland: gegevens 2006. Rapport SenterNovem: 3UA0708, Vereniging Afvalbedrijven:VA07001IR.R, SenterNovem, Utrecht.

Wernham C., M. Toms, J. Marchant, J. Clark, G. Siriwardena & S. Baillie 2002. The migration atlas: movements of the birds of Britain and Ireland. British Trust for Ornithology, T. & A.D. Poyser, London.

Weyhenmeyer G.A., Blenckner T. & Pettersson K. 1999. Changes of the plankton spring outburst related to the North Atlantic Oscillation. Limnol. and Oceanogr. 44: 1788-1792.

Whelan C.D., Monaghan P., Girdwood R.W.A., & C.R. Fricker 1988. The significance of wild birds (*Larus* sp.) in the epidemiology of campylobacter infections in humans. Epidem. Inf. 101. 259-267.

White G.C. & K.P. Burnham 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, S1: S120-S139.

White G.C. & K.P. Burnham 2010. Program MARK: Survival estimation from populations of marked animals. http://warnercnr.colostate.edu/~gwhite/mark/mark.htm; accessed 22 Jul 2011.

Whitfield J. 2008. Does `Junk Food' Threaten Marine Predators in Northern Seas? Science 322: 1786-1787.

Wiens J.A. 1989. The Ecology of Bird Communities, 2. Processes and variations. Cambridge Univ. Press, Cambridge.

Wietfeld J. 1977. Untersuchungen an Speiballen der Silbermöwe (*Larus argentatus*) im Naturschutzgebiet Grober Knechtsand (Elbe-Weser-Mündung). Vogelwelt 98: 221–229.

Wiggins D.A. & R.D. Morris 1987. Parental care in the Common Tern Sterna hirundo. Ibis 129: 533-540.

Wilkens S. & K-M. Exo 1998. Brutbestand und Dichteabhängigkeit des Bruterfolges der Silbermöwe (*Larus argentatus*) auf Mellum. J. Ornithol. 139:21-36.

Williams G.C. 1966. Natural selection, the cost of reproduction and a refinement of Lack's principle. Am. Nat. 100: 687-690.

Wilson L.J., C.A. McSorley, C.M. Gray, M. Catherine, B.J. Dean, T.E. Dunn, A. Webb & J.B. Reid 2009. Radio-telemetry as a tool to define protected areas for seabirds in the marine environment. Biol. Conserv. 142: 1808-1817.

Wilson R.P., J. Cooper & J. Plötz 1992. Can we determine when marine endotherms feed? A case study with seabirds. J. Exp. Biol. 167: 267-275.

Wilson R.P., W.S. Grant & D.C. Duffy 1986. Recording devices on free-ranging marine animals: does measurement affect foraging performance? Ecology 67: 1091–1093.

Wilson W.H. & R.E. Ruff 1988. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (North Atlantic): Sandworm and bloodworm. U.S. Fish. Wildl. Serv. Biol. Rep. 82(11.80). U.S. Army Corps o f Engineers, TR EL-82-4. 23 pp.

Winkler D.W. 1987. A general model for parental care. Am. Nat. 130:526–543.

Winkler D.W. & P.E. Allen 1996. The seasonal decline in Tree Swallow clutch size: physiological constraint or strategic adjustment? Ecology 77: 922–932.

Wise M.H. 1980. The use of fish vertebrae in scats for estimating prey size of otters and mink. J. Zool., Lond. 192: 25-31.

Wit A.A.N. de 1988. Onderzoek naar telmethoden voor grote kolonies met Zilvermeeuwen en Kleine Mantelmeeuwen (deel 1). Rijksinstituut voor Natuurbeheer, Arnhem.

Witte J.Y. & J.J. Zijlstra 1978. The species of fish occurring in the Wadden Sea. In: Dankers N., W.J. Wolff & J.J. Zijlstra (eds) Fishes and fisheries of the Wadden Sea: 10-19. Report no. 5, Final report of the Wadden Sea Working Group, Balkema, Rotterdam.

Wittenberger J.F. & G.L. Hunt Jr 1985. The adaptive significance of coloniality in birds. In: Farner D.S., J.R. King & K.C. Parkes (eds) Avian Biology, VII: 1-78. Acad. Press, New York.

Wolf P.A. 2003. Audouins Meeuw op Neeltje Jans. Dutch Birding 25: 205-206.

Wolff W.J. (ed.) 1976. Proceedings of the Conference of Wadden Sea Experts held at the island of Schiermonnikoog, The Netherlands, 26-28 November 1975. Contr. nr. 3, Wadden Sea Working Group, Publ. Office Government, The Hague.

Wolff W.J. 2005. Non-indigenous marine and estuarine species in The Netherlands. Zool. Meded. 79: 3-116.

Woltman D. 1914. Van enkele vogels op Schiermonnikoog. De Lev. Nat. 19: 43-45.

Wooller R.D., Bradley J.S. & Croxall J.P. 1992. Long-term population studies of seabirds. TREE 7(4): 111-114.

Wooller R.D., J.S. Bradley, I.J. Skira & D.L. Serventy, D.L. 1990. Reproductive success of Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. J. Anim. Ecol. 59: 161-170.

Wooller R.D., J.S. Bradley, I.J. Skira & D.L. Serventy1989. Short-tailed Shearwater. In: Newton I. (ed.) Lifetime reproduction in birds. Acad. Press.

Wooller R.D. & Coulson J.C. 1977. Factors affecting the age of first breeding of the Kittiwake, *Rissa tridactyla*. Ibis 119: 339-349.

Woutersen K. 1992. De Stormmeeuw *Larus canus* als broedvogel in de Schoorlse Duinen. Sula 6: 81-92.

Woutersen K. & Roobeek K. 1992. Broedgevallen van de Stormmeeuw *Larus canus* in het binnenland in Noord-Holland. Sula 6: 51-55.

Wright P.J. & Bailey M.C. 1993. Biology of sandeels in the vicinity of seabird colonies at Shetland. Fisheries Research Services Report 15/93. Marine Laboratory, Aberdeen.

Wright P.J., Barrett R.T., Greenstreet S.P.R., Olsen B. &Tasker M.L. 1996. Effect of fisheries for small fish on seabirds in the eastern Atlantic. In: Hunt G.L. & R.W. Furness (eds) Seabird/fish interactions, with particular reference to seabirds in the North Sea: 44–55. ICES Cooperative Research report No. 216.

Wynne-Edwards V.C. 1935. The habits and distribution of birds on the North Atlantic. Proc. Boston Soc. Nat. Hist. 40: 233-346.

Yen P.P.W., J.B. Sydeman, S.J. Bograd & K.D. Hyrenbach 2006. Spring-time distributions of migratory marine birds in the southern California Current: Oceanic eddy associations and coastal habitat hotspots over 17 years. Deep-sea Res. II-Oceanogr. 53: 399-418.

Zack S. & B.J. Stutchbury 1992. Delayed Breeding in Avian Social Systems: The Role of Territory Quality and "Floater" Tactics Behaviour 123: 194-219.

Zijlstra M. & M.R. van Eerden1995. Pellet production and the use of otoliths in determining the diet of cormorants *Phalacrocorax carbo sinensis*: trials with captive birds. Ardea 83: 123–131.

Zipperle A. & K. Reise. 2005. Freshwater springs on intertidal sand flats cause a switch in dominance among polychaete worms. J. Sea Res. 54:143-150.

Zomerdijk P.J., Orden C. van, Zwart K, Verkerk W., Muusers B., Fabritius H.E. & Vries C. de 1971. Broedvogels van Noord-Holland Noord. Publ. Vogelwerkgroep Noordhollands Noorderkwartier, Uitg. Heijnis Tsz, Zaandijk.

Zwarts L. & Esselink P. 1989. Versatility of male curlews *Numenius arquata* preying upon *Nereis diversicolor*: deploying contrasting capture modes dependent on prey availability. Mar. Ecol. Progr. Ser. 56: 255-270.

Zwarts L. & Wanink J.H. 1984. How Oystercatchers and Curlews successively deplete clams. In: Evans P.R., J.D. Goss-Custard & W.G. Hale (eds). Coastal waders and wildfowl in winter: 69-83. Cambr. Univ. Press., Cambridge.

Zwarts L. & Wanink J.H. 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, burying depth and behaviour of tidal-flat invertebrates. Neth. J. Sea Res. 31: 441-476.

Zydelis R., J. Bellebaum, H. Österblom, M. Vetemaa, B. Schirmeister, A. Stipniece, M. Dagys, M. van Eerden & S. Garthe 2009. Bycatch in gillnet fisheries-An overlooked threat to waterbird populations. Biol. Conserv. 142: 1269-1281.

Acknowledgements

Many, many people have contributed to these studies: seawatching data, beached bird surveys, discard experiments, ship-based seabird surveys, colony work and tracking studies. Results of the Kelderhuispolder studies form the main body of work underlying this thesis and aspects of this work can be found in most chapters. With regard to this part of the work, first and foremost my volunteer co-worker, friend and highly committed (field) assistant Arnold Gronert must be acknowledged for his dedication and friendship through the years. Without his help, only some of the results now reported, would have been possible. Arnold Gronert, who became involved in 2006 and stayed until 2012. He participated in 183 (33%) of the 559 colony visits in this period, working 815 hours in the field (38% of a total of 2137 field hours). Apart from that, Arnold must be acknowledged for his careful examination of students and other volunteers entering the scene. He was and is also invaluable in his ring-reading activities in one of the key foraging areas of Herring Gulls breeding at Texel, where he spent countless hours along the mainland coast (breakwaters and beach) between Schoorl aan Zee and Den Helder. Thanks, Arnold. **Students** participating in the Kelderhuispolder studies were, in chronological order, Vicky Hunt (2006, University Cornell, USA), Sharon Boekhout (2006, Larenstein, Leeuwarden), Tim van Nus (2007, Larenstein, Velp), Janne Ouwehand (2008, RUG, Groningen), Natalia Gallego (2008, UvA, Amsterdam), Cosme Damián Romay Cousido (2009, Univ. A Coruña, Spain), Rim Lucassen (2010, RUG, Groningen), Suzanne Poiesz (2012, UvA, Amsterdam) and Estefania Velilla (2012, Univ. Maastricht). Never a dull moment in a seabird colony, but it was with these dedicated people that it was so much fun to be out in the field. I thank you all.

Many people were interested to participate (and help) in the colony as **volunteers**, and from 2006-2012 I enjoyed the company of Geert Aarts, Henrike Andresen, Janneke Bakker, Rob van Bemmelen, Anja Berg, Allert Bijleveld, Lotte van Boheemen, Roeland Bom, Michelle Boonstra, Niels Bot, Sander Bot, Willem Bouten, Wiepke Brugge, Rob Buiter, Maarten Buteijn, Daan Camphuijsen, Martin Camphuijsen, Gepke Camphuysen, Anja Cervencl, Fred Cottaar, Anne Dekinga, Evelien Dekker, Rob Dekker, A.R.G. van Dijk, Jacintha van Dijk, Adriaan Dijksen, Lieuwe Dijksen, Debby Doodeman, Yaiza Dronkers, Sjoerd Duijns, Anne Evers, Natalia Gallego, A. Garbut, Stefan Garthe, Ricardo Gasol, Roser Gasol, Petra de Goeij, Rineke Gronert, Merel den Held, Hester Helsloot, Denise Hermans, Vincent Hin, Sander Holthuijsen, Pieter Honkoop, Job ten Horn, Piet van den Hout, Nicole Janinhoff, Roos Kentie, Romke Kleefstra, Maarten van Kleinwee, Ineke Knot, Wouter Koch, Christine Koersen, Eva Kok, Martin Koopman, J. van Koot, Casper Kraan, Suse Kühn, Tiedo van Kuijk, Coby Kuiken, Dirk Kuiken, Mardik Leopold, Jutta Leyrer, Suzan van Lieshout, Georgina Massouraki, Els van der Meer, Jaap van der Meer, Wilma Mossink, Martijn Pallandt, Monica Parsons, Helma van Pijkeren, Yvonne Radstake, Marijke Rauch, Damian Cosme Roumay, Milou de Ruijter, René de Ruijter, Sanne de Ruijter, Jelmer Samplonius, Carry Schaap, Stijn Schep, Jordi Segers, Judy Shamoun-Baranes, Tal Shamoun-Baranes, Cees van Slooten, Jeremy Smith, Bernard Spaans, Peter Spannenburg, P.J. van Spreeuwel, Anne Tasker, Mark Tasker, Bas Teunis, Tineke Troost, Les Underhill, Kees Verbeek, José Verbeek-Cottaar, Hans Verdaat, Lisa Verwoerd, Yvonne Vittali, Anne Vollmer, Kees de Vries, Dennis Waasdorp, Jan Zorgdrager, and Miranda Zutt. Other visitors to the colony were Jan Musch and Tijs Tinbergen (Musch & Tinbergen), Menno Reemeijer (NOS, Het Filiaal), Rob Buiter (VARA Vroege Vogels, Teleac), Els van der Meer and pupils (Stichting Kopwerk), Jop de Vrieze (NRC). Bas Teunis, who kindly prepared the wonderful cover drawing of displaying Lesser Black-backed Gulls, spent two months (2010-11) on a mission to collected as many photographs as possible to document the behaviour of gulls in the early breeding phase. RUG students that participated as part of their courses at NIOZ were (2005) K. Prent, J. Reinders, S.L.J. Wartenbergh, (2006) A.R.G. van Dijk, J. van Koot, P.J. van Spreeuwel, (2007) Martijn Pallandt, Jelmer Samplonius, Cees van Slooten, (2012) Marijke Rauch, and Lisa Verwoerd.

Every year, the end of the season meant: an extra **ringing sessions** of fledglings with a group of volunteers to enlarge the number of colour-ringed youngsters, particularly in seasons that few young fledged from our own study plots. Field assistants during these ringing sessions 2006-2012 were Geert Aarts, Henrike Andresen, Janneke Bakker, Rob van Bemmelen, Anja Berg, Allert Bijleveld, Judith van Bleijswijk, Sharon Boekhout, Jonne Bonnet, Joop Bonnet, Pierre Bonnet, Sander Bot, Daan Camphuijsen, Gepke Camphuysen, Anja Cervencl, Fred Cottaar, Jenni Cremer, Jacintha van Dijk, Debby Doodeman, Sjoerd Duijns, Vania Freitas, Petra de Goeij, Arnold Gronert, Chiel Gronert, Rineke Gronert, Denise Hermans, Vincent Hin, Pieter Honkoop, Piet van den Hout, Jasmijn Hulleman, Nicole Janinhoff, Roos Kentie, Maarten van Kleinwee, Christine Koersen, Laurens van Kooten, Casper Kraan, Suse Kühn, Tom Leopold, Mardik Leopold, Jutta Leyrer, Suzan van Lieshout, Luc Meeuwisse, Brecht de Meulenaer, Jeroen Mos, Tim van Nus, Bram Oosterbeek, Dörte Poszig, Jeroen Reneerkens, Harmen Riphagen, Damian Cosme Romay, Lucy Schmaltz, Jonathan Shamoun, Tal Shamoun, Judy Shamoun-Baranes, Jeremy Smith, Kees Verbeek, Hans Verdaat, Jan Zorgdrager, Miranda Zutt, and Tim Zutt.

Through the years, shorter and longer term **scientific collaborations** occurred with Judith van Bleijswijk and Anneke Bol (DNA, analysis 2007, 2012, NIOZ), Peter de Boer (SOVON), Willem Bouten (2008-12, Univ. Amsterdam), Karel ten Cate (2007 Univ. Leiden), Fred Cottaar (2006-12 ringgroep IJmuiden), Stefan Garthe (2007, 2008, FTZ Büsum), Veit Hennig (2007, Univ. Hamburg), Jutta Leyrer (2007-10, NIOZ), Emiel van Loon (2009-12, Univ. Amsterdam), Pieternella Luttikhuizen (DNA, 2012), Kees Oosterbeek (2008, SOVON), Gregor Scheiffarth (2007, Vogelwarte Helgoland), Judy Shamoun-Baranes (2008-12, Univ. Amsterdam), Arie Spaans (2006, colour-ring data), José & Kees Verbeek (2006-12 ringgroep IJmuiden), and Anne Vollmer (2007, Univ. Leiden). Some tracking data derived from the Argos satelliet PTTs on gulls breeding at Vlieland have been used in this thesis with special permission from SOVON and the German “Institut für Vogelforschung” in Wilhemshaven. Both were engaged in a large international study financed by the “European Space Agency” (ESA), together with the "Computational Biogeography and Physical Geography” unit of the University of Amsterdam and the "Centrum voor Limnologie (NIOO-KNAW)". All organisations and researchers are kindly acknowledged and thanked for their help and interest in the gull studies at Texel.

Permissions, **licenses**, and all sorts of **technical advice** were provided by Woutera van Andel (Vogeltrekstation Heteren), Edwin Baaij (UvA, GPS base station and hardware), Henk Brugge (Ecomare, fish for suppl. feeding experiments), Maarten Brugge (traps), Kees Bruin (SBB), Anne Dekinga (NIOZ, base station receiver), Aris Ellen (SBB), Marcel Groenendaal (SBB), Jos Hooijmeyer (RUG, solar panels), Job ten Horn (NIOZ, base station receiver), Henk van der Jeugd (Vogeltrekstation Heteren), Risto Juvaste (colour rings), Peter Rock (colour rings), Bernard Spaans (radio transmittors), Gerrit Speek (Vogeltrekstation Heteren), Erik van der Spek (SBB), Jan Witte (SBB), and Salko de Wolf (rehabilitation). Chris Pool and Nanneke van der Wal (Proefdierdesk bureau KNAW) kindly intervened when the necessary paperwork for animal experiments (even if just blood sampling) was incomplete and were a great help throughout to facilitate the studies.

The **field work at Texel** had not been possible without the co-operation of Staatsbosbeheer in all seasons. Staatsbosbeheer Texel granted permission to work in the Kelderhuispolder, a nature reserve closed for the general public. I am particularly thankful to Kees Bruin, Aris Ellen, Marcel Groenendaal, Erik van der Spek en Jan Witte for help and co-operation and the friendly atmosphere throughout our field work periods and beyond. It is hoped that these studies will help conserve the breeding populations within these dune areas in years to come.

I am much indebted to the **recent ring-readers**, who provided the much needed data to study movements and survival. Since 2006, substantial amounts of data (>25 sightings of a total of 17,414 recoveries) were received from Sytze Algera, Ruud Altenburg, Peter de Boer, Roland-Jan Buijs, Ruud Costers, Fred Cottaar, Cosme Damian Romay, Michael Davis, Patrick Derrien, Pieter Duin, Alain Fossé, Michel Fouquet, Roland Francois, Salvador Garcia, Gerrit Goedhart, Delfin Gonzalez, C.J. de Graaf, Benjamin Griard, Arnold Gronert, Antonio Gutierrez, Rob Hoeben, Job ten Horn, Miguel Juan, Hans Keijser, Maarten van Kleinwee, Brian Knott, Mardik Leopold, Henry van Lierop, Bob Loos, Rim Lucassen, Frank Majoor, Javier Marchamalo, Gabriel Martin, José Manuel Méndez, Benny Middendorp, Mars Muusse, Theo Muusse, Tim van Nus, Janne Ouwehand, Christian Pedersen, Suzanne Poiesz, Peter Rock, Juan M. Ruiz, John Sanders, Jean Michel Sauvage, Rebekka Schüller, Roy Slaterus, Tom van Spanje, Dick Veenendaal, Francisco Giron Veiga, José & Kees Verbeek, Kees Verbeek, José Verbeek-Cottaar, H.J.P. Vercruijsse, Hein Verkade, Paul Veron, Fred Visscher, Rob Voesten, Peter Volten, Willem vd Waal, S. Waasdorp, Pim Wolf, Salko de Wolf, Jan Zorgdrager, and Carl Zuhorn. I would like to specifically acknowledge the work that “the IJmuiden team” did over the years, including the maintenance of a colour-ringed population on a neigbouring island in IJmuiden. Fred (Cottaar), Kees (Verbeek), and José Verbeek-Cottaar, you were great company during several field trips, and produced extremely useful data through the years in IJmuiden. It was so sad to learn that Kees’ health now fails and I can only hope that at least some of the fun and love for fieldwork can be kept up for as long as possible.

Acknowledgements, specific for each of the main chapters are listed below. Many of the people mentioned earlier have contributed one way or the other and their help was much appreciated. For **Chapter 3,** Geert Aarts (IMARES, Texel) kindly processed and provided black box data for commercial nearshore fisheries in Dutch waters, the Ministry of Economy, Agriculture and Innovation (EL&I) granted permission to use these data. The work would not have been possible without the continuous support and voluntary assistance of Arnold Gronert, active as co-worker in most field seasons. For **Chapter 4** the authors are grateful to Risto Juvaste who produced the colour-rings, the radios were provided by the NIOZ waders group (courtesy Theunis Piersma and co-workers). The study was financially supported by the NIOZ (CJC research fund) and was conducted as a Master Project for Groningen University (JO). We thank Geert Aarts and Allert Bijleveld for comments and help with statistical analysis and Sander Bot for mental support and comments on the manuscript. Scott Hatch kindly commented on an earlier draft of this paper. For **Chapter 5**, 462 ring-readers have contributed, with (excluding any of the authors of this chapter) the most substantial contributions by Ruud Altenburg, Peter de Boer, Cosme Damian Romay, B.W. van Dijk, Michel Fouquet, Salvador Garcia, Gerrit Goedhart, Diek Groenewald, Andreas Guyot, Job ten Horn, Maarten van Kleinwee, Javier Marchamalo, Gabriel Martin, Mars Muusse, Theo Muusse, Tim van Nus, Janne Ouwehand, Peter Rock, Juan Ruiz, John Sanders, Norman Deans van Swelm, José & Kees Verbeek, Kees Verbeek, José Verbeek-Cottaar, Harry Vercruijsse, Hein Verkade, Willem van der Waal, Pim Wolf, and Jan Zorgdrager. Adriaan Rijnsdorp kindly updated the long-term trends in Dutch beamtrawl fisheries. For **Chapter 6**, the authors are grateful to the ringers of the Herring Gulls in 1986-1988 B.A. Nolet, K. de Rijk, and J. Van der Kamp, D. de Bruyn, G. Kasemir, A. van Klinken, R. Noordhuis, R.T. Kiewiet, A. de Wit, A.L. Spaans, J. Jager, L.J. Dijksen, A.A.N. de Wit, A. Bergfeld, C.J. Ooyevaar, F. Nauta, F. Cottaar, R.J. Wanders, N.D. van Swelm, C.M. Berrevoets, and E.O. Neve. Secondly, I am much indebted to the numerous observers who have submitted their observations and without whom the entire project would have been impossible. Some particularly productive readers of colour-rings (excluding any of the authors) must be mentioned: E.J. Alblas, T. Bakker, Y. Bergkamp, C.M. Berrevoets, W. Boeykens, L. Boudolf, H. Buckx, R-J. Buijs, R. Costers, F. Cottaar, A. Deutsch, K. van Dijk, L.J. Dijksen, A.A. Dijkstra, A.H.V. Eggenhuizen, F. Faber, R. François, S.C.V. Geelhoed, G. Goedhart, G. van Gool, C.J. de Graaf, A. Gronert, N.F. van der Ham, H. Hin, G.M. Janse, J. Jukema, J. Kloppenburg, E. Klunder, P. de Knijff, H. Koffijberg, K. Koffijberg, B. Koks, G. Koolhof, D. Kuiken, M. van Leeuwen, B. Loos, E.J. Maassen, F. Majoor, B. Middendorp, J.M. van Muiswinkel, F.B. Nauta, J. Nienhuis, A.M. van der Niet, B.A. Nolet, R. Noordhuis, J. Nowakowski, A. Ouwerkerk, O. Overdijk, B. Oving, A. van Poppel, P. Raevel, J. Rampen, J. Regeer, M. Roos, T. van Schie, J.M.M. Snijders, S.F. Steeneken, W. Steenge, L. Stegeman, N.D. van Swelm, P. Tak, R. Ubels, J.C.G. Vegelin, K. Verbeek, B. Vercruysse, H.J.S. Verkade, H. Van de Wetering, L. Van Wijngaert, G.F. Wilmink, B. Winters, A.A.N. de Wit, J. de Wit, P. Wolf, J. Zijp, and H. Zwaagstra all contributed at least 100 sightings or recoveries of colour-ringed Herring Gulls. SOVON (Joost van den Bruggen) and Waterdienst (Ministry of Transport and Public Works) kindly provided colony data (population censuses) over the past decades (1985-2005). Geert Aarts (NIOZ) was helpful with the statistical analysis of some data and provided useful feedback when the results were discussed. Theunis Piersma and Norman D. van Swelm kindly commented on earlier versions of the manuscript. For **Chapter 7,** Lieuwe Dijksen (SOVON) provided an update on population censuses of gulls breeding in the area since the 1960s. Allert Bijleveld, Daniël Camphuijsen, Anja Cervencl, Fred Cottaar, Cosme Damian Romay, Job ten Horn, Roos Kentie, Maarten van Kleinwee, Rim Lucassen, Tim van Nus, Janne Ouwehand, Rebekka Schüller, Mark Tasker, José Verbeek-Cottaar and Jan Zorgdrager, contributed substantially with ring-reading activities in the Kelderhuispolder. Bernard Spaans (NIOZ) kindly introduced the first author into the world of software program MARK and survival analysis. For **Chapter 8,** Michael Kemp (UvA-BiTS) wrote the R script used to designate unbroken trips. Natalia Gallego Garcia tested the various (chick) growth curves in 2008, using data collected between 2006 and 2008. Jaap van der Meer (NIOZ) and Emiel van Loon (UvA-BiTS) kindly provided statistical advice and helped with the interpretation of the collected data. We thank Edwin Baaij (UvA-BiTS) for technical support throughout this project and the research infrastructure was supported by BiG-grid, LifeWatch and the Dutch national e-science center. For **Chapter 9**, Sharon Boekhout, Jacintha van Dijk, Vicky Hunt, Tim van Nus, Cosme Damian Romay, Nora Spaans, and Hans Witte sorted the fast majority of prey samples. Vicky Hunt, Rob Dekker, Gerhard Cadée, Marc Lavaleye (all NIOZ), and Mardik Leopold (IMARES Texel) all assisted in various ways with specific prey identification problems. Emiel van Loon (University of Amsterdam) kindly provided advice on analytical techniques. For **Chapter 10**, we thank Edwin Baaij for technical support with UvA-BiTS and Michael Kemp for initial R scripts. The research infrastructure was supported by BiG-grid, LifeWatch and the Dutch national e-science centre. For **Chapter 11**, I am grateful to the numerous observers on board research vessels in the NIOZ and NZG/DGW programmes during 1987-92. The Tidal Waters Division of the Ministry of Transport, Public Works and Water Management financed the RV Holland programme, from which part of the data were obtained, and which was conducted by volunteers of the Dutch Seabird Group. Mardik Leopold and Rob Dapper were helpful by providing a list of the NIOZ data. Jaap van der Meer analysed the feeding ranges of gulls. Piet Duiven provided the corpses of adult Herring and Lesser Black-backed Gulls. Mardik Leopold, Han Lindeboom, Ruurd Noordhuis, Theunis Piersma, and Arie Spaans commented on earlier drafts of this paper. This study was part of a research project at The Netherlands Institute for Sea Research on scavenging seabirds in the southern North Sea, financed by the Ministry of Education and Sciences. For **Chapter 12**, the bird behavioural studies were facilitated by the BiG Grid infrastructure for eScience (www.biggrid.nl). S. Kolios has to be acknowledged for land use classification, E.E. van Loon for helpful discussions, T. Piersma for commenting on an earlier version of this manuscript together with R. Nager, P. Battley, G. Hayes and two anonymous reviewers. For **Chapter 13**, the tracking studies were facilitated by the BiG Grid infrastructure for e-Science (www.biggrid.nl) and were conducted by the Royal Netherlands Institute of Sea Research in collaboration with the Institute for Biodiversity and Ecosystem Dynamics of the University in Amsterdam, co-funded by the Netherlands Ministry of Transport and Public Works (Masterplan Wind at Sea). Part of the studies of Northern Gannets were funded by the European Commission, Directorate General for Fisheries and Maritime Affairs, project Q5RS-2000-30864. For **Chapter 14**, Tom van Spanje provided food samples from the Wormer- & Jisperveld colony. Sharon Boekhout, Daan Camphuijsen, Jacintha van Dijk, Vicky Hunt, Tim van Nus, Janne Ouwehand, Nora Spaans, Cosme Damián Romay and Hans Witte assisted with the sorting and analysis of prey samples. Carl Zuhorn (SBB Vlieland) kindly provided information on the occurrence of certain mammals at Vlieland. Financial support to analyse part of the samples was provided by Waterdienst, Ministry of Transport and Public Works in 2008.

There is a number of people and organisations that I would like to thank, even though the involvement with the work presented in this thesis may have been remotely or indirectly. My brother Martin, for introducing me into the world of natural history, the Christelijke Jeugdbond van Natuurvrienden (a terrible name for a useful organisation) for providing general knowledge and the development of social skills (no matter how rudimentary now). I would like to thank Rob Bijlsma, a great inspiration and the very reason that I failed to finish school, but who changed the way I look at the animal kingdom and on how one should observe and record things. I am grateful to Jelle van Dijk and Frank de Miranda for sharing their interest in seabirds with me, and the same is true for Maarten Platteeuw, Kees Woutersen, Frits-Jan Maas, Nick van der Ham and many other seawatchers “of the first hour”. In the early 1980s I was happy to develop my skills as a seabirder not just by observing them, but also during autopsies and museum studies. From that period, I have great memories of working with Jan Andries van Franeker, Kees Roselaar, Tineke Prins, Henk Sandee, Jan Wattel, and Rombout de Wijs, among others. From the Dutch Seabird Group, an organisation in which seawatchers and beached bird surveyors came together as a result of their mutual interest in seabirds, I have excellent memories of working with Jan Andries van Franeker and Yvonne Hermes, Mardik Leopold, Steve Geelhoed, Arend-Jan van Dijk, Edward Soldaat and I would like to acknowledge friends and colleagues from the ESAS group, notably Peter Hope Jones, Mark Tasker and Andy Webb as co-founders, but also Jan Durinck, Arne Follestad, Stefan Garthe, Ommo Hüppop, Mardik Leopold, Henrik Skov. A special word of thank you, no doubt unexpected for him, for James Williams, who learned me to design and handle a database (no, to *think* database), after which life was so much easier. From the ICES working group for Seabird Ecology I would like to thank the core of the team, for sharpening my thoughts on seabirds and fisheries issues: Tycho Anker-Nilssen, Rob Barrett, John Chardine, Morten Frederiksen, Bob Furness, Stefan Garthe, George Hunt, Bill Montevecchi, Norman Ratcliffe, Jim Reid, Mark Tasker, and Richard Veit. The Vlieland team, named team ASADI by some, Peter de Boer, Guus van Duin, Lenze Hofstee, Leon Kelder, Romke Kleefstra, Jeroen Reneerkens, Menno van Straaten, and Carl Zuhorn for good company, food and drinks at Vlieland. Let’s hope our Zwaluw facilities are recognised as a vital aspect of the waterbird censuses on the island.

In 1992, I became based at Texel following an invitation to start a research project on the effects of fisheries discards on seabirds at the NIOZ. Mardik Leopold and Han Lindeboom issued that invitation, which effectively meant that a dream came true to work at a genuine research institute, on a Wadden Sea island, close to the coast. My life and that of Gepke has changed ever since and we are both still very grateful for this invitation and the trust given that the proposed work should be completed satisfactory. A genuine regime shift for me personally, and we love our life on Texel. Mardik and Katja Philippart were instrumental during that initial phase (and before), leading to an ever-lasting and much enjoyed friendship. I am grateful to know that Mardik happily accepted the invitation to perform as one of the *“paranymphs”* for the defence ceremony. Even though our work trajectories became more separated in recent years, I hope and trust that both our friendship and scientific collaborations will continue in years to come. Mardik and Katja, you both have been invaluable after that sudden shock that struck in March 2013. I thank you so much.

The **Royal Netherlands Institute for Sea Research (Royal NIOZ)**, via Henk van der Veer and Theunis Piersma, provided the necessary facilities, finances and scientific backgrounds for these and earlier studies at NIOZ. Many other NIOZ staff have contributed one way or the other. Early studies of gulls foraging on discards in commercial fisheries were part of a research project at The Netherlands Institute for Sea Research on scavenging seabirds in the southern North Sea, initiated by Han Lindeboom and Mardik Leopold, financed by the Ministry of Education and Sciences. I am grateful to the numerous observers on board research vessels in the NIOZ, Alterra, NZG/DGW, and IMARES programmes during 1987-2010.

At the NIOZ, I much enjoyed the “bird group” as and informal research laboratory with highly dedicated, skilled and friendly co-workers, in a constantly changing configuration over the years. Many direct colleagues, post-docs, AIOs, students, assistants, representatives of other NIOZ departments and other staff from the institute, have one way or the other contributed to these. I have also profited from exchanges with the nearby institute RIN, later IBN or IBN-DLO, Alterra-Wageningen and now IMARES, including personnel moving from one to the other institute or back and frequent collaborations during specific research projects. The number of people is too large to be mentioned complete (not in the least as a result of failing memory), but I surely enjoyed working with Geert Aarts, Bert Aggenbach, Henrike Andresen, Maarten van Arkel, Rob van Bemmelen, Magda Bergman, Allert Bijleveld, Nynke Bloksma, Roeland Bom, Jan Boon, Oscar Bos, Sophie Brasseur, Maarten Brugge, Gerhard Cadée, Jenny Cremer, Kaat Croes, Rogier Daan, Cindy van Damme, Rob Dapper, Daliborka Barjaktarov, Tanja Compton, Anne Dekinga, Rob Dekker, Jacintha van Dijk, Jan Drent, Sjoerd Duijns, Piet Duiven, Pim Edelaar, Bruno Ens, Fram Fey, Eelke Folmer, Mark Fonds, Jimmy de Fouw, Jan Andries van Franeker, Vania Freitas, Ysbrand Galama, Steve Geelhoed, Matthijs van der Geest, Jan van Gils, Petra de Goeij, Jack Gootjes, Santiago Gonzalez, Ruud Groenewegen, Henk de Haas, Joke Hart, Willem Hart, Henk Hobbelink, Sander Holthuijsen, Pieter Honkoop, Piet van den Hout, Andrea Keijser, Roos Kentie, Anita Koolhaas, Hilde Kooijman, Casper Kraan, Mark Lavaleye, Piet-Wim van Leeuwen, Mardik Leopold, Jutta Leyrer, Tamar Lok, Pieternella Luttikhuizen, Hans Malschaert, Jaap van der Meer, André Meijboom, Maarten Mulder, Gerard Nieuwland, Ada Nooy, Henk Offringa, Thomas Oudman, Wim Pool, Peter Reijnders, Dan Ruthrauff, Jan van Santbrink, Meike Scheidat, Stefan Schouten, Jeremy Smith, Bernard Spaans (even if he cannot read green rings), Kees van der Star, Alina Stadnitskaia, David Thieltges, Hans Verdaat, Tony van der Vis, Irene Wernand-Godee, Chris Winter, Hans Witte, Richard Witte, Piet de Wolf, Pim Wolf and many others. NIOZ heads of departments Jan Beukema, Han Lindeboom, Jaap van der Meer, and Henk van der Veer are thanked for the opportunities provided to work at Texel. Jaap van der Meer, for enjoyable sea trips, running a joint project, sharing a joint interest in (mammalian) wildlife, statistical advice and for his suggestion to start studies in the colonies at Texel following the IMPRESS project. Rob Dekker for early morning coffee’s, for sharing his expert knowledge of marine invertebrates, his general friendship, and his useful and enthusiastic co-operation with the investigation of the quality of marine bivalve resources on breakwaters and within the Marsdiep area through the year. Job ten Horn, a more recent addition to the group but excellent companion during seawatching, ring-reading, and for technical advice. Anne, for providing his expert advice on the electronics and other parts of Houston Control and for hitting back when I hit. Anne’s better half, Anita, for great company at work. Special words of thanks for my workroom-mate and lovely friend Petra de Goeij, always capable of cheering up a day’s work, thanks also for being yourself wherever we meet with your unbeatable capacity to turn a chilly atmosphere into something enjoyable. Thank you so much for your friendship when life was miserable, Petra.

After entering **the world of gulls**, Arie Spaans was of great help and he supported the ideas generously from the very beginning of the work. Moreover I came across and was often much helped by numerous gull aficionados, including Roland-Jan Buijs, Theo Muusse, Mars Muusse, Ruud Altenburg, Frank Majoor, Maarten van Kleinwee, Jan Zorgdrager, Norman Deans van Swelm, Peter Rock, Michael Davis, Patrick Derrien, Alain Fossé, Michel Fouquet, Roland Francois, Salvador Garcia, Delfin Gonzalez, Benjamin Griard, Antonio Gutierrez, Miguel Juan, Javier Marchamalo, Gabriel Martin, José Manuel Méndez, Viola Ross-Smith, Juan M. Ruiz, John Sanders, Jean Michel Sauvage, Chris Thaxter, Francisco Giron Veiga, and Paul Veron.

In 2008, a start was made with what would turn out to be a long-lasting and highly productive collaboration with the Computational Biogeography and Physical Geography” unit of the University of

Amsterdam: the group led by Willem Bouten, with Edwin Baaij, Emiel van Loon, Judy Shamoun-Baranes and several other co-workers and many students. Willem needed “targets” for his rapidly developing GPS loggers and the Texel colony turned into a test arena. Co-operation with him was and still is both a pleasure and a great privilege. The mutual benefit was obvious from the start and a stream of publications is the result of our joint efforts. Emiel is the highly useful statistician on the background, who’s invaluable help has rescued many a paper. What he also shows is that statisticians do not need to be arrogant; a much appreciated characteristic of an extremely clever and helpful scientist. Edwin is the technological heart of the enterprise, never impatient, and always willing to help if the technology let us down. Much if not most of the success of the entire collaboration, however, is thanks to Judy Shamoun-Baranes, who became a fine friend and colleague, and who kindly agreed to be that other *paranymph* during the defence ceremony. She participated in, or first-authored, all of the resulting papers and drafts and the joint supervision of a rapidly growing number of students is a daily joy. I want to thank her and her two great kids, but also her husband on the background, for all the time she spent over the years to make the logger studies a success and to enhance the possibilities we have to study these animals. Tal, thank you for not taking the plastic soldiers home to Jonathan.

In recent years, I became more frequently involved with researchers working at Groningen University and I treasure discussions with great scientists that I highly respect, including Christiaan Both, Rudi Drent, Irene Tielemans, Joost Tinbergen, and others during more or less informal meetings and work presentations.

I would like to thank co- and lead-authors of papers and manuscripts included in the thesis: Geert Aarts (IMARES), Edwin Baaij (UvA), Peter de Boer (SOVON), Willem Bouten (UvA), Fred Cottaar (IJmuiden ring group), Stefan Garthe (FTZ), Arnold Gronert, Emiel van Loon (UvA), Janne Ouwehand (RUG), Judy Shamoun-Baranes (UvA), Arie Spaans, Kees Verbeek (IJmuiden ring group), and Harry Vercruijsse. I would also like to thank the co-authors of relevant papers that are highlighted within this thesis, but that were not included in full: Anthony Bicknell (Plymouth Univ.), Roland-Jan Buijs (Buijs Eco Consult), Hallgrimur Gunnarsson (Iceland), Gunnar Hallgrimsson (Univ. Iceland), Daniel Oro (IMEDEA), Beth Scott (Univ. Aberdeen), Olafur Torfason (Iceland), Stephen Votier (Plymouth Univ.), Sarah Wanless (CEH), and Andy Webb (JNCC).

I was privileged to have eminent scientists in the reading committee, including Professor Christiaan Both (Groningen), Regius Professor Pat Monaghan (Glasgow), and Professor Chris Perrins (Oxford). All three went through a comprehensive manuscript and their helpful suggestions, plus those of the two promotors, helped shape it into the current format. Apologies if the work should have been done better, I am still keen to learn. At the NIOZ, I am much indebted to Henk van der Veer, for his help and facilitation as head of the MEE department throughout this project and for his enthusiasm when the thesis was nearly completed. I am very glad he agreed to perform as a co-promoter. And obviously Theunis Piersma, a great inspiration and example for many years, who took me serious way before I deserved that (if I ever did), who was the very reason that this thesis was written in the first place, and who has been instrumental in getting me and keeping me at NIOZ. Theunis is a great inspiration for many (wannabe) scientists around the world and I hope I didn’t consume too much of his time and still performed. I see it as a privilege that he paved the way for me to deliver this thesis at Groningen University, even though my background was unusual and largely inadequate, and I am honoured to have him as a promoter and friend.

I’d like to thank my offspring, Daan and Marjolein, and my wife Gepke, while I apologise for all my absences while being in the field or sitting behind a desk. Gepke was fully aware of what happened and joined many excursions and trips. I trust that Daan and Marjolein also learned to understand what fascinated me even though they themselves developed other interests and skills. Keep going you two and please keep surprising me with your excellent personalities. Dear Gepke, now that your health is failing, I can only hope that we will have more field trips and quality time together in the near and hopefully also distant future and know that this book is dedicated to you.

Appendix 0 - Base material of this thesis

Data collections and short history

Much of the research presented in this thesis is purely descriptive, which was considered an essential first step into a long-term project where the basics still needed to be elucidated. Obviously, a descriptive approach raises concerns about correlations versus causations. Conceptual models will have to be developed, parameterised and rigorously tested in near-future work. This thesis should provide a solid basis for future (field-) experiments and more precise research questions. Underlying the work presented in this thesis are many years of field study and field experiments. Even though emphasis on gulls was a relatively recent aspect of my professional work on seabirds, ever since a personal fascination for seabirds began (on 18 October 1973, 09:30h), I have been collecting and often published data that now came in as useful. I chose to exploit and use most these data and (parts of) publications that were based on them throughout.

Seawatching (1973-1988) Systematic seawatching, a technique of birdwatching that developed strongly in the late 1960s and early 1970s, formed the most important source of information on the seasonal occurrence and migratory movements of seabirds and waterfowl off the Dutch coast. As a novel technique, at a time when powerful (often Japanese) binoculars suddenly became financially affordable and in widespread use, seawatchers discovered that many true seabirds were in fact much more common than previously though. The technique, in which effort-corrected data were collected on a grand scale, also produced important insights in year-to-year fluctuations and seasonal patterns of migratory movements of true seabirds, waterfowl, waders, gulls and terns (Camphuysen 1985). Being heavily involved in seawatching in the 1970s, I was given the opportunity to work on the first comprehensive publication reporting seawatching results, published as a special issue of *Limosa* (Camphuysen & Van Dijk 1983). Co-workers in these early years of seawatching were Rob Bijlsma, Pieter Bison, Gerard Dumay, Mennobart van Eerden, Jelle Van Dijk, Nick van der Ham, Frank Janssen, Joop Kooyman, Frits-Jan Maas, Anja van der Niet, Jan den Ouden, Peter Meininger, Maarten Platteeuw, Adri Remeeus, Jacques Ruinaard, and Kees Woutersen, building on on seawatching studies by pioneers such as Luit Buurma, Jelle van Dijk, and Frank de Miranda. While many of the more common species of gulls, notably Herring Gulls, were in fact ignored by seawatchers during their censuses (*"At none of the observation sites has this common species* [Herring Gull] *been recorded systematically"*; Camphuysen & Van Dijk 1983), later observers (notably Nick van der Ham) have produced useful data from which the relative abundance in nearshore waters could be analysed.

Beached bird surveys (1977-2011) Systematic beached bird surveys (counts of dead birds that has washed ashore) commenced in the 1950s and 1960s, basically to demonstrate what damage was done by the frequent spillages of mineral oil into seas and oceans on the vulnerable wildlife living there. I became involved in these surveys in 1974 and have co-ordinated a national, year-round beached bird monitoring programme since 1977 till the present day (Nederlands Stookolieslachtoffer Onderzoek, NSO). Key co-workers in the early years have been Chris Braat (Haarlem), Klaas van Dijk (Groningen), Frank van den Ende (Amsterdam), Jan Andries van Franeker (Amsterdam), Kees de Graaf (Den Helder), Simon Hart (Zeeland), Gepke Jonker (Amsterdam), Ep van Hijum (Friesland), Frits-Jan Maas (Texel), Jan den Ouden (Amsterdam), Hans Schekkerman (Castricum), Jack van Velzen (Den Helder), but many, many others have contributed over the years. Following a series of cyclostyled newsletters, a quarterly journal was issued to report results to contributors, finally leading (via a merge with newsletters produced for seawatchers united in the Club van Zeetrekwaarnemers) to the seabird journal *Sula*. A first comprehensive report on results of beached bird surveys in The Netherlands was produced in the late 1980s (Camphuysen 1989a), commissioned by Vogelbescherming Nederland (Zeist) and Werkgroep Noordzee (Amsterdam), followed by overviews in the mid- and late 1990s (Camphuysen 1995b, 1997) and a serious of topical papers, often addressing the (generally declining) effects of oil on seabirds (Camphuysen 1998, Dahlmann *et al.* 1994, Camphuysen *et al.* 1999, Camphuysen & Heubeck 2001, Heubeck *et al.* 2003, Camphuysen 2010, 2011a). It became clear during this work, certainly when oil became less and less important as a cause of death among stranded seabirds, that factors such as cold weather (Camphuysen & Derks 1989), shortages of food causing oceanic birds to starve and "wreck" (Blake 1984, Camphuysen 1989bc, Camphuysen & Leopold 1996, Camphuysen 1992a, 2003), entanglements in marine litter (Camphuysen 1990a, 1994c, 2001a, 2008b), or deviations in seabird abundance such as invasions (Camphuysen & Van IJzendoorn 1988ab, Camphuysen 1992b, 1996, 2008a) could be important to explain certain events. Oil as a factor of interest was gradually pushed towards the background and more ecologically relevant questions became addressed. Older sets of data, from diaries and publications produced in the first half of the 20th century, were located and included into the database. With a database ready at hand, now spanning a period of over 110 years (1901-2011), detailing the results of beached bird surveys over *c.* 71,500 km of (Dutch) coastline during which 270,200 dead birds have been found (including over 63,250 gulls), it was clear that some relevant patterns and trends should be analysed and included in this thesis.

Seabirds at sea studies (1985-2010) While seawatchers discovered many new aspects regarding the occurrence of seabirds and migrating waterfowl in Dutch waters, the urge to explore open sea became deeper and deeper. Early contacts with British investigators in the late 1970s and early 1980s (Barry Blake, Tim Dixon, Peter Hope Jones, Mark Tasker and later also Andy Webb; the Seabirds at Sea team, Nature Conservation Council, Aberdeen) led to a general consensus as to how ship-based offshore censuses should be performed. Standardisation of data collection was seen as a vital aspect, since the need to collaborate and share data between research institutes and countries around the North Sea was foreseen in the early start of offshore seabird surveys. UK researchers could start in the late 1970s, but for us in The Netherlands, after some preliminary work in 1985, a start was facilitated only in the second half of the 1980s thanks to Henk Baptist (Dienst Getijdewateren, Zeeland), providing access on board MV *Holland* for volunteers of the Dutch Seabird Group, and to Kees Swennen/Mardik Leopold, who opened up opportunities at NIOZ, Texel. Numerous surveys were conducted since, mostly between 1987 and today, onboard a variety of vessels of opportunity, exploring the North Sea and (sub-)Arctic waters at first, (sub-)tropical and (sub-)Antarctic waters in later years. A strong coalition between Mardik Leopold and myself over the years, and an international network with co-workers in Norway (Arne Follestad), Denmark (Jan Durinck, Henrik Skov), Germany (Stefan Garthe, Ommo Hüppop, Phillip Schwemmer), Belgium (Eric Stienen, Henk Offringa, Jan Seys), Portugal (Ivan Ramirez), Spain (Pep Arcos), and of course the United Kingdom (Jim Reid, Carolyn Stone, Mark Tasker, Andy Webb, James Williams and many others) led to the accumulation of a vast amount of data (European Seabirds at Sea database), and the production of a number of distribution atlases (Camphuysen & Leopold 1994, Stone *et al.* 1995, Skov *et al.* 1995).

Discards projects (1992-1995) My professional career at the Royal Netherlands Institute for Sea Research commenced in 1992 when I was appointed by Mardik Leopold and Han Lindeboom to start investigating the effects of discards (unwanted biota dumped into the sea in commercial fisheries) on seabirds. A local or regional study onboard commercial beamtrawlers in the Southern Bight soon developed into a series of international, EC-funded research projects, led by NIOZ, in which the effects of discarding on seabird populations throughout the North Sea were studied. Key co-workers in these discards projects have been Belen Calvo, Kenny Ensor and Bob Furness (Glasgow University, UK), Stefan Garthe and Ommo Hüppop ('Vogelwarte Helgoland', Germany), Jan Durinck and Henrik Skov (Ornis Consult, Denmark), Genevieve Leaper and Mark Tasker (JNCC, UK), Arne Follestad (Norsk Institutt for Naturforskning, Norway), Henk Offringa and Chris Winter (NIOZ, Texel).

The results of these projects have been published in three comprehensive reports (Camphuysen *et al.* 1993, Camphuysen 1994a, Camphuysen *et al.* 1995) and a number of topical papers (Camphuysen 1993, 1994, 1995, Garthe *et al.* 1996, Camphuysen & Garthe 1997, 2000). Still, however, a large amount of the data collected were 'underexplored'. The results of all these 'discards-projects' are highly relevant to the studies of gulls (common scavengers at trawlers in the southern North Sea), and both publications and so far unpublished data have been used in this thesis. The projects have produced two rather different types of data: (1) information on the at-sea distribution and species-specific tendencies to scavenge around fishing vessels, and (2) detailed information on consumption rates, species and size selection and dominance hierarchies among scavenging seabirds around trawlers at sea (including the vulnerability to kleptoparasitism).

Seabird offshore foraging ecology (1995-2010) When the discards projects had finished, ship-based seabird surveys continued. Inspired by the discards projects, in which the simple counting and monitoring of seabirds per unit area were combined with ecological studies at sea, new tools were developed to investigate and quantify the foraging behaviour and interspecific feeding interactions of seabirds at sea (Camphuysen &

Garthe 2004). The techniques paid off, and seabird surveys became considerably more meaningful over time (Camphuysen & Webb 1999). A new, large, EC-funded research project aimed at studying predator-prey interactions in a marine ecosystem impacted by industrial fisheries for sandeels. In this project, the IMPRESS project, information from fisheries and fish stocks, oceanographical features and prey availability, at-sea foraging performance of seabirds, seabird distribution patterns and breeding success rates were combined. The study area was the east coast of Scotland, the main prey species was the Lesser Sandeel *Ammodytes marinus*, the principal predators were Northern Gannet *Morus bassanus*, European Shag *Phalacrocorax* aristotelis, Black-legged Kittiwake *Rissa tridactyla* and Common Guillemot *Uria aalge*, the main fishery involved was the (Danish) industrial fishery. Although *Larus*-gulls did not form the prime target of ecological attention, quite some spin-off of useful data accumulated (Camphuysen 2005, Camphuysen *et al.* 2006), particularly on the natural feeding behaviour of a whole range of seabirds and marine mammals at sea, whether or not in multi-species feeding frenzies or as solitary feeders, that were tapped in **Appendices 7** and **8** of this thesis.

Breeding biology and foraging ecology of Laridae (2006-2012). The main body of work underlying this thesis are the results from field studies in a mixed colony of Lesser Black-backed Gulls and Herring Gulls in Kelderhuispolder at Texel, where breeding biology, foraging ecology and demography have been investigated. It was Jaap van der Meer, as head of MEE department (NIOZ) at the time, who suggested that these studies should commence. Two reasons were given: (1) a continuation of work such as under the EU IMPRESS project (linking breeding performance with food supplies and oceanographic/environmental conditions at sea), but (2) while working in an ecosystem that was closer to the core activities of the NIOZ MEE department (*i.e.* the Wadden Sea and nearshore waters of the southern North Sea).

It was an ambitious undertaking, given the multi-disciplinary work under IMPRESS with no less than 11 research institutes and a multi-million Euro budget involved. The colony studies at Texel had to be set-up from scratch, basically alone, with a 4000 Euro per annum budget and the help of few students and volunteers. It should thus not come as a surprise that this mission is not yet completed. However, part of what *has* been achieved is included in this thesis and this provides insight in the (current) dietary choices and preferences of the two study species, their foraging arena, foraging habitats and feeding range, their reproductive success, nesting densities, breeding habitat preferences, breeding biology (timing, clutch volumes, clutch size, hatching and fledging success), cannibalistic behaviour, annual survival and migratory movements. Since 2006, over 1300 gulls have been colour-ringed (as fledglings or as adults) at Texel, and these will provide further data on annual survival, site fidelity, dispersal and migratory movements, recruitment rates and longevity in years to come.

The advantage of an island population is the smaller number of parameters that has to be taken into account in comparison with the mainland. Mammalian ground predators, for example, are scarce and the species list is shorter. The Red Fox, a species that arguably changed the breeding opportunities for many ground-nesting species in much of mainland Noord- and Zuid-Holland, is absent at the island (…so far). Breeding colonies on Texel, at least currently, are generally quiet, situated as they are in fenced-off nature reserves, rather distant from popular tourist resorts and substantial human settlements. Food resources of island nesting gulls may be more restricted, given that foraging habitats are less diverse than in most mainland areas. However, this had to be investigated first, given that prey preferences, feeding habitats and foraging ranges were largely unknown at the start of this project. Finally, being on the same island as the research institute is a huge advantage, because even short spells of 'favourable' weather can be used efficiently for field work activities, independent as we are for boatmen or other external access arrangements.

Co-workers students through the years have been Arnold Gronert (2006-2012, Sharon Boekhout (2006,student Larenstein, Leeuwarden), Vicky Hunt (2006, University Cornell, USA), Tim van Nus (2007, Larenstein, Velp), Janne Ouwehand (2008, RUG, Groningen), Natalia Gallego (2008, UvA, Amsterdam), Cosme Damián Romay Cousido (2009, Univ. A Coruña, Spain), Rim Lucassen (2010, RUG, Groningen), Estefania Velilla (2012, Univ. Maastricht), and Suzanne Poiesz (2012, UvA,

Colour-ring studies A large set of data was kindly provided by Arie Spaans, who had retired from Alterra (Wageningen), and this involved data that had accumulated after three colour-ringing campaigns in 14 different colonies of Herring Gulls in The Netherlands in the late 1980s (1986-1988). The database was in need of restoration and the network of ring-readers had to be reassured that this their sightings of colour-ringed gulls were still (or over time now even more so!) important and useful. When this was completed, a gold-mine of information was accessible, simply awaiting analysis and publication, and still growing (van Kleinwee &

Camphuysen 2010). Key co-workers over the years, apart from the initiator of the project (ALS) himself, have been the ringers A. Bergfeld, C.M. Berrevoets, D. de Bruyn, F. Cottaar, L.J. Dijksen, J. Jager, J. van der Kamp, G. Kasemir, R.T. Kiewiet, A. van Klinken, F. Nauta, E.O. Neve, B.A. Nolet, R. Noordhuis, C.J. Ooyevaar, K. de Rijk, N.D. van Swelm, R.J. Wanders, and A de Wit. Equally important, however, have been the dedicated ring-readers that have reported their sightings, including (top-10 only) H.J.P. Vercruijsse (16,857 sightings), A. Gronert (6043), A. van Poppel (5813), R. Costers (4377), K. Verbeek (4226), F. Cottaar (3770), B. Winters (3733), J. Rampen (3483), G. Goedhart (3000), and H.J.S. Verkade (2870). A first paper based on this material (on Herring Gull dispersal) was published recently (Camphuysen *et al.* 2011) and the data have further been explored in **Chapter 6**, and **Appendices 4** and **6**, addressing issues such as site-fidelity, annual survival and others.

Dataloggers It had always been a dream to be able to use modern data loggers, in particular to monitor the foraging whereabouts of the study species at sea in great detail (less so to monitor the migratory pathways and wintering areas, although the spin-off of the work in that direction turned out to be equally fascinating). An early opportunity, kindly provided in 2007 by Stefan Garthe (FTZ, Büsum), was set left unused, because the need to recapture incubating gulls a few days after the loggers were deployed was considered undesirable. I have been extremely fortunate to be able to collaborate in 2008-2012 with the research group of Willem Bouten at University of Amsterdam, who were able to provide high resolution GPS loggers, basically in exchange for access to a study colony and data. A further (financial) boost was given by a short research project commissioned by the Ministry of Transport and Public Works, in which the presence and abundance of Lesser Black-backed Gulls around windfarms at sea needed to be investigated (2010-2011; Camphuysen 2011b). Key co-workers in the GPS-logger projects were Willem Bouten, Edwin Baaij, Judy Shamoun-Baranes, and Emiel van Loon and results have been used throughout this thesis from recently published topical papers (e.g. Camphuysen *et al.* 2010, Shamoun-Baranes *et al.* 2010) and ongoing analyses. The logger deployments (devices with solar panels to recharge the batteries from which the data can be downloaded automatically by a receiver station in the colony, without the need to handle the birds) have provided an enormous amount of data, that was vital to enhance knowledge of nest attendance (daily time budgets), foraging range, foraging habitats, foraging flight patterns/feeding activities, resting and preening behaviour, and even migratory movements and (previously unknown) central place foraging activities from temporary stop-over sites and in wintering areas.

Appendix 1 – Human attitude, taxonomic considerations, the fossil record

Our attitude towards gulls

In the early 20th century, Herring Gulls were thought to threaten the sheer existence of tern colonies (Van Dobben 1934, Thijsse 1936, Tinbergen 1939, 1953, Mörzer Bruyns 1958). Famous Dutch naturalist Jan Drijver (1934) in his book "*Texel, het vogeleiland*" (Texel, the bird island) devoted an entire chapter on "*De meeuwen en hun wandaden*" (gulls and their misdeeds). Conservation measures, from which gulls had only just profited in the 1920s and 1930s, were openly regretted (see also Thijsse 1936). Rooth (1957) collected prey items in colonies of Herring Gulls, but failed to find the supporting evidence for the devastating effects of gulls on other birds:

> "*Indien het nemen van jonge vogels als prooi door broedvogel-zilvermeeuwen een zodanige omvang zou hebben gehad, dat het voor het voortbestaan van de belaagde soorten van betekenis was geweest, was dat stellig bemerkt.*[1]"

He was the first nor the last researcher who failed to find evidence that gulls were responsible for declining population trends in other species. In 1958, M.F. Mörzer Bruyns of the Institute for Nature Conservation and Research (RIVON) wrote an essay on "*Gulls which are a menace to other species*". Herring Gulls were thought to "*…endanger[ing] other breeding birds and in places even threatening them with extinction.*" A list was provided of 18 wild bird species, "poultry", and two species of mammals of which eggs and/or young were taken by gulls. In the 1960s and 1970s, Herring Gulls were considered a threat for Common Eider *Somateria mollissima* and Shelduck *Tadorna tadorna* ducklings (Tinbergen 1953, Hoogerwerf 1973, 1974). Swennen (1989), from a combination of observations and field experiments, demonstrated that gull predation on ducklings only significantly affected weakened chicks during scarcities of food (the 'unfit'). Ducklings that were able to find food, on more constantly favourable feeding sites (the 'fit') had a high chance to survive.

A rather different tone is used in *"The Herring Gull's World"* (Tinbergen 1953) and certainly in *"Klieuw"* (Tinbergen 1948), where Herring Gulls are depicted as interesting, highly social and curious birds. There is a short chapter on the "gull problem" in the first book, but Tinbergen was clearly more fascinated by the behaviour and family life of these birds. His field experiments on chick behaviour are world-famous. In *"Klieuw"* his observations were presented for a more general (and younger) audience. Both books have been reprinted several times and as Konrad Lorenz remarked in the foreword of *The Herring Gull's World*: *"If Karl von Frisch's name will, for all future time, be associated with the honey-bee, Niko Tinbergen's will always call to mind his work on gulls."* Indeed, the behaviour, the postures, the vocalisations and the intra-specific clashes of the Herring Gulls studied at Texel reminded me constantly to Tinbergen's comprehensive descriptions of the behaviour of these birds in his books and in numerous papers (Tinbergen 1929abc, 1932ab, 1936abc, 1937, Booy & Tinbergen 1937, Tinbergen 1948, 1949, Tinbergen & Perdeck 1950, Tinbergen 1952, 1953, 1955, 1956, 1960ab, 1970, 1971, 1978).

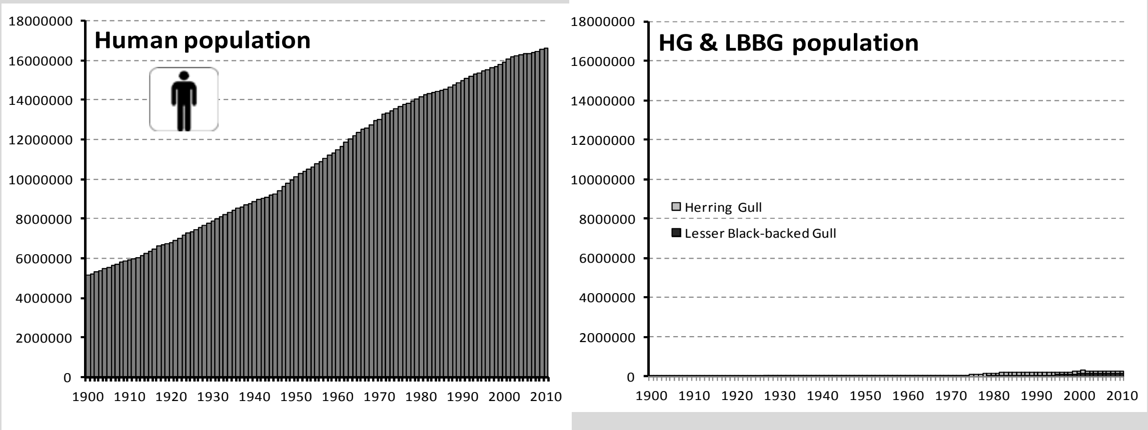
An overpopulation - Whatever 'too many' gulls is, and how many breeding pairs we should be willing to tolerate, is unclear. The Dutch human population is considerably larger than the breeding population of gulls (^{App}Box 1.1). Tinbergen (1953) described the colonies of Herring Gulls on the Frisian Islands and in Holland and Germany as "overcrowded" and used the population levels at the time as an explanation for food shortages that apparently led to egg robbery and cannibalism. There were only some 20,000 pairs breeding in the entire country when the book was published (Appendix 2). Mörzer Bruijns (1958) considered 10,000 breeding pairs of Herring Gulls quite enough and saw this as the upper limit. If the censuses are correct, there are currently about

---

[1] "If Herring Gulls would regularly take young birds as prey and if that would have affected the populations of other birds, we would have noted." (Rooth 1957)

150,000 pairs of Herring Gulls and Lesser Black-backed Gulls breeding in The Netherlands. Gulls have benefited from their abilities to invade new habitats and exploit new resources (Alerstam 1990, Rock 2003, Kelcey & Rheinwald 2005, Rock 2005). Animals come to be disliked when they interfere with the way in which we utilize the environment, compete with us for resources, damage constructions or spread disease (Furness & Monaghan 1987). The opportunistic aspects of the behaviour of gulls coupled with a high local abundance makes that many consider them as pests (Furness & Monaghan 1987).

Box 1.1 – Overpopulation?



Trends in the human population (n, left), and in Herring Gulls and Lesser Black-backed Gulls combined (n, pairs x2; same scale, right) in The Netherlands, 1900-2010.

To put the marked population increase of Herring Gulls and Lesser Black-backed Gulls throughout the 20th century[1] in a perspective, the estimated Dutch human population[2] (left) was plotted on the same scale as the number of breeding pairs of Herring Gulls and Lesser Black-backed Gulls in The Netherlands combined (right). The gull populations are barely visible in the graph. Currently, there are nine breeding pairs (Herring Gulls and Lesser Black-backed Gulls combined) per 1000 human inhabitants in The Netherlands. If we humans were to share the eggs for breakfast, it would mean one each…every 37 years.

Source: [1]this thesis, [2]Centraal Bureau voor de Statistiek 2012

Taxonomic considerations

Currently, 54 species of gulls are recognised worldwide (Gill & Wright 2006), some 23 species of which that are known to occur at least occasionally in The Netherlands (Van den Berg & Bosman 1999, Bijlsma *et al.* 2001, Wolf 2003, Ebels *et al.* 2006; Appendix 2). The subspecific identity of the Lesser Black-backed Gulls and European Herring Gulls nesting in The Netherlands may not seem to be of much significance in an ecological study. However, we might be able to understand more of the history of colonisation, hybridisation and range expansion if at least we knew where the colonising birds came from and how they are related to taxa already present in an area. The phylogenetic relationships with numerous taxa (subspecies or forms, or even distinct species according to some taxonomic conventions) around Europe, in the arctic and in the New World are highly complex and likely the result of long-term climatic oscillations, such as quaternary glacial cycles (Voous 1960, Liebers & Helbig 2002).

Lesser Black-backed Gull *Larus fuscus* Linnaeus, 1758

There has been a considerable uncertainty and debate about the taxonomy of Lesser Black-backed Gulls colonising The Netherlands in the 1920s and 1930s (Brouwer 1927, Van Dobben 1931, Van Marle & Voous 1943). Snouckaert van Schauburg (1908) had listed only a single form (as a rare winter visitor): *Larus fuscus fuscus*, the Lesser Black-backed Gull. Van Oordt & Verwey (1925), in their follow-up avifauna, made a distinction between the Scandinavian Lesser Black-backed Gull *L. f. fuscus* (a passage migrant in Sep-Nov with single cases in January, May, and in summer) and the British Lesser Black-backed Gull *L. f. affinis* (very rare, three examples). It should be noted that Lesser Black-backed Gulls of which a subspecific identity could not be ascertained were ignored in that work. These may have included gulls of the 'intermediate' type.

Van Marle & Voous (1943) looking into this matter, concluded that a whole range of mantle colours occurred, but also that according to their museum experience, *graellsii* and *intermedius* were probably inseparable in the field. Most Dutch and certain German (Niedersachsen) breeding birds were rather dark mantled, however, and it has later been suggested that in fact *L.f.* intermedius was involved rather than *graellsii* (Brouwer & Haverschmidt 1928, Tinbergen 1929, much later also Rijsdijk 1968ab, Van Orden & Ooyevaar 1971, Hausmann 1969). Drijver (1957), however, remarked that Lesser Black-backed Gulls nesting on Texel all belonged to the 'lighter British form' (*Larus fuscus graellsii*). Authors like Van Orden *et al.* (1967) copied this opinion and were rather firm in their conclusions not only that *graellsii* was the breeding form on Texel, but also that *intermedius* was a passage migrant and rare summer visitor with only a single record during the breeding period. This was repeated ten years later (Dijksen & Dijksen 1977, Strijbos 1977). It was Rijsdijk (1968ab) who provided material (colour slides) on the basis of which it was concluded that *intermedius* was nesting for the first time in The Netherlands in 1966 (two pairs near a Black-headed Gulls colony in Europoort) and 1967 (4 pairs, same place); a view that was promptly supported by prominent ornithologists of that time (CNA). Dijksen (1996a), in a more recent review, listed all three forms (nominate included) for Texel, but did not draw any conclusions regarding the subspecific status of breeding birds or passage migrants. Glutz von Blotzheim & Bauer (1982) also refrained from drawing firm conclusions, suggesting that *L.f. intermedius* was the more likely subspecies in this part of Europe, but that a comparative study covering the entire range between Denmark and Spain had to be awaited.

Barth (1968) observed, from a fairly small sample size, that Herring Gulls *L. a. argenteus* and Lesser Black-backed Gulls *L. f. graellsii* breeding in France, Belgium and The Netherlands showed upperpart grey tones and biometrics that were intermediate between the British *L. a. argenteus* and *L. f. graellsii* and Scandinavian subspecies *L. a. argentatus* and *L. f. intermedius*. Muusse *et al.* (2011), studying gulls at a Dutch colony near Moerdijk, confirmed that a majority of Herring Gulls belonged to the pale 'British form', but found that the modal grey mantle tone of many Lesser Black-backed Gulls was closer to the population mean for *intermedius* from southwest Sweden than to (British) *graellsii*. Ring recoveries confirm that British *graellsii* can be found breeding in several Dutch colonies, but the dark upperparts of many Dutch birds likely originate from Scandinavia (Muusse *et al.* 2011).

Teixeira (1979) suggested that The Netherlands had been colonised simultaneously from the west (British *graellsii*) and from the northeast (*intermedius* from Denmark and southern Scandinavia), and that both types had mixed such that subspecific identification was now impossible. It is unclear what the factual basis is for this idea. Cramp & Simmons (1983) simply listed The Netherlands under the breeding range for *intermedius*. Sangster *et al.* (1999) concluded that the form *intermedius* was not 'diagnosably distinct' from *graellsii* and that *intermedius* had to be considered conspecific with *graellsii*. In this paper they considered Lesser Black-backed Gulls *L. graellsii* and Baltic Gulls *L. fuscus* as being specifically distinct, based on differences in morphology, moult, and ecology. This position was abandoned only a few years later (Sangster *et al.* 2003), when studies were published in which mitochondrial DNA variations in gulls were found to indicate that *fuscus*, *graellsii* and *intermedius* shared the same haplotype, with no significant differences in haplotype frequency, and that the three forms had to be considered a single species, namely Lesser Black-backed Gull *Larus fuscus* (Liebers & Helbig 2002).

Voous (1960) united all Palaearctic forms of the circumpolarly distributed group of Lesser Black-backed Gulls and Yellow-legged Herring Gulls in one species: *Larus fuscus*. This group formed several complicated but continuous chains of populations, showing geographical variation in the intensity of the mantle coloration. With the exception of the northeast Siberian forms they all had yellow legs. Voous (1960) concluded that along the north-western coast of Europe, the Lesser Black-backed rather than the Herring Gull must originally have been the autochthonous form of the circumpolarly distributed group of large gulls. Voous suggested that Lesser Black-backed Gulls were "driven away" by the Herring Gull (a Nearctic invader) and he considered the settling of the Lesser Black-backed Gulls in Denmark (since 1920) and in the Netherlands (since 1926) recoveries of once lost territory.

Based on a mitochondrial haplotype network (model of gene flow relationships among 10 Lesser Black-backed Gull populations), however, Liebers & Helbig (2002) were able to evaluate the conflicting proposals regarding the origin and spread of Lesser Black-backed Gulls colonising Western Europe. Earlier proposals varied between an origin either from a *cachinnans*-like ancestor in the Aralo-Caspian basin (Mayr 1940) or from an *atlantis*-like source population in the NE Atlantic Ocean (Dwight 1922). Lieber & Helbig (2002) concluded that differentiation into *intermedius* and *graellsii* happened only very recently, as indicated by genetic uniformity and lack of population structure among these two forms. The paucity of contemporary mtDNA structure was considered to reflect "the historical legacy of a rapid and recent westward and southward expansion from Fennoscandia along with considerable population growth". The Netherlands, in other words, were colonised from the east and/or northeast rather than from the west (see also Liebers *et al.* 2004).

European Herring Gull *Larus argentatus* Pontoppidan, 1763

European Herring Gulls were part of the ongoing debate. While Dwight (1925) referred to two distinct species, Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus*, he was puzzled by the characters of *Larus cachinnans* in the Aralo-Caspian basin: "*Unless we are prepared to consider the Herring-Gull (L. argentatus) and the Lesser Black-backed Gull (L. fuscus) one and the same species, because of cachinnans, the connecting link, we must consider cachinnans a full species combining the characters of both."* Stegmann (1934) reviewed the issue (in a 'somewhat revolutionary paper'; review in *Ibis*) and drew conclusions on the basis of a then unique collection of birds including many individuals sampled in northern Europe and Asia. He united all gulls into a single species, *Larus fuscus*, with 16 forms or subspecies (*argentatus, argenteus, smithsonianus, thayeri, leucopterus (= glaucoides), vegae, birulae, taimyrensis, atlantis, michahellisi, ponticus, cachinnans, mongolicus, californicus, brittanicus (=graellsii, = affinis), and fuscus*). Meinertzhagen (1935) closely followed this proposition, and enlarged the account of (known) winter quarters. It was realised that, while in Holland and in the UK forms of the Herring- (*argentatus*) and black-backed (*fuscus*) gulls were breeding in mixed colonies, they did not (or seldom) interbreed. Moreover, with a stronger tendency to breed in coastal localities in Herring Gulls rather than in Black-backed gulls, Meinertzhagen (1935) realised that ecological aspects ("habit") and not only plumage would support separation. Incidentally, the type locality for *Larus fuscus argenteus* was Texel Island, Holland.

There was no long-lasting support for the view of a single species with 16 forms and Herring Gulls and Lesser Black-backed Gulls were generally separated as distinct species in most later publications. The debate continued as to whether *atlantis, michahellis* or *cachinnans,* or any of the other forms were belonging to one or the other group or had to be considered full species (not further addressed here). Van Marle & Voous (1943), while referring to Stegmann's paper, reviewed museum specimens and concluded that Dutch breeding birds could be separated from Swedish (or Baltic) Herring Gulls on the basis of wing pattern an biometrics. They concluded that the Dutch population should be referred to as to *Larus argentatus argenteus*, whereas the birds from the Baltic (frequently wintering in The Netherlands) were *L. a. argentatus*. This view is still generally held, even though there is a considerable overlap in morphological characteristics of the two taxa, so that individual birds cannot always be identified with certainty.

Voous (1960) treated Herring Gulls as the Nearctic representative of a circumpolarly distributed group of Lesser Black-backed Gulls and Herring Gulls (the ring-species model). The

“Herring Gull ring-group” comprised more than 20 taxa of large gulls (Dwight 1925, Mayr 1942, Glutz von Blotzheim & Bauer 1982); a connected series of neighbouring populations, each of which could interbreed, but for which two “end” populations existed, too distantly related to interbreed. On the grounds of the conspicuous resemblance between the British and the North American Herring Gulls, Voous (1960) assumed that the Herring Gull was a recent colonist in northwestern Europe, having in various places driven out or at least numerically surpassed the original west European inhabitant, the Lesser Black-backed Gull. According to Voous, this colonisation took place during or shortly after the last great glaciations.

Based on mitochondrial DNA variation among 21 gull taxa, Liebers *et al.* (2004) showed that members of the “Herring Gull complex” differentiated largely in allopatry following long-distance-colonisation events. What earlier authors (Geyr von Schweppenburg 1938, Mayr 1942, Glutz von Blotzheim & Bauer 1982) regarded as ‘herring gulls’ turned out to be an assemblage of several distinct taxa, which were not each other’s closest relatives. Liebers *et al.* (2004) found a circumpolar ring of interbreeding populations to exist but that the endpoints did not overlap. More importantly, Liebers *et al.* (2004) found no genetic evidence for a closure of the circumpolar ring through colonisation of Europe by North American Herring Gulls. Closure of the ring in the opposite direction may be imminent today, however, with Lesser Black-backed Gulls about to colonise North America (Howell & Dunn 2007).

The fossil record

Gulls (Laridae) are a bird family within the order Charadriiformes and are closely related to twelve families of wading birds (Jacanas Jacanidae to Seed Snipes Thinocoridae), sheathbills Chionidae, skuas Stercorariidae, terns Sternidae, skimmers Rynchopodidae and auks Alcidae (Del Hoyo *et al.* 1996). The Cretaceous Ichthyornis (>65Ma) was believed to be a small, gull or tern-like bird with teeth (Marsh 1872ab). It is currently assumed to have been an ecological equivalent of modern seabirds, close to the ancestry of modern birds, but representing an independent lineage (Clarke 2004). Ichthyornids appear to have been a side branch of bird evolution that died out, leaving no descendants (Dixon 2007). Charadriiforms have a scanty Paleogene record in Europe (Mayr 2009). Gull ancestors, “*Larus” elegans* and “*L.” totanoides* are known from the Upper Oligocene of France (28-34 Ma; Hugueney *et al.* 2003; Mourer-Chauviré *et al.* 2004). Both species have an abundant fossil record in early Miocene French fossil sites. These birds were small, the size of small terns, with fairly long legs (16-23 Ma; Mayr 2009). The exact phylogenetic affinities of these birds with respect to extant Laridae and Sternidae still need to be determined (Mayr 2009).

Gearing up gulls with GPS loggers is a delicate process that has to be done both quick but careful; a result is shown on page 99, shortly after release. Excessive preening at a bathing place is a first response of these birds, immediately after being handled.

Appendix 2 - When exploitation came to a halt: 18th -20th century

> *"Schoon 'er eene aanmerkelijke verfcheidenheid onder de Zee-Meeuwen is, munt deeze toch genoegzaam uit, door de Kleur en Grootte. Buiten twyfel is het de Allergrootfte Aschgraauwe Meeuw van Ray, in 't Engelsch Herring-Gull, dat is de Haring-Meeuw genaamd…Nestelen en broeden overvloedig op 't Eyerland aan Texel, [waar] hunne Eyeren aldaar in menigte opgezogt worden, zynde niet alleen goed tot fpyze, maar ook by fommigen een lekkere verfnapering"*[1]
>
> Nozeman & Houttuyn 1797

Herring Gull ("Groote Zee-meeuw, Larus cinereus"), an abundant breeding bird of Eyerland, Texel, where their eggs are collected in large numbers. Illustration in Nozeman & Houttuyn 1797 (Photo Bert Aggenbach, NIOZ).

Herring Gulls were common breeding birds in The Netherlands in historical times, at least since the 18th century. At Texel they certainly bred on Eyerland ("egg-land"), but probably also elsewhere. Early authors had difficulties with the identification and taxonomy of gulls. As late as in 1826, immature or juvenile forms were often described as separate taxa (AppBox 2.1). Apart from being uncertain about the identification of species, some early authorities relied on second hand information regarding the breeding occurrence of birds and failed to rigorously check their sources (Dijksen 1996b, Eigenhuis 1996). Despite all uncertainties, however, there is little doubt that at least the European Herring Gull *Larus argentatus argenteus* (hereafter simply Herring Gull) and the Black-headed Gull *[*formerly *Larus] Chroicocephalus ridibundus* were native, colonial breeding birds for centuries.

Gull populations in the 19th century The status of most gull species in The Netherlands before 1900 is still quite unclear. Herklots (1853), summarised existing knowledge for the mid-19th century, suggesting that four species of gulls were breeding in The Netherlands at the time (AppBox

---

[1] *Even though there is a considerable variety in sea gulls, this species is exceptional because of its colour and size. Without doubt, this is the largest, pale grey gull mentioned by Ray, Herring-Gull in English. Breeds in large numbers on the Eyerland at Texel, where the eggs are collected to serve as food or snack (Nozeman & Houttuyn 1797).*

2.2). Albarda (1897), only listed Herring Gull and Black-headed Gull as breeding birds. The Mew Gull *Larus canus* was described as a winter visitor, of which a breeding colony was found on Texel in the past (“*vroeger*”). Earlier claims of nesting Great Black-backed Gulls *Larus marinus* on Texel (Houttuyn 1763, Schlegel 1852, 1854-58, 1860ab) were regarded erroneous (“eene dwaling”). The status of the Lesser Black-backed Gull *Larus fuscus*, a species for which we have no breeding evidence in historical times (unless confused with Great Black-backed Gulls), is perhaps even more obscure. Herklots (1853) and Schlegel (1860ab) both referred to this species as a migrant in autumn, with young birds as uncommon winter visitors. Schlegel (1878) adds that Lesser Black-backed Gulls (*“Kleur volkomen als bij de Mantelmeeuw, maar de poot en geelachtig, en hierdoor, zoo als door de mindere grootte gemakkelijk van de voorgaande te onderscheiden”*[2]) breed in Britain, but are otherwise distributed as the Great Black-backed Gull. He is not very clear about a possible breeding status within The Netherlands (*“broedt zelfs aan de kusten van Groot-Brittanje, maar, zoo als het schijnt, niet aan de onze, alwaar zij gewoonlijk in September aankomt en doortrekt*[3]*”*). Snouckaert van Schauburg (1901) reports the shooting of an adult in October 1900 in Hornhuizen (Groningen) and comments: *“Van deze soort, die bij ons te lande niet talrijk voorkomt, worden slechts zelden oude exemplaren waargenomen; meest worden jeugdige vogels in het grauwe kleed aangetroffen.”*[4]

Box 2.1 – The “Wagel dress”

The “Wagel”, known as the Great Grey Gull or Grisard or Burgo-master *Larus nævis* from Linnaeus, was in fact the juvenile Great Black-backed Gull (or any other large gull, given that “the young of all the British Gulls, ..., for the first year or two,...appear in the Wagel dress”). Bewick (1826) had just realised that Wagel’s were immature gulls. *“We have continued the name and description of this bird as a distinct species, though it is now familiarly known to be the young of the Black-backed Gull. We may observe here that the young of all the British Gulls, except perhaps the Kittiwake, and Black-headed Gull, have the whole plumage more or less spotted with ash grey on a dull white; for the first year or two, they all appear in the Wagel dress, scarcely differing in anything but in shade and size.”*

The “Wagel dress”

Source: Bewick T. 1826. A history of British Birds, Vol. II. Edw. Walker, Newcastle

Apparently, a steep decline in the breeding populations of gulls occurred after the mid-19th century. At Texel, colonies of Herring Gulls at De Hors [the current study area] and near Den Hoorn colonies disappeared around 1890 (Drijver 1934). Some were known to breed in low areas of Dijkmanshuizen and in Mielanden, but because the eggs were taken by humans, isolated breeding attempts usually failed. Around 1900, only two species of gulls were still able to breed in The Netherlands (Black-headed Gull and Herring Gull), but the populations were small.

Colonisations in the 20th century - In the 20th and early in the 21st centuries, eight new species of gulls colonised or tried to colonise The Netherlands. A total of 22 species occur at least occasionally in our region, of which ten as breeding species (Hustings & Vergeer 2002;

---

[2] *Colour as in black-backed gull, but feet distinctive yellowish and smaller*

[3] *Breeds even along the coast in Britain but, apparently, not along our coasts, where she normally arrives as a passage migrant in September*

[4] *Of this species, that is uncommon in our country, adult individuals are rarely seen; most are young birds in a dull plumage.*

Box 2.2 – Gulls in The Netherlands in the 19th century

Herklots[1] summarised existing knowledge for the mid-19th century as follows, suggesting that four species bred in The Netherlands (presumed breeding species in bold):

Larus marinus, Linné, De Mantelmeeuw	**Great Black-backed Gull**	"Broeit, in zeer klein getal, op de duinen langs onze kusten. Standvogel" [*Breeding in small numbers, resident*]
Larus fuscus, Linné, De kleine mantelmeeuw	Lesser Black-backed Gull	"In het najaar, op den doortrek langs onze kusten. De jongen overwinteren niet zelden." [*Passage migrant; young birds overwinter]*
Larus argentatus, Brünnich, De Zilvermeeuw	**European Herring Gull**	"Broeit in de duinen. Standvogel" [*Breeding, resident*]
Larus canus, Linné, De kleine zeemeeuw	**Mew Gull**	"Broeit in de duinen. Standvogel" [*Breeding, resident*]
Larus glaucus, Brünnich, De burgemeester	Glaucous Gull	"Na zwaren noordweste storm, in het koude jaargetijde" [*Storm-driven winter visitor*]
Larus tridactylus, Linné De drieteenige meeuw	Black-legged Kittiwake	"In het koude jaargetijde, op den doortrek aan onze zeekust" [*Winter visitor, coastal*]
Larus ridibundus, Linné De kokmeeuw	**Black-headed Gull**	"Broeit op de meren…, Verhuist in het najaar" [*Breeding inland lake, migration in autum*]
Larus capistratus, Temminck De kleine kokmeeuw	species unknown	"Op den doortrek, in het koudere jaargetijde, langs onze zeekusten" [*Winter passage, coastal*]
Larus minutus, Pallas De dwergmeeuw	Little Gull	"In den zomer waargenomen, somtijds, zeer zeldzaam, op den doortrek in het najaar aan het zeestrand" [*Summer sightings, rare in autumn along the coast*]

Source: [1]Herklots J.A. 1853. Bouwstoffen voor eene Fauna van Nederland, onder medewerking van onderscheidene Geleerden en Beoefenaars der Dierkunde. Eerste Deel. E.J. Brill, Leiden.

Camphuysen & de Vreeze 2005; Boele 2012; AppBox 2.3). The process of colonisation by gulls often began with interbreeding between the newcomer and closely related established taxa. Brouwer (1927), Tinbergen (1929), van Dobben (1931) and Voous (1946) found Lesser Black-backed Gulls hybridising with Herring Gulls in the late 1920s. The first Mediterranean Gulls *Ichthyaetus melanocephalus* breeding in The Netherlands hybridised with Black-headed Gulls in 1933 (Vijverberg 1935). Breeding of Yellow-legged Gulls *Larus michahellis* was first established in 1985, when a male was found nesting with a Lesser Black-backed Gull, and another with a Herring Gull, in the large mixed colonies of the port of Rotterdam (Europoort and Maasvlakte; Van Swelm 1998). As soon as the number of individuals of the colonising species increased, the phenomenon died out or became rare. No known hybrid pairs were formed during first breeding attempts of Little Gulls *Hydrocoloeus minutus*, Great Black-backed Gulls *Larus marinus* or Black-legged Kittiwakes *Rissa tridactyla*.

Current winter visitors, passage migrants and vagrants (12 species) originate mostly from the New World (4) and the high arctic (5), with some representatives from Asia (2) and the Mediterranean (2) (AppFig. 2.1). It is speculative to forecast any further colonisations, but given climate change, these would more likely originate from the Mediterranean region (e.g. Slender-billed Gull *Chroicocephalus genei* or Audouin's Gull *Ichthyaetus audouinii*) rather than from the arctic. It is interesting to note that two Mediterranean species are recent additions, as vagrants, to several national lists in NW Europe and that in some cases these were either repeated sightings (of different individuals) or even flocks of birds rather than isolated events (Wolf 2003, Ebels *et al.* 2006 and other recent reports).

When reconstructing population trends over the 20th century, marked changes in abundance (AppFig. 2.2) and species composition (AppFig. 2.3) are found. **Black-headed Gulls** were the most numerous breeding species throughout. During the first half of the 20th century, less than 50,000 pairs of Black-headed Gulls were nesting in The Netherlands (Van Dijk 1998). After decades of increase, the population peaked in the early 1980s at some 225,000 pairs. During

Box 2.3 – Gulls in The Netherlands since 1900

All species of gulls observed in The Netherlands since 1900, including first breeding attempts (B, year). Breeding species are in bold, taxonomic conventions following the IOC Birdlist of the world[11].

Species	Scientific name	br	First breeding or status
Ivory Gull	*Pagophila eburnea* (Phipps, 1774)		*(vagrant, high arctic)*[2]
Sabine's Gull	*Xema sabini* (Sabine, 1819)		*(passage migrant, high arctic)*[3]
Black-l. Kittiwake	*Rissa tridactyla* (Linnaeus, 1758)	B	<2000 offsh. platf.[1]
Slender-billed Gull	*Chroicocephalus genei* Brème, 1839		*(vagrant, Mediterranean)*[2]
Bonaparte's Gull	*Chroicocephalus philadelphia* (Ord, 1815)		*(vagrant, New World)*[2]
Black-headed Gull	*Chroicocephalus ridibundus* Linnaeus, 1766	B	<1900 [3-4]
Little Gull	*Hydrocoloeus minutus* Pallas, 1776	B	1942 Friesland[6]
Ross's Gull	*Rhodostethia rosea* (MacGillivray, 1824)		*(vagrant, high arctic)*[2]
Laughing Gull	*Leucophaeus atricilla* Linnaeus, 1758		*(vagrant, New World)*[2]
Franklin's Gull	*Leucophaeus pipixcan* Wagler, 1813		*(vagrant, New World)*[2]
Mediterranean Gull	*Ichthyaetus melanocephalus* Temm., 1820	B	1933 Schouwen[5]
Audouin's Gull	*Ichthyaetus audouinii* Payraudeau, 1826		*(vagrant, Mediterranean)*[2]
Pallas's Gull	*Ichthyaetus ichthyaetus* Pallas, 1773		*(vagrant, Asia)*[2]
Mew Gull	*Larus canus* Linnaeus, 1758	B	1908 Rottumeroog[7]
Ring-billed Gull	*Larus delawarensis* Ord, 1815		*(vagrant, New World)*[2]
Great Bl.-backed Gull	*Larus marinus* Linnaeus, 1758	B	1993 Delta area[9]
Glaucous Gull	*Larus hyperboreus* Gunnerus, 1767		*(passage migrant, arctic)*[3]
Iceland Gull	*Larus glaucoides* Meyer, 1822		*(passage migrant, arctic)*[3]
European Herring Gull	*Larus argentatus* Pontoppidan, 1763	B	<1900 [3-4]
Caspian Gull	*Larus cachinnans* Pallas, 1811	B	2012 Amerongen[12]
Yellow-legged Gull	*Larus michahellis* J.F. Naumann, 1840	B	1985 Europoort[10]
Lesser Bl.-backed Gull	*Larus fuscus* Linnaeus, 1758	B	1926 Terschelling[8]

References: [1]Camphuysen & de Vreeze 2005, [2]Van den Berg & Bosman 1999, [3]Bijlsma *et al.* 2001, [4]Snouckaert van Schauburg 1908, [5]Vijverberg 1935, [6]Brouwer & Haverschmidt 1942, [7]Van Pelt Lechner 1908, [8]Bouma 1929, Tinbergen 1929, [9]Vercruijsse & Spaans 1994, [10]Van Swelm 1998, [11]Gill & Donsker 2010, [12]Boele 2012

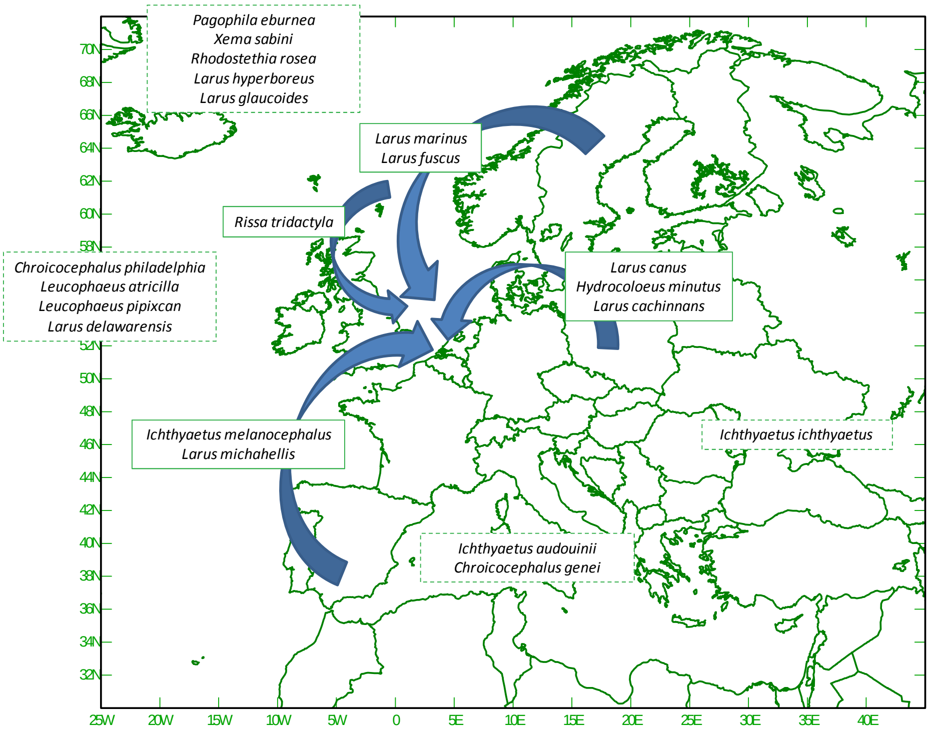


Figure 2.1 Colonisation of The Netherlands by gulls since 1900 and the origin of species observed as passage migrants or vagrants (including five taxa from the New World). Arrows indicate directions of colonisation; dashed boxes list species of which colonisations attempts are not known.

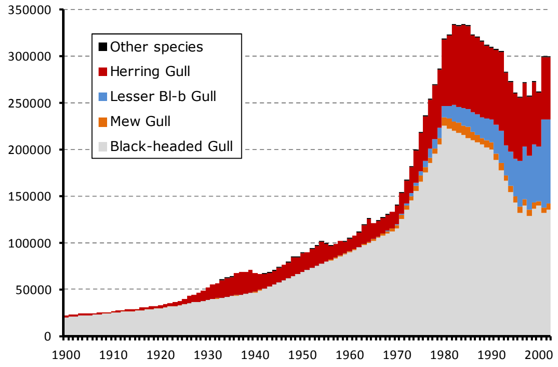


Figure 2.2 Reconstructed population trends (p) for 9 species of gulls breeding in or colonising The Netherlands in the 20th century (multiple sources; see text).

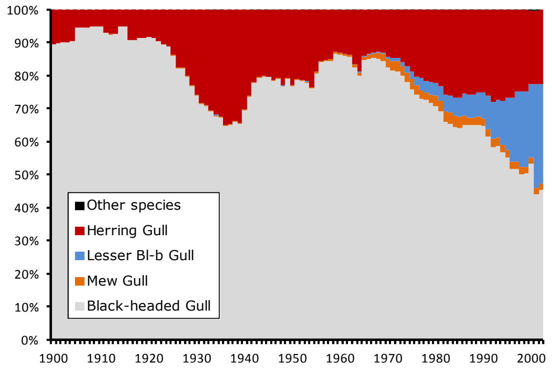


Figure 2.3 Species composition (%) for 9 species of gulls breeding in or colonising The Netherlands in the 20th century (multiple sources; see text).

the late 1980s and the early 1990s, however, a considerable population decline occurred. In the late 1990s, the population was estimated at 132,000 pairs, only 123,000 pairs were breeding in 2005 (Van Dijk *et al.* 2007). Common or **Mew Gulls** first nested in 1908 (Keijl & Arts 1998). Numbers remained low at first, but in the early 1960s, just over 1000 pairs were counted, mainly in the Wadden Sea area and in Noord-Holland. Numbers increased sharply in the 1970s, especially in de mainland dunes. In the mid-1980s, with over 11,500 pairs breeding, more than 50% were found in Schoorl (Noord-Holland). Red Foxes (re-) appearing in Noord-Holland drastically reduced the reproductive success and eventually also the number of breeding pairs (Woutersen 1992, Woutersen & Roobeek 1992). Mainland Mew Gulls dispersed, formed smaller colonies, and commenced breeding on roofs in towns. At the same time, numbers of breeding Mew Gulls slightly increased in the Wadden Sea and Delta areas (Keijl & Arts 1998). Between the mid 1980s (*c.* 11,500 pairs) and the late 1990s (*c.* 6000 pairs), the Dutch population almost halved. Breeding numbers of **Little Gulls** (Koks 1998), **Mediterranean Gulls** (Meininger & Flamant 1998), **Great Black-backed Gulls** (Koks & Jongenelen 1998), **Yellow-legged Gulls** (Van Swelm 1998), and the offshore nesting **Black-legged Kittiwakes** (Camphuysen & Vreeze 2005, Camphuysen & Leopold 2008) have thus far been relatively small. Population trends of Herring Gulls and Lesser Black-backed Gulls are summarised below.

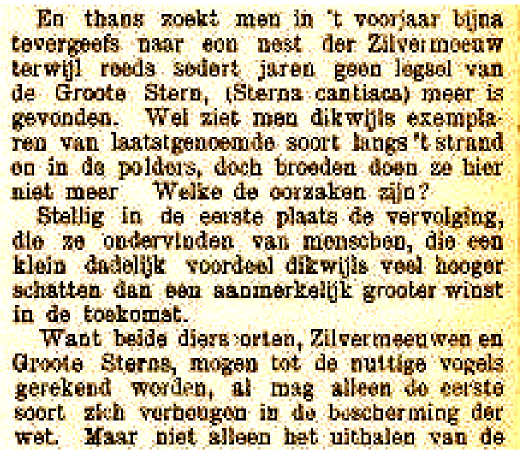
Herring Gulls and Lesser Black-backed Gulls in The Netherlands in the 20th century

In the sections now following, a chronological description of population developments of Herring Gulls and Lesser Black-backed Gulls is provided. Note that colony counts, summarised per decade, were not necessarily accurate. Census techniques have seldom been documented and the reconstruction includes some interpolations of data in case of missing values. Many publications refer to breeding pairs, but it is usually unclear if active nests, occupied territories or simply the total number of birds divided by two (or any other factor) were presented. In this chronological overview, some of the driving factors are touched upon, where appropriate, but the drivers are dealt with later in this appendix.

1900-1910 (1300-2300 bp Herring Gull, Lesser Black-backed Gull not breeding)

Around 1900, a few thousands of Herring Gulls were breeding in The Netherlands and most colonies were exploited (^{App}Fig. 2.4). The small population size in the late 19th century resulted from ruthless and widespread egg collecting, shooting, hunting, and persecution (Spaans 2007). In 1907, the widespread egging was halted ("Vogelwet 1907", Royal Decision July 1907). Permission was granted only under special circumstances, for example in so-called "Vogelarijen". Successful nesting for Herring Gulls had in fact only been possible in situations where eggs were collected systematically, but only until a certain date, to allow for some reproductive success and to safeguard future yields from the same site. Albarda (1897) listed Herring

Gulls as *"abundant residents, very common along the coast, breeding in colonies in the dunes".* Snouckaert van Schauburg (1908) suggested that Herring Gulls were mostly breeding on 'the islands' (i.e. in the Wadden Sea), in dunes and on sand banks. Leege (1907), visiting the Dutch Wadden Sea islands in 1906, was much more precise and he concluded that few pairs of Herring Gulls bred at Texel, hundreds on Vlieland, few on Terschelling and Ameland, 50 pairs on Schiermonnikoog and about 1000 pairs on Rottum.



En thans zoekt men in 't voorjaar bijna tevergeefs naar een nest der Zilvermeeuw terwijl reeds sedert jaren geen legsel van de Groote Stern, (Sterna cantiaca) meer is gevonden. Wel ziet men dikwijls exemplaren van laatstgenoemde soort langs 't strand en in de polders, doch broeden doen ze hier niet meer. Welke de oorzaken zijn?

Stellig in de eerste plaats de vervolging, die ze ondervinden van menschen, die een klein dadelijk voordeel dikwijls veel hooger schatten dan een aanmerkelijk grooter winst in de toekomst.

Want beide diersoorten, Zilvermeeuwen en Groote Sterns, mogen tot de nuttige vogels gerekend worden, al mag alleen de eerste soort zich verheugen in de bescherming der wet. Maar niet alleen het uithalen van de

"Currently, it is almost impossible to find a nesting Herring Gull in spring and Sandwich Terns have not nested for years. We do see these terns foraging along the beach and in polders [?], *but they do not longer breed here. What could be the reason?*

Obviously, the relentless persecution by man, who value short term profits higher than possible future revenues. While both species, Herring Gulls and Sandwich Terns, are seen as useful species, only the former enjoys protection by law."

Figure 2.4. Clipping from Texelse Courant, 9 November 1902.

Van Pelt Lechner (1900) had reported serious declines in the Rottum population, from *c.* 5000 pairs in 1869 to less than 2500 pairs around the turn of the century. This decline had continued, partly because much of Rottum had been washed away by the sea (Leege 1907). Snouckaert van Schauburg (1908) does not provide information on Herring colonies in the Delta area or on the mainland, but Tesch (1907) mentions colonies in 'the mainland dunes' ("Hollandsche duinen") and near Hoek van Holland, but not at Texel. In fact, however, between 1900 and 1905 a few pairs of Herring Gulls were nesting west of Den Hoorn at de Hors on the south tip of Texel, but due to frequent disturbances and egging, the species disappeared (Anon. 1902, Drijver 1936). Herring Gulls nested at Schouwen, where eggs had been collected in 1881, but the population around the turn of the century was probably rather small (Heerebout 1982, Werkgroep Avifauna Natuur- en Vogelwacht Schouwen-Duiveland 1986). Lesser Black-backed Gulls were described as winter visitors (Sep-Mar) in very small numbers with occasional reports in summer (Albarda 1897, Snouckaert van Schauburg 1908).

1910-1920 (1350-2900 bp Herring Gull, Lesser Black-backed Gull not breeding)

Further protective measures were implemented around 1912 ("Vogelwet 1912"; Anon. 1912), and several colonies became protected as a result of private initiatives (Staatsboschbeheer, Vereeniging tot Bescherming van Voogels). For the first time in history, colonies could develop without disturbance, and as a result, the numbers of Herring Gulls increased. Thijsse (1912ab), after a visit to the "Vogelarij" at Rottum, described the practice of "controlled egging" (allowed only after special permission until 15 June, 3-egg clutches remained untouched throughout, a single licence is provided) and the apparently successful measures to protect the colony by the warden of the island. It was also following this visit, however, that concerns were expressed that Sandwich Terns *Sterna sandvicensis* suffered from increased predation by Herring Gulls (Thijsse 1912b). On the neighbouring island Schiermonnikoog, where 50 pairs of Herring Gulls bred, the colony was fully protected and an increase was foreseen (Woltman 1914). A few nests of Herring Gulls were found in dune areas between Zandvoort and Noordwijk (Verwey 1915), but large numbers occurred only in the more traditional sites. An increase in breeding numbers was reported from Den Haag (Van der Vliet 1918). Vijverberg (1917) is one of the first authors to mention anything about the diet of Herring Gulls, in this case of birds nesting at Schouwen (Haemstede). Apart from a single Common Starfish *Asterias rubens*, numerous pellets were found to contain crushed Common Mussel shells *Mytilus edulis*.

1920-1930 (2700-13,500 bp Herring Gull, Lesser Black-backed Gull colonising, <10bp)

Numbers of breeding Herring Gulls steadily increased and new sites were colonised. Between 1925 and 1930, the total breeding population amounted to 8000-10,000 breeding pairs in 20 colonies (^{App}Table 2.1; Haverschmidt 1942, Mörzer Bruijns 1956). The entire coastline had been colonised and Mörzer Bruijns (1956) specifically mentioned that these birds did not cause any problems and that their numbers were therefore not too large. Relatively large Herring Gull colonies were known to occur at Rottum, Noorwestplaat, Schiermonnik-

Table 2.1. Estimated numbers of Herring Gulls breeding in The Netherlands in the late 1920s to late 1950s (after Ardea 17: 14-18, Ardea 28: 96, Haverschmidt 1942 and Mörzer Bruijns 1958).

Location	**1926**	**1938**	**1948**	**1957**
Rottum	800	1000	2200	1150
Noordwestplaat*)	275	175		
Schiermonnikoog	3500	4000	2000	1400
Ameland	5	400	750	175
Terschelling	1300	6000	1600	1750
Vlieland	500	2500	800	900
Texel	300	1800	4000	1800
Callantsoog	30	800	1350	1200
Schoorl	n.d.	50	n.d.	970
Bergen	250	500	400	150
Heemskerk	n.d.	3100	2000	1400
Kennemerduinen	n.d.	n.d.	n.d.	600
Zandvoort	n.d.	n.d.	n.d.	40
Noordwijk	45	100	100	30
Wassenaar	80	600	400	1000
De Beer	n.d.	0	n.d.	275
Voorne	0	20	n.d.	0
Scheelhoek	0	0	60	70
Goeree	0	0	0	5
Schouwen	"100s"	5000	4000	1800
Walcheren	0	0	0	45
Saeftinghe	0	0	1	250
Braakman				41
	7085	26045	19661	15051
Estimated	10000	26000	19000	15000

*) Not separated from Rottum in later years

oog, Vlieland (Wadden Sea islands) and in Zwanenwater (mainland coast Noord-Holland), smaller settlements occurred at Terschelling, Texel (Wadden Sea), Bergen (mainland Noord-Holland), Wassenaar (mainland Zuid-Holland) and Schouwen (Delta area; Van Oordt & Verwey 1925). Between Noordwijk and Bergen, occasional breeding pairs were found. Meyendel (Wassenaar), where 250 breeding pairs were reported (Groot 1921, Schierbeek 1926, van Dijk *et al.* 1981, van Ommering & van der Salm 1990; *Ardea* 18:21, *DLN* 30: 244, *Ardea* 25:82), was first mentioned as a breeding site, while Tinbergen (1939, cited in Van der Hammen 1978) indicated that Herring Gulls had occurred near Wassenaar as breeding birds "for centuries". Bouma (1927), from the colony in Wassenaar, is the first to mention domestic refuse (margarine wrappings) and mammals (Rabbit *Oryctolagus cuniculus*) as Herring Gull prey items.

In the mid-1920s, Lesser Black-backed Gull were still considered scarce winter visitors and passage migrants in small numbers (mostly Aug-Nov; Van Oordt & Verwey 1925). The first three breeding attempts of Lesser Black-backed Gulls were recorded in 1926 at Boschplaat, Terschelling (Bouma 1929, Tinbergen 1929abc). In 1929, more or less isolated pairs of Lesser Black-backed Gulls were found nesting in at least three colonies of Herring Gulls: Schiermonnikoog (possible breeding; certain in 1934; Haverschmidt 1942), Terschelling (see above) and Schouwen (Rutten 1929). On Haamstede on Schouwen, Lesser Black-backed Gulls were probably breeding in 1927 and 1928, while 3 pairs were found in 1929 (Haverschmidt 1942). Haverschmidt (1942) listed totals of 5 pairs (or nesting attempts) for 1927 and 1928, 6 in 1929, and 9 in 1930. In 1928, a more accurate investigation at Terschelling indicated that the birds did not all belong to the same type: there was a considerable variation in mantle colours (Tinbergen 1929c). There were 5 birds resembling the *intermedius*-type, one bird was rather dark and approximated the nominate race in colour, while another was light with pale yellow legs. There were two other fairly dark birds, one of which was mated with a Herring Gull (three eggs). According to the wardens, at Terschelling, chicks hatched in the first half of June.

1930-1940 (13,500-26,000 bp Herring Gull, 10-20 bp Lesser Black-backed Gull)

Number of Herring Gulls breeding in The Netherlands continued to increase and with that concerns about what was described as 'an overpopulation' were expressed more and more often (Van Dobben 1934):

> *Tenslotte zou ik graag de nadruk willen leggen op de wenschelijkheid, alle meeuwenkolonie's aan een contrôle te onderwerpen. Er zijn er b.v. in ons land, die nog ongestoord doorgroeien, omdat de schade ervan op het moment niet zoo gevoeld wordt. Later kunnen we er echter de grootste last mee krijgen. Om in dit opzicht verrassingen te*

> *voorkomen, hebben we immers de aangewezen taktiek, om verdere uitbreiding van het aantal meeuwen door het schudden van een funk percentage eieren, bv. 2 per nest, te voorkornen. In de laatste jaren heeft het geslacht Larus de vogelbescherming voor moeilijke problemen gesteld. De geweldige toename, in ons land vooral van zilver- en kap-meeuwen, aanvankelijk met vreugde begroet, heeft tenslotte door het brutale ,,Draufgangertum" van deze vogels de vorm van een ware meeuwenplaag aangenomen. Andere vogels, die we graag willen behouden, zijn hierdoor dusdanig in het gedrang gekomen, dat een beperking van het aantal meeuwen noodzakelijk is geworden. Er is geen sprake van een uitroeien van de meeuwen. Zij moeten onze kusten blijven versieren, en de steden opvroolijken, en dat in groot aantal! Het gaat slechts om een beperking, misschien is het al voldoende, om verdere uitbreiding van het aantal te voorkomen, en verplaatsingen te bewerken.*[5]

Substantial settlements now occurred in dune areas in Noord- and Zuid-Holland (Ardea 28, 96 cit. in Zomerdijk *et al.* 1971and cit in Van Dijk *et al.* 1981). It was clear that an important anthropogenic resource for Herring Gulls were the numerous refuse dumps (every village had at least one, larger towns used a fair number of dumps; Binsbergen (1935). "Damage on eggs and chicks of other birds" inflicted by Herring Gulls, however, was now considered a serious problem (Mörzer Bruijns 1956). Many regional newspapers published public discussions about the (presumed) damage done by Herring Gulls. Even though some wardens argued that the evidence was lacking, and even while studies of the diet of these birds showed that chick predation was apparently negligible (e.g. Bakker 1937), for the general public, many scientists and conservationists alike, the damage done by Herring Gulls was evident, even if their arguments were often subjective:

> "*Het felle oog en de forse snavel maken duidelijk, dat van nesten van andere vogels, welke door de Zilvermeeuw zijn ontdekt, weinig overblijft*." (subscript of photograph in Mörzer Bruijns 1956).[6]

Some 30 pairs of Herring Gulls were found nesting at Texel in 1919, 50 pairs in 1920 and around 1500 pairs in the early 1930s (Drijver 1934). Breeding gulls (Herring Gulls and Black-headed Gulls) were now considered a significant threat to other wildlife and to farmer's properties.

> *"Zij zwermden uit de polders naar de boerderijen en de dorpen en kwamen al spoedig tot de ervaring, dat piepkuikens in smaak niet onderdoen voor leeuwerikjes en kievitjes, en dat het niet eens zoo moeilijk was een booze kloek te overrompelen… Zelfs de jonge musschen en spreeuwen onder de dakpannen, al was het ook in de kom der dorpen, waren niet meer veilig."* (Drijver 1934).[7]

New, poorly planned initiatives were meant to turn the tide. Nest were disturbed and eggs were removed, but while intended to stop the increase, these actions had an adverse effect: the few and dense colonies were disturbed, but more small colonies became established in other areas, even closer to human settlements in places. In 1938, persecution started at all existing colonies at the time, but again in a poorly organised set-up, so that more breeding pairs resettled and dispersed. The total Herring Gull population in 1938 was estimated at 25,800-26,300 pairs (^{App}Table 2.1). The quality of this count was doubted, however, because counts were mainly done by "jachtopzieners" and reserve wardens "with variable interests" (Haverschmidt 1942). During 1939, in some of the larger Herring Gull colonies owned and managed by the State Forestry Service, stringent control began to be organised by the Herring Gull Commission, and about 10,000 adult Herring Gulls were killed by poison (strychnine nitrate; Mörzer Bruijns 1958).

Meanwhile, the population of Lesser Black-backed Gulls expanded slowly. At the Boschplaat, Terschelling, numbers increased slowly (1930 9, 1931 10, 1933 10, 1936 14, 1939 14pairs; Haverschmidt 1942). Mixed pairs (Herring Gulls x Lesser Black-backed Gulls) occurred annually since 1928, and were still found in 1933, but not in 1936 and 1939. The species was found breeding at Schouwen in 1931 and 1939 [no figures] (Haverschmidt 1942), isolated pairs were found in Schoorl and probably at Texel in 1934 (Haverschmidt 1942; Ardea 24, 55; cit. Zomerdijk *et al.* 1971). Breeding at Texel was confirmed in 1935,

---

[5] *Finally, I would like to emphasise the need to control all gull colonies. In our country there are colonies for example that can increase undisturbed, because the damage inflicted by the gulls is currently not so serious. We may get problems with them later, however. To avoid unpleasant surprises, we can minimize colony growth by killing (by shaking them) a fair proportion of the eggs, for example two per nest. In recent years the genus Larus has brought about difficult problems for conservationists. The enormous population increase, in our country mostly of Herring Gulls and Black-headed Gulls, initially welcomed with joy, turned into a gull plague, particularly because of the brutal behaviour of these birds. Other bird species, that we would also like to keep, have ran into trouble, so much so that a reduction of the number of gulls is inevitable. We wish to keep them as coastal birds and as visitors of our cities, in large numbers even. We are only suggesting a reduction of the growth of the existing population, or to make them move to areas where they do not cause problems.*

[6] *That bright eye and the heavy bill clearly show that nests of other birds, once detected by the Herring Gull, will be robbed*

[7] *They swarmed from the polders to the farmyards and the villages and soon discovered not only that small chickens taste just as nice as chicks of larks and lapwings, but also that the angry mother hen could be intimidated successfully. Even young sparrows and starlings hidden in nests under roof tiles, even those in villages, were no longer safe.*

when a pair of Lesser Black-backed Gulls was found the Westerduinen (Makkink 1935), mixed pairs were found at Vlieland in that same year (Haverschmidt 1942). Makkink (1935) described the birds at Texel and concluded that "*the grey of the mantle was very light, considerably lighter than that of the birds … on the isle of Terschelling. The light was now favourable and in all positions the grey of the mantle appeared intermediate between the grey of Larus canus canus L. and of L. fuscus subsp. from Terschelling. On the spot where the bird alighted I found afterwards a secondary, which I compared with the corresponding ones of a dozen adult birds in the Museum of Natural History at Leiden, which were all determined as L. fuscus affinis Reinh.*"

1940-1950 (13,750-20,500 bp Herring Gull, 15-45 bp Lesser Black-backed Gull)

During the second World War, 1940-45, direct observations of gulls were sparse and no census could be made (Mörzer Bruijns 1958). The use of gull eggs by the general public increased markedly, particularly so at the end of the war when human resources were at their minimum (Brouwer & Junge 1945, 1946). But even in 1941, Strijbos (1941) reported that hardly a single Herring Gull fledged from the mainland colonies: egging was widespread and in a small town as Egmond, up to 200 egg collectors would depart each morning on egging "excursions", taking any clutch they encountered in the dune area (many other species of ground-nesting birds included). Still, and much to the regret of the most fanatic, the widespread use of land mines made certain colonies no-go zones and Herring Gulls could nest there relatively undisturbed (Mörzer Bruijns 1956). In 1947, colony census was organised. The total number of breeding pairs was not as high as in 1939 (about 16,000 pairs were counted). In 1948 19,000 pairs were counted (^{App}Table 2.1). After the war, by order of the National government, an intensified campaign of systematic destruction of Herring Gulls began (Strijbos 1941, Mörzer Bruijns 1958, Braaksma 1968). At De Beer, Scheelhoek and Kwade Hoek, hundreds of gulls were shot and poisoned per annum (Ann Reports Natuurmonumenten, De Beer). Between 1946 and 1954 so many eggs were destroyed that the entire "surplus production" was removed (Mörzer Bruijns 1956). As a result, the population increased only slowly. It was intended to keep part of the Wadden Sea (notably Vlieland and Griend) and within the Delta area at least De Beer and dunes areas at Voorne and Goeree "free" of Herring Gulls (Mörzer Bruijns 1956). The systematic persecution of Herring Gulls certainly prevented a successful colonisation in the northern parts of the Delta area (Meininger *et al.* 2000). In Noord-Holland, so far, breeding occurred almost exclusively in dune areas. From the late 1930s and early 1940s on, however, inland breeding attempts have been documented indicating a further range expansion (Oude Zeug 1939, Warmenhuizen 1941-43, Geestmerambacht 1942; Van Oordt 1941, Zomerdijk *et al.* 1971). Perhaps as a result of frequent disturbances and egg-destructions within the major colonies, Lesser Black-backed Gulls increased only slowly in numbers. Breeding at Meijendel was for the first time reported in 1946 or 1948 (Van Dijk *et al. 1981*, Van Ommering & van der Salm 1990). The total breeding population of Lesser Black-backed Gulls in the late 1940s numbered only 40-50 pairs (Teixeira 1979)

1950-1960 (12,850-23,700 bp Herring Gull, 20-85 bp Lesser Black-backed Gull)

From 1949 to 1955, Herring Gull numbers fluctuated around an average of *c.* 19,000-20,000 pairs (Mörzer Bruijns 1958). A further expansion of breeding sites was recorded at Texel, where Herring Gulls were now nesting near De Geul and in the Slufter valley in the northwest of the island (Drijver 1957). The population showed a tendency to increase, although almost every year large numbers of eggs were taken and young and even adults were killed. At De Beer, between 1950 and 1960, annually some 431 ± 143.0 adult gulls were shot and poisoned (Ann Reports Natuurmonumenten; from Meininger *et al.* 2000). In 1954, 1955 and 1956 control measures were carried out more drastically throughout the country, especially in the larger colonies, because of the anticipated damage inflicted by Herring Gulls to other birds. Thousands (1954: 12,000; 1955: 10,000, 1956:7,300) of breeding birds were poisoned with bread or an egg containing 50 mg of strychnine-nitrate laid out near the nests. The effect of the 1954 campaign was noticeable in 1955 (breeding population 23,000 → 18,000) and that of 1955 in 1956 (18,000 → 14,500). The campaign of 1956 seemed to be without effect (^{App}Table 2.1), although about 25% of the breeding population was killed (14,500 → 15,000). It is suggested that the stabilisation, or even slight increase, had been caused by immigrating gulls from abroad. Mörzer Bruijns (1958 argued that "the stringent control on eggs and young in the Dutch colonies already carried out since 1946 and especially since 1954, made it improbable that these gulls originated from the Dutch population". Control measures were continued in 1957 in attempts to reduce the breeding population to about 10,000 pairs in the 1960s (Mörzer Bruijns 1958).

The total breeding population of Lesser Black-backed Gulls in the late 1950s still numbered less than 100 pairs (Teixeira 1977). In the northern part of the Delta area, a first breeding of Lesser Black-backed Gulls at De Beer was recorded in 1957 (Ten Kate 1959). In Meijendel, at least 10 pairs of (British) Lesser Black-backed Gulls were reported to nest plus a mixed pair (Lesser Black-backed Gull x Herring Gull (Blaak 1957).

1960-1970 (13,600-23,600 bp Herring Gull, 25-825 bp Lesser Black-backed Gull)

In the early 1960s, several new factors influencing population trends were identified, including the effects of organochlorine pesticides (Koeman 2007) and a modernisation of the fishing fleet (Rijnsdorp *et al.* 2008). Poisoning of (Herring) gulls, resulting from pollution of the Dutch coastal waters with organochlorine pesticides, became a serious issue during the 1960s, even though the effects were only studied in depth for terns Sternidae and Common Eiders *Somateria mollissima* (Spaans 1998b, Koeman 2007). Double beam trawling, introduced in the early 1960s, proved a successful fishing method to catch deep burying flatfish. In less than 10 years, the otter trawl fleet was replaced by a highly specialised beam trawling fleet. Engine power, the size of the beam trawl, the number of tickler chains and the fishing speed increased rapidly and fishing activities expanded into previously lightly fished grounds and seasons, enhancing foraging opportunities for scavenging seabirds on a grand scale (Rijnsdorp *et al.* 2008). In the mid-1960s, the destruction of adult gulls from "unwanted" colonies came largely to halt. In the 1960s, a public environmental awareness developed, partly in response to the book *Silent Spring* (Carsons 1962, Lytle 2007). It became more and more obvious that the continued development of industrialised countries reached a point at which an environmental crisis threatened the stability of the system (Singer 1968, Schaefer 1970). Our natural environment became something to protect (culminating into the 1970 European Conservation Year) rather than to ruthlessly exploit. With hindsight, this combination of factors in the 1960s and 1970s may have changed the tide for nesting gulls: a period of rapid population growth followed (AppFigs. 2.5-6).

Table 2.2 Population trends (rounded, estimated numbers) of Lesser Black-backed Gulls and Herring Gulls breeding in The Netherlands from 1960 to 2005 in the Wadden Sea area, in coastal colonies on the mainland (Noord- and Zuid-Holland), in the Delta area and deeper inland (from Spaans 1998ab, and SOVON database).

	Lesser Black-backed Gull						**Herring Gull**				
	Wadden	Mainland	Delta	Inland	Totals		Wadden	Mainland	Delta	Inland	Totals
1960	80	0	1	2	80	1960	6250	5460	1880	5	13590
1965	170	20	0	0	190	1965	13690	1820	1470	1	16980
1970	700	90	30	3	820	1970	16140	1460	2580	0	20180
1975	4500	300	200	4	5000	1975	31610	2980	6390	1	40980
1980	9670	1460	840	10	11980	1980	46520	7080	17040	110	70750
1985	14540	2770	2070	20	19400	1985	54440	9970	24370	100	88880
1990	13510	1770	9270	90	24640	1990	49910	3450	23760	20	77140
1995	20780	980	18900	340	41000	1995	38090	2910	28130	460	69590
2000	32610	1700	31610	950	66870	2000	29570	2150	28690	620	61030
2005	53090	4310	33970	630	92000	2005	32710	3740	16110	170	52730

During the 1960s, Herring Gulls in mainland colonies declined, and a marked increase was found on the Wadden Sea islands (AppTable 2.2). In the Delta area, a substantial increase occurred in the late 1960s. Following the continuing disturbances and destructions, Herring Gulls in mainland Noord-Holland bred almost exclusively in coastal dune areas (Zwanenwater 9 colonies, totally 110p, Schoorl 245 pairs in 1969, Schoorl-Egmond 10p, Egmond-Wijk aan Zee 70-100p). Counting colonies was difficult, as a result of the persistent disturbances of nesting locations. In Noord-Hollands Duinreservaat the population declined from from 500 to 100 pairs between 1953 and 1965. The colony at Schoorl was still frequently disturbed, and while 800 pairs bred in 1967, only 245 pairs occurred in 1969. The total breeding population in the late 1960s in Noord-Holland was estimated at only 450-500p. (Zomerdijk *et al.* 1971). Shooting Herring Gulls was still commonplace within the dune areas and Van IJzendoorn (1968) reports "dozens" of shot Herring Gulls found in Midden Heerenduin (Duin & Kruidberg near Castricum) in 1965-1967. Numbers in Zuid-Holland (Goeree-IJmuiden) reached an absolute low as a result of a combination of chemical pollution, destruction (Amsterdamse Waterleiding Duinen colony and De Beer), and culling (Wassenaar). The breeding site at Scheelhoek near Stellendam was increasingly unsuitable as a result of vegetation succession (Van Dijk *et al.* 1981).

From the mid-1960s on, numbers of Lesser Black-backed Gulls increased significantly in most colonies. On the Wadden Sea islands, the population increased from 80 to 700 pairs with a marked spurt at the end of the decade (AppTable 2.2). In Noord-Holland, around 1969, 12 pairs were reported breeding in Schoorl, a few pairs were found between Wijk aan Zee and Egmond. The Zwanenwater Nature Reserve was referred to as "a former breeding area" (Zomerdijk *et al.* 1971). In Wassenaar, c. 23 pairs were breeding in 1960-67 (Van Dijk *et al.* 1981). A "few breeding pairs" were found in Europoort in the mid-1960s (Rijsdijk 1968ab, cit in Meininger *et al.* 2000).

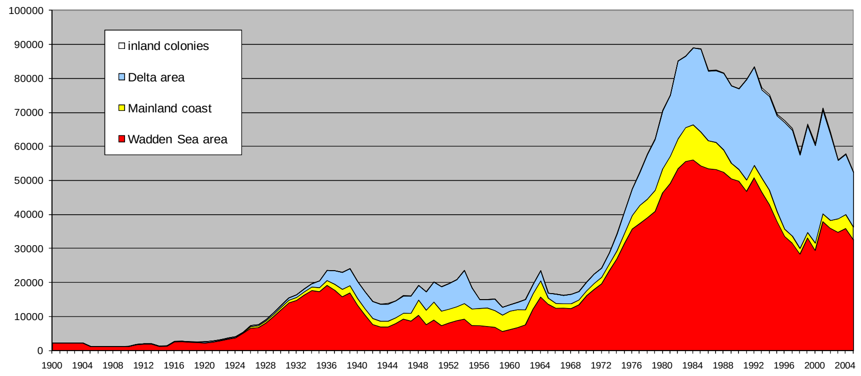


Figure 2.5. Reconstructed population trends (breeding pairs) for Herring Gulls breeding in The Netherlands in the 20th century (multiple sources; see text).

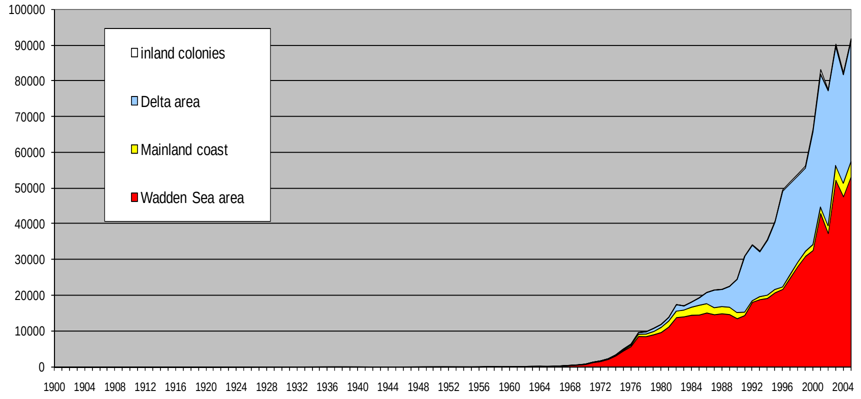


Figure 2.6. Reconstructed population trends (breeding pairs) for Lesser Black-backed Gulls colonising The Netherlands in the 20th century (multiple sources; see text).

1970-1980 (20,200-70,750 bp Herring Gull, 825-12,000 bp Lesser Black-backed Gull)

The population of Herring Gulls "exploded", from just over 20,000 in 1970 to well over 70,000 pairs in 1980 (AppTable 2.2), as a result of substantial increases in all breeding areas. Several factors may have contributed to this trend: the systematic persecution was halted, chemical pollution (drins released in the Botlek area) with immediately lethal effects was much reduced, large open rubbish dumps became established all over the country providing a rich resource of food, and coastal fisheries with beamtrawlers intensified even further (Rijnsdorp *et al.* 2008). Spaans (1979b) reported a 14% per annum increase in breeding numbers of Herring Gulls. Within the Wadden Sea area, the increase was more prominent in the western part than in the eastern part, where the effects of chemical pollution in the 1960s had been smaller. The population in a single mainland colony (Meijendel) increased from 1183 pairs in 1973 to 3257 pairs in 1979 (Spaans 1980 cit. in Van Dijk *et al.* 1981), but most other colonies increased at similar rates (Geelhoed *et al.* 1998). Breeding numbers at the Maasvlakte increased from 450-500 pairs in 1977 to 1000 pairs in 1979, with another 200 pairs at Europoort. In Zuid-Holland as a whole (Goeree-IJmuiden), the population increased from *c.* 2000 pairs in 1975 to *c.* 4900 pairs in 1979 (Van Dijk *et al.* 1981).A new colony was formed in the Grevelingen basin.

The increase in number of breeding Lesser Black-backed Gulls was even more spectacular. Spaans (1979a) reported a 30% per annum increase in breeding numbers and highlighted the end of systematic destruction of gull colonies as a vital factor. The largest coonies were now at Terschelling (8410 pairs in 1977, 7350 pairs in 1978). The numbers of breeding Lesser Black-backed Gulls in Schoorl increased from 12 pairs in 1969 to 21 in 1970. In Wassenaar, a rapid increase from 50 pairs in 1969, 80 in 1970, 406 in 1976 to 750 pairs in 1979 was found (Spaans 1980, Van Dijk *et al.* 1981). Also the colony in Europoort increased rapidly (Meininger *et al.* 2000). Further developments included: first breeding in the Amsterdam Waterleiding duinen in 1972, 2 pairs in 1979, Kennemerduinen 1 pair in mid 1970s, 2 pairs in 1979, Maasvlakte 60-80 pairs in 1977, 120 pairs in 1979 (Spaans 1980, Van Dijk *et al.* 1981). Breeding numbers in the Delta area increase from a mere 30 pairs around 1970 to 840 pairs in 1980.

Prior to 1968 the Red Fox *Vulpes vulpes* was no more than a rare vagrant in mainland dune areas (Broekhuizen *et al.* 1992). Introductions of Red Foxes in the mainland dune areas occurred in the late 1960s and early 1970s. These foxes managed to establish viable populations and colonised new coastal areas between Den Helder and Hoek van Holland. The effects on ground nesting gulls were immediately obvious in (Bouman *et al.* 1991, Woutersen 1992). Gulls responded by a marked increase in the incidence of roof-nesting (Eulderink *et al.* 1990) and by emigration to neighbouring colonies (Texel, Maasvlakte/Europoort; Meininger *et al.* 2000).

1980-1990 (70,750-89,200 bp Herring Gull, 12,000-25,000 bp Lesser Black-backed Gull)

Population trends were more variable in this period. Herring Gulls peaked at around 90,000 breeding pairs in the mid- and late-1980s, but then stabilised or declined (Spaans 1998c, Dijken 1999). A population decline in the late 1980s was particularly strong in mainland colonies (10,000 to 3500 breeding pairs; AppTable 2.2). In the northern Delta area, Herring Gulls settled that had been driven away from mainland colonies as a result from predation by Red Fox (1980-1995 explosive population growth to 10,000 pairs at Maasvlakte/Europoort; Meininger *et al.* 2000; Norman Deans van Swelm in litt.). The increase in breeding numbers of Lesser Black-backed Gulls slowed down after 1985, declines were found in mainland colonies in the same period, but breeding numbers in the northern Delta area quadrupled (Van Ommering & van der Salm 1990, Geelhoed *et al.* 1998, Dijken 1999, Meininger *et al.* 2000; AppTable 2.2). Small inland breeding populations of Herring Gulls declined in the late 1980s, but continued to increase in Lesser Black-backed Gulls.

Ground-nesting gulls in Zuid-Holland and Noord-Holland continued to suffer from Red Fox predation. The breeding population of Lesser Black-backed Gulls at Meyendel, one of the most prominent sites in mainland Zuid-Holland, increased from 850 to 1800 breeding pairs between 1984 and 1988, but rapidly declined to 1140 pairs in 1989, 450 pairs in 1990, less than 100 pairs in 1991 and only 2 pairs in 1993. Herring Gulls at Meyendel peaked at 3100 pairs in 1987, but declined to 1250 pairs in 1989, 170 pairs in 1990, 25 pairs in 1991 and went more or less extinct thereafter (http://www.vwg-m.nl/soorten/Zilvermeeuw; accessed 31 Jul 2011). It would be an oversimplification to blame all population trends in mainland gull populations on Red Fox activities, but under pressure of this predator (absent within the Wadden Sea area), many large colonies fell apart. New, smaller colonies were formed in industrial areas, in inland meadows, on roofs of buildings in major cities and on islands or relatively fox-free areas in the Delta area and in IJmuiden. Overall, the breeding numbers on the mainland declined markedly in both species (Spaans 1998abc). The virtual absence of nesting large gulls in much of mainland Noord-Holland (just south of Texel; Ruitenbeek & Cottaar 2010ab) in the 1990s and in more recent years must therefore be seen as an artefact. It is not the result of a scarcity of suitable breeding habitat.

1990-2000 (62,800-85,000 bp Herring Gull, 25,000-67,000 bp Lesser Black-backed Gull)

A change in domestic waste management became established in The Netherlands, and many refuse dumps were closed as a result. Dump sites were largely covered up, and increasing amounts of waste were incinerated rather than dumped. Meininger *et al.* (2000) observed that this trend coincided with a stabilisation and gradual decline of breeding numbers of Herring Gulls in the northern Delta Area after the mid-1990s. In 1997, the largest colony in the country at that time (Saeftinghe, Westerschelde) numbered 10,000 breeding pairs (Spaans 1998c). Since the open refuse dump at Texel was closed and covered up in 1992, the population declined by as much as 36% in six years time (11,150 pairs in 1992, 7200 pairs in 1998; Dijksen *et al.* 1999). Herring Gulls in the Wadden Sea area declined from 50,000 pairs to less than 30,000 pairs in just one decade (Spaans 1998c, Dijken 1999). In coastal mainland colonies, Herring Gulls declined from 3500 pairs to just over 2000 pairs in the same period. In the Kennemerland area (IJmuiden-Haarlem), in the early 1990s, 590 pairs of Herring Gulls were breeding, 85% of which in cities (mostly IJmuiden, some in Haarlem), and only 15% in dunes (Kennemerduinen and Midden Herenduin; Geelhoed *et al.* 1998). Numbers stabilised in the Delta area, while inland settlements increased spectacularly (20 pairs in 1990, nearly 500 pairs in 1995, over 600 pairs in 2000). Meanwhile, Lesser Black-backed Gulls continued to increase, from nearly 25,000 pairs around 1990 to c. 67,000 pairs around the turn of the century (AppTable 2.2). Mainland colonies remained more or less stable, but in the Delta area and in the Wadden Sea district the increase continued. inland settlements increased spectacularly (90 pairs in 1990, 340 pairs in 1995, to 950 pairs in 2000). In the Kennemerland area (IJmuiden-Haarlem), in the early 1990s, only 80 pairs of Lesser Black-backed Gulls were breeding, nearly all (99%) in cities (mostly IJmuiden, some in Haarlem), and only 1% in dunes (Geelhoed *et al.* 1998). At Texel, with only 2979 pairs nesting in 1995, a 73.3% increase occurred in only three years to 11,161 pairs in 1998. The authors explain this increase partly by the decline of Herring Gulls (Dijksen *et al.* 1999).

2000-2010 53,000-67,800 bp Herring Gull, 67,000-92,000 bp Lesser Black-backed Gull)

Around 2005, when the demographic studies at Texel were about to start, Herring Gulls breeding in The Netherlands had declined to *c.* 52,750 breeding pairs. With 32,700 pairs in the Wadden Sea area, this remained one of the key breeding areas. Around 3750 pairs nested in coastal areas of the mainland, just over 16,000 pairs in the Delta area and only a few hundreds were known to breed further inland (AppTable 2.2). Around 92,000 pairs of Lesser Black-backed Gulls were estimated to nest in The Netherlands (53,000 pairs in the Wadden Sea area, less than 4500 pairs in coastal colonies on the mainland, nearly 34,000 pairs in the Delta area and just over 600 pairs deeper inland. Inland colonisations continued to occur (Poot 2008), but numbers tended to remain fairly low. At Texel, there was no colony census in 2005, but in 2004 6024 territories of Herring Gulls were found (650 pairs at De Schorren, all other pairs in dune reserves). Lesser Black-backed Gulls, all nesting in dune reserves, were estimated at 14,454 pairs in 2004. Considering the result of the only earlier census in this period, 6592 pairs of Herring Gulls and 13,426 pairs of Lesser Black-backed Gulls in 2001, the former species was still considered to be in decline, while the latter continued to increase in numbers. By far the most important (mixed) breeding colony was that in the Geul area (southern tip of the island), of which the Kelderhuispolder study colony forms an integral part.

In summary - Following conservation measures, the Herring Gull population increased to *c.* 15,000 pairs in the late 1930s (12.2% increase per annum; Anon. 1918, Spaans 1998c) and that increase was considered a problem. Measures to keep the breeding population at or around 10,000 pairs were partly successful, but this required relentless persecution, including the destruction or removal of clutches and the killing of thousands of adult birds. The widespread culling came to an end in the 1960s, when Herring Gulls (among other seabird species), notably those nesting in coastal mainland colonies and in the western Wadden Sea, suffered from the effects of chlorinated hydrocarbons in the marine environment. The releases or leakages of the most toxic substances came to a halt in the late 1960s. The number of Herring Gulls subsequently increased from around 20,000 breeding pairs in the late-1960s to a maximum of nearly 90,000 pairs in the mid-1980s (11.5% increase per annum; Spaans 1998c). In the Delta area, the number of breeding pairs stabilised in the 1980s, but then increased by 41% (2.8% per annum) to 31,000 pairs in 1996. In the Wadden Sea area, numbers stabilised during the 1980s, but then declined by 40% (4.2% per annum) to 34,000 pairs in 1996. Herring Gulls on the mainland North Sea coast increased until the mid-1980s and then decreased by 79% (12.3% per annum) to 2100 pairs in 1996.

Thus, the population increase of Herring Gulls took place with two spurts of growth: from the mid-1910s to the late 1930s, and from the late 1960s to the mid-1980s (^{App}Fig. 2.5). The period in between was marked by heavy persecution (Spaans 2007). Herring Gulls occasionally nested inland during the 1940s (Strijbos 1942a) and have regularly done so from the 1960s onwards, with around 530 breeding pairs in the mid-1990s. Since the 1970s, the species has regularly nested on buildings in towns up to 25 km from the coast; in 1995-96 at least 1500 pairs were breeding on roofs of buildings (Spaans 1998c). Deeper inland, however, few birds bred successfully and the population has thus far remained small.

Following a long period with small breeding numbers after the colonisation in the late 1930s, the Lesser Black-backed Gull increased strongly to 50,000 pairs in the mid-1990s (Spaans 1998b) and subsequently to *c.* 90,000 pairs in the early 21st century (Van Dijk *et al.* 2007; ^{App}Fig. 2.6). Until the mid 1970s, breeding numbers were small and *c.* 70% were found in the Wadden Sea. This proportion dropped to 51% by 1991-96, while the relative importance of the Delta area increased from 4% to 47% (Spaans 1998b). The proportion of gulls breeding on the mainland North Sea coast initially increased to 14% by 1985, but then fell to 2% by 1991-96. An important issue in mainland colonies, both for Lesser Black-backed Gulls and Herring Gulls, was the introduction of Red Foxes into coastal dunes areas. Local ground-nesting birds dispersed or declined, roof-nesting increased, and many gulls emigrated from mainland colonies in Zuid-Holland towards the northern Delta area (Europoort/Maasvlakte) and from colonies in Noord-Holland to safer locations in IJmuiden and to Texel. Since the mid 1980s, Lesser Black-backed Gulls have regularly been found nesting on roofs of buildings up to 25 km from the mainland North Sea coast. In 1993-96, some 500 pairs were breeding on buildings (Spaans 1998b).

Drivers influencing gull population dynamics

Several drivers may affect population dynamics of gulls breeding in North Sea coastal ecosystems and in the Wadden Sea, and many of them have been briefly touched upon in the chronical overview above. Examples are fisheries, pollutants, eutrophication, and invasive species in the marine environment, but there are also more terrestrial issues such as agriculture and waste management, or global factors such as climate change. Some drivers are important for some time, others continue to affect the functioning of marine systems. Some drivers boost populations, others cause declines or act more indirectly or have delayed effects, by affecting for example fecundity or recruitment rates. In the literature, many of these drivers have been treated as isolated actors inducing environmental change. Animal populations rarely show simple patterns of growth or decline, because complex mechanisms interact over time in intrinsically complex processes (Lebreton & Clobert 1991). Multiple drivers act in concert, and ecosystem responses may become amplified or suppressed. The effects of persecution, exploitation, mammalian predation, domestic refuse dumps, fisheries, and chlorinated hydrocarbons have often been highlighted in published accounts. Issues such as eutrophication, climate change, oil pollution, severe winters, or other environmental conditions have so far not often been mentioned as important factors triggering population changes in large gulls nesting in The Netherlands. What follows here is a brief overview of such environmental conditions, human attitudes (changes in the conservation status and culling activities) and the economic changes in human society briefly touched upon before, that may have influenced the size of the breeding populations and the distribution of colonies throughout the 20th and early 21st centuries.

Early exploitation – In the 19th century and around 1900, Herring Gulls colonies were frequently raided by humans in search of eggs (for food). Besides, gulls were shot for fun in coastal holiday resorts. Around 1912, protective measures were implemented to safeguard colonies from egging and other forms of disturbance and the demand for seabird feathers had come to a halt. As soon as the first protective measures became established, the breeding population increased and new colonies became established. There is little doubt that the exploitation of seabirds, around Europe, in fact around the world, had a devastating effect on breeding populations (Croxall *et al.* 1984, Feare 1984). The relaxation of early exploitation is probably one of the main factors explaining the rapid growth of many seabird populations through the 20th century.

Early conservation - There were some protective measures for gulls in the late 19th century, considering their 'usefulness' for agriculture and forestry (*"diersoorten, nuttig voor landbouw en houtteelt"*; Anon. 1880, 1892, 1893), but eggs were still taken from nests on a grand scale and adults were illegally shot. At Rottum, erosion and an associated decline of breeding habitat were considered issues leading to a steady population decline (Leege 1907). Elsewhere, frequent disturbances and egging were thought to prevent Herring Gull colonies from increasing. In 1907, the widespread egging was halted ("Vogelwet 1907", Royal Decision July 1907). Permission to collect eggs for human consumption was granted only under special circumstances, for example in so-called "*Vogelarijen*" (see below). Protective measures were implemented around 1912 ("Vogelwet 1912"; Anon. 1912), and several colonies became protected as a result of private initiatives (Staatsboschbeheer, Vereeniging tot Bescherming van Voogels). For the first time in history, colonies could develop without disturbance. At Texel, where Herring Gulls had disappeared as breeding birds around 1890 (a few birds were found nesting in 1912; Van Eecke 1912), a re-colonisation occurred in 1914 (Drijver 1934). Nearly 30 pairs were found breeding in 1919, 50 pairs in 1920 (Drijver 1920, 1934). Breeding was successful, because the colony was protected by the Nederlandsche Vereeniging Tot Bescherming Van Vogels. The colonisation may have occurred, however, because Herring Gulls breeding at Zwanenwater (mainland Noord-Holland) were still persecuted in order to protect the vegetation. There is no doubt that the early conservation measures had a strong positive effect on the reproductive success and survival of Herring Gulls nesting in The Netherlands, so much so, that the conservationists were 'unpleasantly surprised' by the unwanted side effects of a rapidly expanding population.

Egging - After 1907, eggs of gulls and terns could no longer be collected for consumption, except in so-called "vogelarijen" with a special permission that had to be renewed annually (Thijsse 1912a). At Rottum and the nearby Noordwestplaat (eastern Dutch Wadden Sea), egging was permitted until 15 June. Egging has a negative effect on the reproductive success of birds, but in long-lived seabirds, the effects of egg removals are less devastating than direct kills of mature birds (Schreiber & Burger 2002). A new breeding season would provide new reproductive perspectives. Moreover, the "vogelarijen" provided protection of nests that would have been unavailable on other sites. Egging never stopped completely, but it became illegal. Most people currently believe that the eggs of gulls are not edible ("they taste like fish!"). While this is obviously not true, that rooted belief has greatly reduced the risk for gulls to loose their eggs.

Persecution and control New settlements of Herring Gulls and the population increase in general were not welcomed by everyone. Early measures to protect breeding sites were questioned, because Herring Gulls were thought to relentlessly plunder nests and kill offspring of other birds (Thijsse 1912b, Drijver 1920, 1934, Mörzer Bruyns 1958). Even though evidence (apart from the occasional sighting of a kill) was lacking, during the 1920s and 1930s, the pressure increased to bring the increase of Herring Gulls to a halt. During 1939, in some of the larger Herring Gull colonies, owned and managed by the State Forestry Service, stringent control measures were organised by the "*Herring Gull Commission*", and about 10,000 adult Herring Gulls were killed by poison (strychnine nitrate). Large scale egging (or the destruction of eggs or embryos) became part of the campaigns that were organised between the late 1930s and the mid to late 1960s (Mörzer Bruijns 1956, 1958). Eggs were taken on a grand scale during World War II, when the systematic destruction of gulls and their nests relaxed a bit, but when egg collectors removed virtually all eggs in certain areas (Strijbos 1941). Since the late 1960s, taking eggs of colonial seabirds is more or less illegal, but it still occurs locally for human consumption. There were indications that some reserve wardens, whether or not specifically instructed to do so, destroyed clutches of Herring Gulls to keep the numbers down, but exact figures are unavailable.

Shortly after the war, the Herring Gull population was shown to have slightly increased, even though almost every year large numbers of eggs were taken and young and adult birds were killed (Mörzer Bruyns 1958). Persecution was therefore intensified. In 1946-1954 so many eggs were taken and both young and adult gulls were killed in The Netherlands every year, that the annual surplus was eliminated. During these years, the total population stabilised at about 20,000 pairs, which was still twice the number conservationists "hoped" for and what was seen as an acceptable number of breeding pairs. Further measures to reduce the number of nesting Herring Gulls were taken and in the absence of immediate success, this developed into a systematic campaign of mass destruction in 1954, 1955 and 1956. Thousands (1954: 12,000; 1955: 10,000, 1956: 7300) of breeding birds were poisoned by placing some bread or an egg containing 50 mg of strychnine-nitrate near the nests. The effect of the 1954 and 1955 campaigns was noticeable, but that of 1956 seemed to be without effect, even though *c.* 25% of the breeding population was killed. An unexpected increase of 7000 birds was assumed to be the result of immigrating by gulls from abroad. The control on eggs and young in Dutch colonies carried out since 1946 would make it unlikely that these 7000 were (only) Dutch recruits. From 1947-1966, some 90,000 adults were either shot or poisoned and some 500,000 eggs were destroyed (Spaans 2007). Cullings were particularly severe in colonies at Vlieland (18,000 adults killed), Castricum-Wijk aan Zee (15,000), and Schouwen (18,000; Spaans (2007; $^{\text{App}}$Fig. 2.7). Between 1945 and 1966, approximately 90,000 adult Herring Gulls were destroyed.

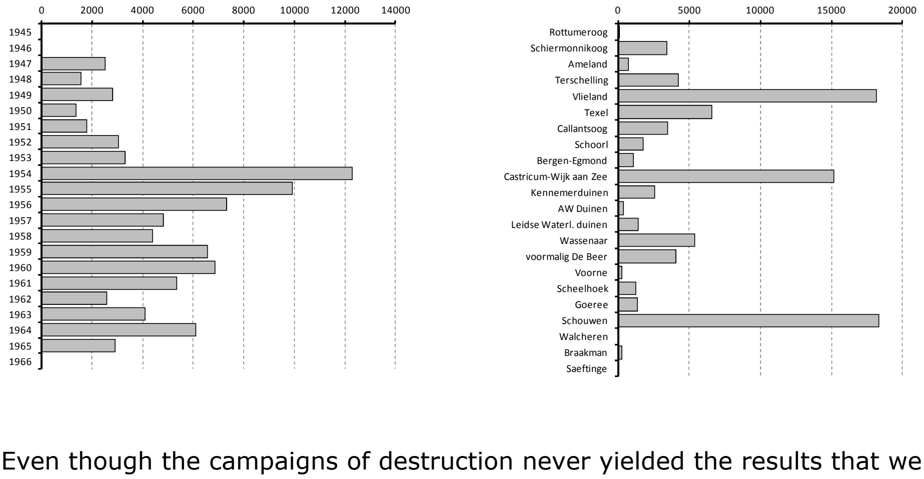


Figure 2.7. Number of Herring Gulls poisoned or shot during 1946-66 per year (left) and per colony (right, from north to south).

Source: RIVON, Spaans 2007).

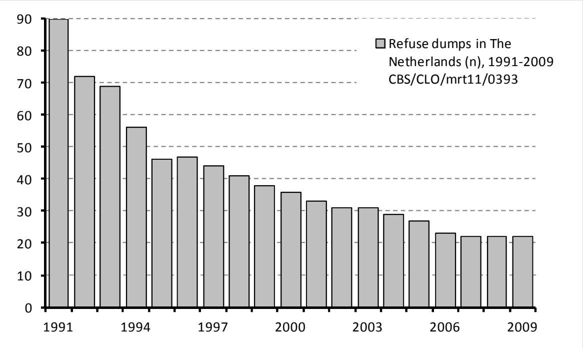
Even though the campaigns of destruction never yielded the results that were hoped for (*c.* 10,000 breeding pairs as a Dutch population and certain areas completely free from nesting Herring Gulls), it is quite evident that the inflicted mass mortality has suppressed the expansion and growth of colonies. In the mid-1960s, this type of systematic destruction came to an end. It stopped partly because the success of systematic persecution was disappointingly small, but also because of an alarming decline in breeding success of a number of seabirds and marine mammals in the Wadden Sea area, due to intoxication, following discharges of pesticides by Shell Chemie in Botlek near the mouth of the River Rhine (Koeman *et al.* 1969, Koeman 1971; see below). Large-scale anti-gull measures were stopped in The Netherlands in 1967, and in Britain and Germany in the late 1970's (Vauk & Prüter 1987, Tasker & Becker 1992). Small-scale culling still occurred in areas where gulls were considered to pose a hazard to public health, but a marked increase in breeding numbers of Herring Gulls and Lesser Black-backed Gulls followed.

Mammalian predators – Ground-nesting seabirds are vulnerable for mammalian predators (McChesney & Tershy 1998, Ratcliffe 2004). Intentionally released mammals such as cats, rabbits, pigs or goats have caused major seabird population declines, notably on (small) island populations around the world (Jones & Byrd 1979). The same is true for rats and mice (for example) that may have landed on islands unintentionally. For large gulls breeding in coastal areas in The Netherlands, until the late 1960s, there were no predators other than feral cats to (potentially) cause significant problems in colonies. Red Foxes were fairly common only in southeastern parts of the country (Limburg, east Noord-Brabant, Gelderland (Veluwe and Achterhoek), Overijssel and locally in Utrecht, Drenthe and SE Friesland (IJsseling & Scheygrond 1943, Broekhuizen *et al.* 1992). For colonies along the mainland coast of Noord- and Zuid-Holland, this changed following some releases (apparently) of Red Foxes in Kennemerduinen and in Noordhollands Duinreservaat around 1968 (Broekhuizen *et al.* 1992). The animals managed to establish viable populations and the effect on ground-nesting birds in dune areas was substantial. In the late 1960s, 1970s and early 1980s, Red Foxes increased in numbers, colonised new coastal areas between Den Helder and Hoek van Holland. Locally, small numbers became established in the Delta area, but the effects on ground nesting gulls were most obvious in mainland colonies (Cottaar & Maassen 1989, Bouman *et al.* 1991, Costers 1992, Woutersen 1992, Keijl & Arts 1998). The Wadden Sea was free of Red Foxes (Mulder 1996) until an unfortunate, but deliberate release of a couple including a pregnant female at Vlieland in 2009 (Mulder 2011). Eight young were born on the island, but most animals were eliminated in a concerted effort between wardens and hunters (Mulder 2011). Many mainland colonies were plundered by foxes and eventually either fell apart (smaller settlements) or declined substantially. Gulls responded by a marked increase in the incidence of roof-nesting (Kooistra 1985, Eulderink *et al.* 1990, Van der Helm 1992, Cottaar 2004, Roobeek 2010, Gijsbertsen 2011) and by emigration to neighbouring colonies (Schoorl and Callantsoog towards Texel, Meyendel and other Zuid-Holland dunes areas towards Maasvlakte/ Europoort), where foxes were either absent or where more or less fox-free ground could be colonised (Costers 1992, Meininger *et al.* 2000).

Waste management – Around the 1930s, Herring Gulls were well known scavengers of rubbish dumps, that could be found near virtually every village and town (Binsbergen 1935). At the time, the economic situation made people value matter differently than today and rubbish dumps contained mostly organic waste and ashes that didn't serve any further purpose. Pigs, crows, gulls, starlings and sparrows were common visitors of these dumps. The smell of the village dumps in summer was legendary, so much so that even determined bird photographers refrained from getting close to these sites on warm days. The few observations that have been published suggest that mostly immature gulls, rather few adults, frequented these dumps in summer: *"Den geheelen zomer waren er de jonge zilvers te vinden - die op de broedplaatsen geen boodschap hebben"*), while peak abundances of Herring Gulls on dump sites occurred in winter, when also the adults joined in ("*het hoogtepunt werd bereikt in de dagen na Kerstmis, ontelbare kippenkoppen en konijnenbotjes leveren voedsel aan de groote schare vogels*"; Binsbergen 1935). After the second World War, the economic situation gradually improved and disposable materials were developed that soon led to a huge amount of waste; a trend that has continued ever since (Thompson *et al.* 2009). With a rapidly growing human population, and the associated need to build new houses,

Box 2.4 National change in waste management

A change in waste management led to a decline in capacity and accessibility of open rubbish dumps. After 1990, according, the number of actively used refuse dumps declined from 90 in 1991 to just over 20 in 2006 and stabilised at that level (Figure). In fact, around 2006, 24 sites were still in use or in a start-up phase, another 17 were in final stages of decommissioning, and one site was closed only temporarily. From the perspective of scavenging gulls, the resource had been more concentrated (fewer large sites), but was also less accessible (dump sites were earlier covered up). The total capacity of waste dumps amounted to 58,000,000 m^3 in 2006, with important sites at relatively great distances from the coast (Overijssel, Gelderland, Noord-Brabant) and in Noord-Holland.



Number of refuse dumps in use in The Netherlands, 1991-2009[1]

Refuse dump facilities in The Netherlands in 2006: number recently closed or being decommissioned, sites currently used or licensed for near-future use, and capacity

Province	**Decommissioning**	**Exploitation / start-up**	**capacity (m^3)**
Groningen	5	1	*c.* 700,000
Friesland	2	1	*c.* 1,300,000
Drenthe	1	1	*c.* 5,250,000
Overijssel	3	3	*c.* 8,500,000
Gelderland	5	5	*c.* 8,800,000
Flevoland	1	2	*c.* 4,000,000
Utrecht	1	1	*c.* 2,500,000
Noord-Holland	3	4	*c.* 7,800,000
Zuid-Holland	1	2	*c.* 4,500,000
Zeeland	1	1	*c.* 1,800,000
Noord-Brabant	5	2	*c.* 7,100,000
Limburg	8	1	*c.* 5,300,000
Total	36	24	*c.* 58,000,000

Sources: [1] CBS, PBL, and Wageningen UR 2011, [2]Werkgroep Afvalregistratie 2007

smaller dumps near villages were closed and larger ones, away from cities and villages, were opened. Spaans (1971) described mid-winter censuses at all (104) such large dumps in Friesland, Groningen and Drenthe in 1967 and found some 26,000 Herring Gulls foraging. On one particularly important site, the compost works of Vuilafvoermaatschappij NV (VAM) in Drenthe), where the organic refuse of some 1 million people was processed at the time, some 8000 Herring Gulls were present. Spaans (1971) found that numbers of gulls at dumps fluctuated considerably through the winter and that certain sites were more important than others. The total number of Herring Gulls feeding at the 104 refuse dumps in winter 1967/68 varied between 20,000 and 39,000 (or even 50,000) individuals. When individual dumps were ranked according to the number of humans living nearby (assuming that dump size and thus the feeding resource for gulls would increase with a larger resident human population nearby), a positive correlation was found between numbers of inhabitants and the numbers of gulls at the dumps, which was thought to reflect the effect that the amount of available food had on the distribution of scavenging gulls (Spaans 1971). While Spaans (1971) rejected the 0-hypothesis that the tidal rhythm within the neighbouring Wadden Sea influenced the numbers of gulls at dumps, he showed that in fact there was a negative correlation between the area of exposed Cockle *Cerastoderma edule* beds (as a proxy for feeding possibilities on mudflats) and the number of gulls at dumps.

The ringing programme of Herring Gulls in the 1980s produced sightings of 1807 different individuals at 54 different landfill sites throughout the country. The same ringed birds in the 1990s produced sightings of 1337 individual birds at 46 different locations. In the 2000s, however, with most of the originally ringed individuals probably dead, but with new ringing programmes established, 105 individual birds were reported from only 8 refuse dump and waste processing plants:

Groningen, vuilstort	53.20°N	6.62°E
Wijster, vuilstort VAM	52.78°N	6.52°E
Medemblik, vuilstort	52.77°N	5.07°E
ICOVA vuilverwerking Kajuitweg 1 Amsterdam	52.41°N	4.83°E
Barneveld, vuilstort	52.17°N	5.63°E
Vuiloverslag Breda	51.60°N	4.77°E
Bergen op Zoom, vuilstort	51.50°N	4.33°E
Nieuwdorp, vuilstort Midden Zeeland	51.47°N	3.72°E

In the 1970s and 1980s, open refuse dumps were increasingly causing problems and illegal dumps of highly toxic waste materials were highlighted as scandals in the media. Costly clean-up operations were required and it was realised that national waste management simply had to change (Boersma *et al.* 1984). In the years following more and more open rubbish dumps were decommissioned (^{App}Box 2.4), which meant that a rich resource for scavenging gulls gradually reduced in size.

Climate change – Climate exerts an incompletely understood linkage with marine productivity through the transfer of energy from the atmosphere to an ocean surface layer of variable thickness (Kawasaki 1985). In that surface layer (the euphotic zone), several components of climate (solar radiation, wind, temperature) impact productivity. These variables are correlated, but their oceanographic implications and hence their impact on biological processes differ (Raymont 1963, Kawasaki 1985). Climate has always changed on the long geological time scales, but rarely so much and so rapidly as during the last century (Houghton *et al.* 1990, Folland & Karl 2001, Møller 2011). Marked recent changes in the Northern Hemisphere were a widespread reduction in temperature variability, a decline in Arctic sea-ice extent, and the proportion of total precipitation derived from heavy and extreme precipitation events over land in the mid- and high latitudes. Warming from 1910 to 1945 was initially concentrated in the North Atlantic and nearby regions. The Northern Hemisphere showed cooling during the period 1946 to 1975 while the Southern Hemisphere warmed (Climatic Research Unit and UK Met Office, Jones *et al.* 2001). North Atlantic cooling has recently reversed and the patterns of global temperature change since the 1970s are related in part to the positive westerly phase of the North Atlantic/Arctic Oscillation, the NAO Index[8] (Folland & Karl 2001).

As a natural cause of demographic change, climate may influence the breeding success of seabirds (Jouventin & Weimerskirch 1991, Reid *et al.* 1999, Durant *et al.* 2003, Frederiksen *et al.* 2004). Seabirds characteristically have high adult survival rates, deferred maturity, and low reproductive rates and (some of) these parameters may be expected to be buffered against environmental fluctuations (Reid *et al.* 1999). The two case studies mentioned above suggest that easy to measure meteorological parameters have affected seabird breeding success or mortality rates indirectly through changes in the food chain (Thompson & Ollason 2001, Sandvik *et al.* 2005). The North Sea ecosystem undergoes cycles with marked changes, observed as altered biomass of individual species spanning a range of life forms from algae to birds (Corten 2001,

---

[8] The North Atlantic Oscillation (NAO) is an important mode of variability of the atmosphere of the Northern Hemisphere. The NAO index is often defined as the difference of sea-level pressure between two stations situated close to the "centres of action" over Iceland and the Azores. The NAO has a large climatic influence on the North Atlantic ocean and surrounding land masses and it is a major controlling factor in basic meteorological variables such as wind, temperature and precipitation throughout the whole of Europe and eastern North America. Jones *et al.* 1997, Stephenson 1997, Folland & Karl 2001, Hurrell 1995, Fromentin & Planque 1996, Weyhenmeyer *et al.* 1997, Drinkwater *et al.* 2003, Reid *et al.* 1999, Levitus *et al.* 2000.

Beaugrand *et al.* 2002, 2003, Edwards & Richardson 2004). Many of the recent biological events (and probably many of the historical, less well known events) have been shown to be a response to coincident changes in oceanic input and water temperature (Reid *et al.* 2001). It is a long way, however, from shifts in atmospheric pressure via a change in water temperature to changes in biological resources and shifts in fecundity or survival in a given top predator. Long-term data series will be required to test the significance and causal relationships of any correlations found. Studies of the possible effects of climate change should always be considered against synergistic [acting together or strengthening] effects of other drivers of marine ecosystems (Philippart & Epping 2009). For ecologically different species, under influence of the same climatic events, the effect of climate change can be different as a result.

The Northern Hemisphere has been warmer since 1980 than for any period during the last 2000 years (Philippart & Epping 2009). Observations of the sea surface temperature (SST) from the western Wadden Sea, where the gull studies took place, have shown a steady warming trend between ~1980 and the early 21st century (Van Aken 2010). Philippart & Epping (2009) listed a whole range of possible consequences of climate change that could stress structure and functioning of the food web and may result in a cascade of effects. Extreme scenarios involved changes in the surface of tidal and subtidal areas, between autotrophy and heterotrophy[9], between pelagic and benthic production, and between import and export of energy and matter. An increased frequency of mild winters would favour macrobenthic species that are sensitive to low winter temperatures. The reproduction of warm-water species, such as Pacific Oyster *Crassostrea gigas*, might for example be stimulated by higher temperatures (Diederich *et al.* 2005). For other, cold water species, a warming trend is likely to cause problems. Examples would be the greater weight losses in bivalves during winter (as a result of continuing metabolic activity with higher temperatures) and reduced spatfall for bivalves such as Soft-shell Clam *Mya arenaria*, Common Mussel and Cockle (Honkoop 1998, Beukema 2002). Increases in precipitation within Europe and the consequential increase in river runoff and subsequent lowering in salinity may lead to shifts from marine to more brackish species such as a shift within polychaetes from lugworms (*Arenicola marina*) to nereid polychaetes (*Hediste diversicolor* and *Alitta virens*; Zipperle & Reise 2007). These are just some examples of foreseen changes that would have an impact on resources of bird utilising the intertidal zone, such as Herring Gulls.

Møller (2011) reviewed existing knowledge on climate change and birds. Numerous examples were discussed illustrating what changes have occurred already. Relevant for Laridae are questions regarding the rigidity of the annual cycle: what determines the duration of its component parts? Specific issues are the timing of breeding (prospecting, laying dates), clutch size, duration of incubation and the nestling periods, possible mismatches between food peaks, breeding date and an optimal timing of reproduction, the duration of the breeding season and the wintering period, the timing and duration of migration. Further aspects include inter-specific competition, range expansions of similar species (potential competitors), and the abundance of prey (impoverished communities, alien invaders). None of these factors are necessarily problematic for gulls, but all aspects require phenotypic plasticity (Piersma & Van Gils 2011). What *is* problematic is that climate effects are translated into numerous changes in the food web, in all sorts of directions (even if just considering shifts in abundance), and that population-level effects on generalists such as large gulls will be notoriously difficult to disentangle.

Severe winter weather (cold winters and winter mortality) **-** Lesser Black-backed Gull migrate south and winter mortality cannot be measured within The Netherlands. Herring Gulls, however, winter in The Netherlands, in Belgium and in northern France. The local breeding population around colonies may in winter have been replaced by wintering birds breeding further to the north, so that finds of carcasses in breeding areas may refer to individuals that originate from other parts

---

[9] Autotroph = organisms able to synthesise organic matter from carbon dioxide with sunlight as an energy source (plants); Heterotroph = organisms unable to synthesise organic matter themselves (animals and bacteria); Baretta-Bekker *et al.* 1998

of Europe. From beached bird surveys in winter (Nov-Apr) over the past 4 decades (1973/74 and 2011/12) along the North Sea coast (34,362 km surveyed; 9348 Herring Gulls found dead, mean 0.27 dead Herring Gulls km^{-1}), a distinct increase in winter mortality was found in normal (0.38 ± 0.00 km^{-1}, n= 3) and cold winters (0.56 ± 0.28 km^{-1}, n= 2) relative to mild seasons (0.23 ± 0.09 km^{-1}, n= 28; ^{App}Table 2.3). From a slightly shorter series of winter counts within the Wadden Sea area (1980/81-2011/12, 15,337 km surveyed, 4202 Herring Gulls found dead, 0.27 km^{-1}), a similar effect could be demonstrated. Rankings and categorisations of the IJnsen index are based on measurements at De Bilt. Along the coast (in this case an IJnsen index based on measurements collected at De Kooy near Den Helder), 'normal' and 'cold' conditions are relatively rare, and not only in recent years (^{App}Fig. 2.8). Wintering conditions for Herring Gulls are often assumed to have become more favourable in recent years (which would also explain why more and more Lesser Black-backed Gulls spend their winter in northern France, Belgium, the UK and even in The Netherlands in recent years), but the IJnsen index does in fact show only a gradual, non-significant decline since the 1940s.

Table 2.3**.** Densities of dead Herring Gulls in winters of different quality based on the IJnsen index (measured at De Kooy) along the North Sea shore (left) and in the Wadden Sea area (right), from NSO beached bird surveys (Dutch Seabird Group, CJ Camphuysen unpubl. data).

Nov-Apr, North Sea shoreline, 1973/74-2011/12					**Nov-Apr, Wadden Sea, 1980/81-2011/12**				
Characterisation	IJnsen	Mean	SD	n=	Characterisation	IJnsen	Mean	SD	n=
Extremely mild	<3.2	0.22	0.10	19	Extremely mild	<3.2	0.26	0.12	16
Very mild	3.3-5.7	0.27	0.07	7	Very mild	3.3-5.7	0.25	0.15	5
Mild	5.8-9.7	0.14	0.04	2	Mild-Rather mild	5.8-16.6	0.31	0.10	7
Rather mild	9.8-16.6	0.25	0.08	6					
Normal	16.7-28.4	0.38	0.00	3	Normal-Cold	16.7-44.3	0.39	0.11	4
Cold	28.5-44.3	0.56	0.28	2					
n=				39	n=				32

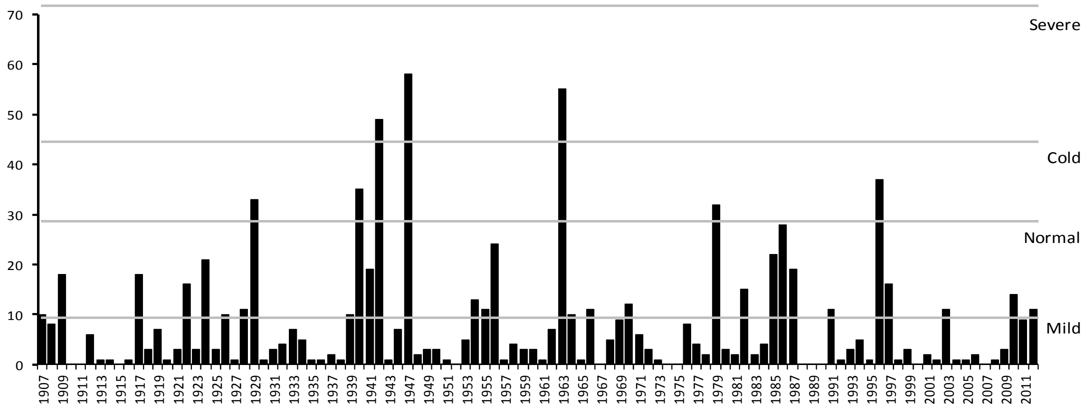


Figure 2.8. IJnsen index for De Kooy (Den Helder, The Netherlands), Nov-Mar 1906/07-2011/12 (no value for 1944/45). The IJnsen index is adopted for a quantitative classification of the winter temperatures, based upon the number of frost days (v, $T_{min} < 0°C$), ice days (y, $T_{max} < 0°C$) and very cold days (z, $T_{min} \leq 10$ °C). With these numbers, known for the winter season (November-March). The IJnsen index (V) is calculated as $V = 33(v^2/12100 + y/50 + z/30)$. For De Bilt (an inland location in The Netherlands), based on data collected in 1707-1990, the severity of winters ranged from V <3.2 (extremely mild) to >82.1 (extremely severe, via 16.7-28.4 (normal winters; Engelen *et al.* 2001). Compared with De Bilt, the measurements at De Kooy indicate a fairly mild winter climate for the Dutch coastal area (7 'cold' winters in a century).

Fisheries, discards - There are direct and indirect effects of fisheries on seabirds Tasker *et al.* 2000). Seabird mortality from entanglements in fishing gear can lead to marked population declines (Zydelis *et al.* 2009, Anderson *et al.* 2011, Pascoe *et al.* 2011). On the other hand, seabirds benefit from fisheries, because many fishing activities increase the food supply or enhance the availability of prey for birds. The practice of discarding unwanted fractions of a commercial catch is clearly beneficial for scavenging seabirds (Garthe *et al.* 1996). Furthermore, major shifts in fish stock composition, for example due to overfishing of large predatory fish, have led to a (relative) increase in smaller fish, suitable for consumption by seabirds (Camphuysen & Garthe 2000; Camphuysen 2001b). In an ICES study released in 2003, Mark Tasker, Kees Camphuysen, Stefan Garthe and Tycho Anker-Nilssen reviewed the alteration of the composition of the [North Sea] seabird community by fisheries. It was concluded that gulls in the southeastern North Sea had obviously benefited considerably from fishery induced changes in food supply, but the effects coincided with several important aspects either stimulating or suppressing further growth of the population (Tasker *et al.* 2003). Moreover, negative and positive impacts of fisheries on seabirds can occur at multiple spatial and temporal scales. To make things more complicated, a single fishery can potentially have simultaneous positive and negative impacts on a species of seabird.

Earlier studies had demonstrated the importance of fish in the diet of large gulls, certainly in the chick phase (Harris 1965, Spaans 1971), but proving the scale of fisheries effects can be difficult, due to confounding and interacting combinations with other anthropogenic effects or with oceanographic factors that influence the availability of marine resources. Herring Gulls and Lesser Black-backed Gulls breeding in The Netherlands have often been studied from a feeding community context (Spaans & Noordhuis 1989, Noordhuis & Spaans 1992, Camphuysen 1995). Throughout this thesis, however, evidence is provided that while these taxa do occur in (large) mixed colonies throughout Europe (nesting communities), their foraging ecology in most areas is quite different (Goethe 1955, Verbeek 1977a, Garthe *et al.* 1999). Nevertheless, some resources are shared and competed for (Camphuysen 1994b, 1995a).

Fisheries effects may act directly on species or indirectly by affecting the abundance of competitors in mixed feeding systems. While numbers of seabirds breeding or feeding in a given area should reflect the carrying capacity of that region in terms of the amount of food available to them, prey availability is not the same as the size of prey stocks present in an area. Several factors influence the accessibility of prey for seabirds and the profitability (in terms of intake rates achievable) of a given area. It is tempting to use fisheries statistics (such as landings data) to assess prey availability, but in fact these statistics may fluctuate independently of prey stock size and prey availability is also different for predator species using different foraging and feeding techniques (Ashmole 1971, Camphuysen & Garthe 2004). Fishery effects may be difficult to detect with simple population monitoring. However, shifts in prey availability may directly affect the reproductive output (chick growth, young fledged), or activity patterns and time budgets of adult birds, well before any trends can be detected in breeding numbers. This is the reason that the Kelderhuispolder studies have focussed on vital rates such as hatching and fledging rates, chick growth and the timing of events, rather than on the population size. In fact, it took a few years (and triggered by disappointment after overseeing existing population censuses) before assessments of breeding densities and population trends became part of the annual work.

With regard to gulls, North Sea fisheries effects are assumed to have been largely positive. Large gulls are high on the list of incidental entanglements in fishing gear (Camphuysen 1990, 1994c, 2008b), but overall numbers are low and entanglements are unlikely to have an effect on the population level. Fisheries in the southern North Sea have become increasingly beneficial for scavenging seabirds after the early 1960s, when otter trawlers were replaced by a beamtrawl fleet. The marked increase in the number of beamtrawlers in the 1970s and 1980s ($^{\mathrm{App}}$Fig. 2.9) may have been of prime importance for the more offshore oriented Lesser Black-backed Gull. Camphuysen (1995) and Garthe *et al.* (1999) suggested that Lesser Black-backed Gulls, who dominated in numbers at these offshore fleets, have filled that empty niche rather than have outcompeted Herring Gulls. In more recent years, both fleet size and fisheries effort declined with likely (negative) consequences for birds relying on a steady supply of fisheries discards (Rijnsdorp *et al.* 2008, Poos 2010, Rijnsdorp *et al.* 2011; $^{\mathrm{App}}$Fig. 2.9). Several papers within this thesis report on the (presumed) effects of this recent decline in discards production on gull populations.

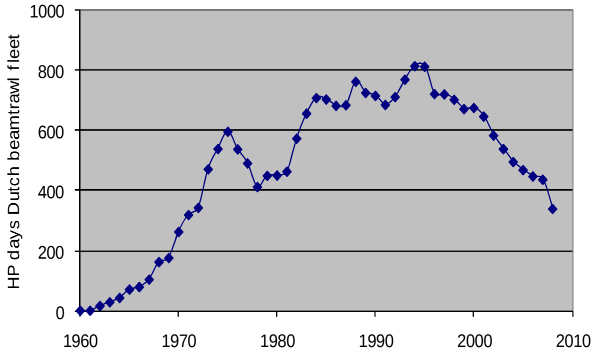


Figure 2.9. Dutch beamtrawl fisheries since the early 1960s, expressed as "horse power days" (from Rijnsdorp *et al.* 2008; updated by A. Rijnsdorp).

Bivalve dredging - In the Wadden Sea, a wetland of international importance, Common Mussel cultures occur in sublittoral areas, while mechanical cockle fisheries were licensed annually after evaluation of available resources. In the 1990s and early 21st century, wintering Common Eiders *Somateria mollissima* and Oystercatchers *Haematopus ostralegus* experienced shortages of food coinciding with particularly intense mechanical fisheries for bivalves. Common Eiders were forced to increasingly use alternative resources in the North Sea (*Spisula subtruncata*; currently commercially extinct; Camphuysen *et al.* 2002). Numbers of dead Oystercatchers in winters 1975-1996 varied with the number of cold days (severity of a winter) and prey biomass. High mortality was observed in the moderate winters of 1976 and 1991 (with low food stocks), and relatively low mortality in the cold winter of 1982 (a large food stock; Camphuysen *et al.* 1996).

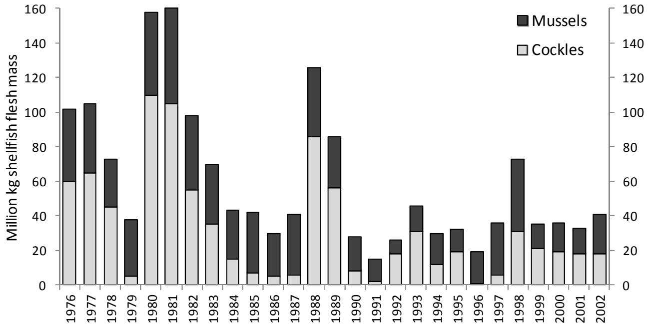


Figure 2.10. Stock assessments of mussels and cockles (flesh mass) in the western Wadden Sea, 1976-2002. Mussels are mostly subtidal in this part of the Wadden Sea (after Brinkman & Smaal 2003).

Bivalves are important prey species for Herring Gulls foraging in the intertidal zone, but the effects of the mechanical fisheries nor natural fluctuations in bivalve stocks have never been evaluated for gulls. The declining mussel and cockle stocks in the western Wadden Sea may have had (negative) population level effects for Herring Gulls breeding at Texel and Vlieland, particularly so in the mid-1980s and early-1990s (^{App}Fig. 2.10). Suction-dredging of cockles had long-lasting negative effects on recruitment of bivalves, particularly the target species, in sandy parts of the Wadden Sea basin (Piersma *et al.* 2001). Large scale disturbances that destroy organisms with a role in maintaining habitat stability, such as the mussel and cockle beds in the Wadden Sea, are likely to result in slow recovery dynamics, particularly in wave disturbed soft-sediment habitats. Positive effects on foraging opportunities for gulls could result from mussel transports and (temporarily) exposed cultures. Some negative and some positive effects, only on Herring Gulls, are thus expected to (have) occur(red).

Eutrophication - The enrichment of natural waters with inorganic nutrients, eutrophication, was formerly known only as a problem in freshwater environments (Nelissen & Stefels 1988). In freshwater, an increased loading with inorganic nutrient salts (notably nitrogen [N] and phosphorus [P]) could strongly increase algal biomass. In certain parts of the North Sea, the Wadden Sea, and in other marine coastal areas, similar phenomena have been reported (Postma

1985, Beukema & Cadée 1986, 1987, Brockmann *et al.* 1990, Valiela 2006, Klein & van Buuren 1992). From 1955 to the mid 1980s loads of both N and P in the Dutch coastal area, the Wadden Sea included, increased steadily (Gieskes & Kraay 1977). Increases in the amounts of N and P that have occurred in the North Sea mostly came from discharged sewage (both treated and untreated) and from farmland through both aquatic and airborne routes (Van der Veer *et al.* 1989; Brockmann *et al.* 1990, Tasker & Becker 1992). The actual amount of nutrients exported by fresh water and by air masses to coastal waters is related to the number of people (indiv. km^{-2}) on the watershed (Valiela 2006). For the Southern Bight, the most obvious sources of this eutrophication are the rivers Meuse, Scheldt, Thames and Rhine, with the latter being by far the most important. Its annual discharge is around 70 km^3, or 70% of all the fresh water that reaches the Southern Bight. River Rhine drains those parts of industrialized western Europe that have the highest population density (Gieskes & Kraay 1977).

Immediately after World War II, the river Rhine enriched the continental coastal waters only to a minor degree (0.1 kg sec^{-1} phosphate, 4 kg sec^{-1} nitrogen). In the early 1960s, however, phosphate-containing detergents came into use, and by 1975 the nutrient averages were 0.7 kg sec^{-1} phosphate-phosphorus, and 12 kg sec^{-1} nitrogen. The total supply of phosphorus by the Rhine to the North Sea (50,000 tons annum^{-1}) was now roughly half the amount that reached the southern North Sea each year through Dover Straits in 4000 km^3 of water of oceanic origin. In the 1970s, domestic sewage accounted for 70% of the phosphorus in river Rhine; detergents alone for 44%, the rest from industrial wastes and agricultural land drainage.

Suggestions that the increasing nutrient input into the southern North Sea would result in an increase in the primary production and how atmospheric, groundwater and riverine inputs of nitrogen, phosphorus and silicon influence coastal eutrophication pressures were evaluated by Gieskes & Kraay (1977) and Jickells (2005). In fact, patterns of long-term variability in the plankton of the North Sea were remarkably uniform over large areas. Clearly, the plankton part of the ecosystem responded in a standard, predictable way to large-scale changes in the environment not immediately associated with human activities. The gradual decrease in abundance of the colonial *Phaeocystis poucheti* between 1948 and 1970 and the delay in spring production of *Temora* and *Acartia* since the early 1950s may have been related to a decline of sea temperatures on the European shelf in that period, but in the southern North Sea the annual fluctuations in the phytoplankton did not correspond to temperature variations in any season. In the region most strongly influenced by the eutrophic river Rhine, trends in the annual plankton fluctuations were similar to those in adjacent areas. However, the decrease in diatoms and in copepods was less dramatic than elsewhere, while the increase in microflagellates and other unidentified species between 1966 and the early seventies was greater than in any other region. It is possible that the increased fertilization of this area has stimulated phytoplankton and zooplankton production in the eastern part of the Southern Bight.

An important effect of eutrophication, next to increased productivity in an area, is an increased risk of a complete system deterioration. In some areas of the North Sea (including the margins), excessive enrichment was found, and the consequential high primary production led to excessive sedimentation of decaying phytoplankton and to oxygen depletion in sediments and overlying water (Cadée 1986, De Jonge 1990, De Jonge & Essink 1991, Schaub & Gieskes 1990, Baretta-Dekker *et al.* 1998, Valiela 2006).

The effects of eutrophication are particularly evident in areas with limited water exchange and significant nutrient input, and substantial areas of the southern North Sea were affected (Niermann *et al.* 1990). Annual primary production in the western Dutch Wadden Sea increased from *c.* 40 g C m^{-2} (1950s) to 150 (1960s) and over 500 g C m^{-2} (1986). The biomass of macrozoobenthos in the mid-1990s had more than doubled since 1970. Simultaneously, the meat yield of cultured Common Mussels increased (de Jonge *et al.* 1996). The downside of enrichment was recorded also within the Wadden Sea ecosystems. In the Balgzand area, for example, oxygen values in the water became much reduced (Van Bennekom & Tijssen 1976)

Some eutrophication is likely to be beneficial for certain seabirds. Flocks of gulls and other seabirds are commonly foraging near sewage outfalls all around the North Sea. Eutrophication can lead to an increase in stock of invertebrates, which might be beneficial for seabirds feeding on them. An increased benthos supply in the Wadden Sea between the 1960s and the 1990s may have positively influenced the population dynamics of gull populations in that region (Beukema 1989, Vauk *et al.* 1989). However, the reduction in nutrient supply has not been followed by a decrease in productivity and biomass of phytoplankton (Philippart & Epping 2009, QSR 4.2).

Invasive species - Non-indigenous, exotic, or invasive marine species, have been found in The Netherlands for hundreds of years. Wolff (2005) listed more than 100 algae, cnidarians, worms, crustaceans, spiders, molluscs, bryozoans, tunicates, and fish species that were found in coastal waters of the North Sea, in the Wadden Sea, or within the Oosterschelde and other estuaries in the Delta area (non-indigenous marine and estuarine plant and animal species). At least 112 plant and animal species were known to have been introduced from elsewhere in the world (13 species of which from other parts of NW Europe; Stegenga 2005, Wolff 2005). A category of dubious non-indigenous species enumerated 37 species. The dispersal of exotic species can result from natural processes or from introductions (fouling species on ships' hulls, non-indigenous species in dry ballast or in ballast water, shellfish imports). Several Mediterranean and Ponto-Caspian species arrived via freshwater shipping canals. Some introductions were intentional and some involved escapes from captive populations (aquaria). Relevant for the present study (given the diets of large gulls), are bristleworms Polychaeta, crabs Decapoda, snails Gastropoda, bivalves Bivalvia, and fish Pisces. At least 11 ‘exotic’ species have or could have contributed to the diets of large gulls in The Netherlands:

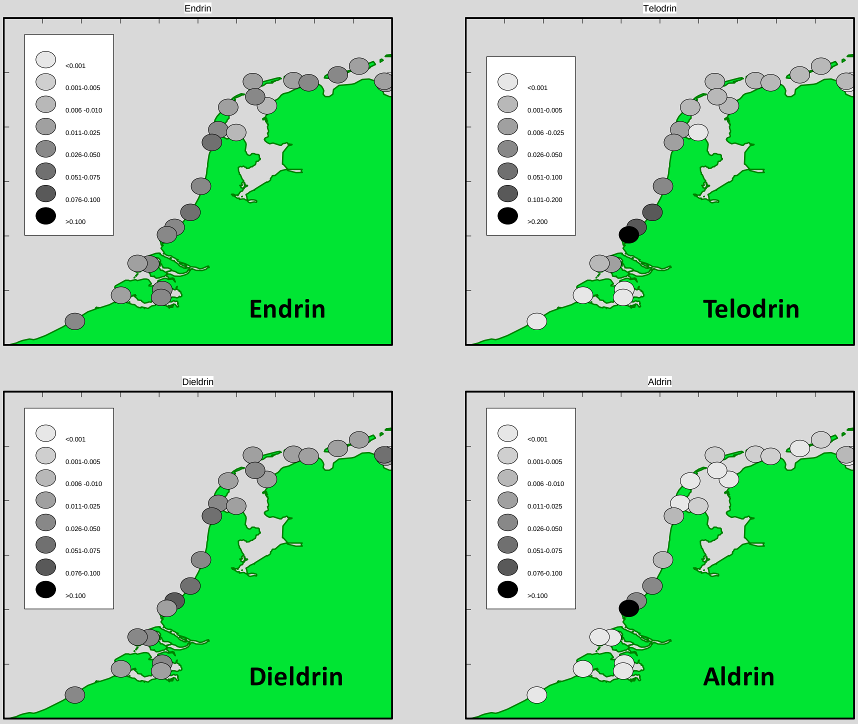
King ragworm *Alitta virens* (first recorded in 1915; currently common),
Chinese mitten crab *Eriocheir sinensis* (1929; currently abundant),
Hairy-clawed shorecrab *Hemigrapsus penicillatus* (2000; currently spreading),
Japanese shorecrab *Hemigrapsus sanguineus* (1999; currently spreading),
Common slipper shell *Crepidula fornicata* (1924; currently localised),
Pacific oyster *Crassostrea gigas* (1964; currently abundant),
Atlantic jackknife *Ensis directus* (1982; currently abundant),
Soft-shell clam *Mya arenaria* <1765; currently common),
Big-scale sand smelt *Atherina boyeri* (1964; currently localised),
Black goby *Gobius niger* (1964; currently localised),
Gilt-head sea bream *Sparus aurata* (2005; currently localised?).

Of these, *Alitta virens* and *Ensis directus* are currently important prey items, notably for Herring Gulls. The two Japanes shorecrabs are increasing the Wadden Sea and are increasingly common in Herring Gulls diets in that area. The Atlantic jackknife virtually replaced some native *Ensis* species, and is currently more abundant than any of these has ever (known) to be. The Atlantic jackknife may therefore be considered an additional food source for gulls (see, however, Gmelig Meyling & Gittenberger 2006 for interactions of jackknifes with other molluscs). The King ragworm *Alitta virens* and the Soft-shell clam *Mya arenaria* are well-established non-indigenous species, first reported around 1915 and 1765 respectively. The other more important prey species, including the two Japanese shorecrab species, Pacific Oysters, Atlantic Jackknife and sand-smelt, are all from a relatively recent date of introduction to the Dutch fauna. The establishment of a viable population of Gilt-head sea bream *Sparus aurata*, first recorded in 2005, needs further confirmation.

Gmelig Meyling & Gittenberger (2006) tabulated the likely origin of 110 non-indigenous species, and found that 25% originated from other areas within the Atlantic Ocean, 5% from the Indian Ocean, 38% from the Pacific, 5% from the Ponto-Caspian region and 27% were from an unknown origin. As means of (likely) transport, 19% were fouling species on ships' hulls, 16% arrived with (commercial) shellfish transports, 9% in ballast waters, 2% in ship’s cargos, 4% via freshwater canals, and 5% were intentionally released. For the remaining 45%, the means of transport were different or unknown. Of these non-indigenous species, 66% were now considered well established, another 11% had become only recently established, 6% had disappeared after a short period of success, and 12% were not established (another 5% unknown). Even though the first introductions date from several hundreds of years ago, Wolff (2005) as well as Gmelig Meyling & Gittenberger (2006), report a higher introduction rate in recent decades. Some of this trend is the result of increased attention for invasive species (observer effort), but since 1978, at least 63 species were introduced, of which a fair number only since the late 1990s.

Box 2.5 – Chlorinated hydrocarbons in the 1960s

Telodrin was an insecticide that was not used in Europe, but that was manufactured, together with many other pesticides, in a chemical industry in the Botlek area, near the mouth of the river Rhine. In August 1964, an explosion occurred in the factory and a large amount of telodrin leaked into the environment[1]. In August 1965 mussels were sampled at about 22 locations along the Dutch coast and in Oostende (Belgium). The residues of chlorinated hydrocarbons appeared to be highest near the mouth of the river Rhine (Zuid-Holland), and declined further to the north and northeast. This pattern corresponds with the outflow of the river water into the sea that moves alongside the Dutch coast in a NE direction and enters the Wadden Sea.



Residues of Endrin, Telodrin, Dieldrin, and Aldrin (ppm) in Common Mussels sampled in autumn 1965 (data from Koeman 1971). The source of these chemicals was a pesticides factory near Rotterdam[2-5].

References: [1]Koeman *et al.* 1968, [2]Koeman 1971, [3]Duinker & Koeman 1978, [4]Rooth 1980, [5]Smit 1981

Source: Koeman J.H. 1971. Het voorkomen en de toxicologische betekenis van enkele chloorkoolwaterstoffen aan de Nederlandse kust in de periode 1965 tot 1970. PhD thesis, University of Utrecht.

Marine pollution (1) Chlorinated hydrocarbons - Pesticides against diseases and insects (agricultural pests) developed during the second World War (1940-45) and were gratefully accepted and applied in The Netherlands. The dangers of the use of pesticides for non-targets species, wild plants and animals (unwanted side effects), were recognised in the 1950s (Mörzer Bruyns 1972). As so often, industrial interests prevailed and no serious action was undertaken. In the early 1960s, however, mass mortalities of piscivorous and molluscivorous birds in the Wadden Sea called for attention. Tissues of large numbers of dead terns, Spoonbills *Platalea leucorodia*, Herring Gulls, Common Eiders and other (sea-)birds were found to have elevated levels of telodrin, aldrin, dieldrin, endrin, and hexachlorobenzene (Koeman 1971, Koeman *et al.* 1972ab, Rooth & Jonkers 1972, Swennen 1972). From a study on the mortality of Sandwich Terns in 1962-65, it was concluded that the death of the birds was caused by the lethal effects of telodrin and dieldrin. Studies on Common Eiders showed that incubating females were particularly susceptible to the toxic effects of chlorinated hydrocarbon compounds. Poisoning by telodrin and dieldrin in 1966-1968 was their main cause of death (Koeman 1971). Experimental studies showed that the acute toxicity of telodrin and dieldrin was particularly high.

The detection of relatively high levels of chlorinated hydrocarbon pesticides in tissues of marine birds in the Wadden Sea in 1964 gave rise to special investigations concerning the origin and the scale of the pollution, and the possible biological implications that these substances could have on the marine environment (^{App}Box 2.5). For all chlorinated hydrocarbons, the highest concentrations were found in Zuid-Holland, just north of the mouth of Nieuwe Waterweg, with declining concentrations further north. Common Mussels in the Wadden Sea in 1965 contained on average 0.0026 ppm telodrin, 0.021 ppm dieldrin, and 0.021 ppm Endrin. Much higher concentrations were found in fish prey of Sandwich Terns in the Wadden Sea (0.05, 0.27, and 0.14 ppm respectively; Koeman 1971).

The effects of the pesticides on breeding Herring Gulls are not well documented. According to Koeman (1971), 'numerous dead gulls', including Herring Gulls, Mew Gulls, and Lesser Black-backed Gulls, were found along the mainland coast of Zuid-Holland, but figures nor a data source were provided. When consulting the database of beached bird surveys (CJC *unpubl. data*), however, an apparently untapped dataset at the time, there is no evidence for a mass mortality. If Herring Gulls along the mainland coast would have died in large numbers in the 1960s, this would have been picked up by these surveys (counts in Zuid- and Noord-Holland relative to the other subregions). If the chlorinated hydrocarbons, particularly Telodrin levels, were responsible and the mortality was acute, a trend in densities as in ^{App}Box 2.5 for Telodrin could even be expected. In fact, densities of Herring Gulls in the 1960s were more or less the same in all subregions, much lower than in the late 1970s and 1980s (^{App}Fig. 2.11). Spaans (1980) observed declines in Herring Gull colonies closest to the areas where concentrations of chlorinated hydrocarbons in mussels were highest (^{App}Box 2.5). Koeman (1971, citing Timmerman & Rooth 1965) referred to the colony of Herring Gulls at Wassenaar (Zuid-Holland), where numbers declined from 1580 pairs in 1964 to 74 pairs in 1965. This is a rather drastic decline for a long-lived seabird such as the Herring Gull, which would suggest at a widespread mortality of adult birds (the vital part of a breeding population). If Herring Gulls were significantly affected by chlorinated hydrocarbons remains unclear. The incident coincided with ongoing persecution of gulls in several breeding sites in Zuid-Holland, notably at the Wassenaar site. Herring Gulls may have been affected, despite the absence of a fasting period during incubation such as in Common Eiders, because of their fish prey in which even higher concentrations of pesticides may have occurred, which is an essential part of their diet during chick care (Spaans 1971).

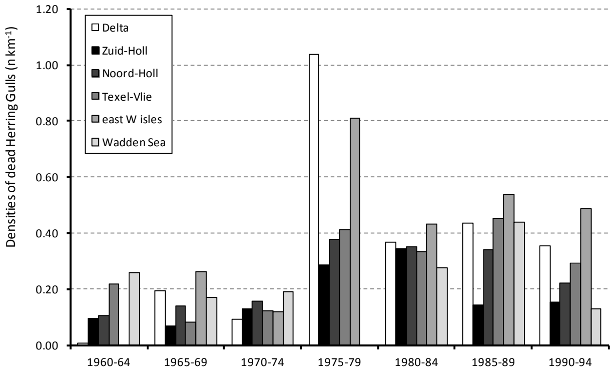


Fig. 2.11 Densities (n km^{-1}) of dead Herring Gulls during beached bird surveys in The Netherlands in the 1960s and in some later decades (5-year means are provided). The shadings correspond with levels of chlorinated hydrocarbons in mussels in the study areas (^{App}Box 2.5).

Source: NZG/NSO beached bird surveys, CJC *unpubl. data*

Legal restrictions led to the elimination of the polluting effluents and a gradual recovery in the seabird populations of the Wadden Sea (Smit & Wolff 1980, Becker & Erdelen 1987). Telodrin was no longer detected in mussel tissue shortly after the first sampling in the summer of 1965, but in 1966 and 1967 it was still present in fish, in terns' eggs at Griend, and in dead Common Eiders on Vlieland (Koeman *et al.* 1968). The mortality in female Eiders peaked in 1965, but was no longer found after 1968 (Swennen 1972). After 1965 the levels of most substances, with the exception of PCB's and DDE, gradually declined (Koeman 1971).

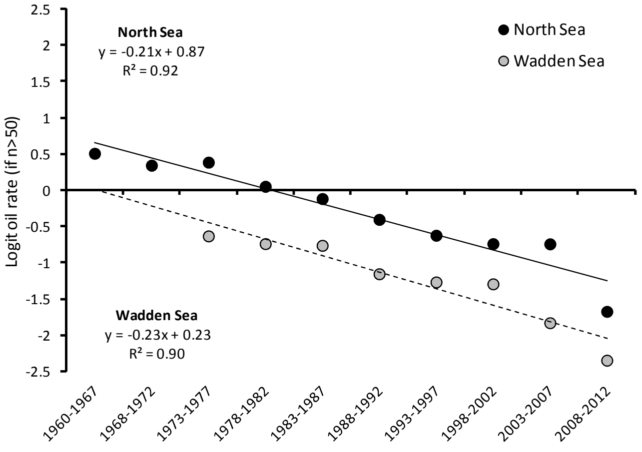


Figure 2.12. Logit oil rate in Herring Gulls found dead along the North Sea shoreline and within the Wadden Sea during beached bird surveys in winter (summarised for 5-year periods; note the first period is 8 years; NZG/NSO unpubl. data, CJ Camphuysen)

Marine pollution (2) mineral oil - Strandings of oiled seabirds have been a signal of the ongoing problem of chronic oil pollution in the North Sea since the beginning of the 20th century (Camphuysen 1989a). Overall numbers of beached birds are subject to enormous fluctuations, being the result of changes in the amount of oil spilled in the marine environment, currents, the frequency of onshore winds and variations in the numbers of seabirds in a given region (Camphuysen 1998, 2010). In contrast, oil rates, *i.e.* the fraction of oiled birds of the total stranded, is relatively constant while specific for different species and regions (^{App}Box 2.6).

As coastal seabirds with a strong tendency to roost onshore (reducing exposure), Herring Gulls are characterised by a strong decline in oil rates from chronic oil pollution (^{App}Fig. 2.12). In the 1960s, 1970s and 1980s *c.* 45-75% of the Herring Gulls found dead on the North Sea coast were contaminated with oil. Current rates are much lower (<20% along the North Sea coast, <5% within the Wadden Sea to 2% along the North Sea coast and <0.5% within the Wadden Sea; NZG/NSO unpubl. data, CJ Camphuysen). Lesser Black-backed Gulls migrate south in the winter period and miss the most critical season for chronic oil pollution in the North Sea (Camphuysen 1989a). Oil-rates are generally calculated over intact corpses of birds: individual birds that had washed ashore while dead or dying (Camphuysen & Van der Meer 1996). Recent studies have demonstrated a remarkable self-cleaning capacity in large gulls (Reijnders 1997, Camphuysen & Gronert 2010b, Camphuysen 2011a). The frequency of oil contamination may thus have been larger than indicated from beached bird surveys. For large gulls, however, currently, oil pollution is a relatively trivial issue.

Box 2.6 – Seabirds and oil pollution

Species-specific oil rates are thought to reflect the risk for birds, or for corpses of birds, to become oil fouled at sea and hence to mirror fluctuations in the amount of oil spilled in different regions[1]. High oil rates are typical for mainly swimming, highly exposed seabirds in areas with frequent oil spills (e.g. around shipping lanes and near the major harbours); low oil rates are typical for mainly flying seabirds away from the busiest shipping lanes:

Oil rates in some common seabird species around the North Sea, from beached bird surveys in The Netherlands, Germany, Denmark, mainland Britain (UK) and on the Shetland Islands, sorted by overall oil-rate in declining order. Life-styles as foraging seabirds and principal feeding habitats were added, after Camphuysen 1998.

	NL	FRG	DK	UK	Shetlands	life-style at sea	habitat
Divers	91	80	70	64	23	swimming	nearshore
Razorbill	83	70	93	61	12	swimming	offshore
Guillemot	82	70	82	58	13	swimming	offshore
Scoters	75	51	72	29		swimming	nearshore
Gannet	86	46	65	29	10	aerial	offshore
Grebes	62	79	78	46		swimming	nearshore
Fulmar	64	25	65	13	6	aerial	offshore
Kittiwake	80	15	52	18	4	aerial	offshore
Eider	25	45	52	27	12	swimming	nearshore
Larus-gulls	43	14	32	10	4	aerial	nearshore
Waders	4	6		4	0	aerial	onshore

A power analysis of the results of beached bird surveys demonstrated the sensitivity of these data as a tool to monitor trends in oil rates of stranded birds[2,3]. Rather subtle changes in oil rates could be demonstrated, indicating positive results of attempts to protect certain sea areas (e.g. the Wadden Sea) and a decline in oil rates over time[1]. Grouped into 5-year periods, using logit-transformed percentages of oiled birds, the oil rates of all bird species combined along the North Sea shoreline and within the Wadden Sea declined significantly[1,3]. Oil rates within the Wadden Sea were significantly lower than those on the North Sea coast (*t*-test, $t_9 = 3.3$, $P < 0.001$[1]. Lower oil rates within the Wadden Sea area than along the North Sea coast were found in each of the ecological subgroups: seabirds ($t_9 = 2.27$, $P = 0.02$), coastal waterbirds ($t_9 = 4.39$, $P < 0.001$), and landbirds ($t_9 = 2.08$, P = 0.03). Seabirds had higher oil rates overall than coastal waterbirds and the declining trends in seabirds were less steep ($b = -0.17$ to -0.18) generally than in coastal species ($b = -0.23$).

Overseeing five decades of beached bird surveys, the proportion oiled (%) of all stranded birds has roughly halved along the North Sea shorelines, while this proportion has declined by no less than 90% within the Wadden Sea area[1]. Seabirds and coastal waterbirds both had high percentages of oil-contaminated carcasses in the 1960s and 1970s. This proportion fell much faster in coastal waterbirds than in seabirds in subsequent decades. Declines were ranged from 30–40% in offshore seabirds that typically occur abundantly in the sea areas where the most intensively used shipping lanes are positioned (large auks, Black-legged Kittiwakes and Northern Gannet). Rather steep declines (57–98%) were found in taxa that mostly occur close to the coast or within the Wadden Sea. Steep declines in oil rates were found in Larus-gulls (>80%), species that do occur widespread in the marine environment in winter but with a tendency to roost and sleep on land rather than on water (contrary to Black-legged Kittiwakes for example). The much speedier reduction in oil-rates in coastal waterbirds, notably so within the Wadden Sea, results from a consistent special 'treatment' of nearshore waters and estuaries considering oil pollution (intensified aerial surveillance, clean-up operations) that has seemingly been effective in reducing oil-rates.

The effects of chronic oil pollution on seabirds were documented for the first time in the early 20th century and levels of chronic oil pollution peaked around the 1960s. Throughout the 1960s, 1970s and 1980s[4-5], chronic oil pollution was a serious cause of death for many seabirds, but the situation has improved markedly since[1, 7-9].

References: [1]Camphuysen 2010, [2]Camphuysen & Van der Meer 1996, [3]Camphuysen 1997, [4]Bourne 1976, [5]Camphuysen 1989, [6]Clark 2001, [7]Camphuysen 1998, [8]Oka *et al.* 1999, [9]Lars *et al.* 2007

Appendix 3. Colony life

This appendix reports on the reproductive success of the sympatric Herring Gulls and Lesser Black-backed Gulls, with emphasis on characteristics of the nesting habitat, nesting densities, egg production, chick growth, hatching and fledging rates, and annual fluctuations in levels of chick depredation at Texel between 2006 and 2012. When these studies commenced in 2006, breeding numbers of large gulls in the Wadden Sea were at an all time high of *c.* 90,000 breeding pairs. Breeding Herring Gulls in the Wadden Sea had just dropped in numbers by almost 40%, but the population of Lesser Black-backed Gulls peaked. After many years of strong and contrasting population trends, however, the populations seemed to stabilise (Stork 2007).

Kelderhuispolder studies 2006-2012

The study area is an undisturbed and ungrazed nature reserve, part of a larger mixed colony (De Geul) on south tip of the island Texel (53°00.5’N, 04°43.1’E; ^{App}Fig. 3.1). This colony had not been studied before. The colony was potentially accessible for research during all weather conditions and throughout the day, without logistic constraints such as boat trips or other access restrictions. There are few mammalian predators (feral cats, some small mustelids). The colony is situated within Natura 2000 area #2 “*Duinen en Lage land Texel*”, site codes NL2003060 (Duinen Vlieland, Waal & Burg, Dijkmanshuizen and De Bol) + NL9802001 (North Sea coastal zone). The Lesser Black-backed Gull (A183) is one of the bird species for which the area is listed, with the objective to maintain a breeding population of *c.* 14,000 pairs within the area.

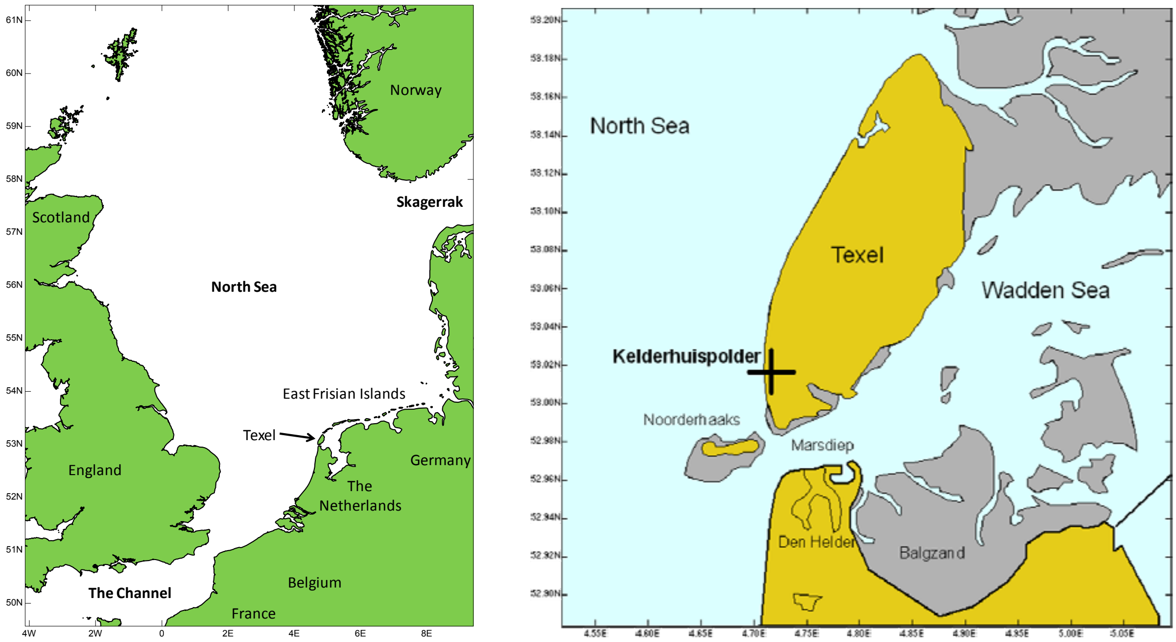


Fig. 3.1 Location of Texel in the North Sea at large and the location of the Kelderhuispolder colony (+) in the western Wadden Sea.

The studies were conducted with a small research budget, one student per annum and volunteer help, restricting possibilities, and choices had to be made to conduct the work in the field and in the laboratory most effectively. Issues of prime importance (each with specific underlying research questions) were insight in the reproductive success, annual survival, recruitment, and foraging ecology (i.e. diet as well as foraging whereabouts) of both species in order to explain the population dynamics and perhaps even to forecast near-future population trends.

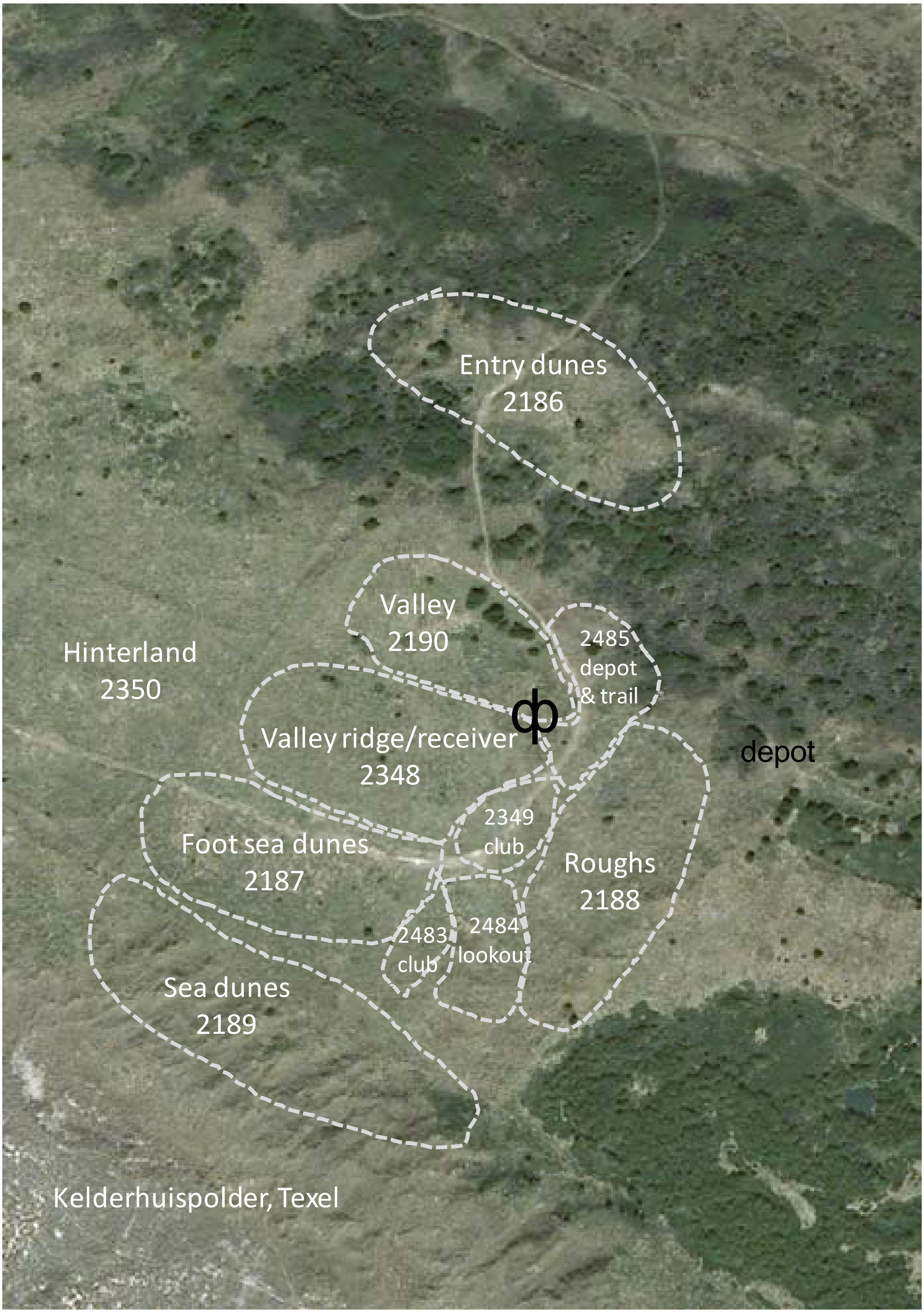


Fig. 3.2. Study plots in the Kelderhuispolder colony mentioned in this thesis and in associated papers. A permanent depot was deployed where all ringing and field work preparations could be done outside the core breeding range of the birds. A receiver station ("Houston Control", ɸ) was erected to automatically collect radio signals (ARTS, 2006-2010) and GPS tracking data (2008-2012) from tagged birds.

Monitoring breeding success - Herring Gulls were studied in three (later four) study plots: Entry Dunes (#2186), Roughs (#2188), and Sea dunes (#2189), plus in later years Valley ridge/HG club/Lookout as a separate area (##2348, 2349, 2484); $^{\mathrm{App}}$Fig. 3.2). In the Sea Dunes area, enclosures were never built and nests were followed only until hatching. The prime study areas for Lesser Black-backed Gulls were Valley (#2190) and Foot sea dunes (#2187), but in later years also the Lookout (#2484) area was used. During the prospecting phase in late April, a nest search was started and maintained every third day, along a pre-set trail through the prime study areas. Nests containing at least a single egg were marked (#), the habitat and the nest itself were photographed and described and a GPS position was recorded and filed (latitude, longitude).

In order to monitor breeding success, it was decided to assess laying dates (in later years also prospector arrival dates), clutch size (*n* nest $^{-1}$), laying sequence (A, B, or C-eggs), egg volume (cc), egg depredation (%), egg mortality (%) and egg-hatching rates(%, *n* nest^{-1}). When found, eggs were numbered in sequence of appearance, measured (max Length x max Width), photographed (to document shell patterns), and the laying and hatching dates were assessed as precisely as possible. During nest visits, the number of eggs was counted, the ink-markings (numbers) were checked, and the condition of the eggs was checked and recorded into a logbook. For each egg, a prediction was made of the expected day of hatching (assuming an 28d incubation period), but the exact duration of incubation (d) was calculated and used for analysis if the laying *and* hatching dates were known. It was decided to annually monitor c. 80 nests of each species until hatching, and to randomly select a maximum of 40 nests to assess fledging rates. The colony is a well-vegetated area and newly hatched chicks would quickly disappear "out of sight" if they would not be stopped. Frequent measurements of chick growth, assessments of causes of mortality and accurate assessments of fledging rates were possible because we used chicken wire enclosures. The use of enclosures was a concrete choice, even though unwanted side-effects may have affected data quality (Walsh *et al.* 1995), because it would provide detailed data on chick developments. Direct counts of unfenced plots can considerably under- estimate the true chick population; a warning issued by Walsh *et al.* (1995) that we confirmed during these studies (hide-observations by Tim van Nus in 2007 and Rim Lucassen in 2009). Because our aim was to obtain productivity data representative of the colony at large, enclosed plots should not be more or less susceptible to depredation than unenclosed sections of the colony. Fortunately, the Kelderhuispolder colonies are not (known to be) under stress from rat or other mammalian predators, in which case enclosure data might have been biased.

Enclosures were built in three study areas of Herring Gulls (Entry Dunes, Roughs, and Valley ridge/HG club/Lookout), but never in the Sea Dunes, which formed the outer boundary of the colony. Enclosures were built also in three study areas of Lesser Black-backed Gulls (Foot sea dunes, Valley, and Lookout), which was basically the high-density area of Lesser Black-backed Gulls in a large dune valley, surrounded by steeper dunes where Herring Gulls were the more abundant species. Chicks were individually ringed when they hatched, and checked every third day, to monitor the fate of each individual until fledging or until an 'untimely' death. During nest visits, all chicks were removed from an enclosure at once and kept in a cotton bag at some distance away from the site. The following data were collected during each nest visit:

Chick condition	Behaviour	Docile and weakened or fit and active
Health status	Condition	Any physical damage or signs of attacks
Bill	Biometrics	Tip to feathers (0.1mm)
Head	Biometrics	Back of the head to tip of the bill (mm)
Wing	Biometrics	Primaries (or down), stretched (mm)
Tarsus	Biometrics	Length of the tarsometatarsal bone (mm)
Body mass	Biometrics	Total mass when handled (g)
Moult	Development	See Box 3.4
Age		Days (d) since hatching

Boluses (if produced during handling by either the chicks or an adult) were bagged, numbered and collected, together with pellets and any chick-feed present in or near the enclosure was sub-sampled. The position of the enclosure relative to the provisioning activities of the parents was reviewed during each visit, to ensure that chicks received the prey delivered to them (when enclosures fail to include the "feeding ground" of a nest, chick-feed may be deposited outside the fence by the parents). If needed, the position of the fence was adjusted and possible escape routes for the chicks (damaged parts of the fence) were repaired.

When chicks were not found during enclosure visits, four options were considered: (1) still present but well hidden in the vegetation, (2) escaped, (3) depredated, or (4) fledged. A first absence despite a thorough search, in the absence of physical evidence of a kill (a ringed carcass in on near the enclosure) or a likely escape (a damaged fence), was logged as "Not found". If the chick was again not found three days later, the bird was logged as "depredated" (if clearly flightless) or as "fledged" (generally with chicks >35d of age with well developed flight feathers). If a chick was found dead, it was logged as "dead" in the absence of any physical evidence for violent attacks, or as "depredated" if stab-wounds were evident or when the carcass was partly eaten (even if perhaps scavenged). In case of doubt, the death was logged as "unknown cause". All carcasses, even those that were incomplete, were collected and deep frozen for later inspection. Field assessments of the cause of death (killed/depredated or 'just died') were verified in the lab.

Data gathered from birds in enclosures include hatching dates (allocating newly hatched chicks to the appropriate egg number), number of chicks under care (*n* nest $^{-1}$), structural growth (mm d^{-1}), mass gain (g d^{-1}), chick depredation (%), chick mortality (%) and fledging rates(*n* pair^{-1}). Just prior to fledging, chicks were marked with a permanent steel ring on the right tibia and an engraved, green PMMA colour ring on the left tarsus to allow for individual recognition at distance after fledging (Camphuysen 2008c). Engravings started with the letter P (prior to 2009) or K (2006-2012), followed by a dot and three more letters as a unique code. Birds were colour-ringed when the tarsus had reached a length of *c.* 60mm, or when the tarsus joint was thin enough (young chicks have a thick tarsus joint, but when around 30-35d of age the leg becomes much thinner as in later life).

We refrained from detailed observations in the colony, except during student projects in 2007 and 2010, so that the parental activities with regard to nest attendance are incompletely known. To monitor presence/absence of adult birds, however, radio tags were deployed in 2006-8 on Lesser Black-backed Gulls and in 2006-10 on Herring Gulls, whereas GPS loggers could be deployed in 2008-2012 to monitor presence and absence of Lesser Black-backed Gulls ($^{\text{App}}$Table 3.1). Most these data still await further analysis, but results have been presented in Chapter 4, 8, 10, and 12.

Table 3.1 The deployment of radio tags and GPS loggers on gulls in the Kelderhuispolder, 2006-2012.

Species	**device**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**
Lesser Black-backed Gull	radio	5	12	34	-	-	-	-
	GPS	-	(1)	6	6	15	9	10
Herring Gull	radio	4	8	10	10	-	-	-

Table 3.2 Colour-ring activities in the Kelderhuispolder, 2006-2012. J = pullus, A = breeding adult, I = breeding subadult (immature).

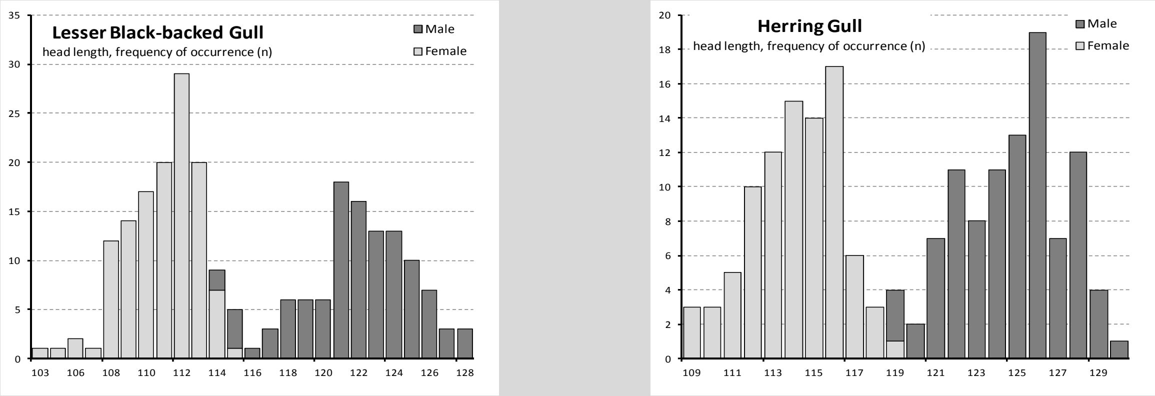
Species	**Age**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**Totals**
Lesser Black-bacled Gull	A	22	24	46	61	29	14	29	225
	J	69	102	81	83	109	109	70	623
Hybrids	J	3							3
Herring Gull	A	7	12	18	35	44	23	33	172
	I				3	2	2	3	10
	J	26	34	55	44	60	17	44	280
Yellow-legged Gull	A					1			1

Box 3.1 Sexing gulls: a non-invasive approach

Male gulls are on average larger than females, but many measurements overlap[1-3]. A non-invasive method was used to sex individual (adult) gulls during handling, following John Coulson and co-workers[1]. The means (±SD) of a number of biometric measurements of male and female Herring Gulls and Lesser Black-backed Gulls from the British breeding population, indicated that in both species, males are, on average, larger than females. These data were used in a discriminant analysis to investigate the accuracy of several body measurements as predictors of sex. In both species, head length (i.e. total length from the back of the head to the tip of the bill) emerged as the most accurate indicator of sex. The accuracy of sexing Herring Gulls on the basis of head length was 95.8 ± 0.9% (mean ± SE, n= 480). In Lesser Black-backed Gulls the accuracy was 95.0 ± 2.0% (n= 121). Using the results of this study, we initially used a cut-off point of head = 118 for Herring Gulls (males larger, females smaller) and 113 for Lesser Black-backed Gulls.

Size differences in a Herring Gull pair

Measuring 'head' in a Lesser Black-backed Gull



Frequency of occurrence of head lengths in Lesser Black-backed Gulls and Herring Gulls breeding in Kelderhuispolder, aged as adults or >4cy birds, and presumed sex, 2006-2012[4]

Over the years it appeared some birds were mis-sexed, and these were often the "smaller males". Lesser Black-backed Gulls breeding at Texel in The Netherlands are on average slightly larger those breeding in the UK[1-3] and studied by Coulson[2]. A plot of the frequency of occurrence of head-length showed a clear bi-modal pattern, but with head = 116 as a probably more appropriate cut-off point to separate two groups, or size-classes of birds, hopefully sexes. We adopted 116 mm as a cut-off in 2011 and 2012 and tested the results with blood samples taken in 2012. Of 16 birds sexed with molecular techniques, the head length varied between 108 and 126mm, including females with a head length of 113 and 114 (5). Mature Lesser Black-backed Gulls from various sources (all collected in summer in The Netherlands), sexed by means of gonadal inspection, were found to have a mean (±SD) head length of 109.8 ± 3.3mm (range 103-114, n= 17) in females and 121.6 ± 2.8mm (range 116-127, n= 17) in males (6). Both the DNA work and the necropsies indicated that a cut-off point of 113mm based on UK birds was too low for Dutch individuals. Too few necropsied Herring Gulls were available for a meaningful comparison (7 adult females, mean ± SD head 111.7 ± 1.6, range 109-114mm, 6 males 123.3 ± 2.7, range 120-127mm)[6]. The UK cut-off point seemed to have worked well for Dutch Herring Gulls and 118mm was used as a sex-discriminant throughout.

References: [1]Harris & Jones 1969, [2]Coulson *et al.* 1983c, [3]Cramp & Simmons 1983, **Sources**: [4]biometrics of ringed adults, Kelderhuispolder 2006-2012 (CJC); [5]sexing based on molecular techniques (DNA) at NIOZ molecular lab, courtesy Anneke Bol, Judith van Bleijswijk, and Pieternella Luttikhuizen (NIOZ); [6]necropsies NZG/NSO 2004-2011 (CJC *unpubl. data).*

Apart from radio tags or GPS loggers, the presence, absence and territoriality of individual birds was monitored during sessions of (colour) ring-reading. Most ring-reading activities were scheduled when few other activities in the field were needed and ring-reading intensity was particularly low during the second half of incubation and during most of chick care. In all, between 2006 and 2012 1314 gulls have been colour-ringed, including 842 Lesser Black-backed Gulls, 462 Herring Gulls, 3 hybrids (LBBG x HG) and one Yellow-legged Gull *Larus michahellis* (^{App}Table 3.2). Results of ring-reading activities have been used to analyse the timing of returns, the participation in the breeding process, pair bonds, site fidelity, annual survival and recruitment rates. During ringing, the adult and subadult breeding birds were sexed by using biometrical data, a non-invasive method developed in the UK (Coulson *et al.* 1983c; Box 3.1).

Breeding success in the Kelderhuispolder, 2006-2012

The breeding results up to 2010 are summarised in Camphuysen & Gronert (2010a) and further updated in this appendix. Contrary to expectations given the recent population increase, was the reproductive success of the Lesser Black-backed Gull often low, particularly as a result of high levels of chick depredation (cannibalism). In Herring Gulls, after many years of consistent decline, chick production was consistently higher. Updated with more recent data (2011-12), the reproductive success was as indicated in ^{App}Tables 3.3-3.4.

Nesting habitat, nest cover - When nests were marked, the habitat and the amount of nest-cover was described and photographed. A standardisation of these descriptions was introduced in

Table 3.3. Breeding success of Lesser Black-backed Gulls, 2006-2012

Breeding season	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**
First eggs	04-May	29-Apr	01-May	30-Apr	04-May	01-May	04-May
Peak egg-laying	10-15/5	6-15/5	7-12/5	9-15/5	11-16/5	10-16/5	16-22/5
Median egg-laying	12-May	09-May	10-May	12-May	14-May	13-May	19-May
Mean egg-laying ± SD	15 May±9.1	10 May±7.4	10 May±4.2	12 May±5.5	14 May±4.9	13 May±5.0	18 May±4.9
Incubation (d)	28	28	28	28	29	26	26
Breeding period	16/5-5/6	16-31/5	13/5-2/6	16/5-5/6	16/5-5/6	17/5-5/6	23/5-10/6
First hatchlings	01-Jun	22-May	29-May	28-May	30-May	27-May	01-Jun
Peak hatching	6-11/6	1-11/6	3-13/6	6-13/6	6-12/6	6-12/6	11-15/6
Median hatching	08-Jun	05-Jun	06-Jun	08-Jun	09-Jun	09-Jun	14-jun
Chick care (40d)	12/6-22/7	12/6-22/7	14/6-24/7	14/6-24/7	13/6-23/7	13/6-23/7	16/6-26/7
First fledglings	17-Jul	10-Jul	10-Jul	14-Jul	11-Jul	10-Jul	10-Jul
Clutch size	2.75±0.54	2.73±0.52	2.84±0.49	2.80±0.46	2.80±0.51	2.82±0.52	2.59±0.64
(n) nests	(57)	(79)	(98)	(114)	(88)	(88)	(97)
3-egg clutch volume	226.4±17.1	224.0±17.1	224.1±15.1	221.2±17.6	226.6±15.7	222.5±20.5	218.5±17.5
(n) nests	(46)	(61)	(87)	(94)	(73)	(74)	(64)
Failed clutches	7.9%	7.2%	10.2%	7.8%	7.7%	18.2%	24.7%
Relaying attempts	9.5%	4.8%	-	1.7%	3.3%	1.1%	3.1%
(n) nests	(63)	(83)	(98)	(116)	(91)	(88)	(97)
Egg depredation	29.0%	15.0%	14.4%	14.9%	9.8%	19.2%	25.2%
Egg mortality	7.1%	5.6%	11.9%	7.9%	6.6%	10.0%	6.7%
Hatching eggs	61.2%	78.1%	73.4%	77.1%	83.6%	70.7%	68.1%
(n) eggs	(183)	(233)	(278)	(328)	(256)	(239)	(254)
Chick depredation	60.3%	66.7%	63.4%	62.3%	35.4%	49.3%	60.7%
Chick mortality	25.4%	12.3%	15.5%	17.9%	34.8%	19.7%	11.5%
Chicks fledged	14.3%	21.0%	16.9%	17.0%	28.6%	31.0%	27.9%
(n) hatchlings	(63)	(81)	(71)	(106)	(161)	(71)	(63)
Fledglings pair^{-1}	**0.26 pr^{-1}**	**0.46 pr^{-1}**	**0.35 pr^{-1}**	**0.37 pr^{-1}**	**0.71 pr^{-1}**	**0.69 pr^{-1}**	**0.57 pr^{-1}**
(n) nests	(35)	(37)	(34)	(49)	(65)	(32)	(30)

2007 (Van Nus 2007). A first description involved the position in a dune landscape: at the top of a dune, along a slope (steep or gradual), or in flat valley areas (^{App}Table 3.5). The position was judged by eye and the absence or scarcity of Lesser Black-backed Gulls nests on dune slopes in the earlier years is an inconsistency in recording rather than a distinct change in nesting positions (Valley and Foot Sea dunes, their main nesting areas, have gradually sloping dunes, in earlier years often described as 'flat areas'). Dune tops, however, highly distinct features in the Kelderhuispolder landscape, are typically occupied by Herring Gulls, not by Lesser Black-backed Gulls.

A more fair comparison between the two species should take the area characteristics (*i.e.* differences between study plots) into account. Steep dunes are characteristic of the Sea dunes, the Roughs, and the Entry dunes; areas where primarily Herring Gulls are nesting. Steep dunes are non-existent in the Valley (2190), the Foot sea dunes (2187) and in the Valley ridge and club areas (2348-9). Lesser Black-backed Gulls were almost completely lacking as breeding birds in the Sea dunes area, but in the Entry dunes and in the Roughs where both species co-occur, in comparison with Herring Gulls, the distribution of nests of Lesser Black-backed Gulls over dune tops slopes and valleys was significantly different (G_{adj}= 26.9, df=2, P< 0.001). Similarly, nesting locations of Herring Gulls in the much flatter Valley, Foot sea dunes, Valley ridge and club areas were significantly different from an expectation based on the nesting positions of Lesser Black-backed Gulls ((G_{adj}= 12.8, df=2, P< 0.01), largely because of their greater tendency to nest on dune tops. Dune top nest positions in the Entry and Sea dunes, but also some of those in the Roughs, provide a spectacular overview over the landscape (sometimes even as far as the mainland coastline) and the colony at large, and dune-top nesting birds were normally the first in-

Table 3.4. Breeding success of Herring Gulls, 2006-2012

Breeding season	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**
First eggs	02-May	26-Apr	25-Apr	23-Apr	26-Apr	24-Apr	27-Apr
Peak egg-laying	7-11/5	4-11/5	5-10/5	4-9/5	2-8/5	1-7/5	4-10/5
Median egg-laying	09-May	09-May	07-May	06-May	05-May	04-May	08-May
Mean egg-laying ± SD	10 May±5.5	08 May±9.0	07 May±4.3	06 May±4.8	05 May±4.6	04 May±4.5	07 May±5.0
Incubation (d)	28	28	27	29	29	27	27
Breeding period	12/5-2/6	10-30/5	8/5-30/5	9/5-30/5	7/5-28/5	8/5-28/5	11/5-31/5
First hatchlings	29-May	23-May	22-May	20-May	23-May	24-May	25-May
Peak hatching	3-8/6	31/5-7/6	31/5-5/6	31/5-5/6	29/5-3/6	29/5-3/6	1/6-7/6
Median hatching	05-Jun	03-Jun	03-Jun	03-Jun	31-May	31-May	3-jun
Chick care (40d)	9/6-19/7	8/6-17/7	6/6-16/7	6/6-16/7	4/6-14/7	4/6-14/7	8/6-18/7
First fledglings	12-Jul	02-Jul	07-Jul	11-Jul	06-Jul	07-Jul	07-Jul
Clutch size	2.71±0.51	2.58±0.69	2.86±0.43	2.69±0.56	2.81±0.48	2.77±0.50	2.64±0.65
(n) nests	(42)	(55)	(69)	(65)	(58)	(56)	(73)
3-egg clutch volume	247.0±23.3	241.9±24.1	249.1±22.4	241.3±23.5	248.1±20.2	248.4±21.0	245.8±24.1
(n) nests	(31)	(38)	(58)	(48)	(49)	(48)	(54)
Failed clutches	14.3%	16.1%	10.8%	10.8%	8.3%	25.0%	15.7%
Relaying attempts	-	1.8%	6.8%	-	3.3%	5.4%	4.3%
(n) nests	(42)	(56)	(74)	(65)	(60)	(56)	(70)
Egg depredation	18.4%	26.0%	18.8%	13.7%	10.6%	14.9%	22.6%
Egg mortality	0.9%	9.6%	13.1%	15.4%	7.6%	20.1%	6.8%
Hatching eggs	79.8%	63.7%	68.1%	70.3%	81.8%	64.9%	70.5%
(n) eggs	(114)	(146)	(213)	(175)	(170)	(154)	(190)
Chick depredation	33.3%	39.1%	25.0%	51.2%	20.0%	16.7%	31.3%
Chick mortality	42.4%	8.7%	25.0%	7.0%	21.8%	46.7%	18.8%
Chicks fledged	24.2%	52.2%	50.0%	39.5%	58.2%	36.7%	50.0%
(n) hatchlings	(33)	(23)	(44)	(43)	(55)	(30)	(48)
Fledglings pair^{-1}	**0.62 pr^{-1}**	**0.80 pr^{-1}**	**1.10 pr^{-1}**	**0.81 pr^{-1}**	**1.33 pr^{-1}**	**0.48 pr^{-1}**	**1.04 pr^{-1}**
(n) nests	(13)	(15)	(20)	(21)	(24)	(23)	(23)

Table 3.5. Nesting positions of Lesser Black-backed Gulls (LBBG) and Herring Gulls (HG) in the Kelderhuispolder dune landscape, 2006-2012.

LBBG	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**Totals**	**%**
Dune top	1			1	1			3	0.5
Dune slope		3	25	49	35	68	75	255	39.3
Flat area	62	80	73	66	55	30	25	391	60.2
HG	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**Totals**	**%**
Dune top	22	26	23	27	16	9	16	139	32.9
Dune slope	13	19	43	31	31	28	33	198	46.9
Flat area	7	11	8	7	12	19	21	85	20.1

Table 3.6. Nesting positions of Lesser Black-backed Gulls (LBBG) and Herring Gulls (HG) within study plots (see ^{App}Fig. 3.2 for an explanation of plot numbers) in the Kelderhuispolder dune landscape, 2006-2012.

LBBG	2186	2188	2190	2348-9	2484	2187	2189	Totals		2187-88	2190-2187
Dune top	1	1			1			3	0.5%	4.4%	0.2%
Dune slope	15	2	82		17	136	3	255	39.3%	37.8%	39.1%
Flat area		26	163	6	47	149		391	60.2%	57.8%	60.7%
Totals	16	29	245	6	65	285	3	649		n= 45	n=601
HG	2186	2188	2190	2348-9	2484	2187	2189	Totals		2187-88	2190-2187
Dune top	39	39			2	1	58	139	32.9%	33.2%	4.2%
Dune slope	83	47	2	4	3	1	58	198	46.9%	55.3%	14.1%
Flat area	3	24	10	29	8	11		85	20.1%	11.5%	81.7%
Totals	125	110	12	33	13	13	116	422		n= 235	n=71

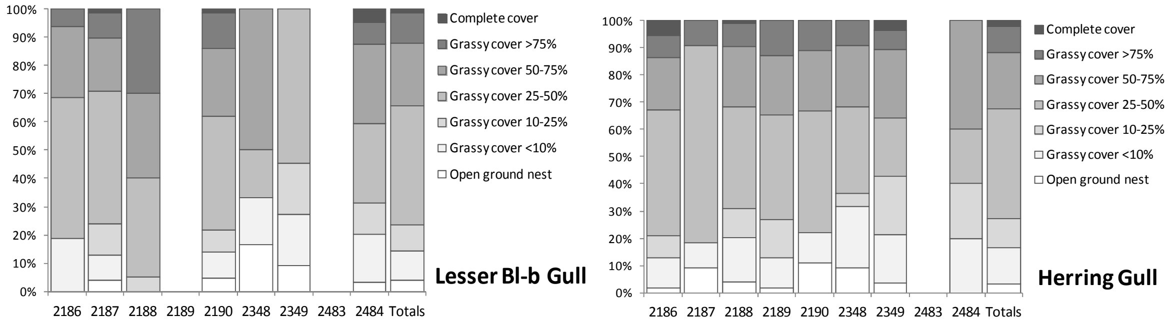


Fig. 3.3. Frequency of occurrence (%) of nests with different amounts of nest cover in the laying phase (during nest marking) within study plots (plot numbers in ^{App}Fig. 3.2), in Lesser Black-backed Gulls and Herring Gulls breeding in the Kelderhuispolder (N >5 per study plots, range), 2006-2012.

dividuals to alert (or inform) the colony about 'unwanted intruders' (humans, dogs, cats), but not necessarily raptors or crows (*personal observations*).

Using a 7-point scale to assess the amount of vegetation covering a nest (^{App}Fig. 3.2), overall, the amount of nest cover recorded at nests of Lesser Black-backed Gulls and Herring Gulls was similar (G_{adj}= 3.66, df=6, n.s.). A majority of the nests (64.4% in Lesser Black-backed Gulls, n= 649, 61.1% in Herring Gulls, n= 422) was more or less half-covered (25-75% cover), and the clutch was usually visible with little difficulty from several angles and from above. Some 15% of the nests (14.2% in LBBG, 16.6% in HG) were more or less completely open nests with at best a tuft of grass on one side. Only just over one tenth of the nests were well-covered (>75% nest cover; 12.0% in LBBG, 11.6% in HG) preventing visual detection from above.

Between study plots, the amount of nest cover at nests varied only slightly (^{App}Fig. 3.3). Between seasons, however, the amount of nest cover encountered at marked nests sites varied considerably (^{App}Fig. 3.4). Between species, these annual fluctuations were fully in concert, indicating that environmental conditions (vegetation growth) were responsible for the differences between years. Individual birds or pairs that were scored in subsequent seasons followed the exact same trend in nest cover as the population at large, supporting this hypothesis. As reported in Camphuysen & Gronert (2010a), hatching success and nest cover were positively correlated in both species. An update and different presentation of egg depredation rates relative to nest cover is provided in ^{App}Fig. 3.4 (including the 2011 and 2012 breeding seasons). Some 35-45% nests that were virtually without cover (open and <10%) lost at least one egg as a result of depredation . Around 20% of the nests with 'proper' nest cover lost at least some eggs. Around 30% of all eggs produced in open nests were depredated, against around 10% of the eggs in nests with more adequate cover.

While mean nest cover showed similar fluctuations per season in both species, egg depredation rates varied independently from year to year. Annual fluctuations in mean nest cover (^{App}Fig. 3.3) and annual fluctuations in egg depredation (%; ^{App}Tables 3.1-2) were not correlated (^{App}Fig. 3.6). Hence, while the amount of nest cover of both species was similar, and while the amount of nest cover was positively correlated with levels of egg depredation within seasons, fluctuations in the availability of cover between seasons did not explain annual differences in egg depredation between species. Mean clutch size and nest cover were positively correlated in both species (^{App}Fig. 3.7). The on average smaller clutch size in open ground nests and nests with little cover could mean that young, inexperienced birds may have been over-represented in these samples. This suggestion was not supported by the (few) immature Herring Gulls that were monitored during a breeding attempt (mean clutch size 2.82 ± 0.4 eggs nest^{-1}, mean nest cover 3.9 ± 1.8, range 2-7, n=11).

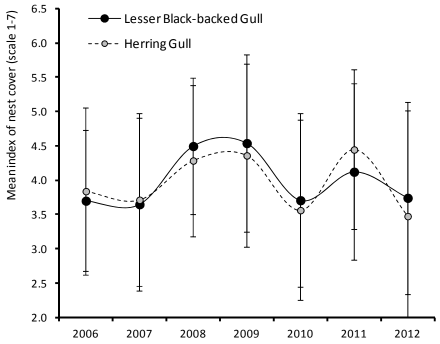


Fig. 3.4. Annual variations in the mean (±SD) cover of nests in the laying phase (during nest marking), in Lesser Black-backed Gulls and Herring Gulls, Kelderhuispolder, 2006-2012.

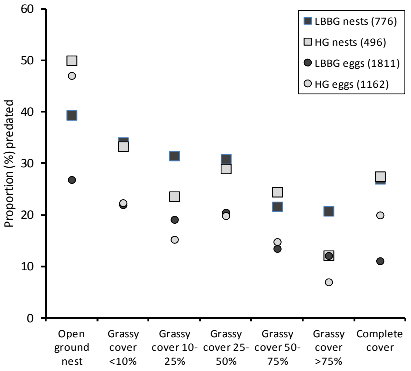


Fig. 3.5. Overall depredation rates (%) of all eggs laid (circles) or any egg in all nests (squares) versus nest cover during nest marking, in Lesser Black-backed Gulls and Herring Gulls, Kelderhuispolder, 2006-2012.

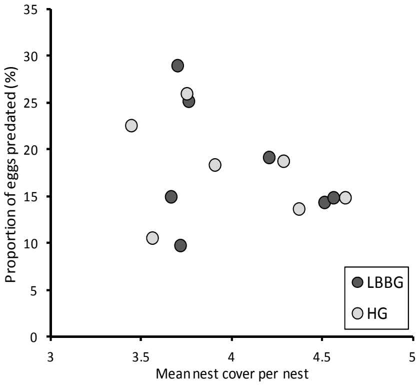


Fig. 3.6. Annual variations in mean nest cover (based on scores on a 7 point scale) related to levels of egg depredation (%), Kelderhuispolder 2006-2012.

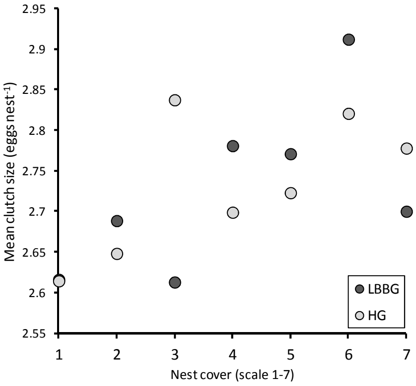
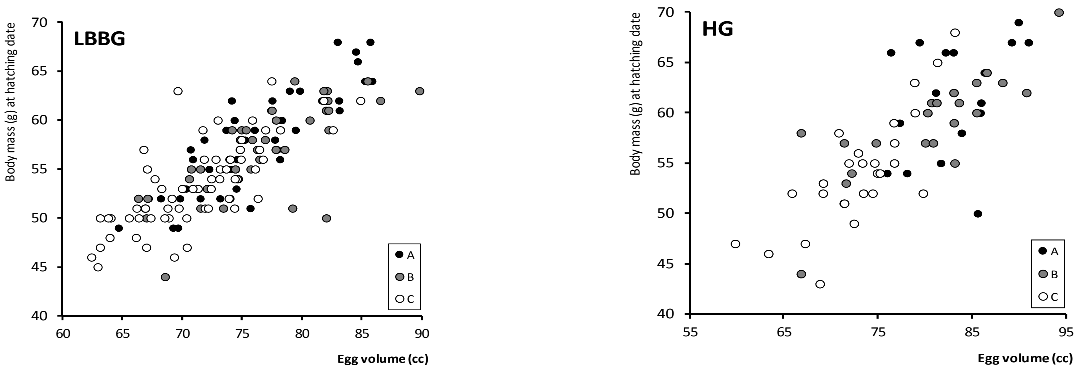


Fig. 3.7. Mean clutch size (eggs nest^{-1}) in nests with different amounts of nest cover, Kelderhuispolder 2006-2012.



LBBG	A-egg	y=	0.906	+ 23.570	R²=	0.755	F=	132.5	df=	1, 43	P<0.0001
	B-egg	y=	0.937	+ 23.225	R²=	0.643	F=	72.2	df=	1, 40	P<0.0001
	C-egg	y=	0.833	+ 26.638	R²=	0.553	F=	72.9	df=	1, 59	P<0.0001
HG	A-egg	y=	0.713	+ 40.677	R²=	0.363	F=	11.4	df=	1, 20	P<0.005
	B-egg	y=	1.195	+ 10.109	R²=	0.701	F=	46.8	df=	1, 20	P<0.0001
	C-egg	y=	0.819	+ 28.836	R²=	0.762	F=	83.4	df=	1, 26	P<0.0001

Fig. 3.8. Egg volume (cc) versus hatching body mass (g) in chicks Lesser Black-backed Gulls (LBBG) and Herring Gulls (HG) for which the exact laying sequence and the body mass on the day of hatching are both known with certainty; Kelderhuispolder 2006-2012 (significance of linear trends indicated in tabulated data)

Box 3.2 – Egg volume

There are several, precise and less precise, means of assessing egg volumes[1-6]. In the studies at Texel a practical, easy and commonly used method was adopted in which the egg volume is calculated from linear dimensions (length and width)

$$\text{Volume} = k\text{LB}^2 \qquad (^7)$$

Where L= maximum length, B= maximum width, and k = a constant. Differences in egg shape have been ignored, even though some eggs are considerably rounder or more pear-shaped than others. The constant (k) used was derived from Spaans & Spaans (1975)[8], to allow for direct comparisons with earlier Dutch (Terschelling) data: **k = 0.5035** (based on 12 Herring Gull eggs). Alternatives, used in other studies are 0.5084 (or 1.01x the 'Spaans'-volume)[2] and 0.476 (0.95x)[9].

Egg dimensions: length and width of eggs of Lesser Black-backed Gulls and Herring Gulls at Texel. Kelderhuispolder, 2006-2012.

LBBG	Length (L)	Width (B)	L/B	**HG**	Length (L)	Width (B)	L/B
mean ± SD	66.7 ± 2.8	46.9 ± 1.5	1.4 ± 0.1		69.6 ± 3.8	48.1 ± 2.2	1.4 ± 0.1
min-max	57.5-75.9	41.6-51.6	1.2-1.7		36.8-79.0	24.7-54.5	1.2-1.7
n=	1869	1869	1869		1226	1226	1226

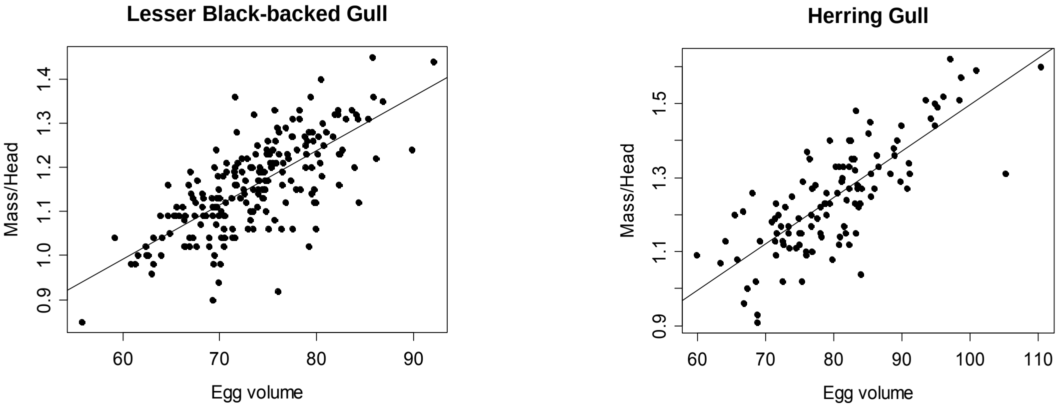
References: [1,2]Barth 1953, 1968 [3,4]Tatum 1974, 1975, [5]Hoyt 1979, [6]Michel & Thompson 2003, [7]Stonehouse 1966, [8]Spaans & Spaans 1975, [9]Harris 1964a.

Egg volume –Bolton (1991) found that chicks from large eggs were not only skeletally larger (tarsus length) but also heavier for their size than those from smaller eggs, both of which could contribute to increased chances of survival. He also found that parental quality was more important than egg size in determining chick survival, suggesting that correlations between survival and egg size found (by other workers in non-experimental situations) may be due to the confounding effect of parental quality. Gasparini *et al.* (2004) considered relaying (in Black-legged Kittiwakes *Rissa tridactyla*) one of three main competing components of quality associated with egg production, each of which could represent parental quality. Assessments of laying dates, egg predation rates and the incidence of replacements clutches were an essential part of the studies at Texel. To test the hypothesis that chicks from large eggs are skeletally larger, heavier or even in better condition (heavier for their size) than chicks from smaller eggs, which could contribute to increased chances of survival, all eggs were measured.

Table 3.7. Egg volume (cc) versus skeletal size (head, tarsus, bill in mm) in chicks Lesser Black-backed Gulls (LBBG) and Herring Gulls (HG) for which the exact laying sequence and the body mass on the day of hatching are both known with certainty; Kelderhuispolder 2006-2012.

Egg volume versus head length											
LBBG	A-egg	y=	1.806	- 10.419	R^2=	0.364	F=	16.6	df=	1, 29	P<0.001
	B-egg	y=	2.086	- 24.686	R^2=	0.273	F=	7.9	df=	1, 21	P= 0.01
	C-egg	y=	0.838	+ 31.148	R^2=	0.078	F=	3.5	df=	1, 41	n.s.
HG	A-egg	y=	2.465	- 32.606	R^2=	0.156	F=	3.1	df=	1, 17	n.s.
	B-egg	y=	2.256	- 25.354	R^2=	0.153	F=	3.3	df=	1, 18	n.s.
	C-egg	y=	2.364	- 37.859	R^2=	0.492	F=	24.2	df=	1, 25	P<0.001
Egg volume versus tarsus length											
LBBG	A-egg	y=	1.550	+ 34.206	R^2=	0.284	F=	11.5	df=	1, 29	P<0.005
	B-egg	y=	3.300	- 10.253	R^2=	0.327	F=	9.2	df=	1, 19	P<0.01
	C-egg	y=	1.974	+ 19.674	R^2=	0.283	F=	15.4	df=	1, 39	P<0.001
HG	A-egg	y=	0.215	+ 80.929	R^2=	0.001	F=	0.0	df=	1, 16	n.s.
	B-egg	y=	1.686	+ 38.549	R^2=	0.072	F=	1.2	df=	1, 16	n.s.
	C-egg	y=	3.668	- 19.945	R^2=	0.542	F=	28.3	df=	1, 24	P<0.001
Egg volume versus bill length											
LBBG	A-egg	y=	1.301	+ 51.557	R^2=	0.054	F=	1.7	df=	1, 29	n.s.
	B-egg	y=	1.703	+ 44.307	R^2=	0.053	F=	1.2	df=	1, 21	n.s.
	C-egg	y=	-0.439	+ 78.242	R^2=	0.005	F=	0.2	df=	1, 41	n.s.
HG	A-egg	y=	5.348	- 11.247	R^2=	0.414	F=	11.3	df=	1, 16	P<0.005
	B-egg	y=	1.634	+ 52.200	R^2=	0.042	F=	0.8	df=	1, 19	n.s.
	C-egg	y=	2.276	+ 33.418	R^2=	0.146	F=	4.3	df=	1, 25	P<0.05

The correlation between egg volume (Box 3.2) and chick mass at hatching was highly significant for A-, B- and C-eggs in both species (^{App}Fig. 3.8). Correlations between egg volume and skeletal measuremens (head, bill, and tarsus) were positive, but seldom significant, perhaps largely because the sample size for specific (sequenced) eggs was still too small (^{App}Table 3.7). Using the exact same dataset but ignoring laying sequence, all correlations were highly significant, except bill length in Lesser Black-backed Gulls. All chicks for which body mass and head length had been assessed at the day of hatching (212 Lesser Black-backed Gulls, 114 Herring Gulls) were used to evaluate the relationship between egg volume and structural size-corrected body mass at hatching (^{App}Fig. 3.9). The results confirm that chicks from large eggs are in better condition (heavier for their size) than chicks from smaller eggs.



LBBG	y=	42.004	+ 24.779	R^2=	0.519	F=	226.4	df=	1, 210	P<0.0001
HG	y=	49.332	+ 18.655	R^2=	0.618	F=	180.8	df=	1, 112	P<0.0001

Fig. 3.9. Egg volume (cc) irrespective of laying sequence versus skeletal size-corrected body mass (Mass / Head) at hatching in 1d old chicks of Lesser Black-backed Gulls (LBBG) and Herring Gulls (HG); Kelderhuispolder 2006-2012 (significance of linear trends indicated in tabulated data)

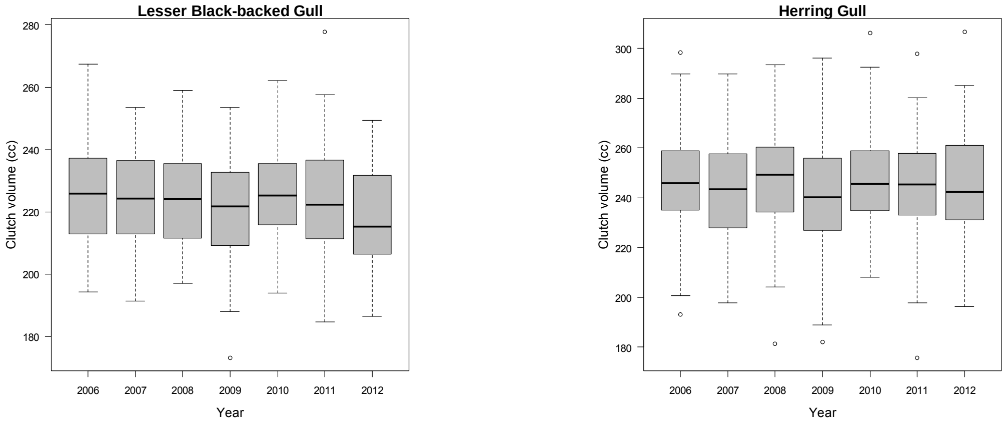


Fig. 3.10. Annual fluctuations in 3-egg clutch volumes (cc, see Box 3.2) of Lesser Black-backed Gulls and Herring Gulls (HG); Kelderhuispolder 2006-2012.

Slight variations in 3-egg clutch volumes between seasons have been reported in Camphuysen & Gronert (2010a). Updated information is provided in $^{\mathrm{App}}$Fig. 3.10 (2006-2012). Clutch volumes in Lesser Black-backed Gulls in 2012 (217.4 ± 15.2, n= 63), the lowest on record, were significantly below all other years combined (224.3 ± 16.2, n= 461; Welch Two Sample t-test $t_{82.6}$ = 3.34, P=0.001). The difference with clutch volumes in the second lowest year, 2009 (221.4 ± 16.0, n= 95), was not significant, however (t_{138} = 1.602, n.s.). Clutch volumes in Herring Gulls in 2009 (240.0 ± 23.7, n= 49), the lowest on record, were not significantly different from other years combined (246.7 ±21.4, n = 281; $t_{63.4}$ = 1.589, n.s.).

Breeding densities Kelderhuispolder

In 2009, 2010, and 2011, the colony was surveyed with a strip-transect census: two observers connected with an 8m long line walked along pre-set transects through the colony, counting well-established nests with and without eggs or young (excluding "play-nests" on territories). The species were identified on the basis of prey remains found at the territory, or by direct observations of birds attending the nest (De Wit 1988, Camphuysen *et al. in press*). As a result of excessive workload in May, the chosen survey dates were often suboptimal. The survey in 2010, however was closest to the preferred date (which would have been 20-25 May for Herring Gulls, 25-30 May for Lesser Black-backed Gulls given their laying dates). De results indicated a study population of *c.* 1000 pairs of Herring Gulls and 2000 pairs of Lesser Black-backed Gulls, with a nesting density of *c.* 360 pairs ha^{-1} ($^{\mathrm{App}}$Table 3.8). The censuses suggested a continuous decline in numbers of Herring Gulls and an increase in Lesser Black-backed Gulls.

Table 3.8. Calculated breeding population (n nests ha^{-1}) of Herring Gulls (HG) and Lesser Black-backed Gulls (LBBG) in the Kelderhuispolder study area (incl. *Hinterland* study plot) in 2009-2011 based on strip transect counts in the early HG hatching phase. The total area is 82,650m².

Numbers		**10/06/2009**	**27/05/2010**	**01/06/2011**
	Herring Gulls	1288	1023	890
	Lesser Black-backed Gulls	1816	1986	2026
	Totals	3104	3009	2916
Densities				
	Herring Gulls ha^{-1}	160	120	110
	Lesser Black-backed Gulls ha^{-1}	220	240	250
	Totals ha^{-1}	380	360	350
Sample size				
	Surveyed	13153 m²	33376 m²	18566 m²
	Sample (%)	16%	40%	23%

Nesting densities between study plots (based on the 2010 census with additional data from the 2009 census for the *Entry Dunes* study plot) varied from 180-700 nests ha^{-1}, with Lesser Black-backed Gulls predominating in the areas with the highest nesting densities and with Herring Gulls in the areas with the lowest nesting densities ($^{\text{App}}$Table 3.9). The percentage of well-constructed nests which did not contain eggs varied considerably from year to year. For Herring Gulls, the 2009 survey was too late for a meaningful assessment of nest contents (many chicks had already ventured into the vegetation), but in 2010 20% (n= 413) and 2011 30% (n= 200) of the nests were empty. For Lesser Black-backed Gulls, empty nests were most numerous in 2009 (59%, n= 289), but lower in 2010 (19%, n= 802) and 2011 (33%, n= 455). Most "empty" nests had never contained eggs and were not used later in the season (from personal field observations during nest monitoring). In fact, during these surveys, scheduled late May and early June, a substantial proportion of the territory holders had either left the colony or paid rather few visits.

A study of territory-holding gulls on a 0.41-ha study plot at Tarnbrook Fell (Lancashire, UK) in 1993 to investigate the occurrence of empty nests showed that of pairs that defended a territory and constructed a complete nest, 27% subsequently failed to produce eggs (O'Connell *et al.* 1997). From annual counts of Lesser Black-backed Gull nests at the Tarnbrook Fell during 1981-1994, the mean percentage of nests which did not contain eggs was both high and remarkably constant from year to year (54±1.9%). Just as on Texel, most "empty" nests did not subsequently receive eggs. These pairs attended their territory significantly less frequently than pairs that produced clutches and achieved significantly fewer mountings. Sixty percent of pairs constructed more than one nest, and 58% of all nests built received no eggs. The rather higher proportion of empty nests in the Lancashire surveys results from a methodological difference: the Texel surveys counted only the best nest per territory, whereas O'Connell *et al.* (1997) counted all empty nests (play-nests included). The 27% of pairs in the 1993 study plot that failed to lay eggs is much closer to the majority of the values obtained at Texel.

Spaans *et al.* (1987) reported an 3-fold increase in nesting densities of the same two species of gulls within a 6 ha study plot at Terschelling of 35 nests ha^{-1} in the late 1960s to 97 nests ha^{-1} in the early 1980s and attributed a number of changes to the change in nesting density (decrease in fledging rates, increase in egg and chick depredation rates, decrease in egg size and chick growth). While it is difficult to compare nesting densities between two study areas directly, the Kelderhuispolder censuses suggest that nesting densities on Texel are indeed very high, possibly some 3.7x higher than at Terschelling in the early 1980s. Within the study area Kelderhuispolder, rather clear variations in nesting densities occurred, with possible repercussions for the egg/chick depredation rates and the reproductive success of the birds breeding there. While summarising all data over all breeding seasons (2006-12), nesting success at hatching (% of nests that hatched at least one egg) was lower for Lesser Black-backed Gulls in areas with the highest breeding densities. In Herring Gulls this effect was absent, but the variation in nesting densities was also much lower. Overall breeding success, comparing nests that fledged at least one chick with nests that failed, tended to be higher in study plots with high densities than in low density areas. The results indicate that the effects of nesting densities on some vital rates are inconsistent and sometimes counterintuitive.

Jehl (1994) studied California Gulls *Larus californicus* at Mono Lake, California, from 1984-93. Numbers had increased 30-fold since 1916 and nesting densities were among the highest reported for the species. He found that the upper critical density approximated 5000 nests ha^{-1}, but even at 7700 nests ha^{-1} there was no effect on egg size, clutch size, or fledging success. Shorter (6-8 yr) sampling periods, however, would have indicated that either positive or negative effects had occurred. Gulls evidently dispersed after the upper critical density was attained, because concentrations above the upper critical density did not persist into subsequent breeding seasons. Jehl (1994) observed that density effects are often inferred from comparing long-term changes in population size (as an index to density) with various population parameters. He concluded that the role of nest spacing is best investigated by comparing the performance of birds nesting at different densities in the same year.

At Texel, we were unable to assess exact nesting densities annually because other activities were prioritised, but also because the fieldwork in colonies with high densities (but nevertheless hidden, difficult to detect nests) such as in Kelderhuispolder caused considerable disturbance. Therefore, the values presented in ^{App}Table 3.9 are best seen as proxies of differences in breeding densities between study plots in the Kelderhuispolder for the entire study period. The variability of hatching and fledging rates between study plots and between seasons was considerable. When pooling the available data and assuming more or less constant densities, the correlation between densities of nests (both species combined) within study plots and egg depredation rates was positive, the correlation with hatching success was the reverse (^{App}Table 3.10). This was true for both species. Similar tendencies were found in chick depredation and fledging rates in Herring Gulls, but not trends were found in Lesser Black-backed Gulls in the phase of chick care (^{App}Table 3.11). In Chapter 4 differences between study plots are discussed in more depth. Later data have confirmed that the two main study plots (Valley and Foot Sea dunes) experienced contrasting trends over time (in chick depredation levels and fledging rates), while we have no data to support the suggestion that nesting densities have reversed in either area (see also below under *Chick depredation*).

Table 3.9. Breeding densities (nests ha^{-1}) of Herring Gulls (HG) and Lesser Black-backed Gulls (LBBG) in the Kelderhuispolder study plots based on strip transect counts in the early HG hatching phase in 2010 (Entry dunes based on the 2009 census).

Study plot	**Lesser Black-backed Gull**	**Herring Gull**	**Totals**	**dominant**
HG club	530	160	700	LBBG
Lookout	410	190	600	LBBG
Foot sea dunes	460	120	580	LBBG
LBBG-club	250	120	370	LBBG
Valley ridge	250	60	310	LBBG
Valley	220	90	310	LBBG
Roughs	140	160	300	HG
Entry dunes	80	190	270	HG
Sea dunes	50	130	180	HG
Total study colony	240	120	360	LBBG

Table 3.10. Egg depredation rates (*n* nest^{-1}) and hatching rates (*n* nest^{-1}) in unnamed study plots with different nesting densities (*n* ha^{-1}, both species combined) and different mean nest cover; pooled data, Kelderhuispolder 2006-2012.

Lesser Black-backed Gull					**Herring Gull**				
Density	Nest cover	Nests	PredRate	HatchRate	Density	Nest cover	Nests	PredRate	HatchRate
					180	4.1	111	0.5	2.0
270	3.3	16	0.3	2.3	270	4.2	123	0.3	2.2
300	3.9	9	0.6	2.9	300	3.9	97	0.5	1.9
310	4.1	237	0.4	2.1	310	3.7	7	0.1	2.0
320	3.9	8	0.3	2.4	320	3.5	21	0.6	1.6
580	4.0	275	0.5	1.9	580	4.0	10	0.2	2.5
600	4.2	73	0.5	2.1	600	3.7	10	0.6	1.6
700	3.4	10	0.7	1.9	700	3.8	26	0.7	1.5

Table 3.11. Chick depredation rates (*n* nest^{-1}) and fledging rates (*n* nest^{-1}) in study plots with different nesting densities; pooled data, Kelderhuispolder 2006-2012.

Lesser Black-backed Gull					**Herring Gull**				
Plot	Density	Nests	PredRate	FledgeRate	Plot	Density	Nests	PredRate	FledgeRate
Valley	0.031	131	1.18	0.63	Entry dunes	0.027	66	0.45	0.98
Foot sea dunes	0.058	123	1.35	0.36	Roughs	0.030	35	0.66	1.26
Lookout	0.060	38	0.84	0.71	HG-club e.o.	0.070	16	1.00	0.56
		292	1.21	0.52			117	0.59	1.01

Box 3.3 - Testing growth models

In a MSc-project, Natalia Gallego Garcia tested four growth models using developments of chicks of Herring Gulls and Lesser Black-backed Gulls from the Kelderhuispolder colony at Texel, using measurements obtained during 2006-2008. In all three years, body mass (g), head length (mm), bill length (0.1mm) and wing length (mm) were measured; in 2007 and 2008 tarsus length (mm) was also measured. The colony was visited with 3d intervals from hatching until fledging of the chicks. The exact age at which chicks were capable of flight varied, but all individuals that reached the age of 40d were recorded as fledglings. For both species, body mass and all measurements of only those birds that fledged were pooled across years, and used to model growth in time (d). The growth models were:

(1) Logistic growth model with 3 parameters

$$y = \frac{a}{1 + b\ell^{-kt}}$$

a is the upper asymptote, *b* is the value of *t* at the point of inflection of the curve, and *k* is the growth rate.

(2) Logistic growth model with 4 parameters

$$y = a + \frac{b - a}{1 + \ell^{(c-t)/k}}$$

a is the upper asymptote, for small values of *t*, *b is* the upper asymptote for big values of *t*, *c* is the value of *t* at the point of inflection of the curve, and *k* is the growth rate.

(3) Gompertz growth model

$$y = a\ell^{-b\ell^{-kt}}$$

a is the upper asymptote, *b* is the value of *t* at the point of inflection of the curve, and *k* is the growth rate.

(4) von Bertalanffy growth model

$$y = a\left(1 - \ell^{-kt}\right)$$

a is the upper asymptote, and *k* is a measure of the rate at which the growth rate declines

An analysis of variance was used to make pair wise comparisons between models. The logistic model with 3 parameters and the Gompertz model could not be compared using an ANOVA, because they have the same number of parameters and the same number of degrees of freedom (n parameters+1). The Akaike's information criterion (AIC) was also estimated for each model and each variable. When comparing two models, the smaller the AIC, the better the fit[1]. When the ANOVA test showed no statistical differences between the models, the simplest model was chosen in this order: von Bertalanffy, being the simplest model, followed by the logistic with 3 parameters and Gompertz models, and the more complex, the logistic model with 4 parameters. When statistical differences were found, the model with the least AIC value was selected.

Both logistic models and Gompertz model fit the data of all variables. Von Bertalanffy model had a poor fit for body mass and did not fit wing length data for Herring Gulls, or wing length data for Lesser Black-backed Gulls. The standard von Bertalanffy model used in the present study can be used to fit most growth data lacking an inflection point, but is not suitable for a sigmoidal growth pattern, like that of body mass and wing length. For this reason, the cubic version of von Bertalanffy model

$$y = a\left(1 - \ell^{-kt}\right)^3,$$

often used to fit either length or weight data containing a growth inflection[2], was used only for these two variables. From all four models tested, the von Bertalanffy was the model with the least fit. Both logistic models and the Gompertz model had a good fit with the data used in this study. However, the choice of the best model should be made based on the objectives of the study and not based on the outcome of the statistical comparisons or the goodness of fit. For example, for the comparison of birds that starve to death, birds that were depredated, and birds that fledged, the use of the logistic or Gompertz model was inappropriate, as these methods require the estimate of the asymptote and cannot be applied to chicks that do not survive to fledging. There are two ways to solve this problem and therefore to make comparisons of this sort. One way is to fit a linear model instead, by using only the points of the linear phase of the growth curve. For body mass, for example, the regression should be made with the points between day 5 and day 25. This method is suitable if the objective of the study is to compare only the growth rates of individuals[3, 4]. However, if the study is intended to compare the growth of chicks during their early days (*i.e.* <5d) or just prior to fledging (*i.e.* >25d), other modes should be chosen or other measurements should be taken.

There were no significant differences between species in growth rates of body mass (*F*=0.17, *p*=0.67), bill (*F*=0.04, *p*=0.83), tarsus (*F*=0.17, *p*=0.67), and head (*F*=0.005, *p*=0.94). The growth rate of wing length was significantly higher in Herring Gulls than in Lesser Black-backed Gulls (*results tabulated below*). The asymptote of the curve for all variables was larger for Herring Gulls than for Lesser Black-backed Gulls.

Values of the parameters estimated from the logistic model. Asymptote (a), point of inflection (b) and growth rate (k) of Herring Gulls (HG), and Lesser Black-backed Gulls (LBBG) are given.

	HG	**LBBG**	**HG**	**LBBG**	**HG**	**LBBG**
	a		***b***		***k***	
Mass	793.4	677.7	16.0	14.6	6.4	5.8
Tarsus	65.4	64.8	5.4	5.0	8.5	7.8
Bill	46.4	45.7	8.0	7.0	12.9	11.8
Head	110.7	109.9	4.6	4.4	12.5	12.3
Wing	338.0	329.5	25.1	22.3	8.5	7.8

The results suggest that from hatching to fledging, Herring Gull chicks grew faster than the offspring of Lesser Black-backed Gulls. However, the only significant difference found between species was wing length (taking more time to develop completely in Lesser Black-backed Gulls). The point of inflection of the wing curve is the latest of any measurement (25d for Herring Gulls and 22d for Lesser Black-backed Gulls) and at 40d, the asymptote is not yet reached. Clearly, after fledging, the wing in both species keeps developing.

References: ^{1}Crawley 2007, ^{2}Ricklefs 1967, ^{3}Bolton 1991, ^{4}Spaans 1971; **Source**: Gallego Garcia N. 2008*. Growth in chicks of Lesser Black-backed Gulls Larus fuscus and Herring Gulls Larus argentatus in the Kelderhuispolder colony, Texel.* MSc thesis, University of Amsterdam, Amsterdam, 26pp, CD. [MSc project 2008, supervision Emiel van Loon, Judy Shamoun-Baranes & CJC]

Chick growth

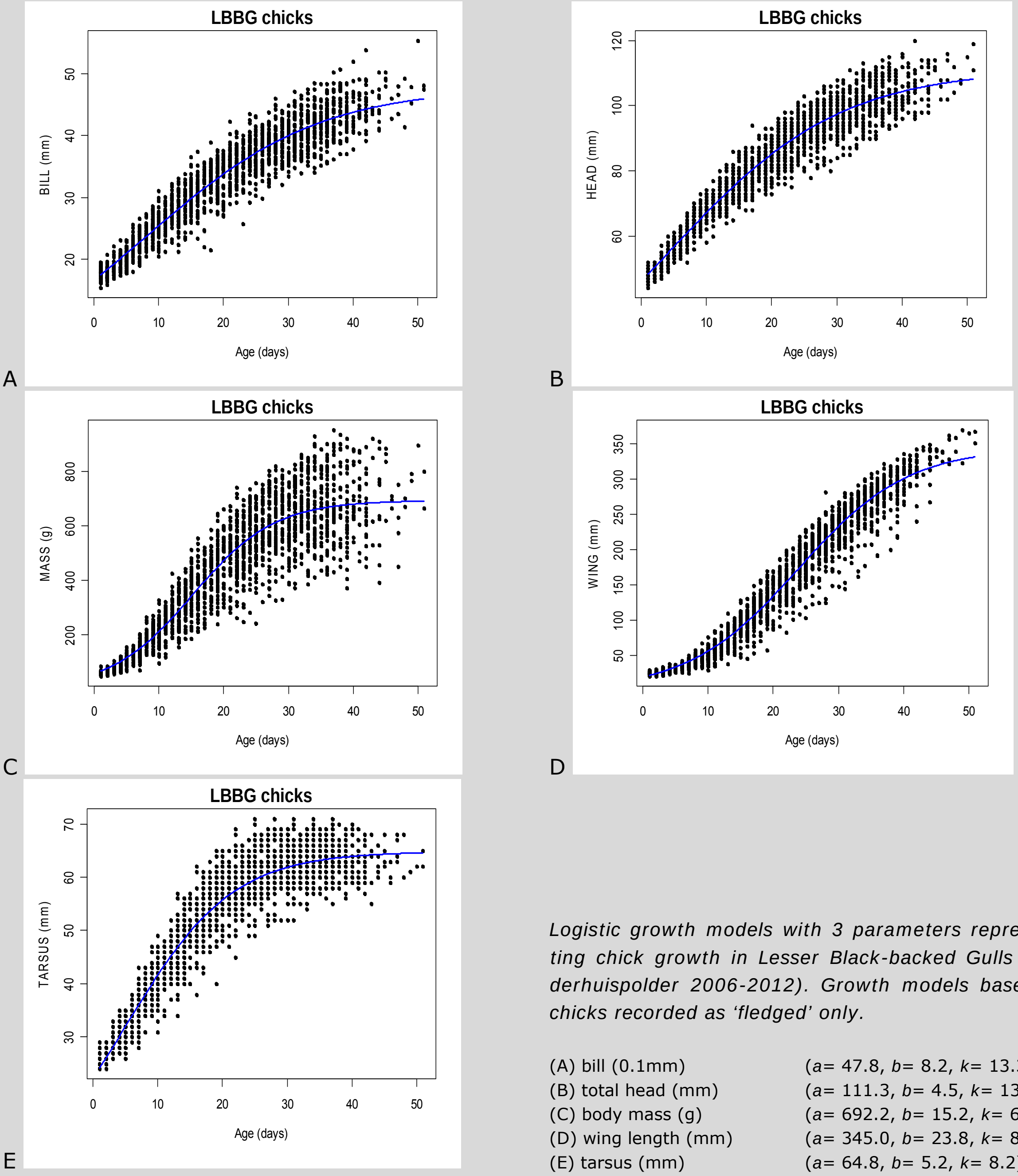
During nest controls in the phase of chick care, chicks were weighed (g) and measured in order to monitor growth. Initially, the measurements included head (back of the head to tip of the bill), bill (tip to feathers) and wing (flattened), but in 2007-2012 the tarsus was measured also. Over the years we obtained 32,142 measurements on 925 chicks ranging from 1-50d of age:

	Chicks	Head	Bill	Wing	Tarsus	Mass
LBBG	647	3937	3922	3938	3591	4045
HG	278	2394	2387	2392	2201	2410

Growth rates could be related to egg size (pre-hatch factors), but were primarily thought to provide information on provisioning rates during chick care (post-hatch factors). Hunt & Hunt (1976) observed that in Glaucous-winged Gull *Larus glaucescens*, in years of both low and high food availability, chick survival was strongly correlated with growth rates. Also, chicks that grew slowly were more likely to be killed by neighbours than fast-growing chicks. Van Klinken (1992) failed to find differences in growth rates between pairs that had received supplementary food and pairs that served as controls, but chick survival was considerably higher in pairs that had received extra food. Pugesek (1993) reported that hatching asynchrony in California Gulls *Larus californicus* resulted in initial mass differences between siblings that persisted and accelerated with time. Fledging success was unrelated to hatching asynchrony but was related to large offspring mass. Parental age was unrelated to hatching asynchrony but heavily influenced the brood's gain in mass. These are just some examples from a wide field of study and numerous publications to explain why attention was paid to chick growth rates. The contrasting population trends in the gulls studied (through changes in reproductive success and survival), are most likely food-related. Periodic fluctuations in growth rates could be due to variations in the capacity of parents to provide sufficient food for the chicks (mirroring patterns in food availability), but differences could also be attributed to a trade-off between present and future reproductive success (Villuendas & Sarzo 2003). None of which is mutually exclusive.

Box 3.4 - Chick growth, 2006-2012

Chick growth was modelled using a logistic growth model with 3 parameters[1]. First, for both species, body mass and all measurements of structural size were pooled across years (2006-12), to model growth in time (d), only using data obtained from chicks that were recorded as fledged

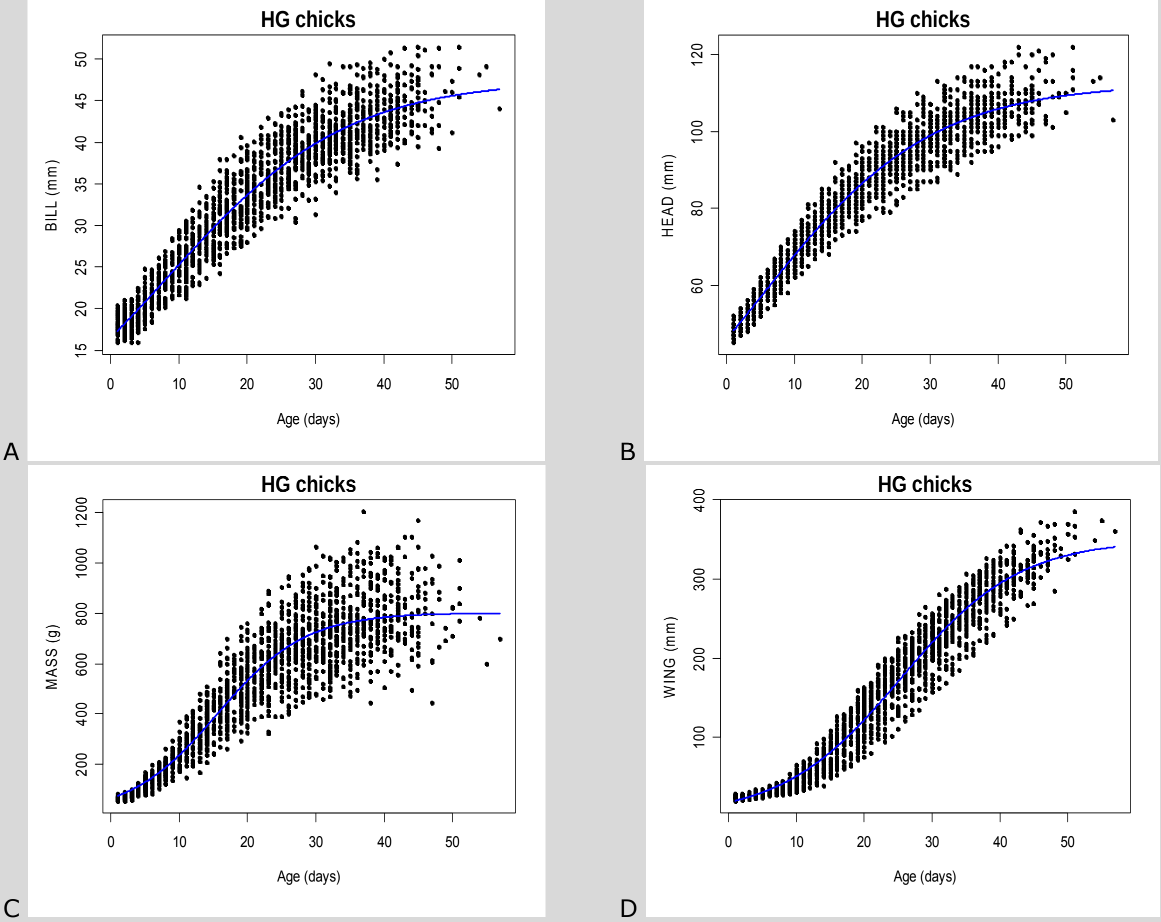


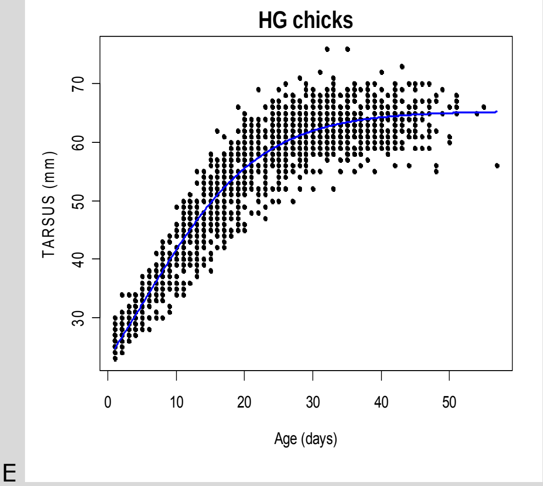
Logistic growth models with 3 parameters representing chick growth in Lesser Black-backed Gulls (Kelderhuispolder 2006-2012). Growth models based on chicks recorded as 'fledged' only.

(A) bill (0.1mm)	(*a*= 47.8, *b*= 8.2, *k*= 13.3)
(B) total head (mm)	(*a*= 111.3, *b*= 4.5, *k*= 13.1)
(C) body mass (g)	(*a*= 692.2, *b*= 15.2, *k*= 6.3)
(D) wing length (mm)	(*a*= 345.0, *b*= 23.8, *k*= 8.4)
(E) tarsus (mm)	(*a*= 64.8, *b*= 5.2, *k*= 8.2)

To investigate annual differences in chick growth (body mass gain as well as structural growth), the logistic growth model[1] was used to model body mass increments, and rates of head and wing length growth in time (d). In this case, all data were deployed, including measurements from chicks that did not fledge (see Tables below). The results confirmed earlier conclusions that Herring Gull chicks generally grow faster than the offspring of Lesser Black-backed Gulls[1]. Deviations from this pattern were body mass and wing and head length increments of Lesser Black-backed Gulls in 2010. In 2010, both species fledged relatively many chicks, but only Lesser Black-backed Gulls chicks experienced higher growth rates than in any other season. In 2010, Herring Gull growth was interrupted by a prolonged starvation event in the second half of June (Chapter 3)[2], which passed more or less unnoticed in the relatively younger Lesser Black-backed Gull chicks. None of the inspected annual growth rates correlated significantly with annual variations in reproductive success (chicks fledged per pair^{-1}; Rank Spearman tests).

Box 3.4 - Chick growth, 2006-2012





Logistic growth models with 3 parameters representing chick growth in Herring Gulls (Kelderhuispolder 2006-2012). Growth models based on chicks recorded as 'fledged' only.

(A) bill (0.1mm)	(*a*= 47.5, *b*= 8.3, *k*= 13.1)
(B) total head (mm)	(*a*= 112.4, *b*= 4.7, *k*= 12.7)
(C) body mass (g)	(*a*= 801.3, *b*= 15.6, *k*= 6.4)
(D) wing length (mm)	(*a*= 349.9, *b*= 25.4, *k*= 8.7)
(E) tarsus (mm)	(*a*= 65.3, *b*= 5.2, *k*= 8.5)

Annual body mass developments for Lesser Black-backed Gulls and Herring Gulls in 2006-2012, estimated with the 3 parameter logistic growth model. Asymptote (a), point of inflection (b) and growth rate (k) ± SE. Growth models based on all chicks.

	Lesser Black-backed Gull			**Herring Gull**		
Year	*a*	*b*	*k*	*a*	*b*	*k*
2006	662.7 ± 18.8	14.7 ± 0.5	5.9 ± 0.3	839.0 ± 30.6	17.1 ± 0.7	6.6 ± 0.4
2007	671.8 ± 12.2	13.9 ± 0.4	5.3 ± 0.3	844.9 ± 12.7	16.0 ± 0.4	6.3 ± 0.3
2008	693.4 ± 8.6	15.2 ± 0.3	6.0 ± 0.2	780.6 ± 12.6	16.4 ± 0.4	6.9 ± 0.3
2009	635.6 ± 12.2	15.2 ± 0.4	6.3 ± 0.3	775.1 ± 19.9	15.5 ± 0.6	6.6 ± 0.4
2010	778.5 ± 15.5	19.5 ± 0.4	7.8 ± 0.2	764.9 ± 12.8	15.4 ± 0.4	6.2 ± 0.3
2011	627.5 ± 12.0	14.4 ± 0.4	5.7 ± 0.3	805.3 ± 23.4	18.0 ± 0.7	7.0 ± 0.5
2012	635.9 ± 10.8	14.7 ± 0.3	5.6 ± 0.3	804.5 ± 20.7	16.6 ± 0.5	6.8 ± 0.4

Box 3.4 - Chick growth, 2006-2012

Annual variations in head growth as an indicator of structural size developments for Lesser Black-backed Gulls and Herring Gulls in 2006-2012, estimated with the 3 parameter logistic growth model. Asymptote (a), point of inflection (b) and growth rate (k) ± SE. Growth models based on all monitored chicks.

	Lesser Black-backed Gull			**Herring Gull**		
Year	*a*	*b*	*k*	*a*	*b*	*k*
2006	106.4 ± 2.0	3.6 ± 0.4	12.2 ± 0.6	113.8 ± 2.6	5.4 ± 0.6	13.1 ± 0.8
2007	109.4 ± 1.1	4.2 ± 0.2	12.0 ± 0.4	113.3 ± 1.0	4.9 ± 0.3	13.0 ± 0.4
2008	111.8 ± 0.7	4.7 ± 0.2	12.6 ± 0.3	112.0 ± 0.9	4.8 ± 0.2	13.2 ± 0.4
2009	108.2 ± 1.1	4.2 ± 0.3	12.6 ± 0.4	111.5 ± 1.5	4.6 ± 0.4	12.6 ± 0.5
2010	114.8 ± 1.2	5.8 ± 0.3	15.0 ± 0.4	112.4 ± 1.1	4.8 ± 0.3	12.6 ± 0.4
2011	108.7 ± 1.3	4.6 ± 0.3	12.6 ± 0.4	117.2 ± 2.4	6.3 ± 0.6	14.9 ± 0.8
2012	110.1 ± 1.2	5.0 ± 0.3	12.7 ± 0.4	114.1 ± 1.1	5.5 ± 0.3	13.3 ± 0.4

Annual variations in wing growth as an indicator of structural size developments for Lesser Black-backed Gulls and Herring Gulls in 2006-2012, estimated with the 3 parameter logistic growth model. Asymptote (a), point of inflection (b) and growth rate (k) ± SE. Growth models based on all monitored chicks.

	Lesser Black-backed Gull			**Herring Gull**		
Year	*a*	*b*	*k*	*a*	*b*	*k*
2006	346.2 ± 13.2	23.8 ± 0.8	8.3 ± 0.3	329.4 ± 18.2	24.7 ± 1.1	8.6 ± 0.4
2007	336.7 ± 6.5	22.9 ± 0.4	8.0 ± 0.2	359.8 ± 4.3	25.7 ± 0.3	8.6 ± 0.2
2008	346.3 ± 3.2	23.0 ± 0.2	8.0 ± 0.1	363.3 ± 5.7	27.0 ± 0.4	9.2 ± 0.2
2009	340.4 ± 8.0	23.9 ± 0.5	8.5 ± 0.2	363.5 ± 9.5	25.9 ± 0.6	9.1 ± 0.3
2010	352.4 ± 6.4	25.6 ± 0.4	8.7 ± 0.2	345.6 ± 8.3	25.3 ± 0.5	8.5 ± 0.3
2011	310.7 ± 7.5	22.9 ± 0.5	7.9 ± 0.2	342.7 ± 11.4	27.0 ± 0.8	8.6 ± 0.4
2012	333.5 ± 6.5	23.6 ± 0.4	8.1 ± 0.2	340.2 ± 6.6	25.4 ± 0.4	8.3 ± 0.3

References: [1]Gallego Garcia (2008), [2]Chapter 3; **Source**: Unpubl. data Kelderhuispolder observations 2006-2012 (base material: 925 chicks; 35,395 growth measurements; CJC).

Growth models - Four growth models were tested to best describe the collected data (Box 3.3) and one of the models was used to evaluate annual variations in chick growth (Box 3.4). The results are general patterns of growth with considerable variability in the later phase of chick care (chicks >20d of age), particularly with body mass. As expected, tarsus developed most rapidly, and size increments more or less stopped around 30d of age. Head and bill developed in a similar way, but were still developing when birds fledged. Body mass stabilised (or fluctuated) from *c.* 30d of age, after a slow start and a growth spurt (near linear growth) between *c.* 5 and 25d of age. Wing development was still in full swing around fledging. Next to measurements of growth (mass and structural size), it was decided to log moult (developments of feathers; Box 3.5). The results show a considerable variation in feather growth with age. While Herring Gulls tended to grow faster from hatching to fledging than Lesser Black-backed Gulls (Gallega Garcia 2008; Box 3.3), in Lesser Black-backed Gulls, the moult scores progressed slightly faster than in Herring Gulls.

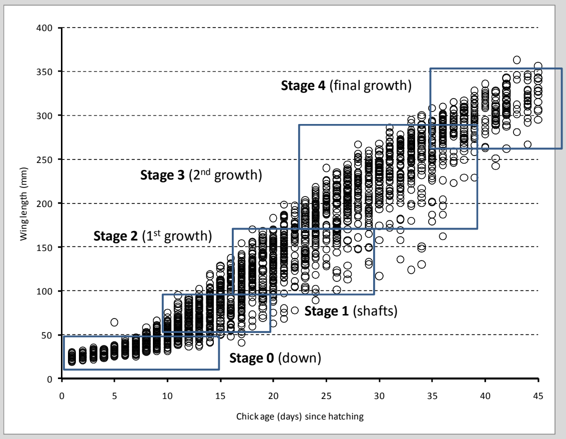
Variations in growth - Pooled data representing annual or multi-year growth rates provide little insight in the aspect of key-interest (Box 3.4): individual or nest-specific periodic fluctuations in structural developments or body mass gain (as a result of differences in provisioning rates). Within seasons, between nests, and between siblings, growth rates could vary markedly. Structural growth increments were nearly always positive, although small drops in size occurred (small measurement errors not excluded). Body mass increments could vary from -95.6 to +82.0 g d^{-1} in Lesser Black-backed Gulls (*n*= 3328 increment assessments) and from -63.3 to +115.0g d^{-1} in Herring Gulls (*n*= 2065). Earlier in the study, it was realised that there were episodic events of collective starvation in chicks of either (often both) species, especially in the second half of chick care. It was later realised that there were episodic events of collective growth spurts also. Chapter 3 reports a key finding of the chick growth analysis: cyclic synchronised starvation events and growth spurts in Lesser Black-backed Gulls and Herring Gulls. Similar drops and gains in body mass in many inspected nests were found during subsequent visits, indicating alternating periods of low and more favourable provisioning.

Box 3.5 - Wing development (growth and moult) in large gull chicks

Chicks of Lesser Black-backed Gulls and Herring Gulls grow rapidly from small downy young to fledglings in a period of *c.* 40 days. The physiological changes, internally and externally, proceed with different growth rates: a change from a "digestive system on legs" during the first weeks to a feathered flying machine when the colony is about to be abandoned. During studies at Texel, we monitored the growth of chicks by measuring body mass and a number of structural size parameters. Only the legs reached 'mature size' prior to fledging, all the other measured parts (head, bill, wing, mass) must have developed further sometime during the first year or even later in life. In the absence of a protocol, we refrained from monitoring the development of flight feathers in the earlier years. Because chick development and chick growth are more than just an increase in length or volume, we decided to start and standardise some observations. From a sample of 64 collected dead chicks (from the 2009 season) we describe stages of flight feather growth with age and with structural size and suggest a simple coding system, based on the feather score system[1], to describe the development of wings in the field (tabulated below, see photographs).

Feather *system based on the system on moult cards[1] and a translation to chick wing development.*

Code	Feather score[1]	Moult stage of chick wing
0		*Down only*
1	*New feather completely in pin*	*Series of blue pins*
2	*Feather emerging from sheath, feather <1/3 final length*	*Sheaths just open, <1/3 feather length*
3	*New feather between 1/3 and 2/3 grown*	*Growing primaries, 1/3-2/3 final feather length*
4	*New feather, >2/3 grown, with waxy sheath at base*	*Growing primaries, >2/3 feather length, waxy base sheath*
5	*New fully grown feather, no waxy sheath remains at base*	*Fully grown wing, P10 is longest feather*



Wing length (mm) against age (d) in chicks of Herring Gulls and Lesser Black-backed Gulls and the successive moult stages that can be recognized within the colony (based on n= 3011 measurements of chicks that were still alive when measured, 2006-2009). The spread of moult stages over age are based on observations in 2009 only.

In later seasons, we consistently deployed this system to monitor the development of flight feathers as an extra parameter indicating chick growth. It appeared that the individual variation in development of flight feathers was considerable. Chicks as old as 18d were found with a fully downy wing (moult stage 0), while some birds would develop feather shafts after only 7d. Moult stage 2, however (a clear development of flight feathers from bursting shafts) was rarely encountered before an age of 2 weeks. Stage 3, well developed greater wing coverts with primaries protruding well beyond those, normally occurred only after three weeks (22d), but often considerably later. Given the individual variation in growth rates, moult scores could be an interesting parameter to indicate if a chick develops 'according to plan'. This would, however, require further study.

Moult stage 0

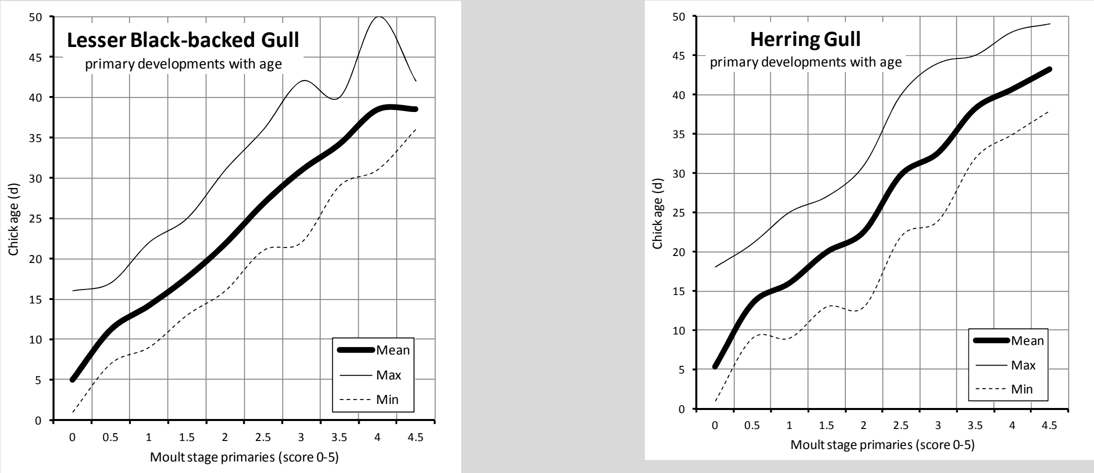
Box 3.5 - Wing development (growth and moult) in large gull chicks

Moult stage 1

Moult stage 2

Moult stage 3

Moult stage 4



Moult stages against age (d) in chicks of Lesser Black-backed Gulls and Herring Gulls (n= 3076 observations, 2009-2012).

Box 3.5 - Wing development (growth and moult) in large gull chicks

Moult scores with age (d) in chicks of Lesser Black-backed Gulls and Herring Gulls, Kelderhuispolder 2009-2012

	Lesser Black-backed Gull				**Herring Gull**			
Moult	Mean age	Min age	Max age	n=	Mean age	Min age	Max age	n=
0	5.0	1	16	301	5.3	1	18	132
0.5	11.2	7	17	109	13.3	9	21	55
1	14.2	9	22	150	16.0	9	25	84
1.5	17.7	13	25	109	19.9	13	27	50
2	21.8	16	31	122	22.5	13	31	78
2.5	26.8	21	36	83	29.7	22	40	61
3	31.0	22	42	86	32.6	24	44	64
3.5	34.2	29	40	56	38.2	32	45	39
4	38.5	31	50	30	40.7	35	48	45
4.5	38.6	36	42	7	43.2	38	49	12

References: [1]Ginn & Melville 1983; **Source:** Camphuysen C.J., C.D. Romay & A. Gronert 2009. *Wing development in large gulls in the chick phase: a manual.* Sula 22: 67-76 [In Dutch]. With additional data obtained in later breeding seasons in Kelderhuispolder.

Abandoning a breeding attempt - Consequences of the trade-off between present and future reproductive success could be to forego breeding, or to give up a breeding attempt (Erikstad *et al.* 1998). In the absence of direct observations of parental care it may be hard to interpret growth data, but on several occasions, an initially prosperous breeding attempt failed after a prolonged period of stabilisation or decline in chick body mass. ^{App}Fig. 3.11 shows two examples of twins under prolonged care that were seemingly abandoned (or not fed sufficiently) after a serious starvation event at between 25-30d of chick age. Many similar examples could be provided, but the data have not been analysed in depth given the uncertainties with respect to parental efforts. In Chapter 8 two further scenarios are discussed: parent birds that give up chick care temporarily, but return to resume provisioning and (often) breed successfully, and adult birds that forego breeding after a prospecting phase in the colony.

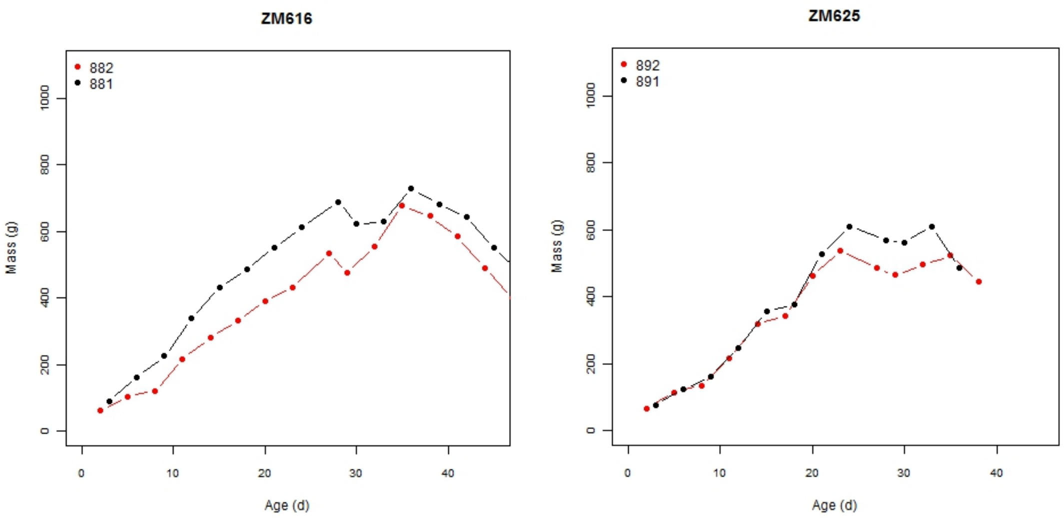


Fig. 3.11. Examples of Herring Gull chick twins in which the parents gave up provisioning at a late stage in development, despite favourable growth in the early chick phase. Both nests were affected by a starvation event (Chapter 3), but in contrast to most other pairs, and after some recovery, provisioning rates declined and the chicks starved to death. Nest numbers and chick numbers are indicated on each graph.

Chick growth and diet - The type of prey used to provision chicks will usually have a profound effect on the growth rates and on fledging success (Brown 1995, Silva *et al.* 2001, Wanless *et al.* 2005, Paiva *et al.* 2006, Romano *et al.* 2006, Whitfield 2008, Flisik & Horn 2010). Prey quality matters. Fish species differ considerably in their calorific value (Harris & Hislop 1978), which means that some (fatty, easy to handle) fish are often preferred over other prey (lean, spiny, or difficult to handle). But even *within* prey species, the quality (calorific value) may vary between seasons (Wanless *et al.* 2005) so that parents may fail to meet the energetic requirements of their offspring. Chick growth rates are discussed as well, but in a dietary context, in Appendix 7 and in Chapter 9, where the foraging specialisations of Herring Gulls are evaluated. Generalist seabirds may be particularly suitable for this topic, because dietary biases are likely to occur with all sorts of effects on the reproductive success.

Chick developments summarised Chick measurements around hatching (1-2d), at 10, 20, and 30d of age, around fledging (c. 40d) and as adults, both sexes combined are summarised in ^{App}Table & Fig. 3.12. The measurements are based on chicks that actually fledged.

Table 3.12. Chick measurements from hatching to fledging, Kelderhuispolder 2006-2012. %ad indicates the measurements of fledglings relative to adult size and body mass. Difference in size between taxa tested using a Welch Two Sample *t*-test. Fledglings include chicks that were monitored from hatching to fledging as well as free-running, near-flying chicks of unknown age, captured mid-July just prior to fledging.

Lesser Black-backed Gull					**Herring Gull**				Difference between species		
Head	mean	sd	n	%ad	mean	sd	n	%ad	*P*=	t	df
Hatchling	48.7	1.8	124		49.1	2.0	96		n.s.	-1.29	175.8
Chick 10d	67.9	3.4	136		68.5	3.9	89		n.s.	-1.12	169.1
Chick 20d	85.0	4.9	131		86.8	5.3	101		**	-2.70	207.1
Chick 30d	97.3	5.3	134		98.5	5.5	101		n.s.	-1.67	211.4
Fledgling	106.2	5.3	440	91%	108.2	5.9	192	90%	***	-4.05	331.3
Adults	116.2	6.2	212		119.7	5.8	153		***	-5.53	336.5
Bill	mean	sd	n		mean	sd	n				
Hatchling	17.9	0.9	124		18.2	1.2	96		n.s.	-1.87	168.1
Chick 10d	25.7	2.2	136		25.5	2.4	89		n.s.	0.87	177.3
Chick 20d	33.9	2.9	131		33.8	3.2	101		n.s.	0.24	205.9
Chick 30d	40.0	2.7	134		39.6	3.1	101		n.s.	0.80	200.0
Fledgling	45.4	2.9	440	95%	45.5	3.5	192	86%	n.s.	-0.35	311.3
Adults	53.3	3.4	212		53.1	3.5	153		n.s.	0.44	320.9
Tarsus	mean	sd	n		mean	sd	n				
Hatchling	26.5	1.3	124		27.0	1.7	96		*	-2.11	140.1
Chick 10d	41.1	3.5	136		41.2	4.2	89		n.s.	-0.18	137.9
Chick 20d	56.1	4.8	131		55.9	4.9	101		n.s.	0.29	199.7
Chick 30d	62.2	3.8	134		62.1	3.8	101		n.s.	0.29	200.0
Fledgling	64.4	3.5	440	100%	64.7	3.3	192	99%	n.s.	-0.82	381.4
Adults	63.8	3.4	212		65.5	3.4	153		***	-4.46	327.6
Wing	mean	sd	n		mean	sd	n				
Hatchling	25.1	2.3	124		25.0	2.2	96		n.s.	0.43	181.0
Chick 10d	52.4	9.8	136		46.6	9.2	89		***	4.44	197.5
Chick 20d	137.6	24.3	131		127.3	24.7	101		**	3.15	213.5
Chick 30d	232.7	25.3	134		220.1	27.1	101		***	3.63	205.1
Fledgling	306.4	25.6	440	72%	306.8	28.8	192	72%	n.s.	-0.17	325.7
Adults	426.5	14.9	212		424.9	15.3	153		n.s.	1.03	312.8
Mass	mean	sd	n		mean	sd	n				
Hatchling	59.9	7.1	124		65.5	8.5	96		***	-5.21	182.6
Chick 10d	217.4	46.3	136		249.3	54.1	89		***	-4.57	167.7
Chick 20d	470.1	97.7	131		536.1	107.3	101		***	-4.83	204.5
Chick 30d	633.4	108.8	134		710.3	129.2	101		***	-4.83	193.8
Fledgling	734.7	120.8	440	89%	817.1	126.3	192	87%	***	-7.92	347.9
Adults	824.6	103.9	212		944.2	108.3	153		***	-10.56	317.4

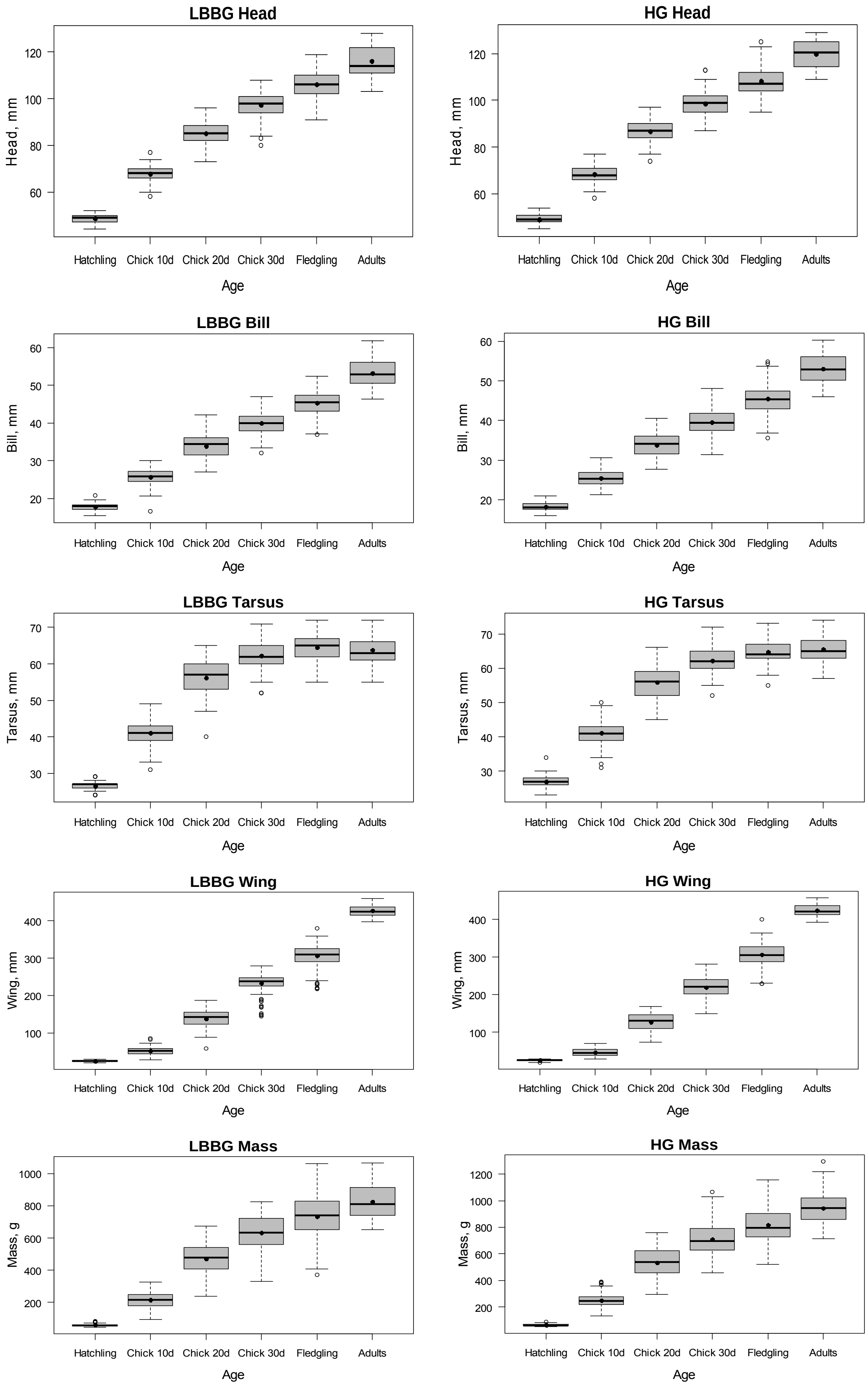


Fig. 3.12. Chick measurements from hatching to fledging, Kelderhuispolder 2006-2012 (see ^{App}Table 3.12).

Box 3.6 - Chick depredation

In 2006, many chicks of Lesser Black-backed Gulls were lost as a result of depredation and breeding success was low. In the absence of direct observations, the cause of this depredation was unclear, though the problem seemed to have worsened after a period of adverse weather in late June 2006. In a student's project in 2007, the characteristics of depredation were studied and quantified with visual observations from two hides (one overlooking the Foot Sea dunes, one overlooking the Valley study plot). Tim van Nus aimed at understanding which species, which areas within the colony and under which conditions gull chicks were most vulnerable. Indications of dietary specialization were looked at, to find evidence for individual birds that contributed disproportionally to the overall levels of egg or chick depredation (specialized cannibals). The methods used ranged from nest- and chick monitoring (the routine colony programme), field observations from hides and a diet study. Two important questions formed the motivation for these studies: (1) which were the main predators, and (2) did the activities of researchers in the colony enhance the depredation risks for nesting birds?

Hides in the Foot Sea dunes (left) and in the Valley (right)

In 2007, the fledging success (0.46 fledglings pr^{-1}) in Lesser Black-backed Gulls was again significantly reduced as a result of chick depredation (66.7%). *Potential* predators in the colony were feral cats, Goshawk *Accipiter gentilis*, Sparrowhawk *A. nisus*, Common Buzzard *Buteo buteo*, Marsh *Circus aeruginosus* and Hen Harrier *C. cyaneus*, Hobby *Falco subbuteo* and Kestrel *F. tinnunculus*, all breeding near or within several km from the colonies. Additionally, Carrion crows *Corvus corone*, Jackdaw *C. monedula* and Magpies, which also prey on eggs and young birds, nest in the vicinity of the colony and are common visitors. A total of 49 depredation events were actually witnessed during observations from a blind (17 eggs, 32 chicks, 89h of observation, 41% of the time with other researchers working in the colony at the same time and potentially causing disturbance). *Observed* predators involved only cannibalistic gulls (taking eggs and chicks of conspecifics or inter-specific), plus a single Carrion Crow (one attempt with an unknown outcome), confirming that intra- and inter-specific depredation of eggs and chicks was most important. Depredation by cats would have occurred at night (out of sight). Apart from some remains of incidental kills (often involving adult gulls, and includes observations in later years), cat depredation was seemingly negligible.

Only 7 depredation events occurred when other researchers roamed the area (20 events expected given observer effort in the hides; $G_{adj}= 9.01$, df=1, $P< 0.001$), suggesting that research activities were not a prime cause of concern. In the single year of study, no correlations were found between the amount of nest cover, vegetation within territories, nest densities, frequencies of aggressive interactions and the incidence of depredation of chicks. Eggs were stolen more frequently from open nests than from nests with extensive cover, a finding that was confirmed when pooling data over more years.

Though little evidence was provided that the presence of researchers in the colony caused extra depredation to occur, our own behaviour was reviewed and adjusted to minimise colony disturbance as much as possible: small research teams, single visits on each day, teams staying close together during the work, chicks to be removed from enclosures for measurements and returned when the work was completed (handling time per enclosure 10-20min max), an avoidance of windy weather (>5B) whenever possible.

Source: Nus T.M.C. van 2007. Inter- & intraspecific depredation within a mixed colony of Herring gulls (*Larus argentatus*) and Lesser Black-backed gulls (*Larus graellsii*). BSc-thesis Van Hall Larenstein, Velp & Royal Netherlands Institute for Sea Research, Texel. [BSc project 2007, Van Hall Larenstein supervision Giel Bongers & CJC]

Chick depredation

Kadlec *et al.* (1969) observed that about one-half of the Herring Gull chicks which hatch die before fledging, and that most of the deaths occurred during the first 5d after hatching. A large proportion of the chicks which die are never found, even when the colony is searched regularly and intensively. Possible causes of the disappearance of chicks are depredation, scavenging or the rapid decomposition of young chicks.

A sudden 'disappearance' at young age, in fact at any age, was a common phenomenon in the Kelderhuispolder colonies. Chick depredation was the key issue explaining these disappearances, but in some years chick mortality (starvation and/or disease) was prominent. Of all 663 chicks under care that were lost from the monitoring programme (excluding presumed escapes from enclosure and birds of which the fate was unclear), 51% were less than 10d of age and the age distribution of chick losses was skewed (2006-2012 data pooled). In total, no less than 68% of the well-documented chick losses were ascribed to depredation (cannibalism, or one species attacking chicks of the other; Box 3.6). When comparing the age distribution of chicks lost as a result of depredation pooling all available data (^{App}Fig. 3.13), it is clear that different mechanisms may be at work in both study species. A majority of the Herring Gull chicks was depredated well before the chicks were really mobile (<7d of age; median 4d), while the majority of the losses in Lesser Black-backed Gulls occurred between 7 and 15d of age (median 10d). In case of the Herring Gull, predators *must* have entered the territories to get the chicks, while the chicks of Lesser Black-backed Gulls may have ventured into neighbouring territories and have put themselves at risk (in fact not an option for many chicks in the monitoring programme within enclosures where only a single nest was fenced in). The age distribution of chicks recorded as "dead" (through starvation or disease, no visible traces of attack) is rather similar for both species, with a median around 9-10d of age:

	Lesser Black-backed Gull		**Herring Gull**	
	Dead	Depredated	Dead	Depredated
Median	10d	9.5d	9d	4d
1st-3rd quartiles	4-16d	4-18d	4-25d	11-15d
sample	141	366	68	88

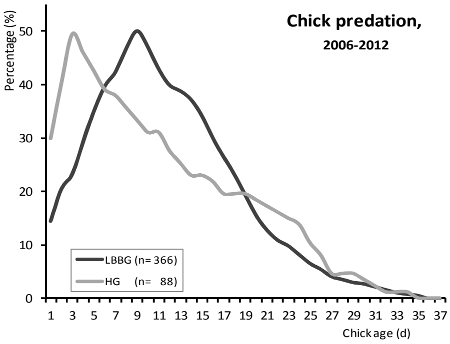


Fig. 3.13. Cumulative percentage (%; increasing from 0-50%, declining from 50-100%) of chick depredation with age (d) for Lesser Black-backed Gulls and Herring Gulls breeding in the Kelderhuispolder , 2006-2012.

High levels of chick depredation in Lesser Black-backed Gulls was one of the features that immediately attracted attention in the early years of the Kelderhuispolder studies. A first student's project, conducted in 2007, aimed at identifying the main culprits causing depredation and at assessing the effect of the observers causing colony disturbance (Box 3.6). We failed to demonstrate an important observer effect; in fact most depredation occurred when there was nobody in the area, or kills occurred a large distance away from the surveyors. The observers themselves observed seemingly opportunistic egg-stealing as part of the disturbance caused by the work conducted in the field, particularly under windy conditions (such conditions were subsequently avoided whenever possible and when disturbance led to egg-stealing, visits were cut short). Aggressive behaviour of adults directed to free-roaming chicks were commonly seen (including violent stabs), but actual chick kills were seldom observed (but see Box 3.7).

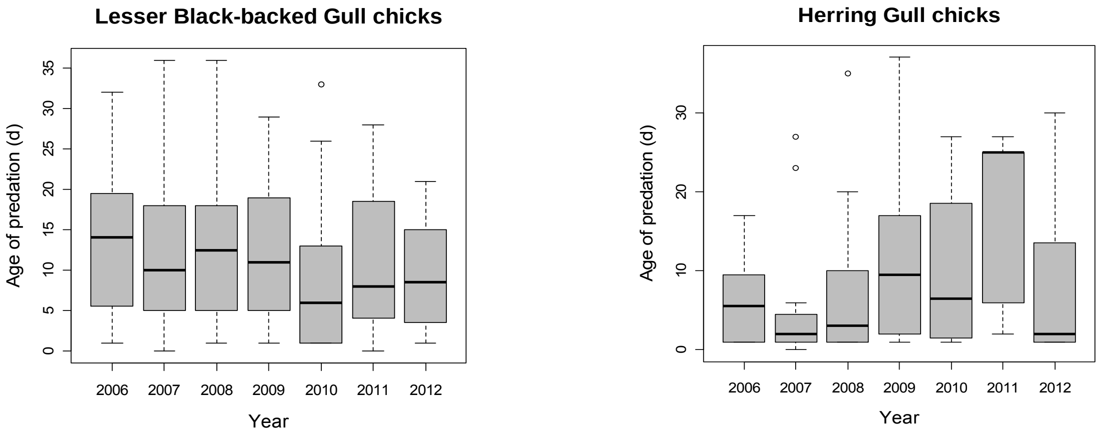


Fig. 3.14. Boxplots of the age of depredated chicks of Lesser Black-backed Gulls and Herring Gulls in the Kelderhuispolder, 2006-2012.

In Lesser Black-backed Gulls the median age at which most chicks were recorded as depredated was fairly similar over the years (AppFig. 3.14). In 2010, when depredated chicks were relatively young, the overall depredation rates were actually the lowest on record (35.5%, n= 161 hatchlings), but an 'unprecedented' 34.8% of the chicks were logged to have died from other caused in that year (AppTable 3.2). The breeding success was slightly higher than in other years. In Herring Gulls in 2011, a season with low reproductive success, only few chicks were logged as 'depredated' (16.7%), but most of those that were had reached a considerable age (23-25d). The age at which most chicks were depredated was apparently more variable, possibly partly as a result of a smaller sample size.

Chick depredation and cannibalism in some other studies - There are many studies reporting cannibalism or high levels inter-specific chick depredation in mixed gull colonies. Some examples that suggest nesting densities as an important underlying factor include:

Spaans *et al.* (1987), reporting on effects of a marked increase in population size and nesting density of Herring Gulls breeding at Terschelling (The Netherlands), found significant reductions in fecundity (0.34-0.44 young fledged pair^{-1} in 1983-1984, compared to 1.25-1.50 young pair^{-1} in 1967-1969) largely as a result from increased cannibalism (intra-specific chick depredation).

In the mid-1990s, the German Wadden Sea island Mellum (53°43'N 08°09'E) harboured about 30% of the Herring Gulls breeding along the German North Sea coast. In 1995, Wilkens & Exo (1998) assessed the reproductive success of Herring Gulls in relation to population densities. The studies were conducted on two study plots with different population densities. The low density study plot was characterised by later clutch initiation and higher fledging rates, mainly as a result of higher chick depredation rates on the high density study plot. Rasa (Flat) Island (Gulf of California islands) is the nesting site for over 90% of the world population of Heermann's Gulls *Larus heermanni* and depredation by Yellow-footed Gulls *Larus livens* on Heermann's Gull chicks is widespread (Velarde 1992). At a high density site in a valley (7100 nests ha^{-1}), the total number of chick depredation events was higher, but the proportion of nests preyed upon was significantly lower than a rocky hill site with 'low' breeding densities (950 nests ha^{-1}). Predatory gulls spent significantly more time searching for prey and made significantly more depredation attempts in the valley compared to the rocky hill and the number of successful depredation events per unit time a predator was present in the observation area and the success rate of predators did not differ between areas. A positive correlation was found between prey and predator numbers and breeding synchronously and densely could thus give the Heermann's Gull an effective defence against this predator. Fetterolf (1983) found that food-stressed chicks in Ring-billed Gulls *Larus delewarensis*

Box 3.7 - Cannibalism

In large gull colonies such as in the Kelderhuispolder at Texel, a considerable proportion of the pre-fledging mortality is attributed to chick depredation. Visual observations have confirmed the occurrence of infanticide (a parent killing its own chick or eating its own egg), cannibalism (chicks or eggs of conspecifics) and inter-specific depredation (chicks or eggs of Herring Gulls taken by Lesser Black-backed Gulls or vice versa). In several years, chick depredation was widespread and involved many aggressive adult birds (mainly Lesser Black-backed Gulls), in other seasons chick depredation was largely confined to rather few, specialised individuals in other seasons. Chicks often suffered from numerous attacks by adult birds before they were killed (numerous stab wounds, bald heads, large wounds in chicks that are still alive) and some were not consumed but left to rot away or were scavenged by other birds at some later date. Part of the chicks was consumed, however, and some of these served as food for other chicks.

A documented case of cannibalism, *12 June 2011*

A documented case of cannibalism - Even though these attacks occurred frequently, we rarely able to witness an attack from the beginning to the end. One such occasion, however, could be observed and photographed on 12 June 2011. An adult Lesser Black-backed Gull walking through the colony, suddenly grabbed an unattended downy young and walked off with it. Neighbouring adults did not respond, other than with some agitated noise and frequent long-calls[1], suggesting that the predator had not invaded another occupied territory. The adult was alone and started stabbing the small chick. Well before the attacked chick was dead, another, only slightly older chick escaped from nearby cover and observed the kill with considerably interest and from a short range.

Box 3.7 - Cannibalism

Begging commenced started well before the prey was actually killed, suggesting that this chick knew exactly what was about to happen. Dried traces of blood on the beak of the adult bird was just another indication that a specialised cannibal was at work. The adult bird killed its prey and commenced with a long-call sequence. Its attending chick responded impatiently, while either begging or pecking the convulsing carcass. The chick was unable to gain access to the carcass, but the adult opened the corpse and presented a small amount of intestines to the attending chick. During a second long-call sequence by the adult, this chick "helped itself" and continued feeding on the intestines. After finishing off the intestines, adult and the chick walked back to what must have been their territory, a few metres away, and the adult started to preen its feathers.

Over the years, within the nest monitoring scheme, at least 8 specialised cannibalistic pairs (or individuals within pairs) have been identified (that includes inter-specific depredation; 7 Herring Gulls, 1 Lesser Black-backed Gull; each at least 30 documented kills/eggs), but in years with particularly high chick depredation levels, numerous adults (mostly Lesser Black-backed Gulls) were involved and the killings were apparently more opportunistic.

Free-roaming Lesser Black-backed Gull chick after numerous attacks by adults

References: [1]Tinbergen 1936c, 1953, 1960a; **Source**: Camphuysen C.J. 2011c. Kannibalisme bij de Kleine Mantelmeeuw *Larus fuscus* op Texel: een gedocumenteerd geval. Sula 24: 83-90.

were subjected to the highest levels of intra-specific attacks and depredation. Poor reproductive output and high levels of chick depredation are both considered important indicators of food limitations in seabird colonies (Hamer *et al.* 1991; Martin 1987; Strann & Vader 1992).

Chick depredation and nest attendance - At Texel, a supplementary feeding experiment was designed to investigate if parents would decrease provisioning effort (and increase their time on guard to protect the young) in response to a reduction of the nutritional requirements of their chicks. Again, Lesser Black-backed Gulls were studied, because depredations levels were much higher in this species. Previous breeding seasons were characterised by high levels of chick depredation (60-65% of hatchlings) and low fledging rates (0.26-0.45 chicks pair^{-1}). To measure nest attendance, adults were instrumented with radio-transmitters.

The experiments were conducted in two study plots (*Foot Sea dunes* and *Valley*), under the assumption that densities in either area as well as other characteristics (e.g. distance to the edge/centre of the colony, species composition, nest cover, habitat) were similar. The colony censuses in later years showed that in fact the nesting densities were rather different (assuming the spatial pattern in densities found in 2009-2012 was similar as in 2008). But before jumping onto the conclusion that the different nesting densities were solely responsible for the observed differences in depredation rates between study plots, the (only currently known) long-term trends are worth a quick evaluation (^{App}Fig. 3.15). A comparison of chick depredation rates over seven seasons showed that the depredation risks in the Foot Sea dunes were initially considerably higher than in the Valley, while the two study plots varied more or less in concert from year to year since 2009. Relatively low chick depredation rates were found in 2010 and 2011. If the levels of chick depredation would simply be positively correlated with nesting densities, the inter-seasonal variation within and between study plots (with a fairly constant or only gradually changing nesting density between seasons) is difficult to explain.

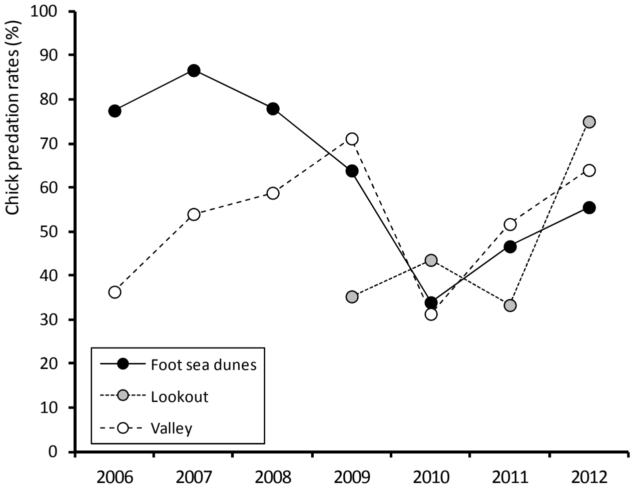


Fig. 3.15 Chick depredation rates in study plots (percentage depredated of chicks that had hatched) per year for Lesser Black-backed Gulls in the Kelderhuispolder study plots *Foot Sea dunes*, *Lookout*, and *Valley* (where the research was concentrated) 2006-2012 (n> 15 chicks per plot per year, total number of monitored chicks: 470).

Appendix 4. Annual cycles

The annual cycles of Herring Gulls and Lesser Black-backed Gulls are characterised by returns from wintering areas to the breeding grounds in late March, *c.* five-month breeding periods that last until August, a complete post-nuptial moult and a retreat to the wintering areas in the course of September and October (^{App}Figs. 4.1-2). The breeding colonies are normally abandoned in the course of August and few adults of either species are seen near or within their breeding colonies in winter. Despite pronounced differences in wintering range (Appendix 5), the first returning adults of both species arrive at roughly the same time at the latitudes of their breeding colony. Early spring arrivals occur roughly one month before the first prospecting breeding birds visit the colony. Within the Wadden Sea area, the birds do not visit their breeding territories until March, and initial visits are brief, often confined to club areas. Early visits do not include overnight stays, and occur mostly in favourable weather (light winds, no rain).

Colony departures are a gradual and secretive process. More and more 'known' (e.g. ringed) individuals are missing, but the actual date of departure is notoriously difficult to assess. Colour-rings were used to keep track of individual birds (Box 4.1). When colour rings are reported from wintering areas or stopovers underway, colony departure has been proven, but since the strike-rates (the likely- hood of sightings) are low, this is an inaccurate way of assessing dates of departure. Modern technology (satellite and GPS tracking) has provided more detailed information on colony departures and returns than ever before. ^{App}Table 4.1 summarises colony departures and returns for eight individual Lesser Black-backed Gulls carrying GPS loggers (tagged in 2010, returning in 2011) from the Kelderhuispolder colony. All birds, failed breeders as well as successful birds, departed earlier than expected (late July, early August, mean 25 Jul ± 5.5d), some used and autumn stop-over in northern France or in the UK (probably to continue primary moult near a predictable food source), and most individuals were wintering at the Iberian Peninsula (see Appendix 5). Nearly all birds had returned at Texel in late March in the next season (30 March ± 6.3d).

Table 4.1 Colony departures and spring returns of 12 Lesser Black-backed Gulls from Texel carrying GPS loggers. Stop-over intervals and locations as well as the period and area of overwintering are indicated for each bird.

Colour ring	Breeding Success	# Fledglings	Chick age at dep	Departure	Autumn stopover	Stopover period	Wintering area	Wintering period	Return
F.AJK	Failed	0		16-Jul	N France	28 Jul-14 Sep	S Spain	24 Sep-8 Mar	29-Mar
F.ABN	Fledged	1	43d	21-Jul	none	none	S Spain	22 Aug-…..	12-Apr
F.AKJ	Fledged	1	46d	23-Jul	UK	23 Jul-20 Dec	C Spain	25 Dec-10 Mar	20-Mar
F.AKK	Fledged	1	58d	01-Aug	N France	2 Aug-1 Nov	C Spain	16 Nov-21 Mar	30-Mar
F.AKU	Failed	0		26-Jul	none	none	UK	2 Aug-31 Mar	31-Mar
M.AMJ	Fledged	2	55-56d	30-Jul	UK	4 Aug-17 Sep	S Spain	27 Sep-21 Mar	30-Mar
M.AMK	Fledged	1	55d	29-Jul	none	none	S Spain	5 Aug-15 Mar	03-Apr
M.AMM	Failed	0		30-Jul	N France	30 Jul-10 Oct	S Spain	16 Oct - 15 Mar	30-Mar
				25 Jul ± 5.5					30 Mar ± 6.3

Age-specific timing and whereabouts through the year

Colour-ring data were used to evaluate the dispersive and migratory movements in the annual cycle of Herring Gulls (Chapter 6) and Lesser Black-backed Gulls (Chapter 5). Colour-rings do provide a wealth of information that should not be put aside given new technological developments. For one, the sample size is much larger, and individuals can be tracked over a considerably longer period (often even life-long, *i.e.* up to 20 or more years!). Different cohorts and age groups can not only be studied simultaneously, but individual birds ringed as fledglings continue to be tracked when they successfully mature. With the high first-year mortality rates, few scientists can afford to tag a substantial number of fledglings with expensive data loggers.

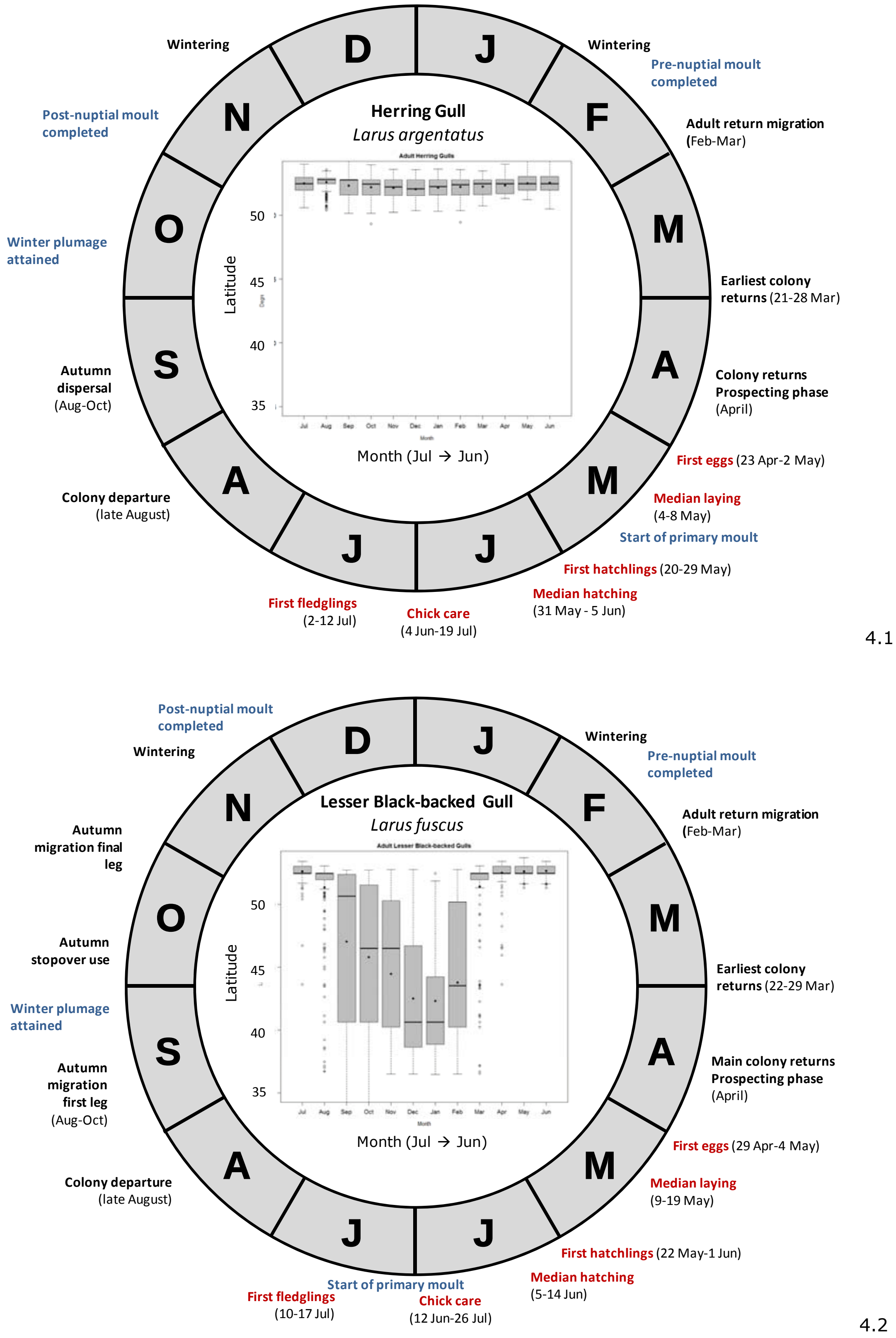


Fig. 4.1-2 Schematic representation of the annual cycle of the Herring Gull (top) and Lesser Black-backed Gull (bottom), based on observations at Texel (2006-2012) and long-term colour-ring sightings throughout Europe (1984-2012). Inset: boxplot of latitudinal distribution of sightings of adults (y-axis scales similar for both species). Mean values are indicated with a solid dot.

Box 4.1 – Colour ringing & ring-reading

The main purpose of colour-ringing birds is to provide possibilities to recognise individuals at distance, without handling or even disturb them. Recovery rates will be markedly increased in comparison with recoveries of the more traditional metal rings[1,2]. Individual birds can be recorded over and over again, resulting into rather impressive and insightful "life-histories"[3]. Several colour-ring programmes became established in The Netherlands, to monitor the dispersal, migration routes, use of foraging areas, annual survival, return rates and other parameters of Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *L. fuscus*[4,5]. One of the more comprehensive studies was launched in the mid-1980s and this project involved the annual ringing of c. 100 fledglings in 12 (later 14) colonies of Herring Gulls scattered along the Dutch coastline between 1986 and 1988[4,6,7]. Around 90,000 documented sightings and recoveries of Herring Gulls ringed in these years have been processed and are available for analysis (Chapter 6)[8]. In the Kelderhuispolder studies, a new colour-ring programme was started[4]. Colour-rings were primarily used to assess site- and partner fidelity, annual survival, and return rates (including recruitment)[2,9]. Over time, when more than one breeding attempt could be monitored, insight in the individual quality of birds will be obtained. Information on migratory movements were an interesting "bycatch"[10].

Herring Gull partners male M.ALP & female F.AJM alert at territory during a colony disturbance.

Lesser Black-backed Gull male M.ADA balancing at Houston Control.

Colour-rings used in the ALS/RIN colour-ring programme[4,6,7] (without metal rings). Photo Maarten van Kleinwee.

Colour-rings used in the CJC/NIOZ colour-ring programme[4,6,7] (with stainless steel metal rings). Photo Fred Visscher.

Another important reason to start a new colour-ring programme was the need to pinpoint foraging areas and roosts of birds breeding at Texel. For Herring Gulls, this has been a successful part of the work (Appendix 9), for Lesser Black-backed Gulls (expected, given the more marine orientation) the results have been more modest and GPS loggers were used to provide more info (Appendices 7-8). The colour-rings have been instrumental in unravelling annual cycles for both species.

In the Kelderhuispolder studies, green, engraved Poly(methyl methacrylate) (PMMA) rings were used, manufactured by Risto Juvaste (Finland). PMMA is a transparent thermoplastic, often used as a lightweight or shatter-resistant alternative to glass. The rings have a 4-letter combination starting with F (ringed as adult females), M (as adult males), K or P (both as fledglings) during 2006-2012 (1314 individuals; Appendix 3). The same rings, but with a distinct code (starting letter Y) were supplied to the study group working at the mainland colony in IJmuiden (369 LBBG, 133 HG, 2 YLG; 2008-2012), in order to obtain some comparative

Box 4.1 – Colour ringing & ring-reading

data on site-fidelity, return rates, migratory movements and annual survival in a nearby but otherwise apparently rather "different" colony (more inland feeding, higher breeding success, earlier egg production). Rings were also provided to colour-ring 25 gulls (14 LBBG, 11 HG) that were instrumented with ARGOS PTTs in 2007 and 2008 on Vlieland by SOVON[14]. Between 2007 and 2011, 95 fledglings were colour-ringed at Vlieland (43 LBBG, 52 HG) with rings that are similar to those used at Texel.

Colour-ring programmes require the interest of birdwatchers that spend time deciphering codes and reporting the observations to the ringer (or database co-ordinator). Ring-readers need feed-back and only a mutual understanding of the importance of ringing reports will result into a successful project. Within Europe, the work of Dirk Raes cannot be praised enough, who constructed and maintained the one and only website on which all the hundreds and hundreds of colour-ring programmes are listed (with contact addresses)[5]. Peter Rock volunteered to co-ordinate the "large gull" colour-ring programmes and he was instrumental in avoiding colour/code overlaps between schemes. Perhaps most importantly are the ring-readers, however, mentioned earlier, without whom colour-ringing would yield only a fraction of the results we currently possess. In the acknowledgement section of this thesis, not all, but a substantial number of these volunteers are named and gratefully thanked. A special word of thanks deserve some of the extraordinary ring-readers, all volunteers, that each have contributed more than 2000 sightings to the database: Harry Vercruijsse (18,375 sightings), Fred Cottaar (11,920), Arnold Gronert (8436), Kees Verbeek (7991), A. van Poppel (6418), Ruud Costers (4560), Gerrit Goedhart (4423), Bert Winters (4003), Jo Rampen† (3716), Hein Verkade (3011), and José Verbeek-Cottaar (2007)[13]. Harry Vercruijsse did not only read an exceptional number of colour-rings as a major contribution to the database, but he also wrote an excellent book on (among other things) survival and recruitment of young birds, ringed between 1986 and 1988, in the colony in Schouwen[12].

References: [1]Rock 1999, [2]Shedden et al. 1985, [3]van Kleinwee & Camphuysen 2010, [4]Camphuysen 2008, [5]http://www.cr-birding.be/ and http://www.cr-birding.org/, [6]Spaans 1984, [7]Camphuysen & Spaans 2005, [8]Camphuysen et al. 2011, [9]Calladine 1997b, [10]Hallgrimsson et al. 2012, [11]Costers & Gronert 1989, [12]Vercruijsse 1999, [13]RIN/NIOZ colour-ring database, 1986-2012 (ALS/CJC), [14]Ens et al. 2009.

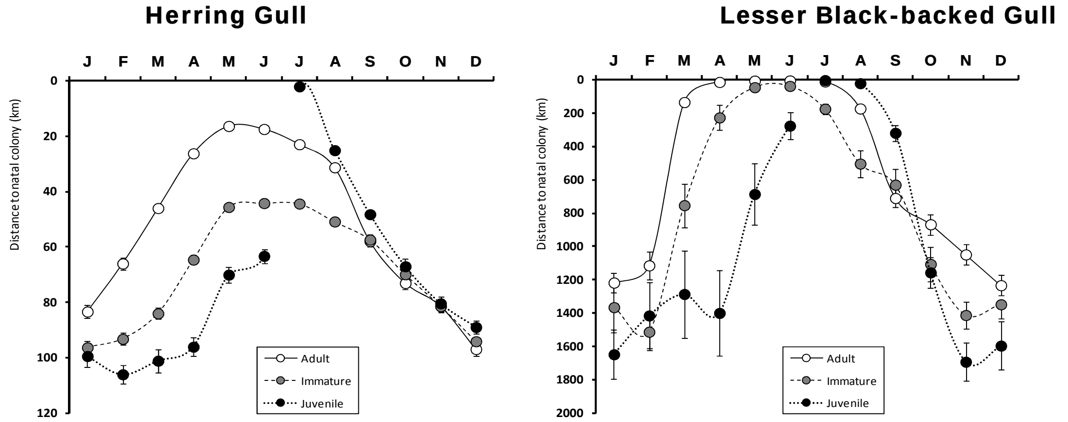
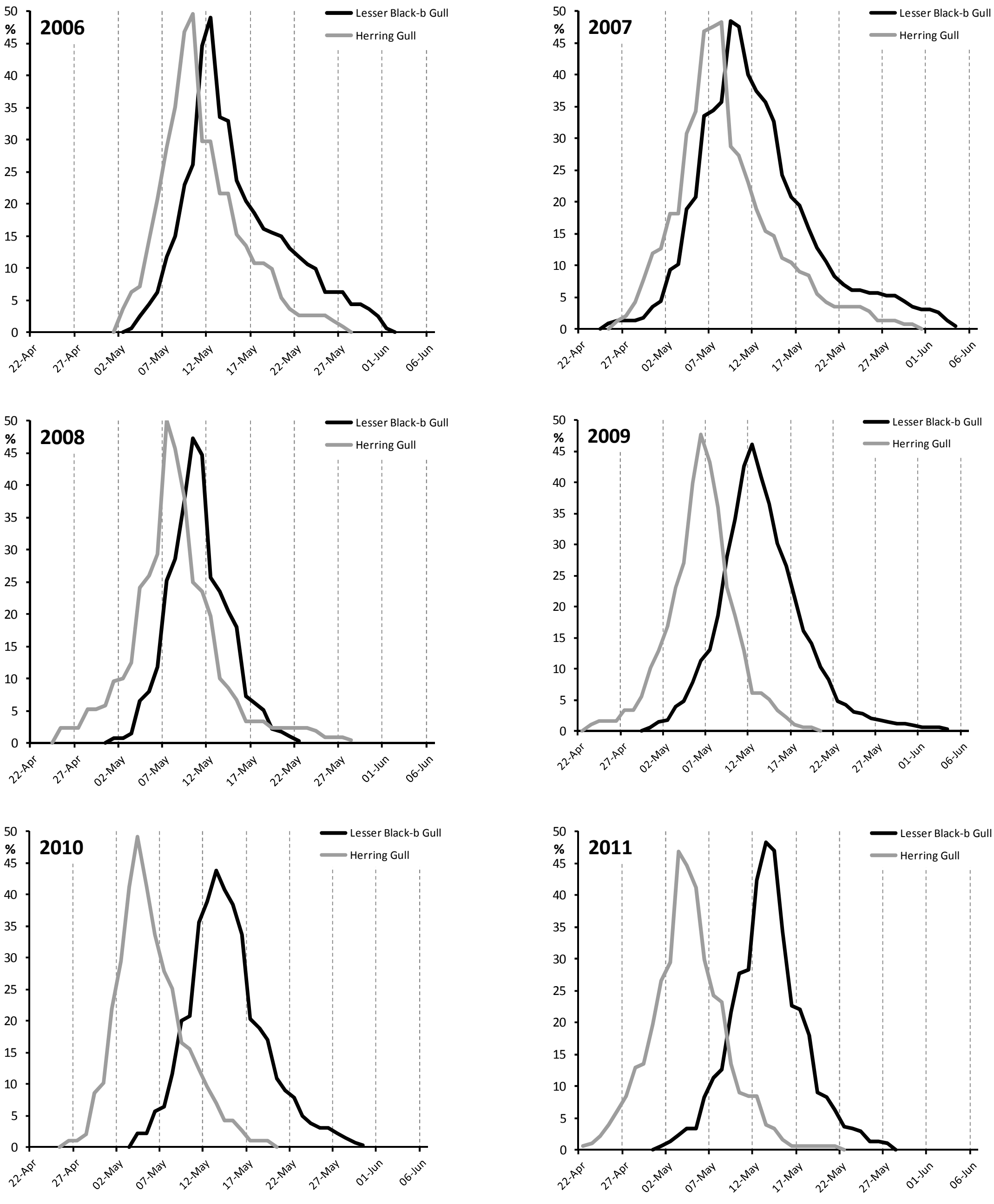


Fig. 4.3. Seasonality in mean distance (km ± SE) from natal colony (n= 86,247 sightings) for adult, immature and juvenile Herring Gulls (top graph) and for adult, immature and juvenile Lesser Black-backed Gulls (bottom graph); all colonies combined, birds colour-ringed in The Netherlands during 1986-2011. For individual birds, a monthly mean geographical position was used.

In both species, juveniles are the last to abandon the colony area, travel relatively fast and slightly further than older cohorts to the south, and do not normally return to the breeding ground in their first summer ($^{\mathrm{App}}$Fig. 4.3). Older immatures (2nd-4th year birds) may spend their summer months closer to or even within their natal colonies, but on average remain well south (rarely north!) of the breeding grounds. For adult Lesser Black-backed Gulls, the Dec-Feb period may be taken as the wintering period. In most of autumn (Aug-Nov) individual birds occur scattered over the entire flyway, some using stopovers, others do not, before the majority of the birds has arrived at the southernmost locations for that season. The spring movements up north are more synchronised (mostly in late February/early March, but into April). Immature birds follow about one month later. In Herring Gulls, the same pattern, albeit on a totally different scale (tens or hundreds rather than thousands of kilometres south of the colonies).



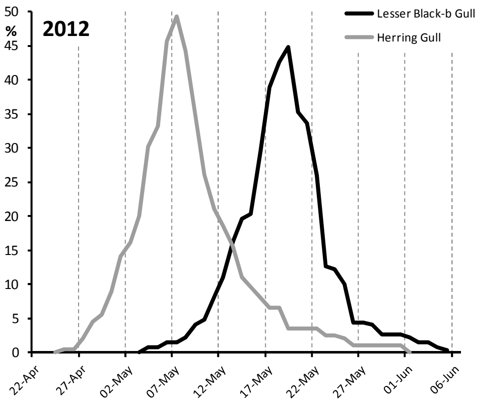


Fig. 4.4 Annual shifts in laying peak in sympatric breeding gulls at Texel, 2006-2012. Mean laying dates (±SD) and the difference (d) between the laying peaks are indicated below:

Year	HG	LBBG	Difference
2006	10 May ± 5.3	14 May ± 8.8	3.8
2007	9-May ± 8.8	11-May ± 7.8	2.3
2008	8-May ± 5.8	10-May ± 4.1	2.5
2009	6-May ± 4.6	13-May ± 5.8	6.5
2010	5-May ± 4.7	14-May ± 5.3	8.9
2011	4-May ± 5.0	13-May ± 5.0	9.3
2012	7-May ± 6.2	19-May ± 5.3	11.1

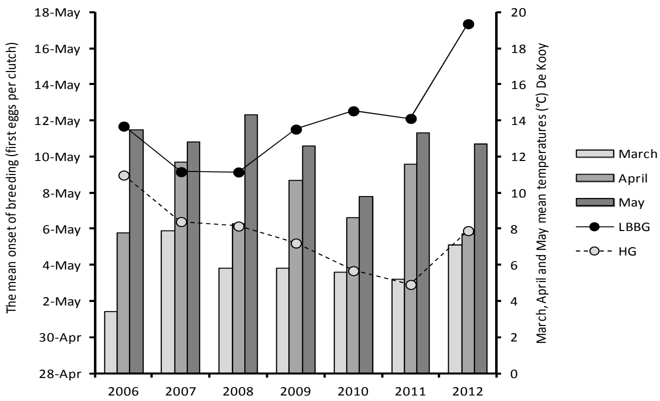


Fig. 4.5. The onset of breeding (annual mean date of first eggs) and monthly mean ambient temperatures (°C) measured at De Kooy (Den Helder); 2006-2012. Temperatures were derived from KNMI (2012).

Spring migration is less synchronised than in Lesser Black-backed Gulls: a more gradual overall process, but again with immatures running approximately one or even 1.5 month late.

The annual return of individual Lesser Black-backed Gulls as prospectors within the Kelderhuispolder colony at Texel has been studied with frequent checks of the presence and absence of colour-ringed individuals, late March-early April (Chapter 5). Certainly in March and early April, colony visits were synchronised with Herring Gulls (during calm weather, no overnight stays). Despite a considerable difference in wintering areas, the arrival as prospecting breeding birds is roughly similar between the two species.

The onset of breeding, egg-laying

The onset of laying sets the calendar for all stages of breeding following, until colony departure. In the Kelderhuispolder, in the prospecting phase, birds visiting the colony were initially shy (March, most of April), as if hesitant, and most simply left the colony with the slightest of disturbance (raptors, cats, human intruders, scientists). Territories became (re-)established gradually, but still, the birds were restless at first and only gradually seemed to gain confidence. Pair bonds were reaffirmed and new pairs were formed both within as well as outside the colony (on beach roosts nearby or on more distant feeding grounds; *unpubl. colour-ring data CJC*). Territories were defended from the pre-incubation through the post-fledging periods (cf. Butler & Janes-Butler 1982). However, only once the eggs were produced, as if the point of no return had passed (see also Tinbergen 1929ab, 1932, 1936, 1953, 1956), territorial defence became really violent.

Egg laying - The onset of laying in the Kelderhuispolder colony, based on the mean laying date of first eggs within clutches, varied from 8 May ± 3.7d (2008) to 17 May ± 4.6d (2012) in Lesser Black-backed Gulls and between 3 May ± 4.6d (2011) and 8 May ± 5.2d (2006) in Herring Gulls. The difference in the onset of laying between the two species increased markedly over time, partly as a result of the progressively earlier dates of laying recorded in Herring Gulls recorded between 2006 and 2011 (2012 was similar as in 2008-9; ^{App}Fig. 4.4).

Several reviewers confronted with the Kelderhuispolder laying dates commented on spring temperatures as a potential explanation for advances or delays in laying dates (not mentioning a possible mechanism). In fact, the laying dates were not correlated with spring temperatures (measured at De Kooy, Den Helder in March-May; KNMI 2012) (^{App}Fig. 4.5) and if temperatures affected the onset of laying, the effect on either species must have been different. The synchronisation in the start of egg-laying in each species is high, with a small variance around the laying peak. On average, over seven years of monitoring (2006-2012), the onset of laying (mean of first eggs produced in all nests monitored), was six days apart for the two species, with Herring Gulls well ahead of Lesser Black-backed Gulls: HG 5 May ± 2.0d, min 2 May, max 8 May; LBBG 11

May ± 2.7d, min 9 May, max 17 May. As in the mean laying date, the gap between the two species in the *onset* of laying increased over time: 2006 → 2012, resp. 2.7, 2.8, 3.0, 6.3, 8.9, 9.2, 11.5d. The widening gap resulted from a near-consistent year-to-year advance in the onset of laying in the Herring Gull, contrasted by a less consistent, but otherwise opposite trend in Lesser Black-backed Gulls.

Breeding synchrony - Darling (1938) suggested that "*the degree of breeding synchrony by social stimulation may be density related*" and that the synchrony of laying in colonial birds was stimulated by interactions between the birds. The larger the colony, the greater the stimulus and laying in larger colonies would therefore be more synchronised than that in small ones. What was thereafter called the 'Fraser Darling Effect' is thus a greater synchronisation of breeding at greater densities. "*A steady toll of the chicks is taken while they are in the down stage. If this period is a comparatively short one for the whole chick crop of the colony, the percentage taken will be less than when the down period of the chick crop is extended.*" (Darling 1938: 69; ^{App}Fig. 4.6).

A density correlated onset of laying was found by some authors (Horn 1970, Nelson 1967), but most authors studying gulls failed to confirm the phenomenon (MacRoberts & MacRoberts 1972, Vermeer 1963, Weidmann 1956, Yom-Tov 1975). Vermeer (1963) studied the breeding ecology and behaviour of the Glaucous-winged Gulls *Larus glaucesens* at Mandarte Island (British Columbia, Canada), in 1961-1962. Data were obtained on pair-bondage, pair formation, philopatry to nest site, egg-laying, clutch-size, incubation, egg and chick mortality, fledging rate, growth, age at first flight and colony departure, annual adult mortality and longevity. No support was found for the Fraser Darling Effect that there would a greater synchronisation of breeding at greater densities. MacRoberts & MacRoberts (1972) recorded the timing of laying and the position of nests in 10 study areas within a mixed Herring and Lesser Black-backed Gull colony on Walney Island (Lancashire, UK). The study areas differed from one another in density of breeding birds and in proportion of each species and the data were collected to determine if evidence could be found for synchrony of reproduction by social stimulation. The gulls showed considerable variability in onset and spread of laying, however, and attempts to correlate densities of breeding birds in each area with median date or spread of laying, average nearest neighbour distance with median date of egg-laying, and median laying date for one species with that of the other species in the same section of the colony, failed to produce evidence for inter- or intraspecific social stimulation of reproduction.

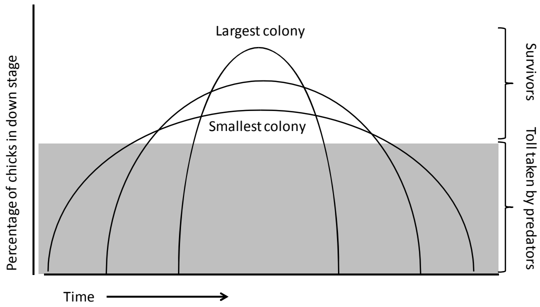


Fig. 4.6. Diagram illustrating how the survival rate is influenced by the "spread" of time in which the eggs of a colony of Herring Gulls are laid (from Darling 1938: 70).

Coulson & White (1960) showed that large colonies of Kittiwakes have a longer nesting period than small colonies, but remarked that while these and other facts cast doubt on the importance of the "Fraser Darling effect", they did not disprove the possibility that neighbouring birds in a colony may stimulate each other. Studies on colonies of Kittiwakes on the Durham, Northumberland and East Lothian coasts to test whether or not social stimulation is of importance to colonial-nesting birds were undertaken. Differences of up to 21d were observed between the mean time of breeding of nine colonies. The differences were greatest in the youngest colonies, and the effect of differences in the age composition of the colonies had to be considered. Females which were breeding for at least the fourth time bred 10 days earlier than females which were breeding for the first time. However, less than 20% of the observed differences in the time of breeding could be accounted for by differences in the age composition. The time of breeding was related to the density of nests within individual colonies. The onset of breeding was earlier at higher densities, but the last birds to breed in each colony did so at the same time. The time of return to the colonies was also related to nest-density and this suggested that the effect on the birds of the density of their breeding neighbours was carried over from one year to the next. It followed from these studies that social stimulation has a distinct effect on the breeding condition of birds within Kittiwake colonies.

At Texel, Lesser Black-backed Gulls breeding in the two main study plots deviated from the mean onset of laying for the colony as a whole in a rather different way, with birds in the higher density area (Foot Sea dunes) commencing slightly earlier, sometimes significantly earlier, than birds in the lower density area (Valley; ^{App}Fig. 4.7). In Herring Gulls, arguably with smaller differences in breeding densities between study plots, but also with slightly smaller samples (monitored nests per plot), the onset of breeding varied between plots and between years, but the differences were small and rarely significant (^{App}Fig. 4.8).

We have no historical data about any of these study plots, and do not know if some of these settlements are of a relatively "younger" date (perhaps with younger, less experienced birds). Several of the currently breeding birds (found everywhere in the colony) were ringed as 15 years ago chicks on Texel or elsewhere (UK, Europoort, IJmuiden). The Kelderhuispolder colony also produced the oldest currently known, ringed Herring Gull for The Netherlands (Box 6.1). As a whole, it is not a recent colonisation. As yet, there is insufficient data to check if females which are breeding for at least several times breed on average earlier than recruiting females.

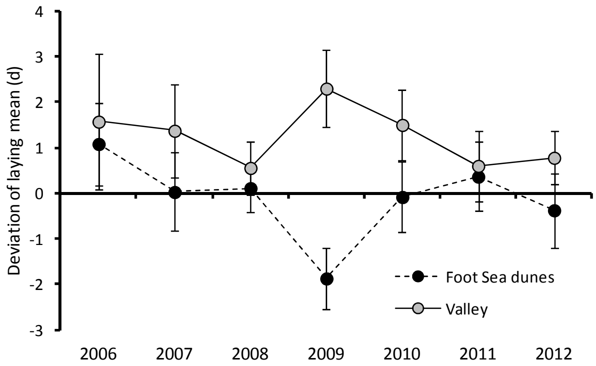


Fig. 4.7. The onset of laying (mean ± SE) in two study plots in the Kelderhuispolder in Lesser Black-backed Gulls.

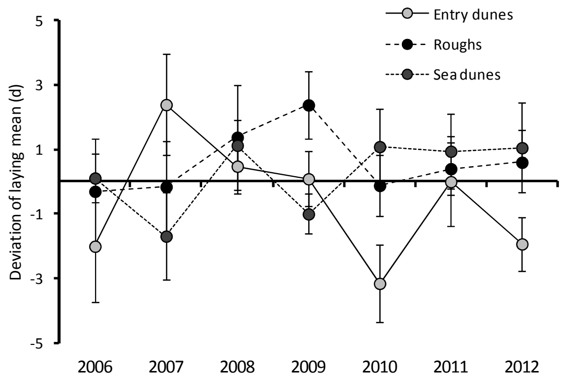


Fig. 4.8. The onset of laying (mean ± SE) in three study plots in the Kelderhuispolder in Herring Gulls

Advances in the timing of laying - Herring Gulls breeding at Terschelling commenced laying at 18-19 May in the late 1960s (1967-69). In the mid-1980s (1983-1984), the laying dates of Herring Gulls at Terschelling had advanced (10-14 May; Spaans *et al.* 1987, 1997b). As shown above, Herring Gulls today, at Texel, breed even earlier (7 May ± 2.2 days, n= 7). There is no recent information on Herring Gull laying dates from Terschelling, but anecdotal information suggests that Texel and Terschelling (just as Vlieland, the island in between) are quite similar in laying dates.

Bukaciński *et al.* (1998) reported a median laying date of 10-12 May in Lesser Black-backed Gulls at Terschelling in 1992, similar to the current median laying date at Texel (13 May ± 2.9d, n= 7). Compared with IJmuiden (only 60km to the south of Texel), however, the Wadden Sea island populations are "late". Unfortunately, exact information is lacking, but both species lay *c.* one week earlier in IJmuiden than at Texel (Fred Cottaar & Kees Verbeek *pers. comm.*). In 1983-1984, breeding success was highest for early breeders, with almost complete failure for late breeders. Spaans *et al.* (1987) concluded that, as a consequence, early breeders contributed more to subsequent generations, suggesting that, if laying date is heritable, this may have contributed to the advance in clutch initiation that occurred since the late 1960s. On the Isle of May, Scotland, in 1968 (Parsons 1976), The onset of laying in Herring Gulls occurred in synchronized groups within the colony. Late-laid clutches were usually situated on the periphery of the colony.

There was no evidence suggesting that differences in the timing of laying corresponded with variations in the timing of prospecting (*i.e.* with differences in arrival times near the colony). However, arrival within the general breeding area is more difficult to measure than actual arrivals within the colony. Paludan (1951) evaluated the pre-egg stage in a mixed colony at Græsholm more extensively. The isolated group of islands in the western Baltic did provide the possibility to monitor both a 'general arrival' (birds arriving near the islands) as well as 'colony visits' (birds entering the actual breeding area), even if none of his birds were colour-marked and could be easily recognised as individuals. A remarkable feature in this colony was the enormous difference in timing between the two species: Lesser Black-backed Gulls arriving 2-4 weeks later than Herring Gulls. Especially the earliest colony visits were, as observed at Texel, weather dependent: cold and windy weather or fog made the birds leave the colony sometimes for some days. Pair formation in Herring Gulls was apparently (re-)established outside the colony, since most birds arrived in pairs. In Lesser Black-backed Gulls, the first arrivals were apparently unpaired, but pairs quickly "dominated the picture". Paludan's (1951) Herring Gulls arrived as early as in February near the colony, and the variable duration of the pre-egg stage was apparently influenced by variations in the occurrence of inclement weather (notably low temperatures) in the early period. Lesser Black-backed Gulls, as a result of their later arrival from the wintering areas, usually missed that period altogether, leading to less variations in the timing of the onset of laying between years. In Herring Gulls, a 28d difference in colony occupation was observed between the earliest (1943) and the latest year (1947). In Lesser Black-backed Gulls that difference was only 11 days. The duration of the pre-egg stage (date of first egg minus date of first colony occupation, 1943-1946) was on average 40.3 ± 6.8d in Herring Gulls and 38.3 ± 2.1d in Lesser Black-backed Gulls, or well over one month. In 1947, a year with a particularly cold winter, the pre-egg stage in Herring Gulls amounted to only 28d (no data for Lesser Black-backed Gull in that season. This resulted in the most delayed laying date for Herring Gulls in this study. And a three-week period could therefore perhaps be seen as a minimum requirement for the pre-egg stage. A three to four week pre-egg (prospecting) stage would fit the data on Texel apparently quite well.

Differences between study plots - Between study plots, small, but usually non-significant differences in the timing of laying were found, suggesting slight differences in breeding synchronisation between smaller areas within the colony. In Lesser Black-backed Gulls, rather distinct and apparently study-plot-specific differences in chick predation rates were reported during a supplementary feeding experiment (Chapter 4), but also in other seasons (^{App}Fig. 3.13). Kim & Monaghan (2005) observed that high-quality individuals may be more able to obtain particular sites, and thus aspects such as the timing of breeding or habitat quality and individual quality are often confounded in correlative studies. Autocatalytic interactions between breeders of different quality could lead to site-specific, apparently collective decisions or behaviour (Deneubourg & Goss 1989). If valid, it underpins the risk of jumping onto false conclusions in research projects with a study-plot approach, when generalisations for the population at large are made.

The timing of moult

(Adult) post-nuptial primary moult - Post-nuptial moult in adult Herring Gulls and Lesser Black-backed Gulls is complete, with primaries descendant, from mid-May to mid-Dec (Cramp & Simmons 1983). The start of primary moult in Dutch Herring Gulls is assumed to vary from mid-May to mid-Jul, with an average of late-May (Cramp & Simmons 1983). The mean duration of primary moult is 6 months and should thus be completed between late-Sep and mid-Nov (average late-Oct; Walters 1978, Cramp & Simmons 1983, Ginn & Melville 1983). Immature Herring Gulls (non-breeding birds) were earlier and had a shorter moulting period: 4.5 months (Walters 1978).

Walters (1978) noted that practically all adult Herring Gulls breeding in study areas around Amsterdam in the late 1970s commenced their primary moult during incubation. This is rather earlier than reported for Skomer and Skokholm (Wales) in the 1960s, where Herring Gulls were found to commence primary moult in the final stage of chick care (Harris 1971). The onset of primary moult is less accurately described for Lesser Black-backed Gulls, but it begins "on breeding grounds" and is completed "in winter quarters" (Stresemann & Stresemann 1966; Cramp & Simmons 1983). The onset of primary moult on Skomer and Skokholm was during the later stages of chick care and early fledging (Harris 1971). On Walney Island (northern England), however, primary moult commenced from mid-May to August (Verbeek 1977c). Lesser Black-backed Gulls identified as *intermedius* from the Oslo Fjord to Möre region in SW Norway commenced with primary moult between mid-May and mid July (average mid June), which was much earlier than more northerly birds (nominate *fuscus*), that were found to initiate wing moult somewhere between mid-July and late September (average 10 August; Barth 1975).

Primary moult at Texel - Adult birds of both species that returned to the colony at Texel in spring were all in full breeding plumage: with soft parts (eye-ring, bill, legs) brightly coloured and their head white, but with their flight feathers being moderately to heavily worn. Many incubating Herring Gulls captured at Texel in May and early June had commenced primary moult. Pooling all available data (2006-2012), sufficient samples are available only for the second (55 females, 46 males) and third decade of May (24 females, 40 males). Fourteen Herring Gulls captured in the first period did not show wing-moult (9 males, 5 females), but in the second 10-day period, just over one third of the incubating birds (31% in females, 35% in males) had just initiated primary moult (mean moult score on a scale from 0-50: 0.6 ± 1.2 in females and 0.6 ± 1.1 in males). That is during or immediately after egg-laying. In the third decade of May, i.e. half way incubation/just prior to hatching, two-thirds of the birds had just commenced with wing moult (63% in females, 65% in males; mean moult score 2.2 ± 2.7 and 1.5 ± 1.9 respectively). The onset of primary moult at Texel was thus similar to the birds nesting around Amsterdam in the 1970s (Walters 1978), and considerably earlier than Herring Gulls monitored at Skomer and Skokholm (Wales) in the 1960s (Harris 1971). Too few Herring Gulls were captured in 2006 and 2007 for a meaningful comparison, but between 2008 and 2012, the proportion (%, n) of Herring Gulls that showed active primary moult in May varied: 2008 41% (17), 2009 59% (39), 2010 40% (37), 2011 40% (28), 2012 35% (34). Moult was slightly more advanced in moulting individuals in seasons with relatively many moulting birds in May (mean moult score 2.4, 2.7, 1.1, 3.4, 2.0 respectively).

Lesser Black-backed Gulls at Texel (30 females and 26 males captured as incubating birds in early to mid-June) were only rarely showing signs of a beginning of primary moult. Of 126 adult females and 108 males captured between 10 May and 24 June (2006-2012), only three females (2%) and six males (6%) had just shed one or two inner primaries. This suggests that the onset of primary moult in the Lesser Black-backed Gulls is generally postponed until the later phase of chick-care. Few photographs made of adult breeding birds in flight in June, and a slightly larger proportion of the birds photographed in July showed signs of the onset of primary moult. This suggests that the primary moult generally commenced 1.5-2 months later than in Herring Gulls (^{App}Fig. 4.9-10), just as reported for Skokholm and Skomer (UK) in the 1960s (Harris 1971).

F.ADZ 16 July 2011

F.ADD 24 June 2011

F.AAD 20 June 2011

F.ACD 25 July 2010

F.AHR 24 June 2011

M.AAJ 25 June 2009 (B Ubels)

M.ABT 24 June 2011

M.AMZ 10 Jun 2010

Fig. 4.9. Actively breeding Lesser Black-backed Gulls, not showing the onset of primary moult in June and July, in and around Kelderhuispolder Texel (photos Kees Camphuysen, Maarten van Kleinwee, Bram Ubels).

M.ACJ 25 July 2010 M.APJ 24 June 2011

M.AMZ 25 July 2010 M.AKL 25 July 2010

Fig. 4.10 Actively breeding Lesser Black-backed Gulls showing the onset of primary moult in late June and July, Kelderhuispolder, Texel (photos Kees Camphuysen, Maarten van Kleinwee).

Among seabirds there is considerable variety of wing-moult strategies, which has presumably evolved to mediate the costs of moult in the context of often complex life histories. Harris (1971) reported from colonies at Skokholm and Skomer (UK) that the moult sequences of the Herring and Lesser Black-backed Gulls were similar and that birds may interrupt the moult so as to migrate without gaps in the wings. As a migratory species, with a complete moult taking about four months, Lesser Black-backed Gulls have to complete their post-nuptial wing-moult in the wintering areas. Processes of moult are scheduled such that normally no migrant has to fly with gaps in its wings (Berthold 2001): many species show interruptions of moult. Wing and tail moult commence at the breeding grounds and discontinued during migration. The remaining old feathers should then be replaced at the wintering grounds. The use of stopovers close to the breeding grounds by some individuals (^{App}Table 4.1 and Appendix 5) could serve as resting stations where foraging is easy and where primary moult could continue and be completed prior to the final lap south to the wintering grounds.

Verbeek (1977c) observed that in Lesser Black-backed Gulls the timing of moult is pliable and that modifications in this timing may occur in a short time (decades). He also found that the entire Herring Gull population on Walney Island (England) began to moult primaries within a shorter period (about 50d) than on Skomer and Skokholm (Wales; about 70d), perhaps indicating that feeding conditions around Walney were better than those around Skomer/Skokholm when the studies were conducted. Better feeding conditions could permit less efficient birds to moult earlier than would otherwise be possible. There is no insight in annual differences in the onset of primary moult in Lesser Black-backed Gulls at Texel, but a variable proportion of Herring Gulls captured in May was moulting (min 40% in 2010, max 59% in 2009; moult score and frequency were positively correlated; 2006 and 2007 data deficient). If a higher percentage of moulting birds would indicate better feeding conditions is doubtful, given the relatively low breeding success (^{App}Table 3.2) in years with a higher percentage of moulting individuals earlier in the season. Note, however, that the sample size is small.

Coastal passage

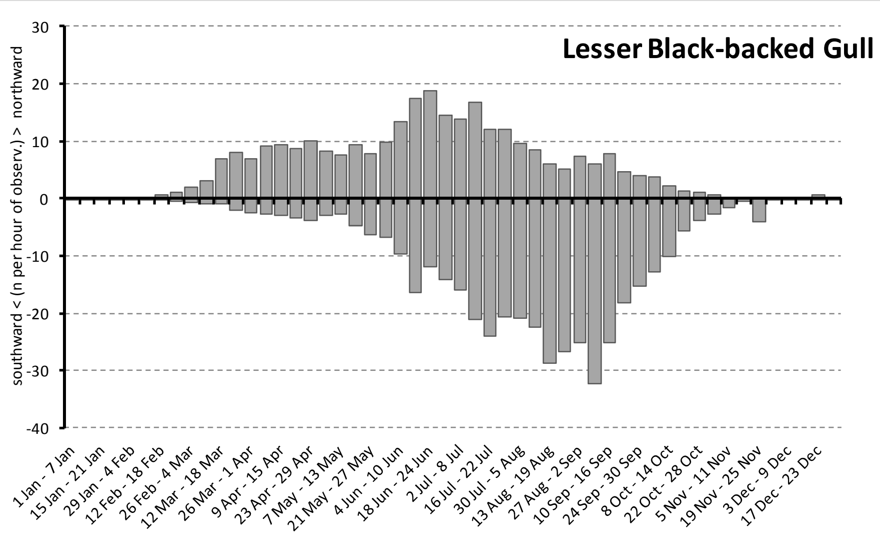
Both species are common seabirds in Dutch coastal waters. Lesser Black-backed Gulls as passage migrants (residents during the breeding season), that are more or less absent in winter. In recent years there are always some, but few, wintering individuals elsewhere in the country. Herring Gulls occur year-round, but a large proportion of the wintering birds may be breeding birds from further north and east. Most Herring Gulls breeding in the Wadden Sea are migratory (covering a short distance) rather than dispersive, and most winter further south (Netherlands, Belgium and northern France; Chapter 6). Seawatchers monitoring coastal passage cannot easily distinguish between migrants and residents, and the incentive to count a species like the Herring Gull is low (Box 4.2). The seasonality in mean distance (km ± SE) from the natal colony (^{App}Fig. 4.3) suggests that other Herring Gulls roam the coastal waters around Texel in winter than in summer (Coulson *et al.* 1984). Most adults move away from their breeding grounds, move south in August and return in February/March; a passage that goes undetected by seawatchers.

Box 4.2 – Seasonal coastal passage

Seawatchers are generally reluctant to systematically record abundant, resident species such as Herring Gulls. Lesser Black-backed Gulls are coastal migrants and are therefore recorded by most (but not all) observers[1,2]. By selecting sites that did count these common species more or less consistently, an effort corrected impression in the seasonal fluctuations in abundance is still possible[3].

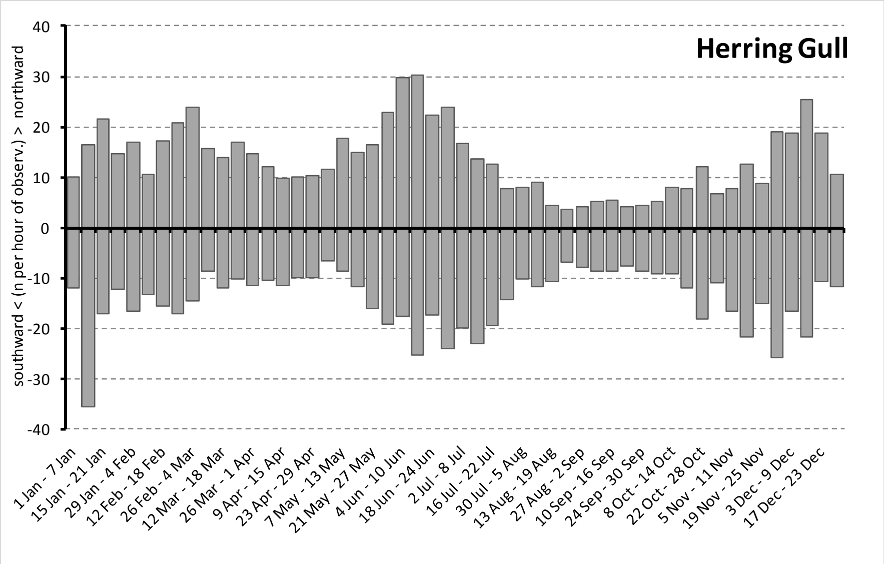
The graphs show southbound movements below the x-axis as negative indices and northbound movements as positives. In typical migrants, one direction would prevail, while more or less resident birds (with local movements) have more or less equal numbers moving in both directions. The seasonal patterns of the two species are strikingly different. Spring migration in Lesser Black-backed Gulls increased in strength from mid-February to late May. Mid-summer passage is characterised by equal numbers moving northward and southward (i.e. foraging flights of local breeding birds). From late July, southbound movements start to dominate the picture and passage peaks in September. Low numbers are seen in winter. The timing fits the ringing data elsewhere in this Appendix and in Chapter 4.

Herring Gull passage is rather different, with 'residents' apparently performing local movements through the year (hence, the interest of seawatchers disappeared). There are however substantial seasonal differences in abundance, with high numbers in winters, low numbers in the early breeding phase (prospecting, egg-laying), a return in numbers from mid-June to early August, low numbers in late August en early September followed by a gradual increase in abundance. The mid-summer peak, if interpreted as foraging flights from local birds as in Lesser Black-backed Gulls, would point at an increased 'interest' in marine resources during chick care.



Coastal passage of Lesser Black-backed Gulls, 1972-2009 (n hour^{-1}; NZG/CvZ unpubl. data*), n= 49,548 obs. hours*

Box 4.2 – Seasonal coastal passage



Coastal passage of Herring Gulls, 1972-2009 (n hour^{-1}*; NZG/CvZ* unpubl. data*), n= 33,897 obs. hours*

References: [1]Camphuysen & Van Dijk 1983, [2]Platteeuw *et al.* 1994, [3]NZG/CvZ database; **Source:** Nederlandse Zeevogelgroep, Club van Zeetrekwaarnemers, seawatching database

Coastal movements of Lesser Black-backed Gulls are better known (Box 4.2) and seawatchers 'welcome' the return of this species in spring after a near-complete absence in winter. As in Herring Gulls, however, different populations mix: more northerly breeding birds travel southward through Dutch coastal waters, but only colour-ringed birds are detected as 'foreign' passage migrants. German, Danish and most Norwegian birds will not be recognised by the plumage characteristics. The annual mass movement of Lesser Black-backed Gulls in September in Dutch waters will have an international composition, and Dutch breeding birds probably form a minority later in autumn (cf. ^{App}Table 4.1 and ^{App}Fig. 4.3). The spring movements will probably also comprise many 'foreign' Lesser Black-backed Gulls.

The seawatching data reveal an interesting aspect: a relatively high abundance of Herring Gulls in coastal waters during chick-care. Aerial seabird surveys in Dutch coastal waters have confirmed high densities of both species around the major colonies, supporting the suggestion that these are mainly 'local breeders' on foraging flights (Baptist & Wolf 1993). Herring Gulls peaked in late June/early July and seawatchers record high numbers of Herring Gulls following trawlers in that period (Platteeuw *et al.* 1994). In August, numbers of Herring Gulls observed at sea declined markedly (aerial and ship-based survey results confirm seawatching data again; Baptist & Wolf 1993, Camphuysen & Leopold 1994), indicating a contraction away from the North Sea coastal waters when the chicks are fledging (see also Appendix 8).

Appendix 5. Different migratory strategies

Three relatively novel data sources were eminent to update and refine existing knowledge: colour ring programmes (Box 4.1), satellite tracking (Box 5.1) and GPS loggers (Box 5.2). Even just the first data-set clearly shows the main differences between the two species (^{App}Fig. 5.1-2).

The annual winter dispersal of Herring Gulls

The annual dispersal by Herring Gulls breeding in The Netherlands has been reconstructed on the basis of colour-ring sightings, collected between 1986 and 2010, following a ringing campaign that was designed to study post-breeding dispersal and winter distribution patterns (Chapter 6). In three consecutive breeding seasons, a total of 4,028 Herring Gull chicks were colour-ringed in 14 Dutch colonies. Of these, 3,153 individuals (78.3%) were reported at least once alive and 453 (11.2%) were recovered dead. In total, 86,723 ring-readings of living gulls were received and processed. One-fifth (20.5%) of all sightings originated from within a 5km radius around the natal colony. Only a small fraction (695 sightings; 0.8%) were reported at greater distances, i.e. at over 300km from the natal colony. Most Herring Gulls remained within a few hundreds of kilometres from the breeding grounds, with most winter re-sightings in Germany, The Netherlands, Belgium and Northern France.

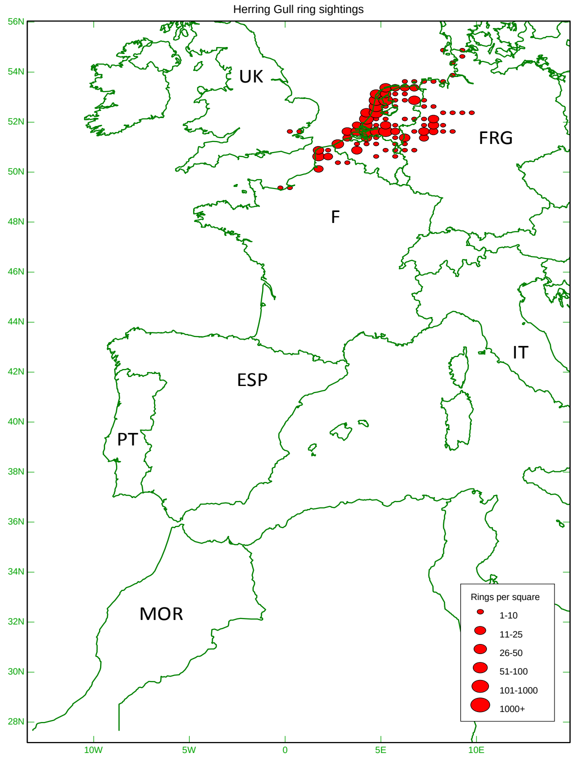


Fig. 5.1. Adult, colour-ringed Herring Gulls reported in the non-breeding season (Sep-Feb, 1984-2011) grouped per 15’latitude x 30’longitude rectangle.

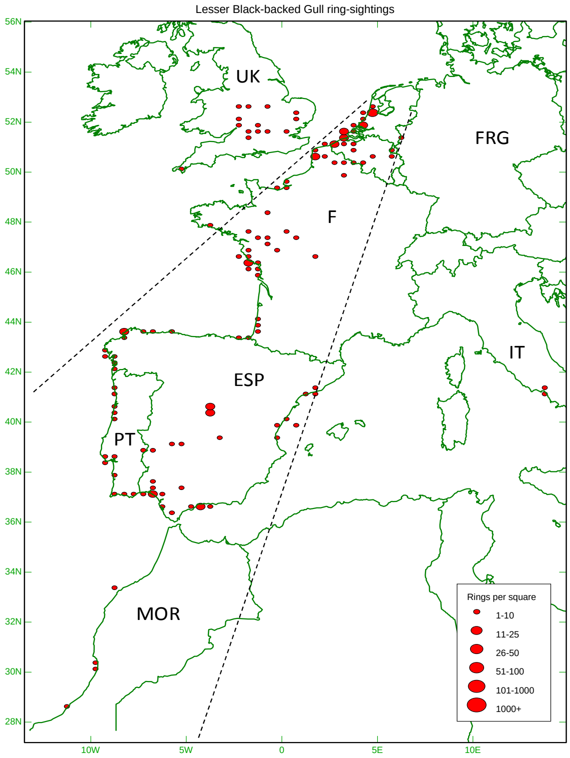
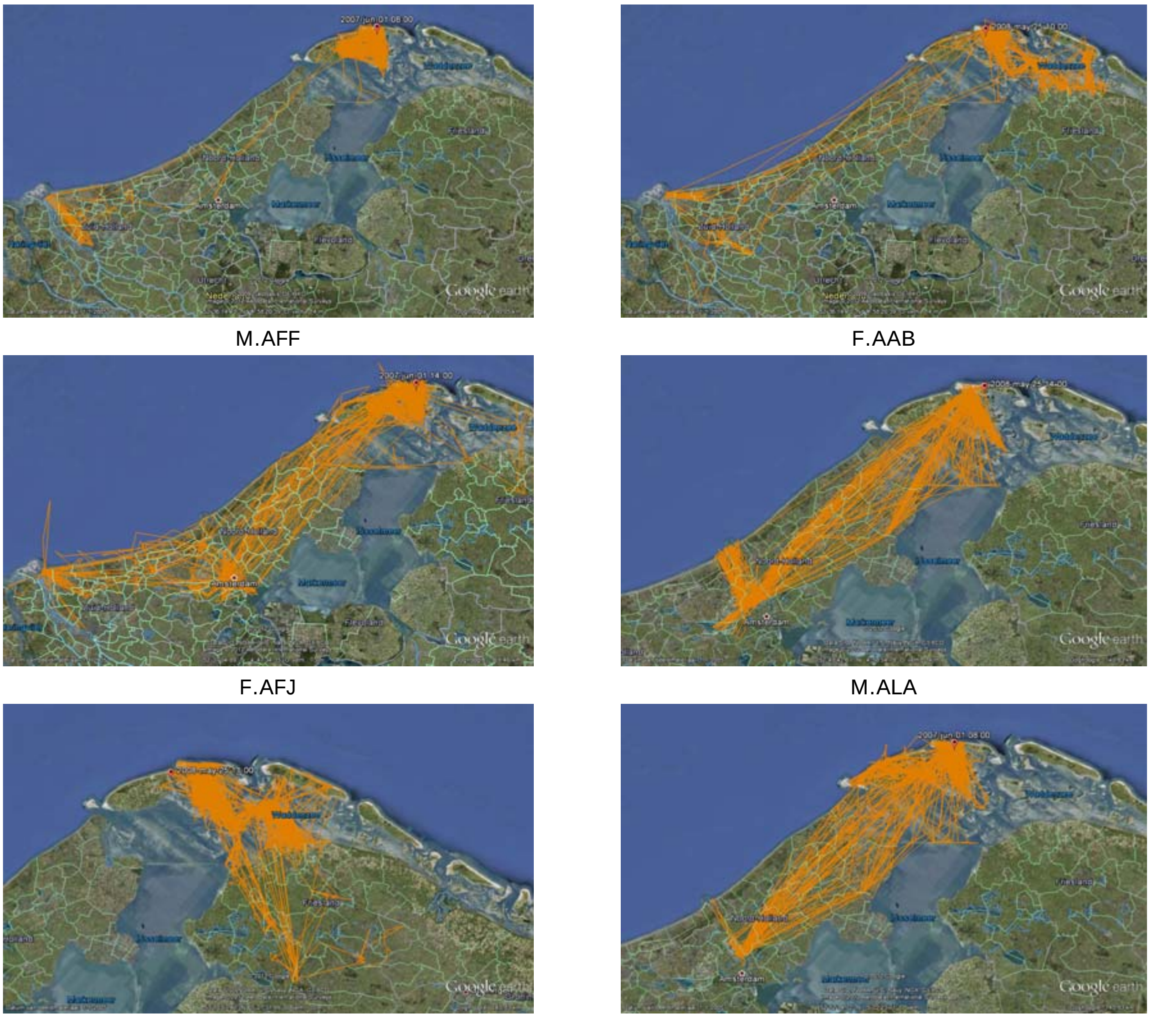


Fig. 5.2. Adult, colour-ringed Lesser Black-backed Gulls in the non-breeding season (Sep-Feb, 1984-2011) 15’latitude x 30’longitude rectangle. Main direction of migration indicated by dashed lines.

Sightings in the UK were rather rare (^{App}Fig. 5.1). Colony-specific differences in travelling distance, dispersal rate, and direction of movements suggested a grouping of colonies in three: (1) colonies on the eastern Wadden Sea islands (Rottumeroog-Vlieland), with significantly higher dispersal rates and movements mostly towards SW to SE, (2) colonies on Texel and along the mainland coast (Callantsoog-Wassenaar), with a shorter mean range and movements mostly to S, and (3) colonies in the Delta area (Europoort, Schouwen and Saeftinghe) with rather short range dispersal in many directions. With reference to studies in other European countries, Herring Gulls breeding in The Netherlands occupied a mid-position between being dispersive and sedentary.

All colour-ring sightings reported in Chapter 6, plus all sightings of newly ringed Herring Gulls in more recent years (554 birds from Vlieland, Texel and IJmuiden), originated from within 49°19'N-55°56'N, 00°00'W-09°45'E; that is The Netherlands, Belgium, northern France and the far west of Germany, with few additional sightings from Denmark and the United Kingdom. Slightly more distant sightings were received from juvenile and immature individuals (mostly further to the east), but south of 49°19'N (N Normandy, France), not a single colour ringed Herring Gulls from these extensive ringing schemes in Dutch colonies has thus far been sighted. The maximum distance travelled in winter did not vary much between adult, immature, and juvenile Herring Gulls, but the timing of outward and return movements was different for each of the age categories (Chapter 6). The age-specific differences were most pronounced in spring, when adults moved towards their home ranges some two months ahead of immatures, who never quite made it to the same latitudes. Immatures, in turn, moved north one month earlier than juveniles. Few first-year birds actually reached the home-range of their native colonies at all.



M.AFF F.AAB

F.AFJ M.ALA

F.AAA F.AFF

Fig. 5.3 The entire range, including all positions obtained from wintering areas, of Herring Gulls carrying Argos PTTs. Some devices have been temporarily defunct in winter (solar panels did not always provide sufficient energy), but there are no indications that any of the birds had moved further away from Vlieland. IfV & SOVON unpubl. data, reproduced with permission.

From more recent deployments of colour-rings (Box 4.1), 39 adult birds ringed in IJmuiden and 89 birds from Texel have been recorded in winter (Nov-Feb). Less than 10% of these birds (8% from IJmuiden, 6% from Texel) has ever been seen in Belgium, nearly 15% (13% versus 15%) in France, and 1% in the UK. These data suggest that in relatively recent years more Herring Gulls have spent the winter within The Netherlands than in the 1980s and 1990s (from recently ringed Herring Gulls, resp. 95% and 91% of the colour-ringed birds was recorded at least once in The Netherlands during the winter months). Adult Herring Gulls from Texel wintered on average *c.* 30km further to the north (*i.e.* nearer the breeding grounds) than in the 1980s and 1990s (Dec-Jan 1990-2005 52.11±0.7°N, 2006-2012 52.27±0.8°N; t_{349}= -1.89, *P*= 0.03).

Satellite tracking - GPS loggers have so far not been deployed on Herring Gulls breeding in the Kelderhuispolder, but SOVON fitted Argos PTTs on 11 adult Herring Gulls breeding at the nearby island Vlieland in 2007-8 (Box 5.1). Tags often gave up mid-winter due to a lack of sunlight to charge the batteries. As a result, some of their winter-movements may have been obscured due to battery failure. Seven birds that have provided substantial overwinter data are listed below (colour ring, Argos tag#, period of functioning and wintering whereabouts; IfV & SOVON unpubl. data, reproduced with permission; ^{App}Fig. 5.3):

M.AFF	#41747	Jun 2007-Jun 2010	wintering Europoort-Rotterdam (Zuid-Holland)
F.AAB	#41750	May 2008-Aug 2010	wintering Europoort-Den Haag-Gouda (Zuid-Holland)
M.AFJ	#41765	Jun 2007-Sep 2009	mainland coast Noord- and Zuid-Holland
F.AFJ	#41766	Jun 2007-Aug 2011	mostly Amsterdam and Europoort, Haarlem, Aalsmeer (Noord- and Zuid-Holland)
M.ALA	#41776	May 2008-May 2010	Amsterdam West, IJmuiden and Bloemendaal (Noord-Holland)
F.AAA	#41779	May 2008-May 2012	Vlieland, Terschelling, Friesland (Friesland)
F.AFF	#41876	Jun 2007-Oct 2009	Amsterdam N (Noord-Holland)

Rings versus tags - Comparing data from the colour-marking programs with the Argos PTTs, the most prominent difference in results are data-points provided by the instruments regarding the occurrence of the birds in the intertidal zone, in the Wadden Sea, and at sea (Ens *et al.* 2009; Appendix 9). Ring-reading is near-impossible in these habitats and colour-ring recoveries are almost by default from areas on land.

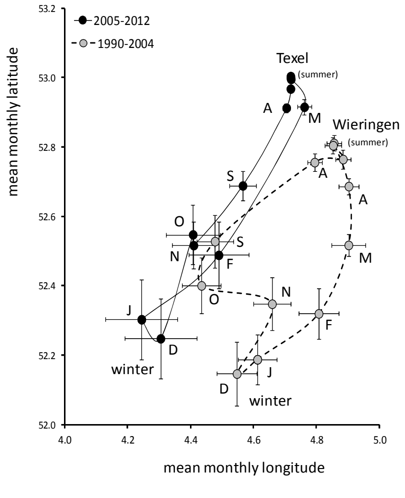


Fig. 5.4 Monthly mean ± SE geographical positions of colour-ring resightings of adult Herring Gulls ringed at Texel in 1986-88 (grey symbols; data from Chapter 6) and in 2006-2012 (black symbols). For each individual bird, a monthly mean geographical position was calculated for each year. The population mean was based on these individual values. Lines connect positions in chronological order, letters indicate months.

Resightings in summer of the older cohorts were never within the breeding colony (no observer effort), but on foraging grounds and roosts to the southeast ("Wieringen"). The historical annual dispersal was slightly further to the south and in late winter and spring more to the east (utilising inland rubbish dumps rather than coastal resorts).

With regard to the winter distribution, these satellite tag data provided rather different data than were obtained in the earlier colour-ring and metal ring programmes. While Camphuysen *et al.*

(2011, Chapter 6) suggested that Herring Gulls breeding at the Wadden Sea islands had a greater tendency to travel south than the more resident birds breeding in mainland colonies, birds tracked with satellite tags from Vlieland moved in fact rather little. The tagged birds from Vlieland had a remarkably small winter range, and popular winter sites in Noord- and Zuid-Holland were visited over and over again (^{App}Fig. 5.3). The paper published in 2011 reports on re-sightings mostly in the 1980s and 1990s and it is possible that migration strategies have changed since (Baker 1980). Indeed, when using more recent re-sightings, of birds colour ringed during 2006-2012 at Texel, it seems that a north-westward contraction of the wintering areas has occurred (^{App}Fig. 5.4), leading to a main wintering area that is similar to that indicated by (few) tagged birds from Vlieland.

Migratory movements of Lesser Black-backed Gulls

There are numerous publications on the migratory movements of Lesser Black-backed Gulls (e.g. Schüz 1934, Holgersen 1938, Barnes 1953, Harris 1962, Baker 1980, Kilpi & Saurola 1984, Rock 2002, Schmaljohann *et al.* 2008, Bosman *et al.* 2012, Hallgrimsson *et al.* 2012). The wintering area of the nominate (*L. f. fuscus*) is from Ethiopia across Uganda and the Congo basin to the Atlantic (easterly flyway), while *intermedius* and *graellsii* winter on the Iberian peninsula and in westernmost Africa (westerly flyway; Kylin *et al.* 2011). Eastern populations, mostly the nominates, migrate along coastlines or the Nile to their wintering grounds in sub-Saharan Africa and have particularly extensive overland migrations. They usually avoid the interior of the Sahara, but occur occasionally far inland when moving upstream along rivers (Schmaljohann *et al.* 2008). Western European birds use the westerly flyway, between Iceland, Norway, Denmark, western Germany to Spain, Portugal and NW Africa (Rock 2002, Halgrimsson *et al.* 2012). There is a migratory divide in southern Scandinavia between populations using south-west or south-east routes, but birds from Kattegat-Öresund colonies (especially Anholt) have been found using both (Cramp & Simmons 1983).

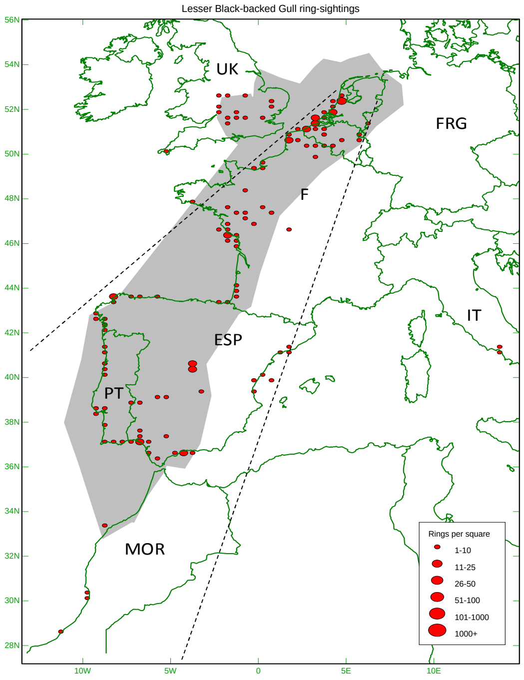


Fig. 5.5 Adult Lesser Black-backed Gulls reported from colour-ring sightings in the non-breeding season (Sep-Feb, 1984-2011) grouped per 15' latitude x 30' longitude rectangle, and the area used by 14 Lesser Black-backed Gulls carrying Argos satellite PTTs in, 2007-2011 (Ens *et al.* 2009, updated).

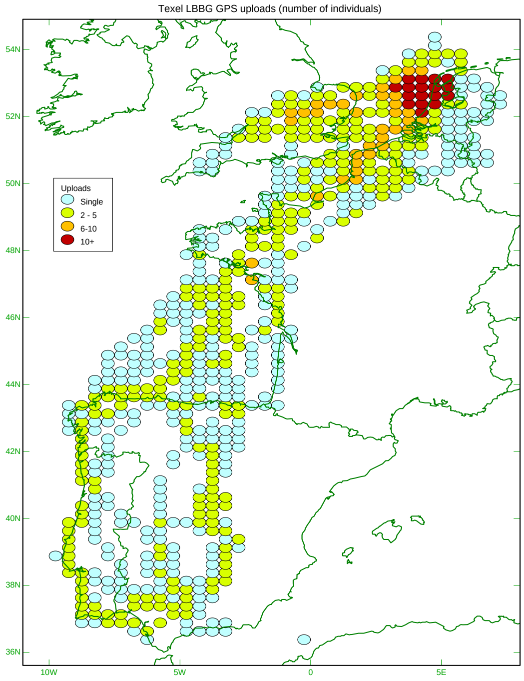


Fig. 5.6 Adult Lesser Black-backed Gulls colour ringed at Texel and carrying UvA GPS loggers: number of individuals per 15' latitude x 30' longitude rectangle through the year (2008-2011). n= 35 tagged birds in total of which 8 individuals have provided overwinter information.

Several colour-ringing schemes became established within The Netherlands in the 1980s and 1990s, but most data sets still await an analysis of recoveries. Data of 132 birds ringed during Herring Gull campaigns in the late 1980s, plus 374 individuals ringed in the aftermath of these events were available plus data from birds ringed in recent years at Texel, Vlieland, Texel, IJmuiden and Leiden (Box 4.1). With most ringing effort concentrated in recent years, an analysis of the data would still be premature. Sightings of Lesser Black-backed Gulls ringed in The Netherlands (NIOZ database) were reported from Algeria (1), Belgium (62), France (153), Federal Republic of Germany (3), The Gambia (1), Italy (2), Mauritania (1), Morocco (34), The Netherlands (331), Portugal (110), Spain (241), and the United Kingdom (36 individual birds). The representation of adult Lesser Black-backed Gull sightings in France, Portugal and Spain is quite overwhelming, indicating that these are probably the main wintering areas for Dutch birds (^{App}Fig. 5.2). In Belgium, France and in the UK some important autumn stop-over areas are situated and in fact, some birds seem and try to overwinter in these rather northerly areas. Sightings in Italy (the same adult in Feb and Sep 2009) and Algeria (a juvenile in Dec-Jan 2006/7, an immature in Nov 2009) are clearly extra-limital (Camphuysen *et al.* 2009). Icelandic birds leapfrog both the Dutch and UK populations (Halgrimsson *et al.* 2012).

Table 5.1. Monthly number of colour-ringed Lesser Black-backed Gulls in Portugal and Spain, 1984-2012.

	J	F	M	A	M	J	J	A	S	O	N	D
Adults	63	50	21	4			1	30	40	42	50	63
Immatures	23	25	18	9	5		8	18	12	28	40	35
First year	23	15	15	8	7	2		5	13	41	30	22
	109	90	54	21	12	2	9	53	65	111	120	120

Colour-ring sightings suggest that immature Lesser Black-backed Gulls are the first to leave the breeding grounds (Appendix 4). Juveniles linger around the colonies until well in August, while most adults abandon the areas *c.* one month earlier. As in Herring Gulls (Chapter 6), the adults are the first to move north from their wintering grounds, followed by the immatures, while many first year birds tend to hang around further south throughout most of the summer. The number of colour-ringed Lesser Black-backed Gulls reported from Portugal and Spain is small through the summer, which is partly an artefact (fewer gulls attract fewer ring-readers), but also an indication that most birds have left the Iberian Peninsula in that season (^{App}Table 5.1).

Table 5.2. Timing of Bay of Biscay crossings in autumn and spring of 12 Lesser Black-backed Gulls from Vlieland (Wadden Sea Islands) carrying Argos PTTs wintering at the Iberian Peninsula. Two additional birds, one wintering in Bordeaux (France), and one wintering the UK but once travelling towards Morocco (bottom rows) were excluded from the analysis. Data SOVON http://www.sovon.nl/, reproduced with permission.

Ring	PTT	2007	2008		2009		2010		2011		Wintering	Autumn	SD	Spring	SD
MAFA	41745	10-Oct	17-Mar	22-Oct	16-Mar						C Spain	16-Oct	8.5	16-Mar	0.7
MAFM	41749	12-Nov	11-Apr		27-Mar		29-Mar				Lisboa/PT	12-Nov		1-Apr	8.1
MAFR	41752	23-Aug	14-Apr	22-Sep	12-Apr	13-Sep	08-Apr				S/C Spain	9-Sep	15.4	11-Apr	3.1
MAFU	41757	27-Nov	28-Mar	09-Dec	26-Mar	01-Dec	20-Mar		10-Mar		NW Spain	2-Dec	6.1	21-Mar	8.1
FAFC	41758	05-Nov	08-Apr								S Spain	5-Nov		8-Apr	
MAFT	41762	26-Sep	29-Apr	07-Oct	06-Apr	14-Oct	10-Apr	11-Oct	09-Apr	08-Oct	W Spain	7-Oct	6.8	13-Apr	10.5
MAFS	41763	28-Aug	05-Apr	13-Jul	26-Mar						S PT/C Spain	5-Aug	32.5	31-Mar	7.1
MAFK	41767		03-Mar	26-Dec	08-Mar		22-Feb				PT	26-Dec		1-Mar	7.1
FAFA	41771	24-Oct	08-Mar		01-Mar	15-Oct	21-Feb				Morocco	19-Oct	6.4	28-Feb	7.5
FAFD	41773	17-Dec	20-Mar	11-Dec	18-Mar						N SP/W PT	14-Dec	4.2	19-Mar	1.4
FAFL	41780	18-Sep									SW Spain	18-Sep			
MAFD	41781	12-Aug	07-Apr	04-Aug	28-Mar						SW Spain/S PT	8-Aug	5.7	2-Apr	7.1
MAFB	41775					07-Jan	20-Mar				UK, 1x MOR	7-Jan		20-Mar	
MAFP*	41764	21-Jul	14-Apr	30-Jun	09-Apr	10-Jul	18-Apr	14-Jul	02-Apr		Bordeaux F	11-Jul	8.8	10-Apr	6.9

Box 5.1 - Satellite tracking

As part of a European Space Agency FlySafe initiative[1], IfV/SOVON used commercially available solar-powered satellite transmitters with a Global Positioning System (Argos GPS-PTT's) on 14 Lesser Black-backed Gulls and 11 Herring Gulls breeding on Vlieland (W Wadden Sea, The Netherlands). The birds were tagged in 2007 (23) and in 2008 (2). The positions of the gulls were updated daily on the SOVON website[2].

Transmitters were programmed with different duty cycles, varying from six to 18 fixes per day. Argos GPS-PTT's were useful to examine the actual *timing* of migration. Of 14 Lesser Black-backed Gulls tagged on Vlieland, 12 were wintering at the Iberian Peninsula (11) or in NW Africa (1). One bird wintered in Bordeaux (France) for at least four consecutive winter seasons, one wintered in the UK, but travelled to Morocco in January 2010 when winter conditions deteriorated.

Herring Gull movements were generally 'extremely' localised and repetitive, with all birds wintering within The Netherlands (mostly in Noord-Holland and Zuid-Holland, 50-100km south-southwest of the breeding colony).

Herring Gull colour-ringed F.AAA with an Argos PTT on the back, Jacob de Vries, Terschelling, Dec 2011.

References: [1]Ens *et al.* 2009, [2] http://www.sovon.nl/nl/content/satellietzenders-bij-meeuwen-en-ganzen; **Source:** http://www. sovon.nl/, Institut für Vogelforschung & SOVON unpubl. data

Satellite tracking - New technology revolutionised our knowledge of the migratory flyways and the timing of individual birds. From 12 birds carrying Argos PTTs (Box 5.1), the winter distribution confirmed results obtained from the colour ringing programme (^{App}Fig. 5.5), but the timing of migration could be examined in unprecedented detail. Of birds that wintered in Portugal, Spain or Morocco, the date of crossing of the Bay of Biscay was used as an indicator of the timing of their major legs of autumn and spring migration towards and from their final destinations in winter. In total, between deployment in 2007 and the last signals received in 2011, 25 autumn crossings and 29 spring crossings were logged (^{App}Fig. 5.6). Autumn migration was considerably more variable in timing (mean 12 October ± SD 44.1d) than spring migration (25 March ± 16.6d; ^{App}Table 5.2, ^{App}Fig. 5.7).

Fig. 5.7 Bay of Biscay crossings of Lesser Black-backed Gull carrying Argos PTTs, 2007-2011 (see Box 5.1 and ^{App}Table 5.2 for further details. IfV & SOVON unpubl. Data, reproduced with permission

Klaassen *et al.* (2011) analysed the data collected with the SOVON Argos PTTs under the expectation that the gulls would achieve high overall migration speeds by travelling via the shortest direct route, travelling during a large part of the day and night, and making few and short stopovers. Fourteen individuals were tracked between the breeding colony at Vlieland and the wintering sites in England, southern Europe and northwest Africa. The gulls did not travel via the shortest possible route but made substantial detours while following the coastline. The gulls did travel during most of the day, and sometimes during the night, but they did not achieve long daily distances (176 km d^{-1} in spring and in autumn). The gulls stopped frequently on travel days to forage. Due to frequent and long migratory stopovers, their overall migration speed was among the lowest recorded for migratory birds (44 and 98 km d^{-1}, in autumn and spring, respectively).

GPS-loggers - Lesser Black-backed Gulls from Texel carrying UvA-BiTS GPS loggers (Box 5.2) have thus far provided eight complete return trips from the breeding grounds to wintering areas at the Iberian Peninsula and in the UK (UvA/NIOZ unpublished data). The area used by these birds (^{App}Fig. 5.6) was again identical to the stopover, migration and wintering areas predicted from colour-ringing (^{App}Fig. 5.5) and were highly similar to the areas used by the birds tagged at Vlieland with Argos PTTs (^{App}Fig. 5.7 and Klaassen *et al.* 2011). The birds from Texel were carefully monitored while breeding, so that their breeding status is fully known. Three failed breeders left the colony 16, 26, and 30 July respectively, but five successful breeders did not stay much longer (21, 23, 29, and 30 July, 1 Aug; Appendix 4, ^{App}Table 4.3). Overall mean departure was 25 July ± SD 5.5d (n= 8). Five birds used stopovers (2x UK, 3x France) for a highly variable length of time (stop-over departure varied between 14 Sep and 20 Dec). One bird wintered within the UK, all others at the Iberian Peninsula. Returns within the colony occurred on average 30 March ± 6.3d (range 29 Mar-12 Apr).

GPS-loggers provide even higher resolution data than Argos-PTTs, and even foraging activities ‘underway’ can be confidently pinpointed (Boxes 5.3-4). In the UK, pig farms (free-roaming pigs and pig-feeders in open fields), and landfill areas were most popular. Roosts were often situated on large buildings, parking lots, in quarries or in fields. In Belgium and northern France, industrial estates were commonly utilised as roosts, landfill areas as feeding sites. Several stop-overs along the coast suggest the utilisation of more marine resources. Again, roosts were often on industrial estates and on parking lots, but also on beaches and in harbours. The Bay of Biscay was an area that was quickly crossed, often with a short stop just prior to and immediately after the crossing. Foraging activities were occasionally logged and were typically at the shelf-breaks, where most fisheries are likely to have been concentrated.

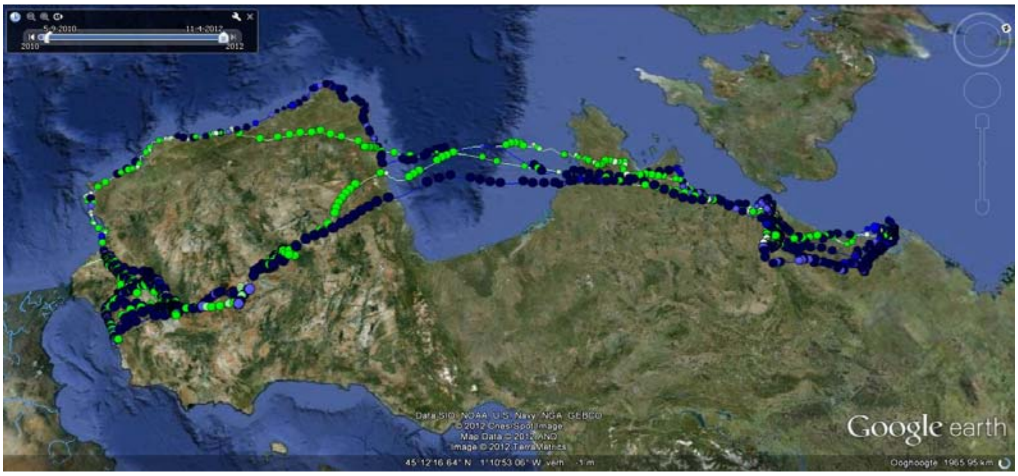
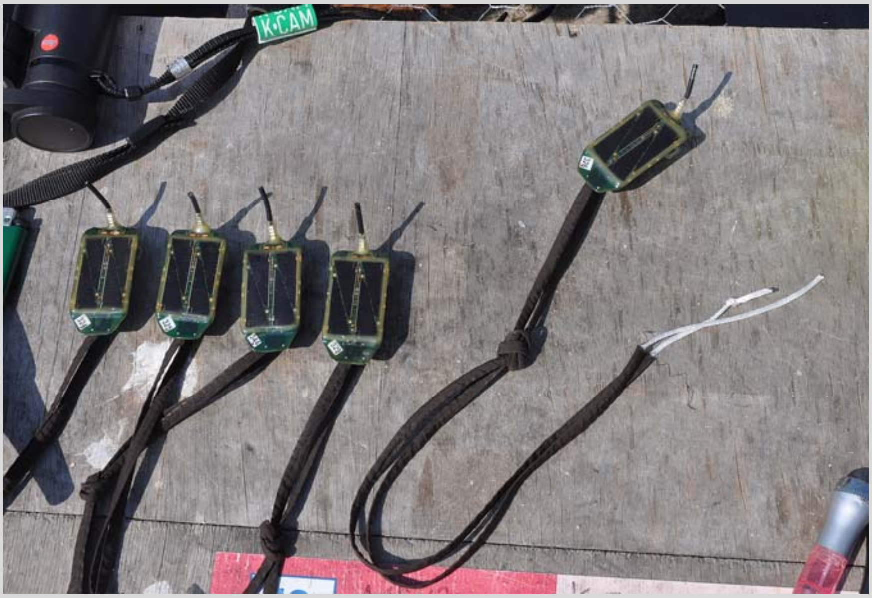


Fig. 5.8 Typical roundtrip from Texel to the wintering areas in southern Spain and back (2x) from a Lesser Black-backed Gull carrying a UvA BiTS GPS logger (M.AMM, GPS #317), tagged on Texel in 2010, retrieved in 2012. Between seasons (winter 2010/11 and winter 2011.12), the trips are near-identical, as in most multi-year data from the IfV & SOVON Argos PTTs.

Box 5.2 – UvA-BiTS GPS loggers

A team at the University of Amsterdam (UvA) developed a flexible, state of the art, Bird Tracking System, the UvA-BiTS. The system includes a solar powered, light weight GPS tag (*c.* 17g) with rechargeable batteries, a tri-axial accelerometer, two way data-communication to a ground station network, automated data processing and visualisation in the Virtual Lab[1,2].

The tracking system enables changing the measurement frequency while the tag is on the bird. In general a GPS fix was taken every 5–20min, during the day and night throughout the entire breeding season. Occasionally, high resolution measurements were taken (every 3–30s) as well. The tag is powered by four solar cells and a 65 mAh lithium polymer battery and gaps in the data occurred when the battery was not sufficiently recharged or the GPS timed out before a fix could be made.



Five GPS loggers lined up and charging (in the sun) prior to deployment

Between 2008 and 2011, in total 34 Lesser Black-backed Gulls have been colour-ringed and tagged with GPS loggers in the Kelderhuispolder. The aim of this study was to quantify the foraging movements, time budgets and habitat preferences of these birds. A comparative analysis of these aspects was conducted between individuals, years, sexes, breeding phases and migration. A further aim was to study the energetic cost of foraging movements by incorporating information on flight strategy selection. In the future it will be tried to link these characteristics to life history traits and fitness. In 2012, another 10 birds were tagged, including 3 pairs.

Potential foraging areas are the North Sea, the island of Texel itself, the Wadden Sea, and the Continental or UK mainland. Each individual GPS position was assigned to one of these five areas: (1) **North Sea**, including the coastal zone and beaches, (2) **Wadden Sea**, (3-4) terrestrial **mainland** areas in The Netherlands, Belgium, Germany or northern France (excluding Texel) or in the UK, (5) the island **Texel**. The first two areas would provide marine or intertidal prey types, the other areas would provide terrestrial prey. The time interval between consecutive GPS positions was used to calculate the proportion of time spent within certain habitats.

GPS logger deployment, (Arnold Gronert (left) and Kees Camphuysen (right)

Box 5.2 – UvA-BiTS GPS loggers

Ground station "Houston Control", 24 April 2010. In this version a radio antenna and receiver system (ARTS) were combined with the UvA BiTS GPS tracking base station. Solar panels and batteries provide the necessary power throughout the season. The onboard laptop computer could be remotely accessed through internet.

The time-series of consecutive GPS-points were grouped into three types of activity bouts per individual bird: '**nest bouts'**, '**short trips**' and '**long trips**'. We defined a nest bout as a continuous period where an individual stays at its nest or in its territory. Based on visual inspection of the data, a 150 m radius around the centre of the colony was used to demark nest bouts. Bathing places and popular roosting sites on beaches occur within *c.* 3 km around the study colony (identified from visual observations of colour-ringed birds); within this area there are few suitable feeding areas except feeding opportunities within the colony itself (e.g. cannibalism), and crowberry *Empetrum nigrum* stands in the surrounding dunes. A short trip was defined as a period where an individual moved out of this 150 m radius but stayed continuously within a 3 km radius from the nest before returning to the colony. A long trip was defined as a continuous period where an individual moved out of the 3 km radius before returning to the colony (a long trip begins once the distance from the nest was >150m and ended when the distance from the nest was < 150m). As there are few feeding opportunities within 3 km of the nest, foraging is associated almost exclusively with long trips. Any nest bouts, short trip or long trips with an interval of 60 minutes or more between two consecutive GPS-locations were usually excluded from further analysis. In addition, if the breeding status was uncertain for specific bouts, these were removed from further analysis. In total, for this thesis and topical papers associated with this work, 6859 complete activity bouts, recorded during May-August 2008-2011, were used (3493 nest bouts, 1167 short trips, and 2199 long trips). The data collected in 2012 (available after August 2012) will be added to the database on a later date.

Lesser Black-backed Gull M.APM with a UvA GPS logger, Kelderhuispolder, 24 June 2011 (MvKlw).

References: [1] http://www.uva-bits.nl/, [2]Bouten *et al.* 2013; **Source:** http://www.uva-bits.nl/

At the Iberian Peninsula, most birds travelled south along the coast, around Portugal, towards southern Spain. The return journey was usually faster: straight through central Spain (via Madrid), up north, and back across the Bay of Biscay (^{App}Fig. 5.8). On the way south, beaches and harbours were common stop-overs. In central Spain, some major landfill areas (popular sites for ring-readers!) and cities formed a major attraction. In southern Spain, roosts were normally situated in quarries or near inland lakes, while many animals utilised the rice-fields near Sevilla as daily foraging areas. Along the costas, some birds utilised fishing vessels along the coast, but again, the time spent at sea was in most birds minimal compared to the time spent on land.

Rings versus tracking data - Comparing data from colour-marking programs with Argos satellite PTTs and GPS-data revealed similar migration routes and wintering areas (^{App}Fig. 5.3-4). A well-known problem with colour-ring data is that human observers are restricted to certain habitats, and attracted to "rewarding" sites for ring-reading, so that an observer bias will always result. The significance of the open sea or certain remote areas on land, for example, can only be fully appreciated from logger data. When combining the results of colour-ring recoveries, Argos PTTs, and GPS loggers, it appears that Dutch birds generally migrate via SE England or Belgium and northern France in a southwesterly direction, cross the Bay of Biscay and winter in Spain and Portugal or (more exceptionally) in NW Africa (^{App}Fig. 5.5-5.8). The timing of these movements is described in Appendix 4.

All data are in perfect agreement with regard to the contours of the flyway: a narrow band (a 30° angle) to the SSW – SW from the breeding grounds. The modern techniques have confirmed that wintering Lesser Black-backed Gulls spend more time on land than at sea. The east and southeast coast of Spain is used by few Lesser Black-backed Gulls from The Netherlands; most birds seem to concentrate on the central and south/western parts of the Iberian Peninsula. Ring-reading activities in NW Africa are sparse, but the logger data, so far, seem to demonstrate that a minority of the Dutch population winters there. Incidentally, the distance record for a Lesser Black-backed Gull from Texel is now set by a GPS-tagged bird moving to and from Guinea-Bissau to winter (Box 5.4). Concurrent ringing programmes, for example that by Roland Jan Buijs using birds ringed in mainland colonies in Zuid-Holland, in which a much larger number of Lesser Black-backed Gulls is colour-ringed, have shown that indeed a small fraction of the birds move south to Senegal, The Gambia and occasionally further to for example Nigeria (R-J. Buijs, pers. comm.).

In contrast with earlier studies using numbered metal rings (Bairlein 2001), colour-rings and most electronic devices give the opportunity to study migratory pathways, stopovers and wintering areas of individual birds in more than one year. All systems revealed that individual birds tend to appear on the same sites year after year. Colour ring sightings are observer dependent, but numerous birds returned in more than one season in front of the same Spanish, French or Portuguese observers. The modern instruments added to that knowledge that most birds move relatively quickly between favourite sites (either underway stopovers or final destinations) and stick to these sites. The GPS data revealed that often in these situations a roost is chosen (building, quarry, lake systems, or otherwise) from where favoured foraging areas are visited in a central-place-foraging modus. Some examples are shown in Boxes 5.3-4. By choosing relatively few locations to stop during migration or to spend the winter, individual birds may obtain intimate knowledge of these favoured locations in terms of safety, risk of disturbance, and food availability.

Electronic devices have turned out to be superior to colour-ring data when issues such as timing are concerned (Appendix 4), but an important limitation is that the sample size is often small. Moreover, few researchers have dared to deploy electronic instruments on young birds (considering the high risks of first-year mortality). Young Lesser Black-backed Gulls have been claimed to winter farther south than adults (Baker 1980, Rock 2002). Hallgrimsson *et al.* (2012) did not find a statistical difference between the latitudinal winter range in birds of different ages, a difference in the latitudinal range during summer, because most adult birds returned to the breeding grounds, whereas especially the younger immatures rarely reached these latitudes. Camphuysen *et al.* [Chapter 5] analysed the seasonality of Lesser Black-backed gulls colour-ringed within The Netherlands and found that juveniles wintered on average 600 km further to the south/southwest than adults (juveniles Dec-Jan c. 37°30'N). Immatures travelled on average further to the south than adults, to mean latitudes (c. 39°30'N) that were intermediate between wintering latitudes of adults and juveniles. The difference in mean wintering latitudes between juveniles and immatures was not significant.

The Argos PPTs revealed that typical elements of a migratory journey are a pre-migratory round trip (several birds), a stopover in northern Europe (all), and a fast migration from stopover to wintering area (all; Ens *et al.* 2009). Some birds carrying GPS loggers performed a pre-migratory, long-distance roundtrip (not just prior to the way south, but also prior to the return flight in spring), but certainly not all individuals. Some birds were so heavily attracted to their stop-over and winter quarters in the UK, that even during the breeding season several trips across the North Sea and back were completed. The UK is an area where few rings are detected and/or reported. The electronic devices now deployed have clearly indicated how important England is for Lesser Black-backed Gulls after the breeding season in The Netherlands. Unfortunately, few British birders are prepared to report their sightings.

Site fidelity

From colour-ring data, there is some evidence that individual birds use the same wintering areas again and again. Of 404 Lesser Black-backed Gulls ringed as adults in IJmuiden and at Texel between 2006 and 2012, 167 individuals (41%) were recorded at any French, Spanish or Portuguese wintering- or stopover-site. Landfill sites where colour-ringed Dutch Lesser Black-backed Gulls have been re-sighted in recent years were Alcalá del Rio, Sevilla (ESP, 37°33'N, 6°0'W), Medina Sidonia, Cadiz (ESP, 36°28'N, 5°55'W), Talavera de la Reina, Toledo (ESP, 39°57.4'N, 4°59.5'W), Los Asperones, Malaga (ESP, 36°43.2'N, 4°30'W), Marchena, Sevilla (ESP, 37°15'N, 5°25'W), Villarrasa, Huelva (ESP, 37°27'N, 6°38'W), Alcazar de San Juan, Ciudad Real (ESP, 39°23'N, 3°11'W), Badajoz, Don Benito, Extremadura (ESP, 38°53'N, 6°58'W), Colmenar Viejo, Vertedero, Madrid (ESP, 40°39'N, 3°46'W), Pinto, Madrid (ESP, 40°15'N, 3°42'W), and Taboeira, Aveiro (PT, 40°39'N, 8°36'W). None of the birds reported more than once, anywhere in this group of countries, was seen on more than 5 out of a total of 120 different sightings locations. This includes birds that were recorded frequently and in several (2-6) subsequent winter seasons (^{App}Table 5.3). The still novel technique of bird tracking has so far confirmed this suggestion. Most tracked birds from which data were collected over more than one winter season (and example in ^{App}Fig. 5.7) not only used the same stop-overs and wintering areas, but also followed more or less the same route to and from (*unpublished* GPS tracking data Kelderhuispolder, IfV & SOVON Argos PTTs).

Table 5.3 Sightings (n), number of sites used (n, %) and number of years from which wintering sightings data were received for Lesser Black-backed Gulls ringed as adult birds on Texel (left) or IJmuiden (right) and reported from France, Spain and/or Portugal (total number of sites in these countries combined is 120).

Ring	Sightings	Sites	%	Years	Ring	Sightings	Sites	%	Years
FABV	34	5	4.2	4	YABR	10	4	3.3	2
FADA	10	5	4.2	5	YACM	19	3	2.5	5
FAKV	11	2	1.7	3	YAJY	44	2	1.7	4
MAAA	23	3	2.5	6	YAKA	13	3	2.5	3
MAAJ	12	2	1.7	5	YAKJ	10	5	4.2	3
MAAV	34	2	1.7	4	YAKK	31	2	1.7	4
MAAZ	11	4	3.3	5	YAPA	13	4	3.3	3
MACH	12	5	4.2	3	YAPB	15	2	1.7	3
MADA	42	5	4.2	4					

The same tendency was found in Herring Gulls (examples in ^{App}Fig. 5.3). The tracking data so far, unfortunately, comprise only relatively few individual birds and an even smaller sample with subsequent winter trips being documented. More data are received every year, however, and when similar tracking data from different research groups working on the same species for a number of years would be combined, it will be possible to conduct a meaningful analysis of site-fidelity in wintering grounds. So far, however, none of the data suggest that "*Gulls lead a fairly mobile life in winter and change their place of residence if the climate or the food supply deteriorates*" (Alerstam 1990). In fact, the available evidence suggest that each bird tends to use a small subset of the wintering opportunities that is available to the population as a whole.

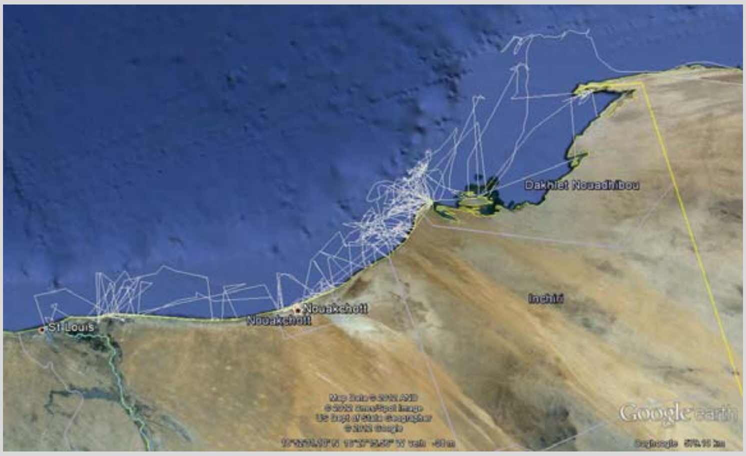
Winter feeding habitats

Of the Lesser Black-backed Gulls carrying GPS tags that have revealed winter data, two individuals wintered in the UK (F.AAW, F.AKU), two in France (F.APR, M.ACT), five in southern Spain (F.AJK, F.ABN, M.AMK, M.AML, and M.AMN), three in central Spain (M.AMA, F.AKJ, and F.AKK), one in Mauritania (M.APM), and one in Guinea-Bissau (M.APN). The **Guinea-Bissau** bird (M.APN) moved within 10d from Texel to a small set of nearshore sandbanks near Sucujaque (12°18'N, 16°38'W) and remained there all autumn and winter before it returned to Texel (Box 5.3). This bird was unusual in its habits of moving exclusively between a number of sandbanks and peninsula's with low human populations. There is no evidence for the utilisation of artisanal fisheries offshore.

Box 5.3 – Wintering in Guinea-Bissau and Mauritania

A record post-breeding movement of a Lesser Black-backed Gull ringed and tagged at Texel was recorded in late summer 2011. Male Lesser Black-backed Gull M.APN (GPS #541, nest KLM542) lost its hatching chicks around 16 June 2011. Just over a week later, on 25 June it left the colony and moved south, first across the North Sea to UK, and then crossed the English channel to France (June 28), continued south along the coast and made some shortcuts over the mainland (skipping Normany and Brittany), crossed the Bay of Biscay diagonally (NE → SW),reached Galicia (NW Spain) and continued towards the Portuguese coast by yet another shortcut and part of the Atlantic between Europe and Africa (470 km). Reached and immediately left Baie de Belixe in SW Portugal and crossed the Atlantic Ocean towards Oualidia (Morocco; Atlantic crossing course 180°, 457km in 9.3 hours, or 49.1 km h^{-1}) and continued along the African coastline as in the map above. The bird reached Guinea-Bissau on 10 July (in a straight line 4875km south southwest of Texel, 325km d^{-1}) and stayed at *~ 12°18'N, 16°38'W*.

This individual, M.APN (GPS 541) remained the entire winter on some offshore sandbanks in a sparsely populated part of northern Guinea-Bissau, west of Sucujaque, travelling from one roost or feeding location to the other in a constantly repeating way.



This individual, M.APM (GPS 540), utilised numerous coastal roosts in Mauritania and fed mostly over the continental shelf (i.e. associated with industrial or artisanal fishing fleets. Most foraging activities were confined to an area west of Cap Timiris. Shown are tracks 6 Nov 2011-4 May 2012

Source: UvA BiTS, *unpubl. data* CJ Camphuysen & J Shamoun-Baranes

The **Mauritanian** bird (M.APM) was more active and utilised several roosts and foraging areas between Nouadhibou (20°55'N) and Senegal (16°32'N), including sites near Nouakchott (18°06'N) and Nouamghar (19°22'N). Foraging trips over the ocean were common, and these included several visits to the shelf break where large freezer trawlers operate (Box 5.3).

Gulls wintering in **southern Spain** (F.AJK, F.ABN, M.AMK, M.AML, and M.AMN) focused on areas around Sevilla (rice fields; 37°14'N, 06°04'W), the port of Malaga (36°43'N, 04°25'W) and the beach and sea area near Huelva (37°09'N, 07°W). Recently created rice fields seemed particularly important for several of these birds and daily foraging trips into these fields were documented. The arrival of an invasive species, the Louisiana crayfish *Procambarus clarkii* (a freshwater crayfish species native to the south-eastern United States) provides ample foraging opportunities for Lesser Black-backed Gulls and other birds (R. Marques-Ferrando & J. Figuerola *pers comm.*). Ring-readers in the area confirmed freshwater crayfish as common prey items. Some birds were foraging in harbours, not only on fish but also on spilled grains and (sunflower) seeds. Offshore foraging (likely around fishing boats) occurred, but most birds spent most time in foraging areas onshore.

Wintering Lesser Black-backed Gulls in **central Spain** (M.AMA, F.AKJ, and F.AKK) focused almost entirely on landfill areas near Madrid and Toledo. Domestic refuse was the principal prey in these areas and colour-ring readers active usually reported the same colour-ringed birds (some tagged birds included) over and over again. The two birds that wintered in **France** (F.APR, M.ACT) spent most time on refuse dumps and in agricultural areas with roosts in quarries or in industrial estates (e.g. roofs of factories, large car parking places). Little time was spent at the sea side, except when moving to and from the wintering area. Finally, two Lesser Black-backed Gulls spent the winter in **England** (F.AAW, F.AKU) and also these spent most their time on inland areas (pig farms, fields, cities, refuse dumps) with roosts in fairly undisturbed areas such as on factory roofs, in quarries, near or on lakes, etcetera. A small number of favoured areas was used with a high frequency, and movements between these sites were usually swift and highly determined.

Colour-ring re-sightings are typically biased towards areas where ring-readers has easy access to the birds without disturbance and this excludes marine areas where seabirds are presumed to occur most of their time. Tracking data do not have that problem and the results were therefore expected to be not only much more complete (unbiased), but also to highlight where that offshore foraging occurred. The data that have accumulated so far, however, all seem to point at a preference to *onshore* or even inland sites for most birds during the entire winter season. These areas are reached by a quick, largely coastal migration, during which foraging occurs both on land and at sea. The stop-overs that some of the tagged birds used for prolonged periods of time (mostly in autumn) were also typically inland sites rather than coastal areas. There are, however, large numbers of gulls in coastal sea areas, on beaches and in harbours throughout the winter, and additional data will be needed to be able to sketch a more representative picture of the wintering habits and habitats of both species of gulls.

Length of the migration - Alerstam (1990) concluded that the length of the migration and the size of the different Scandinavian gull species are negatively correlated: Black-headed Gulls, the smallest, on average migrates the farthest. This finding is put to the extreme by Lesser Black-backed Gulls and Herring Gulls, in which the size difference is rather modest. Herring Gulls (dispersive, semi-residents) and Lesser Black-backed Gulls (long-distance migrants) differ enormously in their non-breeding strategies. Alerstam (1990) described the migration strategies of Scandinavian populations and observed that between 1965 and 1975, wintering Lesser Black-backed Gulls shifted northwards by an average of 1.6 degrees (the equivalent of 150-200km) per annum. *"Maybe in the future significant numbers of adult Lesser Black-backs will begin to winter in the harbours and around tips in Scandinavia?"* Alerstam (1990) explained this marked change by seemingly enhanced resources for wintering birds further to the north: "*Lesser Black-backs from*

England and west Scandinavia winter and live to a large extent as omnivores, especially at refuse tips". A similar shift in wintering distribution had been found somewhat earlier by Baker (1980) and involved ringing results of birds ringed in Britain (Walney Island, Cumbria, 1962-1975). Baker (1980) suggested that this tendency to winter further to the north was either an effect of climate change, an increased inclination to feed on rubbish tips, or the huge increase in population size that has occurred the years. Clearly, none of these factors is mutually exclusive.

At least one third of the adult birds colour-ringed within The Netherlands (1991-2012) were wintering to the north of 45°N latitude (*i.e.* within the UK, northern France, Belgium or even in the southernmost parts if The Netherlands (^{App}Table 5.4). Apparently, the 'classic wintering areas' (the Iberian Peninsula and the coast of northwest Africa bordering the Canaries Current) are not used by all adult birds, but mostly by juvenile and immature birds). If rubbish tips are an important explanation for a tendency to winter further to the north, this would have been reversed in more recent years. There has been a widespread change in waste management in rich industrialised countries since the late 1980s (involving the closure of numerous open refuse dumps; Appendix 2), and open landfill areas are now more common in Portugal and Spain. A meta-analysis of ringing data covering at least the past 3-4 decades would be needed to examine these trends in more depth.

Table 5.4. Proportions (%) of adult (>5cy), immature (2-5cy) and juvenile (first year) Lesser Black-backed Gulls in winter (Nov-Feb) within 5° latitude bands of western Europe based on colour-ring sightings. Note that colour ring-readers effort to the south of 35°N is much less than that further to the north. Base material: re-sighted Lesser Black-backed Gulls, colour-ringed in The Netherlands, 1991-2012 (n= 404 individuals).

Latitude	**Adult**	**Immature**	**Juvenile**	
55-50	17%	3%	4%	UK-Belgium
45-50	20%	9%	4%	France
40-45	24%	27%	13%	
35-40	34%	49%	62%	Iberia
30-35	0%	1%	3%	
25-30	3%	9%	12%	NW Africa
20-25	1%	1%	1%	
15-20	0%	-	-	
<15	0%	-	-	
n=	322	155	121	

A more detailed description of the GPS loggers deployed on Lesser Black-backed Gulls in the Kelderhuispolder colonies at Texel has been published recently:

Bouten B.[1*], E.W. Baaij[2], J. Shamoun-Baranes[1] & C.J. Camphuysen[3] 2013. **A flexible GPS tracking system for studying bird behaviour at multiple scales.** J. Orn. 154: 571-580.

[1] Computational Geo-Ecology, Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands, **Correspondence author* w.bouten@UvA.nl; [2]Science Faculty, Technology Centre, University of Amsterdam, P.O. Box 94216, 1090 GE Amsterdam, The Netherlands; [3]Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands.

Tracking devices and bio-loggers provide crucial information on the ecology and behaviour of birds in their natural environment. An optimal tracking system are lightweight, measure three-dimensional locations, enable flexible measurement schemes, transmit data remotely and measure environmental variables and biological parameters of the individual. We have developed a GPS tracking system that attempts to achieve most of the aspirations of an optimal tracking system for free ranging birds without the need to recapture them. The design, performance and limitations of the system are described. We present measurements on tracked Lesser Black-backed Gulls to show how such a system can generate new opportunities for research at multiple scales. The GPS tracker weighs 12g and includes a GPS receiver, micro-processor, 4 MB of memory for data storage, solar panel and battery. It has a tri-axial accelerometer to monitor behaviour. To maximize flexibility, it is equipped with a radio transceiver for bi-directional communication with a ground-based antenna network, which enables data to be downloaded and new measurement schemes to be uploaded remotely.

Appendix 6 - Annual adult survival, recruitment and parental investment

Annual adult survival

While the fledging rates of Herring Gulls (0.88 ± 0.29 fledglings pair^{-1}) found in Kelderhuispolder were considerably higher than those of the sympatric Lesser Black-backed Gulls (0.49 ± 0.17; $t_{12} = -3.07$, $P < 0.01$, two-tailed), our own colony censuses (2009-2011) indicated a continuing decline in breeding numbers of the former and an increase in the latter species (Appendix 3). Part of the explanation was expected to be found in species-specific differences in annual survival, the age of first breeding and the actual numbers of recruits returning to breed. Data available on fecundity and adult survival in several seabird populations suggest a negative relationship between the two (Weimerskirch 2002). Devoting more energy per individual parent to the raising of young would come at the expense of adult survival (Clutton-Brock 1988, 1991, Pyle *et al.* 1997). The shape of this relationship is convex (^{App}Fig. 6.1), similar to the classical figure representing the optimisation of the trade-off between survival and fecundity or other vital rates (Cody 1966). Cody (1966) proposed a model in which by the "*Principle of Allocation*" maximum contribution to future generations would be achieved by those individuals which utilise, to increase K (carrying capacity), some of the energy conserved by reducing r (the reproductive rate; Williams 1966, Nur 1984).

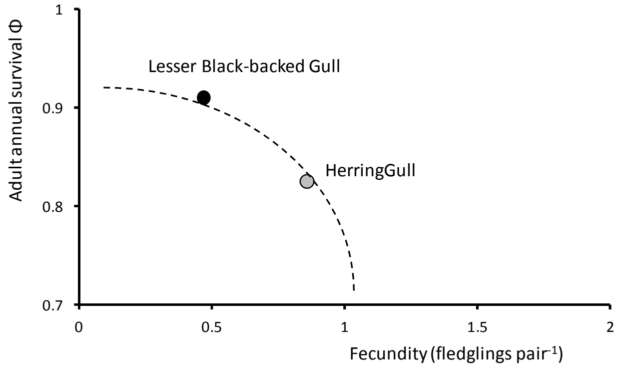


Fig. 6.1 Hypothetical relationship between fecundity and survival in Laridae to achieve a constant population growth rate (λ), a convex curve representing optimisation between survival and fecundity (Cody 1966, Weimerskirch 2002). The plotted values are mean fecundity versus mean apparent annual adult survival for gulls breeding in Kelderhuispolder, 2006-2011.

The apparent survival and fecundity of both species is described in Chapter 7. Apparent survival (*i.e.* survival confounded by permanent emigration), investigated on the basis of the colour-ring programme, amounted to a mean of 79% in female and 86% in male Herring Gulls. Additive year effects rather than sex provided highest model support in Lesser Black-backed Gulls, in which apparent survival for both sexes combined varied between 81% and 100% (mean ≈91%). Given the observed population trends, the lower apparent survival in Herring Gulls than in Lesser Black-backed Gulls found in this study did not come unexpected. An inverse relationship between annual apparent survival and fecundity was indeed found in Lesser Black-backed Gulls (Chapter 7). Herring Gulls, with their consistently lower survival rates, showed a consistently higher fecundity than Lesser Black-backed Gulls (^{App}Fig. 6.1).

Recruitment and the Balance Per Annum

Levels of recruitment were thus far rather low in the Kelderhuispolder. Breeding birds with immature plumage characteristics are rare in these colonies, notably in Lesser Black-backed Gulls, suggesting that current recruits are at least 4 years old (5cy). Some estimates of recruitment rates are required to be able to calculate (or even just estimate) the *Balance Per Annum* (BPA; the difference between the number of chicks per pair surviving to breeding age and the number of adults dying per pair per year; Birkhead & Sears in Perrins 1991).

Between 2006 and 2011, 554 chicks of Lesser Black-backed Gulls and 237 chicks of Herring Gulls were colour-ringed around fledging (*c.* 40d of age). Of the first three cohorts (2006-2008), 254 and 114 chicks respectively could have reached breeding age (5cy) during the period described in this thesis. In fact, only 20% of the chicks (51 out of 254) of Lesser Black-backed Gulls and 13% of Herring Gulls (15 out of 114) were demonstrated to have reached that age (^{App}Table 6.1). Based on a mean fledging rate of 0.49 fledglings pair^{-1} (Table 2.1, Appendix 3), the number of Lesser Black-backed Gulls reaching a reproductive status (≥5cy) was thus 0.10 chicks pair^{-1}. Based on a fledging rate of 0.88 fledglings pair^{-1} in Herring Gulls, a marginally higher 0.12 chicks pair^{-1} was found. Considering an annual adult mortality of 0.18 adults pair^{-1} (Chapter 7) in Lesser Black-backed Gulls, the BPA would be -0.08. With the considerably higher adult mortality

Table 6.1. Annual survival of fledglings colour-ringed in Kelderhuispolder, 2006-2011. For each cohort, first year survival (%) is indicated on the basis of re-sightings anywhere within the NE Atlantic flyway.

Lesser Black-backed Gull								**First year**
Year	Ringed	2cy	3cy	4cy	5cy	6cy	7cy	**survival**
2006	69	23	19	18	14	11	9	33%
2007	102	43	40	34	25	19		42%
2008	83	27	24	18	14			33%
2009	83	25	24	18				30%
2010	108	26	14					24%
2011	109	23						21%
Survival		30%	84%	82%	76%	77%	82%	30.6±7.5%
Sample	554	554	445	337	254	171	69	(6 years)
Herring Gull								**First year**
Year	Ringed	2cy	3cy	4cy	5cy	6cy	7cy	**survival**
2006	26	4	4	2	1	0	0	15%
2007	35	7	6	6	5	5		20%
2008	53	16	16	10	9			30%
2009	45	13	11	7				29%
2010	61	16	11					26%
2011	17	5						29%
Survival %		26%	86%	68%	83%	83%	none	25.0±6.0%
Sample	237	237	220	159	114	61	26	(6 years)

Table 6.2. First returns of ringed fledglings of Lesser Black-backed Gulls and Herring Gulls in Kelderhuispolder (Texel) and at Forteiland (IJmuiden). For each cohort, the percentage that has returned to the colony and the age of first returns has been indicated. Ringing at Forteiland, IJmuiden commenced in 2008 (ringing and sightings data courtesy Fred Cottaar, José & Kees Verbeek).

Kelderhuispolder, Texel								**Forteiland, IJmuiden**						
LBBG		**Age of first return**								**Age of first return**				
Cohort	Ringed	2cy	3cy	4cy	5cy	6cy	Returns	Cohort	Ringed	2cy	3cy	4cy	5cy	Returns
2006	69		1	3			6%							
2007	102		3	4	2	1	10%							
2008	83			5	4		11%	2008	16			6		38%
2009	83			4			5%	2009	32		2	7		28%
2010	108		1				1%	2010	51		9			18%
2011	109						0%	2011	53	2				4%
		0%	18%	57%	21%	4%	5%	Returns		8%	42%	50%	0%	17%
HG		**Age of first return**								**Age of first return**				
Cohort	Ringed	2cy	3cy	4cy	5cy	6cy	Returns	Cohort	Ringed	2cy	3cy	4cy	5cy	Returns
2006	26		1	1			8%							
2007	35			1		1	6%							
2008	53		1	1	1		6%	2008	19	1	1	6	1	47%
2009	45			2			4%	2009	10	2		3		50%
2010	61						0%	2010	8	1				13%
2011	17						0%	2011	7					0%
Returns		0%	22%	56%	11%	11%	4%	Returns		27%	7%	60%	7%	34%

of *c.* 0.35 adults pair^{-1} (annual survival 82.5%), the BPA for Herring Gulls would be -0.23. Both populations may be considered unstable or declining, but the former mainly as a result of low reproductive success, the latter mainly as a result of lower annual survival. Rather few "recruits" (that includes prospecting birds and only few confirmed breeders) have been demonstrated to have returned to the Kelderhuispolder colonies: 5% of all colour-ringed fledglings of Lesser Black-backed Gulls and 4% of all Herring Gulls. If recruitment was based only on these birds, the BPA would be considerably lower, but it is unlikely that all recruits are detected. Further evidence showing that chicks raised at Texel recruit at a relatively high age (if at all) is provided in the comparison of re-sightings within the colonies at Texel and at IJmuiden (^{App}Table 6.2).

Age composition – Though breeding attempts of birds in immature plumage may be fairly common in certain (developing) mainland colonies in The Netherlands, the mean age of first breeding in Herring Gulls is normally probably around 5 or 6 years of age (Vercruijsse 1999). In a dense colony at the Isle of May (Scotland), no 4cy birds (3 yrs of age) were found holding territories or breeding in the 1970s, but some 5cy gulls (4 yrs old) did (Chabrzyk & Coulson 1976). For the Isle of May, it was estimated that the mean age of first breeding was 5.25 years, with 55% of the birds breeding for the first time when five years (6cy) old.

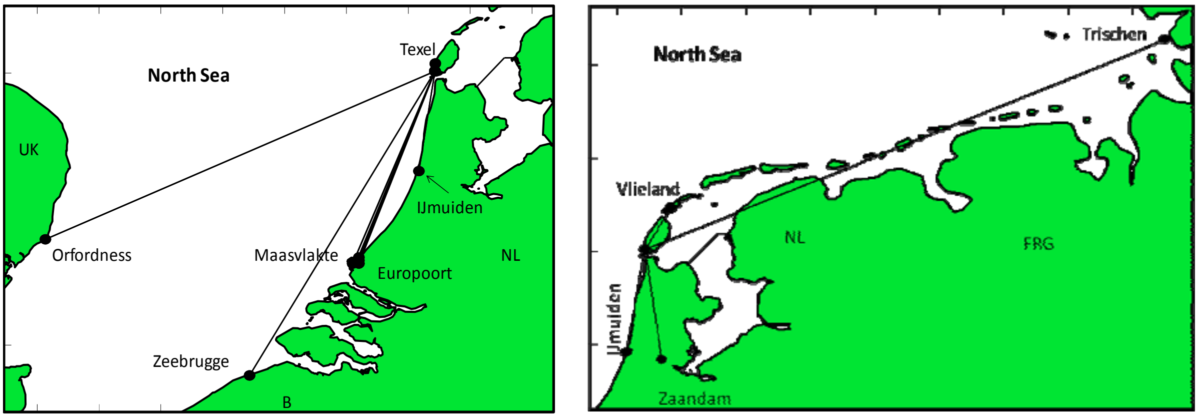
The age composition of the breeding population at Texel is largely unknown, but early recruits (or even immature *visitors*) in the colony are rare. All Lesser Black-backed Gulls that had been ringed in other colonies and that were found to breed in the Kelderhuispolder in recent years were fairly old (9-17 yr). Despite considerable observer effort, only six Lesser Black-backed Gulls that had fledged between 2006 and 2009 were confirmed to have returned to nest and actually breed in Kelderhuispolder, while there are four birds that have moved and recruited and bred elsewhere. The much higher return rates in IJmuiden of prospecting birds are particularly striking, and prospecting or settling recruits are also younger at this mainland colony and first-year survival was higher. Of 152 ringed chicks of Lesser Black-backed Gulls and 44 chicks of Herring Gulls, at least 38 resp. 35% survived its first year against 29% and 26% at Texel (^{App}Table 6.1). To compare the returns of potential recruits in the two colonies for the exact same period (ringing effort 2008-11 versus ring-reading in 2009-2012):

		Kelderhuispolder, Texel	**Forteiland, IJmuiden**
Lesser Black-backed Gull	Returns	4% (n= 383)	17% (n= 152)
	Mean age ± SD	4.2 ± 0.6 cy	3.4 ± 0.6 cy
Herring Gull	Returns	3% (n= 176)	34% (n= 44)
	Mean age ± SD	4.0 ± 0.7 cy	3.5 ± 1.0

Immigration, emigration

With respect to immigration and emigration (or colony dispersal), only anecdotal information is available, again on the basis of ringing data, but this time including some metal-ringed individuals. Within the Kelderhuispolder, adult breeding birds have been encountered that were ringed as fledglings in Orfordness (UK), Zeebrugge (B), Europoort/Maasvlakte and IJmuiden (mainland NL) and from other colonies at Texel. Birds that fledged at Texel in recent years have been found as prospecting individuals at Trischen (Wadden Sea FRG) and Vlieland (Wadden Sea NL), and as confirmed breeders in Zaandam and IJmuiden (mainland NL).

Immigration - Two Lesser Black-backed Gulls ringed as chicks in IJmuiden have recruited in the Kelderhuispolder colonies, 11 individuals originated from Europoort/Maasvlakte, and two from Orfordness (Suffolk, UK) (^{App}Fig. 6.2). All these birds had been ringed as chicks between 1988 and 1997 and were between 9 and 17 years of age (mean 14.3 yrs) when detected as breeding birds at Texel. A recent exception is a bird ringed as chick in Zeebrugge (Belgium) that recruited in the Kelderhuispolder at an age of 5 years, after a prospecting visit one year earlier.



Origin of foreign recruits (immigrants) *Destination of emigrants*

Fig. 6.2 Links between de Kelderhuispolder colony and other Lesser Black-backed Gull colonies based ringed and colour-ringed individuals ringed at Texel and elsewhere.

Emigration - Seven Lesser Black-backed Gulls ringed as young birds since 2006 at Texel have been seen prospecting or were demonstrated to breed in other colonies: K.BAU (Trischen, FRG), K.FAU (IJmuiden, Forteiland), K.LAC (Vliehors, Vlieland), K.NAP (Achtersluispolder Zaandam), P.CAC (IJmuiden, Forteiland), P.CBU (IJmuiden, Forteiland), and P.CDV (Vliehors, Vlieland). Of these, at least three have bred: KFAU (2011-12), KNAP (2011-12), and PCBU (in 2011, prospecting in 2012).

Trends and seasonality in mortality as derived from beached bird surveys

Mortality is an aspect that is notoriously difficult to study during colony work. Birds sometimes disappear, but in the absence of physical evidence, anything could have happened. Since large gulls are coastal seabirds, some insight in seasonal as well as annual patterns and trends in mortality can be evaluated on the basis of beached bird surveys (>50 yrs of data). The data were used to investigate the age composition and the overall densities of dead gulls on the North Sea coastline, in order to check if mortality levels may have changed in recent years. Many fledglings fail to really leave the colony area, but fledglings from coastal colonies (such as those at Texel) often die on the nearby beaches, during attempts to find some food or on the beach roosts where they mix with moulting adults. Beached bird surveys could therefore be a useful tool to quantify seasonal patterns in mortality.

We have seen that the incidence of oil pollution in Herring Gulls has declined significantly over the years (Appendix 2, ^{App}Fig. 2.13) and currently, most gulls die from 'natural causes' (disease, starvation), or from entanglements in plastics or fishing gear or other accidents. We have also seen that the annual cycle and the migratory movements in autumn (or post-breeding dispersal) make that the composition of the population of gulls utilising Dutch nearshore water and on our beaches will change (Appendix 4): there are no or few "local" Lesser Black-backed Gulls in winter (because all these birds are in Portugal and Spain). Although many Dutch Herring Gulls remain here in winter (Appendix 5), their numbers will be augmented by birds from a Baltic, Scandinavian or German origin. This should be kept in mind when consulting the results from beached bird surveys over time.

In ^{App}Fig. 6.3 the monthly densities of dead gulls are provided for each of the years of study (2006-12) against a background of "historical" densities based on surveys between 1980 and 2005. From the material provided in Appendix 2 it is obvious that the breeding population of Lesser Black-backed Gulls increased by a factor 7.5 between 1980 and 2005, whereas that of Herring Gulls peaked reduced in the same period by 25%. Current densities were therefore much higher than 'historical ones' in Lesser Black-backed Gulls, while the reverse was true for Herring

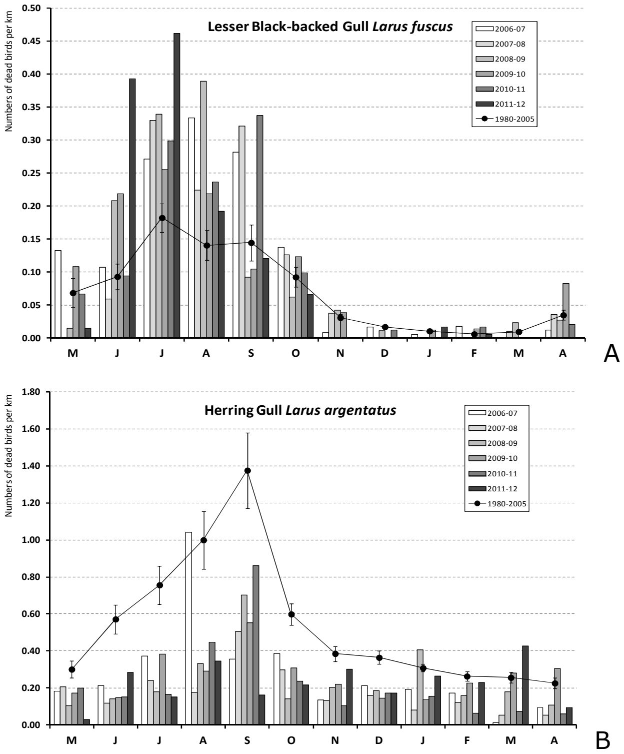


Fig. 6.3 Annual monthly densities of dead Lesser Black-backed Gulls (A) and Herring Gulls (**bottom**) along the North Sea shoreline, based on beached bird surveys 2006-2012 against the long-term mean densities found during beached bird surveys 1980-2005 (average ± SE); NZG/NSO beached bird surveys, unpubl. data; based on 7741counts covering 45,243 km, retrieving corpses of 1817 Lesser Black-backed Gulls, and 15,842 Herring Gulls.

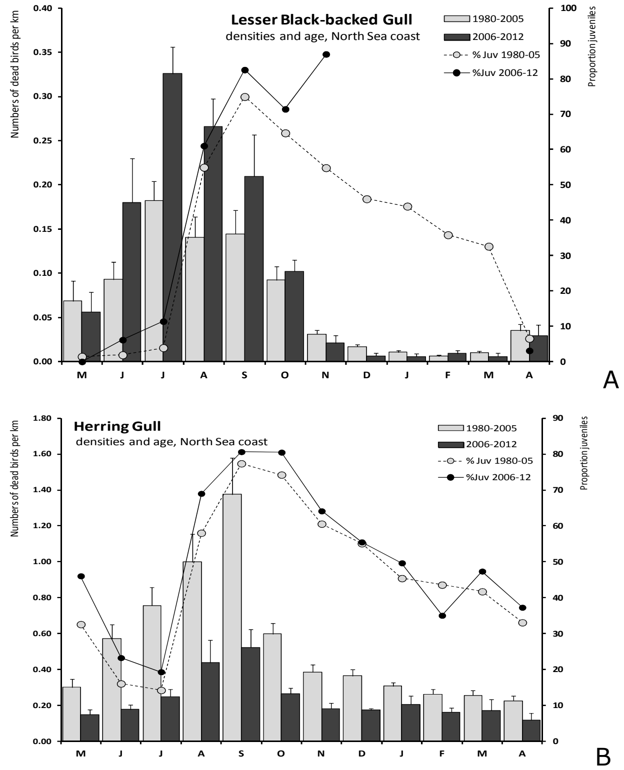


Fig. 6.4 Monthly densities of dead Lesser Black-backed Gulls (A) and Herring Gulls (B) along the North Sea shoreline, based on beached bird surveys 1980-2005 and 2006-2012 (average ± SE) and the proportion (%) of first year birds found dead; NZG/NSO beached bird surveys, unpubl. data.

Gulls. Both species have a late summer peak in densities, which was however more prominent in the historical data of Herring Gulls than it is nowadays. In recent years as well as historically, densities of stranded Lesser Black-backed Gulls increased from April to July followed by a decline. Very low numbers (as expected) are found in winter (Nov-Mar). From April through July, it is mostly adult birds that are found, while juveniles start to predominate in August-October. Over the years, the age composition of the stranded animals remained more or less the same, but current densities are higher (^{App}Fig. 6.4). A similar trend was found in Herring Gulls, except that first year birds remain numerous throughout the winter and into spring (^{App}Fig. 6.5). Juveniles predominated in Aug-Oct, but in June and certainly in July proportionally many adult gulls were found. Recent winters have been relatively mild (^{App}Fig. 2.8), despite some spells of cold weather, and winter mortalities will therefore have been suppressed (^{App}Table 2.3).

Intermittent breeding

Extensive ring-reading activities in the prospecting and early breeding phase resulted in high numbers of re-sightings of birds ringed as breeding birds in previous seasons, with few exceptions at or near the exact same territories as in earlier seasons. However, not all returning birds could subsequently be demonstrated to breed. Some failures to confirm breeding were resulted from difficulties to read rings in vegetated or 'hilly' terrain (steep dunes, esp. in the prime Herring Gull habitat). Confirmed breeding attempts of returning adults were consistently scarcer in Lesser Black-backed Gulls than in Herring Gulls (46% in LBBG, 63% in HG; ^{App}Table 6.3).

"Not breeding" is more difficult to confirm than "breeding", but the difference between the species is considerable in all seasons with sufficient data (^{App}Fig. 6.4). Site-fidelity is such that breeding attempts elsewhere in the colony are unlikely (5 cases have been documented within the colony, 2007-2012; these involved moves from monitored study plots to nearby nesting habitat just beyond the study areas). The percentage (%) of prospecting birds in which breeding was subsequently confirmed is used here to indicate the "breeding incentive", or the drive to breed in a given season. Some birds skipped one, two or even three years and re-appearances as breeding birds were typically very close to or exactly at the original nesting site (certainly in males; divorced females usually moved to another territory). Lesser Blacked-backed Gulls were slightly more frequently found to skip breeding seasons (22% of 208 confirmed re-breeding cases were after one or more years of non-breeding, against 15% in Herring Gull, n= 166; ^{App}Table 6.3). Skipping two or more seasons was fairly rare in Herring Gulls (1%, n= 166), slightly commoner in Lesser Black-backed Gulls (6%, n= 208).

Most of the prospectors that could not be confirmed as breeding birds disappeared from the colony after early May (some returned in July and August). In Lesser Black-backed Gulls (not in Herring Gulls), breeding confirmations (%, ^{App}Table 6.4) and the onset of laying (date, timing, Table 2.1) were negatively correlated: non-breeding (of earlier established breeding birds) tended to be more frequent in delayed seasons (R_S= -0.90, n= 5). The data series is too short, however, to draw firm conclusions. A low frequency of breeding confirmations was particularly striking in 2012, a season with a much delayed onset of breeding. Only 25% of the prospecting Lesser Black-backed Gulls were found breeding later in that season. In Herring Gulls, reproductive success (fledglings pair^{-1}, Table 2.1) and the proportion of confirmed breeding attempts by prospecting individuals were positively correlated (R_S= 0.80, n= 5).

As a result of the difficult terrain the Herring Gulls were nesting in, it was easier to read rings of Lesser Black-backed Gulls at their nest. The difference between the species in apparent non-breeding by prospecting adults (^{App}Table 6.4) may therefore be larger than indicated. At the nearby mainland colony Forteiland in IJmuiden, where nest initiations are earlier than at Texel and where fledging rates are seemingly higher (no concrete data available, just a visual impression), the same colour-rings have been deployed since 2008. Of colour-ringed Lesser Black-backed Gulls returning and prospecting in IJmuiden during 2009-2012, 55.7±10.3% were demonstrated to breed (Texel 2009-2012 46.8±15.8%, ^{App}Table 6.4). Of Herring Gulls returning in IJmuiden, 61.7±12.3% were found breeding (Texel 66.3±11.4%). These values are of the same order of magnitude as those on Texel, even though providing evidence that birds were breeding is far more easy at IJmuiden than at Texel. The results suggest that Lesser Black-backed Gulls at Texel breed on average once every 2.1 years, those in IJmuiden every 1.8 yrs. For Herring Gulls, a highly similar breeding frequency of once every 1.5 (Texel) to 1.6 years (IJmuiden) can be estimated.

Table 6.3. Confirmed breeding in prospecting colour-ringed Lesser Black-backed Gulls (LBBG) and Herring Gulls (HG) in Kelderhuispolder (Texel). Shown are the number of colour-ringed individuals that returned as prospecting birds, the number and percentage in which breeding was subsequently confirmed, and the frequency of season skipping.

		Prospecting	**Breeding confirmed**		**Skipping 1 or more seasons**
Lesser Black-backed Gull	Female	225	98	43.6%	17.3%
	Male	228	110	48.2%	25.5%
Herring Gull	Female	117	73	62.4%	16.4%
	Male	145	93	64.1%	14.0%

Table 6.4. Annual variations in "breeding incentive": the proportion of prospecting colour-ringed Lesser Black-backed Gulls (LBBG) and Herring Gulls (HG) in Kelderhuispolder (Texel) that were later that season recorded as confirmed breeding birds. Shown are the observer effort (hours in the field prior to 10 May to record prospecting birds and the hours spent during breeding), the ringing cohorts evaluated, and for each species the number of colour-ringed prospecting birds (obs), and the number (br) and the breeding incentive (%).

	Observer effort (h)		Ringing	**Lesser Bl.-b. Gull**			**Herring Gull**		
Year	Prosp. Phase	Breeding phase	cohorts	obs	br	br.inc.%	obs	br	br.inc.%
2008	40	224	2006-07	38	26	68%	15	12	80%
2009	73	217	2006-08	69	42	61%	24	18	75%
2010	129	315	2006-09	111	61	55%	52	40	77%
2011	76	184	2006-10	105	48	46%	78	43	55%
2012	77	231	2006-11	112	28	25%	91	53	58%

Parental care and the need for a break - Cody's (1966) model, in which annual survival (and thereby future reproductive success) would be enhanced by those individuals which conserve energy by reducing the current reproductive rate, became again of interest when highly unusual foraging trips were evaluated in the course of a GPS tracking study of Lesser Black-backed Gulls from Kelderhuispolder (Chapter 8). Tracking studies of seabirds occasionally reveal exceptionally long or distant foraging trips. The characteristics, the frequency, and the possible triggers of such unusual trips in comparison to thousands of other, more regular trips were considered in the context of reproductive performance and chick growth. The hypothesis that exceptional trips were conducted exclusively by failed breeders, but not by active breeders during incubation or chick care, had to be rejected. Exceptionally long and distant trips occurred irregularly but annually, in many individual birds and in all phases of breeding, except that in active breeders such trips were relatively rare when the chicks were still young and highly vulnerable (<10d of age). The data seem to suggest that additional time for individual maintenance (e.g. self-provisioning, replenishing exhausted resources) rather than extra effort in chick provisioning (a chick starvation hypothesis) was the most important factor. During a breeding attempt, in other words, apart from giving up, individual birds apparently stepped back and reduce their efforts to enhance their own condition (and fitness). The beached bird survey results suggest that an "untimely death" for an adult in the breeding period is far from unlikely. The individual breaks in chick care were potentially at the expense of clutch or chicks, and compensatory behaviour of the partner was required to bring the breeding attempt to a successful end. The reproductive success in birds that performed exceptional trips was rarely compromised, suggesting that mates compensated indeed for these absences.

Post-fledging chick mortality – Vercruijsse (1999) reported the annual survival and recruitment rates of young Herring Gull at Schouwen (Delta area), following the colour-ringing campaigns in 1986-1988 (Box 4.1). Of 314 fledglings ringed at Schouwen, 37% were demonstrated to be alive after one year (re-sightings in later years, no corrections for detection probabilities). Using the same technique at Texel in 2006-12, the mean first-year survival of Herring Gull chicks ringed at Texel (2006-2011) was a rather lower 25±6%, that of 554 Lesser Black-backed Gull chicks from Texel amounted to 31±7% (^{App}Table 6.1). First year mortality of fledglings, based on demonstrated survival ranged from 70-85% in Herring Gulls and 58-79% in Lesser Black-backed Gulls The annual mortality in subsequent years was considerably lower.

Annual survival rates *after* the first year of life (2-5 yrs of age, just prior to expected recruitment) in Herring Gulls from Schouwen in the late 1980s and early 1990s were high and averaged 87.5±1.0%. Immature Herring Gulls from Texel scored a considerably lower and more variable annual survival of 70.0±5.8%. The annual survival of immature Lesser Black-backed Gulls from Texel (82.5±5.2%; ^{App}Fig. 6.5) was more or less similar as that in Herring Gulls from Schouwen some decades earlier.

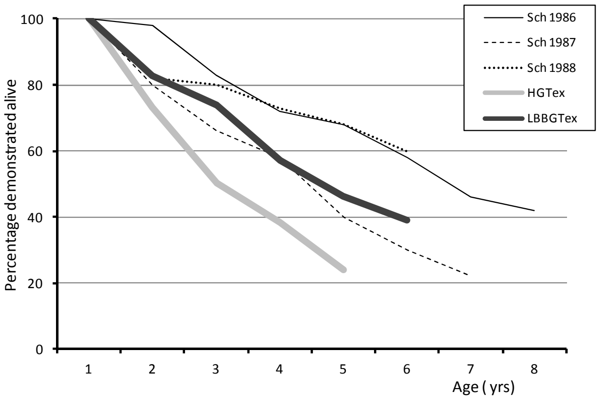


Fig. 6.5 Percentage decline in the number of Herring Gulls (HG) and Lesser Black-backed Gulls (LBBG), ringed as chicks in Schouwen (Sch1986-Sch1988, Herring Gulls only; data from Vercruijsse 1999) or at Texel (2006-2009) *after* the first year of life (*i.e.* after the relatively high losses in the juvenile phase).

Box 6.1 – Longevity records in Herring Gulls and Lesser Black-backed Gulls

A first longevity record of a Dutch Herring Gull involved a bird ringed at the Kelderhuispolder (Texel). From a ring report of Herring Gull 5054793 issued by Vogeltrekstation Heteren[1], a bird found dead on the beach near Den Hoorn (Texel) on 15 July 2006 was ringed as a chick on 14 July 1972 in the nearby Kelderhuispolder. Further details: Distance from ringing location 2 km, direction 329°, time span 12419d (*i.e.* 34.0 yr).

At the longevity list by Staav[2], a Finnish bird is included as the oldest known Herring Gull to date (Helsinki 71386, 32yr 1m), and a British bird as the oldest known Lesser Black-backed Gull (London GM02212, 32.7 yr). Exceeding the maximum age as listed by Staav is another old Dutch Herring Gull of 34.7 yr (Arnhem 5020154)[1].Many seabirds are long-lived and longevity records are in fact biased by ring-loss[3-7]. Aluminium rings should not be used at all for seabirds, but steel rings, if properly deployed, could normally last long enough[8]. Colour-rings are vulnerable and many colour-ring schemes suffer from ring-losses, ring wear (codes can no longer be deciphered) and fading colours. Some fairly old colour-ringed birds are known, with a bird ringed as a chick in Wassenaar (Zuid-Holland) in 1986 currently being a record holder (of the original two rings, one is now lost), with frequent sightings, always at the exact same location in Leiden city, currently (summer 2013) in its 28th calendar year)[9].

ZDGA, currently the oldest known colour-ringed Herring Gull in The Netherlands (27th cy) (M. van Kleinwee)

References: [1]Vogeltrekstation Heteren 2008, [2]http://www.vogeltrekstation.nl/resultaten/longevity-list-roland-staav (Accessed 14 Aug 2012), [3]Harris 1964b, [4]Anderson 1980, [5]Galbraith & Furness 1983, [6]Bailey *et al.* 1987, [7]Van Dijk *et al.* 2012, [8]Kadlec 1975, [9]Van Kleinwee & Camphuysen 2010.

Appendix 7 - Foraging ecology

While it seems that we have a reasonable overview of seabird prey preferences and prey variability, even in the most common species of seabirds, this is in fact not the case (Tasker *et al.* 1999). There is a bewildering variety of prey species, but most form only a small part of the diet. Rather few species/types are 'preferred' or 'important' prey for seabirds, while many should be labelled 'occasional prey'. A point highlighted by Tasker *et al.* (1999), is that few studies tried to address prey selection from a known resource of potential prey. There are obvious methodological problems involved with the assessment of resources for seabirds (a function of prey stock size, suitability and availability), but it remains often speculative why certain seabirds focus one particular prey in one year and another species in the next. Size selection (Swennen & Duiven 1977, 1991; Camphuysen *et al.* 1995), selection of prey of a certain 'quality' or calorific value (Harris & Hislop 1978, Wright & Bailey 1993) and dietary shifts in relation to changing prey stocks (Doornbos 1979, Vader *et al.* 1990) are some confounding factors. The diet studies at Texel were confined to the breeding season, which is one of the concerns expressed by Tasker *et al.* (1999). Given the finding that adult survival in Herring Gulls breeding at Texel is seemingly compromised (Chapter 7), more attention to resources and foraging strategies outside the breeding season may be required in future years. However, the annual cycle and non-breeding dispersal of both species is such that an overlap in the utilisation of resources of birds breeding at Texel can only be expected in summer. When evaluating contrasting population trends of sympatric species, a study of the foraging ecology in the period that matters most (when both species-co-occur in the same general area) seems an acceptable starting point.

Diet studies

At first glance, a diet study seems a pretty straightforward undertaking. It is not. There are numerous methods and techniques to study diets or trophic levels, each with specific shortcomings or advantages (Barrett *et al.* 2007). Results of different techniques can be surprisingly different. Choices had to be made to study the diet of gulls breeding at Texel. Three main questions regarding their foraging ecology were underlying the work: (1) what do they eat, (2) how important is each prey type, and (3) where do they find that food. For more important prey types it would be essential to figure out how the prey was obtained and processed, what size categories were selected, if chicks were provisioned with it, and whether or not there was evidence for inter-specific competition. It was decided to use regurgitated materials (pellets, boluses and other regurgitates). The reasons are explained below. In this Appendix is a lengthy overview of the main prey types and the frequency of occurrence of these prey in the food samples of both species. In separate sections, issues such as individual specialisations and size selection are summarised. More attention is given to a seemingly rather vital aspect of the feeding ecology of both species: their performance and success as scavengers following commercial beamtrawlers and shrimpers (the greater part of the fishing activities off the Dutch coast). Several chapters and appendices in this thesis provide analyses of diet-related studies and some earlier material on the utilisation of fisheries bycatch at sea. The analysis of the diets of gulls nesting at Texel is essentially a project in full progress, with many more results awaiting analysis and interpretation.

Studying feeding habits - The diet of gulls was studied using two rather different methods. The first, more traditional method involved the identification of prey items that had been transported into the colony by the adult birds. Diet sampling was used to establish a link between (foraging) behaviour and fecundity. This method fails to address the prey availability issue. Prey types were too diverse, and the presence of certain taxa was simply unknown to occur prior to our studies, to be able to adequately assess and monitor resources throughout this project. The second method

Box 7.1 Sampling and analysing prey

Food samples were individually bagged and numbered within the colony during nest visits, and labelled on the same day in the laboratory. Label information contained the predator species, type of sample (pellet, regurg, chickfeed etc.), date, study plot, nest site number, breeding phase and if possible the ring-number of an individual bird. Most samples were deep frozen prior to analysis, but boluses tended to be processed immediately to profit from the "fresh" condition of easily digestible prey. Too enlarge the sample size for Lesser Black-backed Gulls, in the Foot Sea dunes, in the Valley and along the trail at the colony entrance (all high density LBBG nesting areas), so called "colony samples" were taken, not assigned to known numbered nests, to be able to evaluated 'seasonal' (*i.e.* between breeding phases prospecting, laying, incubation, chick care, and fledging) shifts in prey choice.

A magnetic stirrer (IKE werke RCT basic), i.e. a laboratory device that employs a rotating magnetic field to cause a stir bar (also called "flea") immersed in water to spin quickly, thus stirring it, was used to separate light and floating aspects of prey samples (usually grasses, moss, feathers, insects and light scales) from more important hard parts (setae, jaws, claws, exoskeletons, shells, otoliths, fish bones etcetera). Left: petri disc with a disintegrated pellet containing fishbones and dry grass.

For analysis, prey items were defrosted, dried, washed, sorted and analysed under an Olympus ZN51 binocular microscope (8-40x magnification) in order to find even minute prey items. Fish prey were identified on the basis of otoliths and other peculiar bones[1-7]. Mammalian and bird remains were identified with a variety of specialised publications[8-9], or with ordinary field guides. Dental aspects, specific bones or external characteristics (claws, spines, fur, feathers), and sometimes even intact mammals or birds could be found in regurgitated prey remains. Most invertebrate prey were identified with a self-made reference collection. Parts of animals (jaws, claws, or other prominent structures) were used to count the number of individuals within a prey sample and regressions were constructed on the basis of reference material to calculate total prey size from particular body parts[1,4,6]. Difficult species were identified with help of specific experts at NIOZ (Gerhard Cadée, Rob Dekker, and Marc Lavaleye).

Database$^{\text{Food sample.DB}}$ entries for each food sample included (1) a unique Sample number, (2) predator Species, (3) Type of sample, (4-6) Date, (7) breeding Phase, (8) name of Location (e.g. Kelderhuispolder), (9) Colony name, (10) study plot name, (11) nest Site number, (12) Individual code (ring or colour-ring), and (13) Sampling type (systematic or opportunistic)

Database$^{\text{Food analysis.DB}}$ entries for each identified prey item included (1) unique Sample number, (2) species ID code, (3) Item measured, (4) Number, (5) aspect measured, (6) size, (7) size category (if estimated only), (8) remarks, and (9) calculated total size of the animal.

Database$^{\text{Taxonomy.DB}}$ entries for individual prey species and prey types included (1) ID, the species code, (2) Group number, (3) Group name, (4) highest taxon in Dutch, (5) highest taxon in English, (6) origin, (7) likelihood as beamtrawler/shrimper discards [yes/no], (8) animal Kingdom, (9) Phylum, (10) Class, (11) Order, (12) Family, (13) Genus, and (14) Species name

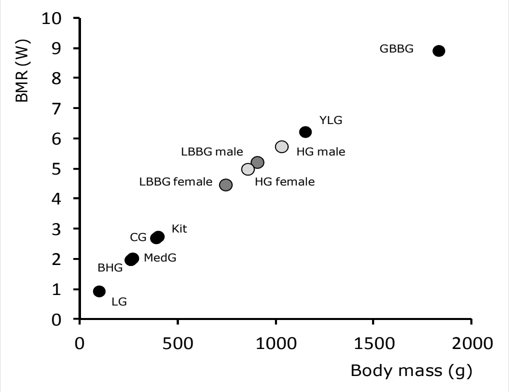
Sources: [1]Wise 1980, [2]Breiby 1985, [3]Mehner 1990, [4]Watt *et al.* 1997, [5]Granadeira & Silva 2000, [6]Leopold *et al.* 2001, [7]Hunt 2006, [8]Husson 1962, [9]Kapteyn 1999 involved direct observations and experiments within feeding flocks, studying prey selection (species and size), preferences, kleptoparasitism and other feeding interactions. In these studies there was a clear link with the resource, but the birds studied were "anonymous" and not necessarily actively breeding at the time of the studies. Also, these studies were restricted to a single, albeit important resource: fisheries discards.

Regarding the traditional diet studies, choices had to be made. There are many methods to study seabird diets, invasive and non-invasive, ranging from simple observations at distance to molecular techniques. How exactly the diet of a predator could or should be studied best has been evaluated recently by Barrett *et al.* (2007).

Box 7.2 - Energetic requirements, energy expenditure

The basal metabolic rate (BMR) represents the minimum rate of energy expenditure in an endotherm under prescribed conditions[1,2]. For birds, BMR is highly correlated with body mass[1-4], and the relationship is linear when expressed logarithmically[5]. Warnings were issued about using allometric equations for predictions[2], but since not everybody will be prepared or facilitated to measure BMR during every study, this will inevitably by common practice. BMR was tested as function of taxonomic order, latitude/region, ocean regime, and season. Passerines and Non-passerines certainly require separate allometric analyses[2,14]. Order, but more importantly latitude, increased the ability of body mass to predict BMR[2].

Bryant & Furness[4] measured BMR for 11 species of seabirds and derived the equation for North Sea seabirds that is reproduced below. This equation was used to calculate the BMR of gulls nesting at Texel, using biometrics collected in the Kelderhuispolder. Males and females of Lesser Black-backed Gulls and Herring Gulls differ considerably in body size and mass and will therefore have a different BMR. Based on the equation of Bryant & Furness[4], the BMR for Lesser Black-backed Gulls and Herring Gulls varied between 4.4 and 5.7W.



Bryant & Furness[4] measured basal metabolic rates (BMR) for 11 species of seabirds, ranging in size from the Black-legged Kittiwakes to Northern Gannets. From these measurements they derived the following equation for North Sea seabirds:

$$BMR\ (kJ\ d^{-1}) = 2.30(body\ mass)^{0.774}$$

The equation was used to calculate BMR for gulls breeding in The Netherlands, while the results were converted into W (J s^{-1}). Body mass from BWPi[5], except mean body mass for male and female Herring Gulls and Lesser Black-backed Gulls [Kelderhuispolder, 2006-2012]. Differences in body mass between sexes for the other species were ignored in this graph.

BMR covers only a part of the energy expenditure. The literature has measurements reported as existence metabolism (EM, the sum of BMR, costs of thermoregulation, digestion, and limited locomotion)[5], or the resting metabolic rate (RMR). RMR, *c.* 1.7BMR[7], may not be measured in the zone of thermoneutrality nor on birds that are postabsorptive[2]. EM and RMR both exclude activities such as swimming, diving, running or flight. EM declines linearly with increasing temperature up to the upper critical temperature of the zone of thermoneutrality of basal metabolism[4]. From a linear interpolation of the equations of Kendeigh *et al.*[6], using the mean ambient temperatures for Texel (measured at De Kooy, Den Helder, 12-17°C[10], May-Aug 2006-2012), the EM for Lesser Black-backed Gulls and Herring Gulls was estimated to vary between 6.7 and 8.6W (*c.* 1.5BMR). With the equations for Scottish seabirds by Bryant & Furness[4], assuming 1.7BMR[7], a RMR of 7.6-9.7W could be estimated. One of the problems with EM and RMR is that unlike BMR, these measurements do not represent limits and are therefore not easily replicable[2].

Body mass (g) and metabolic rates (W) for female and male Lesser Black-backed Gulls and Herring Gulls, using published equations and assumptions (see text).

	Mass	**BMR**	**RMR**	**Flapping flight**	**Gliding flight**	**FMR**
Lesser Bl-b Gull female	745 g	4.4 W	7.6 W	45.4 W	15.1 W	14.3W
male	910 g	5.2 W	8.8 W	53.0 W	17.7 W	16.3W
Herring Gull female	860 g	5.0 W	8.5 W	50.7 W	16.9 W	15.7W
male	1030 g	5.7 W	9.7 W	58.3 W	19.4 W	17.7W

Box 7.2 - Energetic requirements, energy expenditure

Flight is one of the energetically more expensive activities in birds. Flapping flight (a common mode of transport in gulls) is considerably more expensive than sustained gliding flight[7,8]. The metabolic rate of gliding flight was 1.5x, steady horizontal flapping flight ca. 7RMR[7]. From further wind tunnel studies, flapping flight and gliding flight were estimated to increase the metabolic demand by 6x and 2xRMR respectively (RMR = 1.7BMR)[7,9]. Using the equations published by Furness & Cooper[8], the energetic costs of flapping and gliding flights were calculated (tabulated above).

Total costs are encompassed in the field metabolic rate (FMR), which includes energy costs of thermoregulation, digestion, moult, reproduction and all activities during the day. FMR has become the expression signifying daily energy expenditure (DEE) for an animal to live throughout a day during a normal routine[2]. Ellis & Gabrielsen[2] provided the following relationship for seabirds: FMR ($\mathrm{kJ\ d^{-1}}$) = $16.69(\text{body mass, g})^{0.651}$. This FMR would mean 2.3 - 3.7BMR for gulls nesting at Texel. Considerably higher FMR/BMR ratios have been published. Field and activity-specific metabolic rates of free-living Northern Gannets (mean mass 3.2 kg) rearing chicks at Funk Island (Newfoundland) were measured using doubly labelled water and activity timers[11]. FMR averaged 4865 $\mathrm{kJ\ d^{-1}}$ (56W) or 6.6BMR. Regression analyses indicated a metabolic rate of 144 $\mathrm{kJ\ h^{-1}}$ (40W) while at the nest or on water and 349 $\mathrm{kJ\ h^{-1}}$ (97W) during flight[11]. Many studies have assumed a FMR of 3-4 BMR as a fairly conservative, but acceptable estimate of daily energy expenditure for actively breeding adults (and lower values for these same birds outside the breeding season).

A field metabolic rate of 14-18W during breeding following Ellis & Gabrielsen[2], considering an assimilation efficiency of 80%[13], would lead to a daily energy requirement of 1240-1330 $\mathrm{kJ\ d^{-1}}$ for gulls at Texel (female LBBG 1237, male LBBG 1409, female HG 1358, male HG 1527 $\mathrm{kJ\ d^{-1}}$). A FMR of 18-23W during breeding (assuming 4BMR), would lead to daily requirements of 1540-1980 $\mathrm{kJ\ d^{-1}}$ (female LBBG 1538, male LBBG 1795, female HG 1718, male HG 1976 $\mathrm{kJ\ d^{-1}}$).

References: [1]Aschoff & Pohl 1970, [2]Ellis & Gabrielsen 2002, [3]Nagy 1987, [4]Bryant & Furness 1995, [5]Furness & Monaghan 1987, [6]BWP*i* 2004, [7]Baudinette & Schmidt-Nielsen 1974, [8]Furness & Cooper 1982, [9]Furness 1978, [10]KNMI 2012, [11]Birt-Friesen *et al.* 1989, [12]Cairns *et al.* 1990, [13]Anon. 1994b, [14]Lasiewski & Dawson 1967, [15]Anon. 1994a; **Sources:** Kelderhuispolder measurements of adult body mass and chick growth, 2006-2012.

Prey sampling at Texel - Key questions underlying the diet studies at Texel were not the exact energetics of seabirds (*i.e.* consumption rates, prey quality, handling and searching time), but rather differences in food choice (species, size), the dietary overlap between the species, and information on the foraging areas where the food was collected (ultimately to link resources to reproductive performance and survival). Therefore, the decision was made to study the diet on the basis of pellets and other (unforced) regurgitations, including 'chick-feeds'. This method is non-invasive and simple and can provide large samples over time (Barrett *et al.* 2007). It would provide sufficient information of the position of large gulls in the Wadden Sea and North Sea food webs. Together with tracking data and colour-ring sightings, detailed information on the species-specific foraging habitats would be acquired.

Pellet analysis is better used for determining diet composition than for quantification of consumption (Carss *et al.* 1997). Some prey items do not leave hard parts, and processing pellets and reconstructing the numbers of prey and prey sizes is time-consuming. We therefore also examined boluses (regurgitated wet and considerably fresher prey; collected when handling adults or chicks), chick-feeds (fresh prey dumped by adults for the chicks) and other regurgitated material within enclosures (mostly larger bones and plastics as left-overs of chick feeds). Gulls aggregate on clubs within and just outside the colony, where pellets are abundant, but where prey samples cannot always be allocated to a specific species. We focussed on samples taken from marked territories. Some pellet-producing species produce much more regurgitated material than others. At Texel, only Herring Gulls produced large amounts of prey items around their nests, whereas the largely piscivorous Lesser Black-backed Gulls produced inconspicuous, and often only few pellets that were also often dropped at some distance from the nest site. As a result, it was much harder to obtain a sufficiently large sample of prey items for individual pairs of Lesser Black-backed Gulls. To enlarge the sample size, prey samples were also collected in particular colony sections and on clubs where only one species occurred or dominated (the finding location of each prey sample was carefully logged). Sampling and analysis methods are described in Box 7.1.

Energetic requirements - An assessment of the energy budget of an animal is an important component of ecological studies. The basal energy expenditure of an animal determines the minimum requirement of energy (food) and is one of the more constant biological measurements (Fisher 1972). The energy needed beyond the basal metabolic rate (BMR) depends on a variety of factors, including activity, temperature, exposure to weather and wind (or sun), digestion, moult, and other aspects of the maintenance requirement. Energetic requirements are essentially size related, but vary seasonally, regionally and in response to environmental conditions (Box 7.2).

Box 7.3 Common prey types (1)

Lesser Black-backed Gulls and Herring Gulls compared

In 2006-2011, 10,867 food samples were collected in the Kelderhuispolder colony. Of these, 10,234 samples were selected to provide an overview of diets of both gulls (*i.e.* samples from active breeding birds during the pre-hatching or chick care phase). A single prey-sample could contain as many as 13 different prey species or types and 332 different prey types were encountered in all samples. Fish prey, marine Nereid worms, swimming crabs and insects were the most frequently encountered prey-items in Lesser Black-backed Gulls in the egg phase. The diet of Herring Gulls was overwhelmingly dominated by mussels and other bivalves with lower frequencies of occurrence of shore crabs, cannibalistic prey, fish and domestic refuse.

All prey samples during ***pre-hatching***

LBBG	%	HG	%
Pleuron. Limanda	51	*Mytilus edulis*	71
Merl. merlangus	35	*Ensis directus*	9
Nereis longissima	22	large gull egg	8
Liocarc. holsatus	18	*Carcinus maenas*	8
Trach. trachurus	16	*Cerastod. edule*	5
Solea solea	13	*Pleuron/Limanda*	4
Coleoptera	11	*Merl. merlangus*	3
Ammodytes	8	*Rutilus rutilus*	2
unident insect	8	Coleoptera	2
Eutrigla gurnardus	7	chicken	2
n= 2468 (174 sp.)		n= 2758 (190 sp.)	

All prey samples during ***chick care***

LBBG	%	HG	%
Pleuron./Limanda	36	*Mytilus edulis*	55
Merl. merlangus	25	*Pleuron./ Limanda*	12
Liocarc. holsatus	21	*Carcinus maenas*	12
Trach. trachurus	20	*Merl.merlangus*	9
Nereis longissima	8	*Liocarc. holsatus*	8
Ammodytes	7	large gull pullus	7
large gull pullus	6	*Crangon crangon*	6
Solea solea	6	*Ensis directus*	4
Coleoptera	5	plastic packaging	4
Sprattus sprattus	5	large gull egg	4
n= 2509 (191 sp.)		n= 2499 (234 sp.)	

Fish prey and swimming crabs were again the most frequently encountered prey-items in Lesser Black-backed Gulls during chick care, with considerably smaller numbers of nereid worms, cannibalistic prey items and some insects. The diet of Herring Gulls was again dominated by mussels and other bivalves but with distinctly more fish prey. shrimps, cannibalistic prey and some domestic refuse.

Source: NIOZ/Kelderhuispolder diet database (CJC *unpubl. data*)

The diet of Herring Gulls and Lesser Black-backed Gulls at Texel compared

Over the years, more than 300 different prey species and prey types were identified. A total of 370,179 prey items have been logged (*i.e.* 113,046 database entries), of which 66% were measured to assess total body, or a measure to allow for the calculation of prey size. Prey items could have a strikingly different origin and as main categories, the following groups were used:

Origin	n types	Top 5 most frequent types or species
Anthropogenic	92	plastics, chicken, bread, pork, paper
Intertidal	40	mussels, shore crabs, razor clams, cockles, starfish
Marine	83	whiting, flatfish, swimming crabs, horse mackerel, nereid worms
Terrestrial	114	gull's eggs and chicks, insects, earthworms, cattle feed, crowberries
Undetermined	9	mostly 'non-food' such as fossil shell grit, grit, pebbles, unident. organic matter
Pollution	8	seeds and pollen of local flora

A total of 116 different families (animals and plants) were encountered as prey items, but this included 'secondary prey' and plant material that must have blown into the sample prior to or during collections. Most prey were identified only rarely, but some were genuine staple foods (*i.e.*

represented in at least 50% of the diet samples in a study). For Herring Gulls, Mussels *Mytilus edulis* were encountered in 71% of all food samples collected during laying and incubation, and in 55% of all samples collected during chick care (Box 7.3). In Lesser Black-backed Gulls there was no single prey species that would qualify as a staple food, but Plaice *Pleuronectes platessa* and Dab *Limanda limanda*, two similar flatfish species, were encountered in 51% of the samples taken prior to hatching. The composition of food varied in different types of samples. Bread and various species of fish were more likely to be found in boluses (either produced by adults or by chicks), while pellets and chickfeeds (heaps of food dumped at the territory for the chicks during chick care) provided more similar results (Box 7.4). The former prey samples are ‘biased’ towards soft tissue, whereas the latter types are biased towards difficult to digest parts of prey items (shells, bones, etc.). In fact, in both predator species, rather few prey species were found in more than one fifth (20%) of the prey samples analysed:

LBBG egg phase: Whiting *Merlangius merlangius* and the nereid worm *Nereis longissima*
LBBG chick phase: Whiting, Swimming Crabs *Liocarcinus*, and Horse Mackerel *Trachurus trachurus*
HG egg phase and chick phase: none other than Mussels *Mytilus edulis*

Assigning the contents of a given prey sample to just one species, type or place of origin was impossible. The careful and microscopic examination revealed that as many as 13 species, up to to 10 different families and 4 major origins could be encountered in a single prey sample. This suggests that many prey samples represented more than just a singly meal, probably sometimes

Box 7.4 Common prey types (2)

Boluses, pellets and chickfeed samples

Different types of prey samples tended to yield different prey items. In six Kelderhuispolder breeding seasons (2006-2011) a total of 137 Herring Gull boluses were retrieved from adult birds during ringing in which bivalve prey were much less frequently represented than in pellets produced by adult birds. Boluses retrieved from chicks, 518 in total, rarely contained bivalve prey, even if in chickfeeds (deliveries for the chick at the nest site) bivalve prey predominated in frequency of occurrence. In the largely piscivorous Lesser Black-backed Gull, the prey species composition of different types of prey samples was more consistent. The tables below provide the top 8 most common prey types in different prey samples.

Boluses adult birds

LBBG	%	**HG**	%
Merl. merlangus	33	*Mytilus edulis*	28
Pleuron./Limanda	30	*Pleuron./Limanda*	28
Sprattus sprattus	14	bread	19
Crangon crangon	11	*Crangon crangon*	17
Scomber scombrus	8	*Sprattus sprattus*	13
Ammodytes	8	*Merl. merlangus*	9
Trachurus trachurus	7	*Asterias rubens*	6
Solea solea	6	*Ammodytes*	6
n= 84 (48 sp)		n= 53 (50 sp.)	

Boluses chicks

LBBG	%	**HG**	%
Pleuron./Limanda	36	*Pleuron./Limanda*	33
Sprattus sprattus	25	*Crangon crangon*	29
Ammodytes	14	*Merl. merlangus*	16
Crangon crangon	13	*Mytilus edulis*	16
Merl. merlangus	9	*Sprattus sprattus*	12
Liocarcinus holsatus	6	bread	12
Trachurus trachurus	5	*Ensis directus*	8
Ammodytes tobianus	5	*Ammodytes*	8
n= 340 (85 species		n= 178 (74 species)	

Pellets

LBBG	%	**HG**	%
Pleuron./Limanda	47	*Mytilus edulis*	66
Merl. merlangus	32	*Carcinus maenas*	8
Liocarcinus holsatus	20	large gull egg	8
Trachurus trachurus	19	*Pleuron./Limanda*	7
Nereis longissima	18	*Ensis directus*	7
Solea solea	10	*Merl. merlangus*	5
Coleoptera	9	*Cerastoderma edule*	3
Ammodytes	7	large gull pullus	3
n= 4112 (203 sp)		n= 3643 (225 sp)	

Chickfeed

LBBG	%	**HG**	%
Merl. merlangus	42	*Mytilus edulis*	71
Liocarcinus holsatus	35	*Carcinus maenas*	16
Pleuron./Limanda	26	*Liocarcinus holsatus*	11
Trachurus trachurus	22	*Ensis directus*	7
Scomber scombrus	6	*Crangon crangon*	6
Trigla/Eutrigla	6	*Merl. merlangus*	6
Clupea harengus	3	*Pleuron./Limanda*	5
Eutrigla gurnardus	3	*Rutilus rutilus*	3
		Asterias rubens	3
n= 311 (67 sp)		n= 1147 (132 sp)	

Source: NIOZ/Kelderhuispolder diet database (CJC *unpubl. data*) more than a single foraging trip or even more than a day of feeding. Pellet production will probably reflect the amount of indigestible prey matter on different types of food, or the need to expel matter if sharp spines or edges cause irritations of or wounds in the digestive tract.

Expected prey species - Even when diets were more completely known, for example during breeding, few published studies are able to quantify the resources of potential seabird prey. There are obvious methodological problems involved with the assessment of food resources for seabirds, but with insufficient information on prey stock size, availability and profitability, it remains speculative why certain seabirds rely on one prey in one year and on another prey in the next. Size selection, differential selection of prey of a certain 'quality' or calorific value and prey choice or dietary shifts in relation to the prey stock are important aspects which all deserve attention in diet studies. In this introduction I have listed prey species that have been encountered against an expectation based on species known to occur in The Netherlands and in the Dutch sector of the North Sea. A full list of potential invertebrate prey would be exhaustive and non-informative, so the emphasis will be on commoner and relatively conspicuous taxa.

Fish prey - Between 2006 and 2011, 4977 prey samples of Lesser Black-backed Gulls and 5257 prey samples of Herring Gulls were collected from birds that were either actively breeding, or from their chicks. In samples from Lesser Black-backed Gulls, 4139 samples (83%) contained remains of fish, while fish remains occurred in only 1070 samples (20%) from Herring Gulls. From a total of 33 species of marine roundfish found in prey samples from the Kelderhuispolder, the most frequently encountered prey species were:

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Merlangius merlangus	1520	31%	302	6%
Trachurus trachurus	900	18%	98	2%
Ammodytes spp (2 species)	412	8%	60	1%
Eutrigla gurnardus	430	9%	30	1%
Callionymus lyra	264	5%	23	0%
Trigla lucerna	222	4%	25	0%
Sprattus sprattus	139	3%	37	1%
Clupea harengus	126	3%	19	0%
Scomber scombrus	73	1%	8	0%
Gadus morhua	46	1%	14	0%
Trisopterus luscus	38	1%	9	0%

A total of 6 species of freshwater roundfish were found in prey samples from the Kelderhuispolder. The most frequently encountered prey species were:

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Rutilus rutilus	2	0%	121	2%
Perca fluviatilis	2	0%	16	0%
Stizostedion lucioperca	7	0%	6	0%

A total of 8 species of marine flatfish were found in prey samples from the Kelderhuispolder. The most frequently encountered prey species were:

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Pleuronectes platessa	1418	28%	301	6%
Limanda limanda	1105	22%	161	3%
Solea solea	454	9%	74	1%
Buglossidium luteum	70	1%	20	0%
Arnoglossus laterna	51	1%	3	0%

Table 7.1. Fish species in The Netherlands sorted by order (after Nijssen & De Groot 1987), and the number of species encountered in prey remains of Lesser Black-backed Gulls (LBBG) and Herring Gulls (HG) on Texel, 2006-2011. The percentage provides the representation of species per order for the two gull species combined.

Order	Species	LBBG	HG	%	Order	Species	LBBG	HG	%
Petromyzontiformes	3				Gadiformes	16	5	4	31
Lamniformes	3				Batrachoidiformes	1			
Carcharhiniformes	5				Cyprinodontiformes	3	1	1	33
Squaliformes	3				Atheriniformes	2			
Squatiniformes	1				Lampriformes	1			
Rajiformes	11				Zeiformes	2			
Acipenseriformes	1				Gasterosteiformes	3		1	33
Anguilliformes	2				Syngnathiformes	6	3	2	50
Clupeiformes	6	3	3	50	Scorpaeniformes	14	6	5	43
Cypriniformes	25	2	3	12	Perciformes	42	15	14	38
Siluriformes	3				Pleuronectiformes	14	7	8	57
Salmoniformes	10	1	1	10	Teraodontiformes	2			
Stomiiformes	1								
					Totals	180	43	42	26

Table 7.2. Status of fish in Dutch waters (Nijssen & De Groot 1987), and species in prey remains of Lesser Black-backed Gulls (LBBG) and Herring Gulls (HG) on Texel, 2006-2011. The percentage provides the representation of species per category for the two gull species combined.

Status in The Netherlands	Fish species	LBBG	HG	%
Common[1]	53	31	33	62
Rather common[1]	7	3	2	43
Uncommon[1]	45	6	5	13
Incidental	31	2	1	10
Rare	44	1	1	5
All species	180	43	42	26
Commoner species[1]	105	40	40	40
Non discards	144	16	19	14
Common discards (*)	36	27	23	75
% discards	20	63	55	

(*) Van Beek 1990, Camphuysen 1993b, 1994ab, Fonds 1994ab, Groenewold 1996

Box 7.5 – Calorific value of prey

The calorific values of different species of prey fish, offal and other prey vary seasonally, with size[1] or between years[2]. Larger fish tend to have higher calorific values than small ones, but there is considerable temporal variation[1]. It often impossible to obtain precise values for all organisms or occasions when studying the diet of a generalist feeder. The table lists energetic equivalents for some important prey types as they have been employed in other studies. The calorific contents of fisheries discards are often estimated at 3.5 kJ g^{-1} for flatfish, 3.2 kJ g^{-1} for whiting and cod, and 5.0 kJ g^{-1} for gurnards[3]. Haddock liver contains c. 44% fat (17.7 kJ g^{-1}), but beamtrawler offal is mainly from gutted flatfish and small quantities of gadoid whitefish and is therefore assumed to have a lower calorific value: 10-12 kJ g^{-1}[2,3].

Estimated calorific value of major prey types (fat, protein contents and the estimated calorific value (kJ g^{-1} fresh mass)[1,3].

Prey type	calorific value (kJ g^{-1})	Prey type	calorific value (kJ g^{-1})
offal[3]	10.0-12.0 kJ g^{-1}	flatfish[3]	3.5-4.0 kJ g^{-1}
herring, sprat[1,7]	9.6 kJ g^{-1}	elasmobranchs[3]	4.0 kJ g^{-1}
mackerel[8]	10.5 kJ g^{-1}		
horse mackerel[9]	6.2 kJ g^{-1}		
garfish[8]	6.8 kJ g^{-1}	cephalopods[10]	3.7 kJ g^{-1}
gadoids[3,7]	3.2-4.1 kJ g^{-1}	crustaceans[3]	3.5 kJ g^{-1}
gurnards[5]	5.0 kJ g^{-1}	echinoderms[3]	2.0 kJ g^{-1}
sandeels[7]	6.5 kJ g^{-1}	molluscs[3,6]	2.5-3.6 kJ g^{-1}

References: [1]Hislop et al. 1991, [2] Wanless *et al.* 2005, [3]Garthe *et al.* 1996, [4]Camphuysen *et al.* 1995, [5]De Groot *et al.* 1988, [6]Stichting Nederlands Voedingsstoffenbestand; [7]Harris & Hislop 1978, [8]Montevecchi et al. 1984, [9]C. Pusineri *unpubl. data* in Meynier *et al.* 2008, [10]Meynier *et al.* 2008

Table 7.3. Principal habitats of the 105 most common fish species in The Netherlands (see ^{App}Table 7.2) after Nijssen & De Groot 1987, and the number of species encountered in prey remains of Lesser Black-backed Gulls (LBBG) and Herring Gulls (HG) on Texel, 2005-2011. The percentage provides the representation of species per habitat (marine, estuarine/coastal, or freshwater) for the two gull species combined.

Principal habitats	Fish species	LBBG	HG	%
North Sea	53	28	26	49%
North Sea, Estuaries	2	0	0	
North Sea, Wadden Sea	2	0	0	
Coast	4	4	4	27%
Coast SW Nederland	1	0	0	
Coast, Estuaries	3	3	3	
Coast, Freshwater	4	1	2	
Coast, rivers	3	0	0	
Freshwater, Estuaries	1	0	0	15%
Freshwater	25	4	5	
Freshwater (deep inland)	7	0	0	
	105	40	40	40%

In The Netherlands, some 180 fish species occur (excluding 6 species that are currently considered locally extinct; Witte & Zijlstra 1978, Nijssen & De Groot 1987; ^{App}Table 7.1). Of these, 75 species were rare or 'incidental' (^{App}Table 7.2). In prey remains of Lesser Black-backed Gulls, 43 different fish species have been identified, whereas in Herring Gull prey remains 42 species were found representing 10 of 25 possible orders of fish (^{App}Table 7.1).

Of all fish species (n=180), 26% were taken by either Lesser Black-backed Gulls or Herring Gulls or by both (^{App}Table 7.2). Of the commoner species 40% (n= 105) were found at least once. The frequency of occurrence declined according to the abundance of the fish species: 62% of the common fish species (n= 53), but only 5% of the rare fish species (n= 44) were represented in food samples from the Texel colony. Of the commoner (105) fish species, 36 species (34%) are commonly discarded in bottom trawlers off the Dutch coast (^{App}Table 7.2, Box 7.6 and references therein). Of these species, 75% were found in prey remains of gulls at Texel. Ranking fish species to their principal habitat (the 105 commoner species only), 57 (54%) are North Sea fish, 15 (14%) occur along the coast, in estuaries and in river mouths, and 33 (31%) are freshwater species. The representation in gull diets of these prey groups is shown in ^{App}Table 7.3.

In summary, of 47 fish species known to have been taken by these gulls (26% of the species on the Dutch list, n= 180), 38 (81%) species are shared between Lesser Black-backed Gulls and Herring Gulls. Of these "shared" fish, 21 species (45%) are taken only rarely (represented in less than 1% of all food samples containing fish remains for both species). Of fish prey taken by Lesser Black-backed Gulls, 27 species (63%) are well known as fisheries discards, whereas 23 species (55%) taken by Herring Gulls could have been discarded. The estimated calorific value of each of these fish species could be derived from Box 7.5.

Crustacean prey – A total of 23 species of crustaceans were identified from these food samples, mostly Decapoda, but with only few species occurring frequently in anyone of the predating gulls:

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Liocarcinus holsatus	1017	20%	250	5%
Carcinus maenas		0%	524	11%
Crangon crangon	70	1%	146	3%

Various species of Decapod crustaceans are frequently encountered in the Kelderhuispolder food samples. Approximately 40 species of crabs (Brachyura) occur in The Netherlands and in Belgium. Adema (1991) listed 38 species, representing six Superfamilies: Dromioidea (1), Calappoidea (3), Majoidea (14), Corystoidea (5), Portunoidea (12), Pinnotheroidea (3), but a seventh group appeared with two invading species in recent years: represented by *Hemigrapsus sanguineus*, and *Hemigrapsus pensillatus* (superfamily Grapsoidea). The former alien prefers a hard substrate shoreline (*e.g.* a dike) and co-occurred with (and locally outnumerered) the Common Shore Crab, first only in Oosterschelde (Delta), but soon also in the Wadden Sea (Breton *et al.* 2002). The other member of the same genus established a viable breeding population within The Netherlands (Nijland & Beekman 2002). This species is currently particularly abundant on oyster reefs in the Wadden Sea established by yet another invasive species, the Pacific Oyster *Crassostrea gigas.*

From the NIOZ SIBES project, c. 50 species of crustaceans are listed to occur on the Wadden Sea mudflats, representing 8 orders: Decapoda (3), Isopoda (5), Amphipoda (21), Mysidacea (6), Thoracica (3), Rhizocephala (1), Cumacea (4). The smaller Amphipods, Isopods and Mysidacea may simply leave too few remains in pellets and in other regurgitated material to be detected. The Decapods *Diogenes pugilator* and *Pisidia longicornis* would probably have been detected, however, if at all represented. The absence of confirmed Common Shore Crabs *Carcinus maenas* in the diet of Lesser Black-backed Gulls is the most striking difference between the two species. Swimming Crabs (*Liocarcinus* spp.) could in theory been taken from the beach, from the discards fraction of trawlers, possibly even from the intertidal zone. Swimming Crabs are certainly also taken as free swimming organisms at the sea surface, however (Schwemmer & Garthe 2005). Common Shore Crabs are normally attacked at high tide by more or less solitary, swimming Herring gulls in shallow waters near the shoreline. Common Shore Crabs are discarded in large quantities by shrimpers, but not usually by offshore beamtrawlers, whereas swimming crabs are discarded by both (Box 7.6). Brown Shrimps are probably mainly taken in feeding frenzies of scavenging seabirds attracted to shrimpers operating near the coast or within the Wadden Sea.

Of the other typically intertidal crustaceans found in prey remains from the Texel colonies, *Hemigrapsus pensillatus*, *H. sanguineus*, *Idotea pelagic*, *Jassa marmorata*, and *Portumnus latipes*, none featured in the diet of Lesser Black-backed Gulls. Soon after the appearance, both invasive species of *Hemigrapsus* appeared on the menu of specialised Herring Gulls and their frequency of occurrence increased over time. Of 13 other marine crustaceans, 11 were found in prey remains from Lesser Black-backed Gulls, 7 in the diet of Herring Gulls. The most frequently recorded species (in declining order) were, *Liocarcinus depurator*, unidentified Decapods, *Pagurus bernhardus*, *Callianassa tyrrhena*, *Cancer pagurus*, parasitic Copepods (from infected fish prey?), and *Idotea balthica*. None of these species contributed significantly to the diet of the studied gulls (<<1% by frequency of occurrence).

Marine gastropod prey – Seven species of marine gastropods were encountered, with only three species featuring more than five time:

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Polinices polianus	90	2%	4	0%
Littorina littorea	1	0%	10	0%
Nassarius incrassatus	5	0%		0%

The typically intertidal species *Hydrobia ulvae, Polinices catenus, Littorina saxatilis,* and *Hinia reticulate* were rarely encountered, and with the exception of a single *Polinices catenus* all in prey samples of Herring Gulls. Alder's Necklace Shell *Polinices polianus* (syn. *Euspira pulchella*) is an interesting species. This snail was encountered in 90 (2%) of the prey samples of Lesser Black-backed Gulls but only 4x in Herring Gulls. The principal habitat (on sandy bottoms, 10-50m depth, usually buried; Hayward & Ryland 1995) and the size of the measured individual shells (SL 3.8 ± 0.9mm, range 1-7mm, n= 153) make it highly unlikely that these were specifically wanted prey items. They must be considered secondary prey, probably from stomach contents of demersal fish species captured in the deeper parts of the Dutch coastal waters (for example as discards). With few exceptions, all necklace snails were found in samples in which also the remains of either flatfish (Plaice or Dab) or Whiting, or both were present.

Marine bivalve prey – At least 16 species of bivalves have been found in prey samples from the Kelderhuispolder colonies, with one overwhelmingly abundant species (the leftovers of which made the dunes turn blue in the course of a breeding season): the (Blue) Mussel *Mytilus edulis*. The most abundant bivalves were:

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Mytilus edulis	5	0%	3328	67%
Ensis directus	10	0%	356	7%
Cerastoderma edule		0%	136	3%

The five samples with mussels from Lesser Black-backed Gulls were likely mis-assigned to that species. We have no evidence that Lesser Black-backed Gulls (perhaps with the exception of young birds immediately after fledging) deliberately took mussels as prey. The only bivalve slightly more frequently exploited by Lesser Black-backed Gulls was the American Razor Clam *Ensis directus*. Only the flesh, never the shells, were transported into the colony as chick-feeds. While Herring Gulls tended to transport these shells whole (including large specimens).

Shell fragments in a food sample do not automatically mean that a prey species is represented. Many shell fragments were from fossilised shells, indicating a function comparable with stone grit (perhaps as gastroliths facilitating the internal processing of food; Siegel-Causey 1990). There is no doubt about the representation of *Ensis* and *Mytilus* as indications of dietary preferences for these two gulls, but already with cockles *Cerastoderma edule*, the evidence provided is often ambiguous. The frequency of occurrence listed here excludes, for as far as possible, non-food items that were ingested accidentally or as grit.

The Pacific oyster was introduced in the Wadden Sea near Texel in 1976 (Wolff 2005, Cadée 2008ab). The development of the population in the Wadden Sea has been studied regularly (Dankers et al. 2006; Troost 2007; Cadée 2007). Pacific Oysters are consumed by Herring Gulls, but few remains were encountered in the colony. Just as large Common Shore Crabs, Pacific Oysters tend to be dropped from the air by gulls to crush the shell, and the flesh was consumed whenever the bird succeeded. Feeding on Pacific Oysters requires particular skills and is clearly hard work (Cadée 2000, 2001, 2008ab). We have some evidence that relatively few, often immature, highly specialised individuals forage on (loose) Pacific Oysters along the Wadden Sea dike. The shell dropping behaviour is considered pest-behaviour (flat tyres for bicycles are a common side-effect), but there is no evidence Pacific Oysters comprise a consistently and widely exploited resource for Herring Gulls breeding in the Kelderhuispolder.

Cephalopod prey – Only three species were encountered and all were infrequent and therefore likely insignificant as prey for both species: Dwarf Squid *Allotheutis subulata,* European Squid *Loligo vulgaris,* and the European Common Cuttlefish *Sepia officinalis*. Cephalopods were encountered in 9 samples of Lesser Black-backed Gulls and in 2 samples of Herring Gulls. Walter (1997) reported Dwarf Squid from the discards fraction of shrimpers in the East Frisian Islands (Box 7.6). De Bruyne *et al.* (1994) listed 21 Cephalopods for the Southern North Sea (NL and B).

Echinoderms – Commonly discarded Echinoderms by beamtrawlers are Common Starfish *Asterias rubens*, *Echinocyamus pussillus*, Common Brittlestar *Ophiura ophiura*, Sand Star *Astropecten irregularis*, Sea Potato *Echinocardium cordatum*, and Green Sea Urchin *Psammechinus miliaris*. Common Starfish are also readily available at the tideline, both in the North Sea and in the Wadden Sea. Only three species were encountered in prey samples and only Common Starfish were more frequently found (in Herring Gulls):

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Asterias rubens	1	0%	80	2%
Echinocyamus pussillus		0%	1	0%
Ophiura ophiura		0%	1	0%

The absence of frequently discarded biota is striking, which would mean that these animals either get digested whole and leave few traces in pellets and other regurgitates, or they are not favoured as prey by scavenging gulls at beamtrawlers. Other commonly discarded benthic organisms such as Dead man's Fingers *Alcyonium digitatum* and anemones *Actiniaria* spp. were not encountered either. Common Starfish when digested leave highly characteristic white particles in regurgitated material, but most starfish may end up in faeces. Faeces containing Common Starfish grit was frequently observed (but not analysed in this study). Common Starfish were perhaps a commoner prey than indicated here on the basis of regurgitates. The relative high number of Common Starfish leftovers in Herring Gull prey could indicate that most these starfish were taken from the intertidal zone and not from trawlers. Prey types with which Common Starfish were most frequently associated seem to confirm this suggestion (*Mytilus edulis* (48x), *Carcinus maenas* (13x), *Liocarcinus holsatus* (10x), *Pleuronectes platessa* (9x), *Ensis directus* (8x), *Crangon crangon* (7x), rock, grit (4x)).

Amphibians and reptiles – A single and intact Natterjack Toad *Bufo calamita* has been found in a part of the colony with a high density of Lesser Black-backed Gulls. Amphibians may be taken opportunistically from freshwater habitats or even from the surrounding dunes or the colony area itself.

Birds – A total of 17 species of birds have been identified as prey species, but a majority of the (incomplete) remains were not identified. There were simply too few cases to make the considerable effort worthwhile.

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
large gull egg	128	3%	308	6%
large gull pullus	162	3%	172	3%
Passerines	20	0%	35	1%
Non-Passerines	13	0%	19	0%

Cannibalistic prey (eggs and chicks of conspecifics or from the other gulls species) was most frequent. Passerine prey included Meadow Pipit *Anthus pratensis,* Barn Swallow *Hirundo rustica,* Wood Pigeon *Columba palumbus,* Blackbird *Turdus merula,* Starling *Sturnus vulgaris,* Jackdaw *Corvus monedula,* and House Sparrow *Passer domesticus.* Jackdaws were fairly common prey in one season (2009), throughout the colony, but few of the 'monitored nests' produced any leftovers of the still fairly rare prey (Camphuysen *et al.* 2010). Small chicks were offered Jackdaw chicks, but most of the Jackdaw remains in regurgitated prey were adult, or at least free-flying individuals. Observations next to the ferry at Texel confirmed that Herring Gulls were actively hunting adult Jackdaws and tried to bring them down into the sea to drown them. It was the only season that Jackdaws were frequently delivered as prey items and we estimate that at least hundreds of Jackdaws were killed and transported towards the gull colonies in 2009.

Non-passerine birds (apart from large gulls) included Pheasant *Phasianus colchius,* Northern Gannet *Morus bassanus,* Greylag Goose *Anser anser,* Coot *Fulica atra* (chick), Purple Sandpiper *Calidris maritima*, and Sandwich Tern *Sterna sandvicensis* (chick). All these species featured at most once in the prey samples collected in the Kelderhuispolder, suggesting these are all opportunistically taken prey species.

Herring Gulls would seem the most important egg-stealing species considering the data presented above. This may be misleading. Some highly specialised Herring Gulls were monitored feeding on eggs for part of the breeding cycle. Only six pairs of Herring Gulls were found to have consumed 79% of the 308 eggs found in our prey samples. Lesser Black-backed Gulls practiced egg-stealing frequently, but apparently more opportunistically. More importantly, they did not bring many eggs back to their own nest, but rather devoured them at clubs or at the raided nest itself. We did not encounter specialised Lesser Black-backed Gulls with more than a few eggshells as prey remains around their own nest. Peaks in egg predation by the two species are *c.* two weeks apart (^{App}Fig. 7.1), suggesting that this form of cannibalism is triggered by the laying activities of conspecifics (see ^{App}Fig. 4.5). The overall mean date of egg-stealing was 1 June in the Lesser Black-backed Gulls and 18 May in the Herring Gull, which is 19 respectively 11 days after the mean laying date of each species. This gap is probably wider than in reality, as a result of delays in prey sample collecting (on extremely busy days, sampling was sometimes skipped a visit or two if the breeding status of that nest was not expected to change meanwhile).

Adult Lesser Black-backed Gull handling and swallowing a juvenile Starling Sturnus vulgaris*, Kelderhuispolder, 28 June 2008 (CJ Camphuysen)*

Egg stealing by an adult Lesser Black-backed Gull, Kelderhuispolder, 30 April 2012 (CJ Camphuysen)

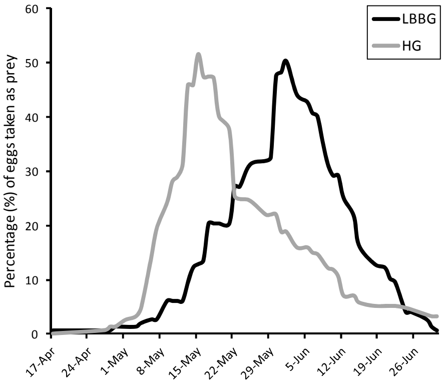


Fig. 7.1 Peaks in egg stealing by Lesser Black-backed Gulls and Herring Gulls from cumulative percentages (decline after 50% was reached) of eggs taken prior to 1st July, Kelderhuispolder 2006-11.

Mammalian prey – At least 10 species of mammals were encountered in prey samples, including small rodents, Moles *Talpa europaea*, Rabbits *Oryctolagus cuniculus* and Hedgehog *Erinaceus europaeus.* Some of these species may be deliberately captured and swallowed, others may have been scavenged in ploughed fields or along roadsides (Chapter 14).

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Oryctolagus cuniculus	12	0%	51	1%
unidentified small mammal	10	0%	13	0%
Microtus oeconomus	16	0%	6	0%
Microtus/Arvelicola	16	0%	3	0%
Rattus norvegicus	7	0%	4	0%
Talpa europaea	2	0%	3	0%

The list of the most frequently encountered terrestrial mammals includes some fairly trivial prey items, such as moles. Moles do not occur in the wild on Texel, so their presence is indicative more feeding trips to the mainland. In mainland colonies of Lesser Black-backed Gulls, moles are a rather important prey species (Camphuysen *et al.* 2006).

Insects – Not many insects were identified to species level, but at least 36 types or species were logged. In total, 886 (18%) of the prey samples from Lesser Black-backed Gulls contained at least some insect remains, against only 280 (5%) samples from Herring Gulls. The most frequently encountered types were:

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Coleoptera	403	8%	108	2%
unident insect	296	6%	69	1%
Carabidae	48	1%	20	0%
Elateridae	43	1%	19	0%
Formicidae	25	1%	20	0%

In the majority of cases (91% of samples of Lesser Black-backed Gulls containing insect prey, and 85% of Herring Gull samples), at most one individual insect prey was encountered, or the fragments were so minimal that the number of individuals could not be quantified. Some insects were encountered perhaps not very often, but sometimes in rather substantial numbers (presented is the number of samples, the proportion of all samples, and the number of individual prey per sample containing this type of insects):

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Diptera	10 (0%)	23 ind sample^{-1}	16 (0%)	707 ind sample^{-1}
Eristalis tenax	2 (0%)	51 ind sample^{-1}	-	-
Formicidae	25 (1%)	62 ind sample^{-1}	20 (0%)	4 ind sample^{-1}
Tipulidae	4 (0%)	34 ind sample^{-1}	3 (0%)	14 ind sample^{-1}
caterpillars	4 (0%)	12 ind sample^{-1}	-	-
Pterostichus	1 (0%)	5 ind sample^{-1}	2 (0%)	17 ind sample^{-1}

Swarming ants Formicidae and various species of Diptera are well known summer phenomena attracting many thousands of gulls (within Europe notably Black-headed Gulls; Källander & Rosenkvist 2000) at times (Seymour 1972, Grant 1992). Hunt & Hunt (1976) ranked swarming insects under the "unpredictable foods" in their study on the exploitation of fluctuating food resources by Western Gulls *Larus occidentalis wymani.* Participating into such feeding frenzies is apparently not without risk. A mass mortality mid-July 2007 (dozens of adults, a single juvenile Lesser Black-backed Gulls freshly dead at the beach near the colony) involved animals that were all stuffed with hundreds of flying ants of a (still) not identified species. There were no other symptoms than these full to overloaded stomachs (with the proventriculus and sometimes even the beak packed with ants), suggesting that the insects may have caused death, for example by releasing a toxic that was (acutely) fatal for these birds (NZG/NSO autopsies, CJC/NIOZ). Some massive swarms of black flies Diptera spp. over the Wadden Sea in May and June 2008, exploited by at least several Herring Gulls and one Lesser Black-backed Gull nesting in the Kelderhuispolder, were found to contain a small fraction of, apparently also airborn water boatmen *Sigara* spp.

Polychaetes – At least 7 polychaetes were found, and some (listed) in fairly high frequencies. Apart from the commoner polychaetes, in declining order of frequency, were also found *Alitta succinea, Nereis pelagica, Lanice conchilega, Hediste diversicolor, Aphrodita aculeate.*

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Nereis longissima	749	15%	50	1%
Alitta virens	63	1%	18	0%
Nereis spp.	24	0%	2	0%

Nereis longissima is an important prey, particularly for Lesser Black-backed Gulls. On average, 9.4 (LBBG) and 8.5 (HG) of the characteristic jaws occurred per sample and several dozens (up to 151, *i.e*. >76 worms) in a single pellet were not unusual. There are many reports of 'sandworms' (Nereid worms) swimming in the water column (Dean 1978), and polychaetes are highly likely to be picked up primarily from the sea surface during swarming events. Reproduction results in death in Nereid worms (semelparous species). Mature males become structurally modified for swimming (epitokous) and swarm in the water column during particular moon phases. Maturation is mainly governed by variations in nocturnal illumination, but certain water temperatures are a precondition for spawning. Swarming at a minimum temperature of 12°C was experimentally induced in *Alitta succinea* around the time of the new moon (Hardege *et al.* 1990). An abrupt increase in temperature caused swarming to occur at different times of the lunar cycle. *Alitta virens* spawns at new moon, but with slightly lower temperatures (Wilson & Ruff 1988). Korringa (1947) reported swarming activities of mature *Nereis longissima* near Boulogne (Pas-de-Calais, F) during the last quarter of the moon . The surface swarming Nereid worms must also be ranked the "unpredictable foods". Many waders are quite capable of subtracting Nereid worms from the mudflats during low tide (Zwarts & Esselink 1989). Even though many Nereid worms will be too deep to be reached by gulls (Esselink & Zwarts 1989), there is no reason to believe that all observed Nereid worm remains were associated with marine spawning events (Ambrose 1986). *Lanice conchilega* and *Hediste diversicolor* are probably most likely to have been taken in the intertidal zone. They were rarely encountered prey, but from both predators in almost equal frequencies.

Of the class Polychaeta, only seven species representing two orders were encountered in gull prey samples: Terebellida (*Lanice*) and Phyllodocida (six Nereid worms). From the NIOZ SIBES project, at least 64 species are known to occur on the Wadden Sea mudflats, representing 10 orders: Capitellida (4), Cirratulida (4), Magelonida (2), Opheliida (2), Orbiniida (1), Phyllodocida (31), Sabellariida (1), Sabellida (1), Spionida (14), Terebellida (4 species). Many of these species will leave few, if any, detectable hard parts in regurgitated gull prey, or we didn't have the expertise to detect them.

Oligochaetes – Earthworms *Lumbricus* spp. (possibly *L. terrestris*) were the only representatives of this group, frequently encountered in tight grass-pellets. Earthworms were represented in 183 (4%) of the prey samples from Lesser Black-backed Gulls, and in 51 (1%) of the samples from Herring Gulls. The detection of the tiny setae and the characteristic snow-white crystalline excretions (Massal 1929) of these worms requires microscopic inspection, and in 2006 we may have been insufficient alert on the presence or absence of setae in certain pellets. There was a positive correlation between the amount of precipitation in summer (mm rain) or the number of rainy days and the frequency of occurrence of earthworms in prey samples during 2006-2010. Earthworms were rarely encountered in 2011 (a relatively wet summer), perhaps as a result of a more superficial inspection of prey samples due to time stress (a bad excuse).

Terrestrial snails – Land snails were always considered rather "dubious" prey. Apart from those listed below, *Cornu aspersum* (4x), *Limax maximus* (1x), and *Cepaea hortensis* (1x) were found. The occurrence of 7 intact *Lauria cylindracea* could perhaps better be considered sample "pollution" rather than indications for genuine prey species. The garden snails *Cepaea* spp. and *Cornu aspersum* were commonly used "schmuck" (decoration) in nests of both species during laying, and broken shells near the nest could mistakenly have been listed as possible prey. The majority of these snails were found in pellets, indicating ingestion. They are perhaps best seen as opportunistically taken prey items, possibly even taken 'locally' (i.e. around the nest).

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
unidentified terrestrial snails	35	1%	27	1%
Cepaea nemoralis	2	0%	20	0%
Lauria cylindracea	3	0%	4	0%

Plants as prey – Many samples contained plant material and the presence of much of it was a consequence of the sampling method. Evidently, some plants were taken as food, but others were ingested as a carrying agent to regurgitate small but difficult to digest (and perhaps irritating) hard particles of other prey. It goes without saying that the exact function/origin of the plant material was not always easy to interpret. Eight plant species have been considered "sample pollution" throughout (see below). Many plants that were presumably prey could not be identified (43x as fibres or leaves, 102x as seed), or they could only be assigned to groups (moss, grasses). The most frequently encountered species and categories were:

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
Zea mays	94	2%	88	2%
Empetrum nigrum berries	90	2%	29	1%
unident plant seed	67	1%	35	1%
unident grass seed	57	1%	6	0%
Poaceae	12	0%	23	0%

Further potential prey species included Triticum seed (4x), Carex seed (2x), Ulmus (2x), *Ammophila arenaria* (1x), Juncus seed (1), Rubus seed (1), *Cornus mas* seed (1), and *Spinacia oleracea* seed (1). Apart from grass or sedge seeds as potential prey are maize and berries of Crowberries probably the only prey type of significance. Crowberries are certainly also fed to chicks and in some seasons the bright purple stains of crowberry-juice-containing faeces occurred all over the colony (colony workers included). Maize may have been harvested on agricultural fields, but processed maize (from cans) was found as well (not listed under this category; see below), or it may have been taken from for example chicken feeders. The diversity of wild plants as prey is small compared to what would be available in the form of berries, seeds or in other forms. Some types require ripening or seed-setting before they are of interest, but otherwise, it would be a fairly predictable but apparently sparsely used terrestrial food resource.

Domestic refuse – This category includes not just dumped materials but also "stolen" food items and prey that may actually have been fed to the birds (bread, chips, crisps, etcetera). The common denominator is that these prey items were taken from us: our garbage dumps, cities, garbage containers or bags, restaurants, ferries, cafeterias or whatever. In total, 286 (6%) prey samples of Lesser Black-backed Gulls and 666 (13%) samples from Herring Gulls were found to contain at least some domestic refuse. The most frequently recorded types were:

	Lesser Black-backed Gull (n= 4977)		**Herring Gull** (n= 5257)	
plastic packaging	19	0%	126	2%
chicken	11	0%	116	2%
bread	36	1%	76	1%
plastic fragments	31	1%	77	1%
bread seeds	46	1%	60	1%
plastic line, thread	43	1%	60	1%

For Lesser Black-backed Gulls, the top five domestic refuse prey types were in fact bread seeds 46x (1%), plastic line, thread 43x (1%), bread 36x (1%), plastic fragments 31x (1x), and plastic pellets 27x (1%). Apart from the bread, many of these smallish plastic particles probably had a marine rather than a terrestrial origin. For Herring Gulls the commonest types were plastic packaging 126x (2%), chicken 116x (2%), plastic fragments 77x (1x), bread 76x (1%), plastic foil 75x (1%), and pork 63x (1%). Most of these materials were clearly of terrestrial origin an frequent visit to garbage dumps seem more evident for this species.

Bread was encountered frequently by both species (in any form 75x in Lesser Black-backed Gulls, 121x in Herring Gulls, frequency of occurrence 2% in both species). An important source for bread are the tourist-loaded ferries to and from Texel, and some individual (colour-ringed or GPS tagged) birds were known to specialise on this feeding opportunity.

Some gulls produced pellets that primarily consisted of glass, plastic, aluminium foil, and other rubbish, but such birds were the exception rather than the rule. Overall, domestic refuse was not overly represented. An overview of bizarre prey and junk food was published earlier (Camphuysen *et al.* 2008), and this included toys (e.g. plastic dolls and soldiers), a mobile phone, a medal, lighters, pencils, and other objects (Box 9.1).

Table 7.4 Representation (frequency of occurrence,%), and number of encountered species and groups by origin of prey items found in food samples of Lesser Black-backed Gulls (n= 4977) and Herring Gulls (n= 5257), Kelderhuispolder 2006-2011.

	Lesser Black-backed Gull				**Herring Gull**			
Origin	Samples	%	Species	Groups	Samples	%	Species	Groups
Marine	4438	89	69	7	1213	23	65	9
Intertidal	129	3	18	6	3925	75	34	7
Terrestrial	1518	31	86	11	1193	23	86	10
Anthropogenic	286	6	51	2	669	13	80	4
Non-food	82	2	2	1	781	15	2	1
Pollution	193	4	4	1	123	2	6	1
Undetermined	63	1	4	3	59	1	3	2

Sample pollution – Samples were taken from sandy soil or grass and often scooped up with a spoon to ensure that also heavy particles (otoliths!) were included. In many samples small plant seeds were encountered that were probably accidentally included and the following seeds were considered to have "polluted" the samples rather than to have been genuine prey items: *Claytonia perfoliata*, *Taraxacum* sp., *Urtica* sp., *Elaeagnus angustifolia*, *Galium aparine*, *Convolvus* sp., *Stellaria media*, and *Epilobium hirsutum*. Grasses were a common "carrying agent" for unwanted, small hard parts (Nereis jaws and tiny earthworm setae were normally found in so-called grass pellets), but the vegetation itself must have been ingested to get rid of particles of prey and it was not logged as prey itself. Grit and fossil shell material were systematically logged as "non-food" items, because the presence or absence of these particles (normally in association with mussels) gave a hint about the likely feeding area. Marine epizoic species are a category of prey species that has been ignored in this review. Epizoans are swallowed with their 'hosts', but are unlikely to have been the target of the foraging bird. Examples are barnacles, sponges, seaweeds and bryozoans, all of which have been encountered occasionally.

In conclusion – From the overview of prey items it is evident that the two species have overlapping resources, but a radically different emphasis (^{App}Table 7.4). Nearly 90% of all food samples of Lesser Black-backed Gulls contained prey from marine origin, against only 23% in Herring Gulls. By contrast, 75% of the prey samples taken from Herring Gulls contained at least some intertidal prey, against only 3% of the samples from Lesser Black-backed Gulls. The frequency of occurrence of prey types from terrestrial sources were of the same order of magnitude, but Lesser Black-backed Gulls took relatively more insects and earthworms, Herring Gulls more mammals and birds. Domestic refuse was clearly more the domain of Herring Gulls, but both species exploited these resources rather frequently. Fish prey are the most frequently encountered marine prey in both species (93% of all samples with prey types of a marine origin in Lesser Black-backed Gulls, n= 4438; 78% in Herring Gull, n= 1213). Demersal roundfish and flatfish predominate strongly in both species, indicating a shared reliance on discards from commercial fisheries (in this region notably beamtrawlers and shrimpers. It is remarkable that locally common fatty fish such as clupeids and sandeels are not taken more. Colonies of Sandwich Terns *Sterna sandvicensis* established at Texel have flourished in recent years and on a diet dominated by these groups of fish. Boluses clearly contained more Sprat than pellets (Box 7.4), and the relative importance of this prey fish may thus have been underestimated.

Prey types can be categorised according to their (likely) origin, but also to expectations regarding their availability (e.g. constant, depending on tidal phase, cyclic, seasonal, or unpredictable). Further categorisation could be the expected inter- and intra-specific competition while feeding (intense kleptoparasitism, interference, depletion or none), or the effort required or the risks involved while accessing a given prey. The aspects required to access the top-10 most important prey species for both species combined would likely be:

	Availability	**Competition**	**Foraging technique / skills**	
Mytilus edulis	tidal	interference	Pecking	On foot
Merlangius merlangus	cyclic	kleptoparasit.	Manoeuvrability	In flight
Pleuronectes platessa	cyclic	kleptoparasit.	Manoeuvrability	In flight
Liocarcinus holsatus	unpredictable	(interference)	Dipping	In flight
Limanda limanda	cyclic	kleptoparasit.	Manoeuvrability	In flight
Trachurus trachurus	seasonal	kleptoparasit.	Manoeuvrability	In flight
Nereis longissima	unpredictable	(interference)	Dipping	In flight
Solea solea	cyclic	kleptoparasit.	Manoeuvrability	In flight
Carcinus maenas	tidal	(interference)	Head plunge diving	Swimming
Coleoptera	weather	(interference)	Pecking	On foot

Specifically for Lesser Black-backed Gull, none of its top-10 prey items has a availability according to the tidal cycle, one is seasonal (Horse Mackerel), three are unpredictable (swimming crabs, Nereid worms, sandeels), one is weather dependent (Coleoptera) and the rest is cyclic (all discards). In Herring Gulls, the tidal cycle is of profound influence of the availability of at least three of the top-10 prey items (bivalves and shore crabs), four are cyclic (discards), two seasonal (gull chicks and eggs) and one unpredictable (swimming crabs).

Foraging techniques deployed by gulls include shallow plunge diving (max depth is just the entire body under water), dipping, surface pecking, surface seizing, and aerial pursuit at sea and behind fishing vessels (Ashmole 1971, Camphuysen & Garthe 2004, Appendix 8). On land, gulls follow ploughs and other contraptions on agricultural fields, in flight and on foot, they walk fields pecking for insect prey, trample grass for earthworms, and use hit-and-run techniques for food in cities and in (actively worked) refuse dumps (Frieswijk & Bresser 1965, Horton *et al.* 1983, Coulson *et al.* 1987, Schwemmer *et al.* 2008). Some (swarming) insect prey is captured in aerial pursuit. On freshwater areas they may deploy the same techniques as at sea. In the intertidal zone, birds flock on breakwaters to loosen attached mussels (on foot), walk mudflats, and swim along the shoreline to head-plunge for prey such as starfish and shorecrabs. Big prey may be airlifted and dumped on the ground to get access to soft inner parts (Cadée 2001, 2007, 2008a).

Individual specialisations

When considering the dietary spectrum of an individual pair of breeding gulls, a minimum amount of information is required. Food samples were collected for as far as they could be found at marked nests, but differences in behaviour, prey choice, or other factors made that the number of samples collected per pair was often low, but certainly varied (mean 3.8, range 1-42 samples per pair in Lesser Black-backed Gulls, mean 8.0, range 1-69 samples per pair in Herring Gulls). The positive relationship between the number samples taken and the number of prey species found was linear when the number of samples was expressed logarithmically (^{App}Figs. 7.2). The results suggest that prey-diversity in Lesser Black-backed Gulls is higher in the egg-phase than during chick care (fewer samples are required to find a considerably higher number of prey species prior to hatching). In Herring Gulls the opposite trend was found: a higher diversity of prey species with a lower sampling effort during chick care. In Herring Gulls, rather many pairs deviated considerably from the overall trend suggesting dietary specialisations (many samples collected but with few different species). For both species it is clear that, preferably, something in the range of 10-20 samples per nest per breeding phase would be required to more or less fully appreciated the dietary choices of a single pair. A sample size that high is a luxury that was rarely within reach, despite frequent searches within all territories.

Aspects of individual specialisation (or the specialisation of pairs) are addressed in Chapters 9-10. The Texel GPS tracking studies of Lesser Black-backed Gulls revealed substantial differences in the foraging behaviour between the sexes (Chapter 10). The proportion of time spent in different habitats varied between tagged individuals representing a continuum of habitat use from almost exclusively terrestrial, to almost exclusively marine. Sexually distinct foraging strategies were discovered, that were maintained throughout incubation and chick-care. Individuals differed in foraging behaviour and foraging range, trip duration and the proportion of time at sea increased with structural size of the birds. During foraging trips, the marginally larger males travelled farther from the colony than females, spent more time in the North Sea. Males were feeding mostly for fish discards at offshore trawlers with few alternative resources nearby. Females foraged predominantly on land or in the Wadden Sea, where they utilised shrimp fishing vessels nearer the colony. Females, accessed a wider variety of resources and must have had a broader prey spectrum, by exploring a whole suite of alternative foraging opportunities in a variety of habitats nearer the colony.

In Herring Gulls, inter-pair dietary specialisations were related to fecundity parameters (Chapter 9). Individual pairs were found to specialise on specific resources, discrete parts of the overall prey spectrum, with rather clear fitness consequences. The dietary spectrum and the level and incidence of dietary specialisations changed when the energetic demands increased during chick care. Prior to hatching, most pairs focussed entirely on bivalve prey, but 25% of the pairs had distinct dietary biases. During chick care, prey spectra diversified overall during chick care and fewer specialists were detected (cf. ^{App}Fig. 7.2). Both chick growth and fledging rates were positively correlated with the amount of fish prey provided. Particularly low chick growth rates were found in pairs that had a dietary bias towards crustacean prey

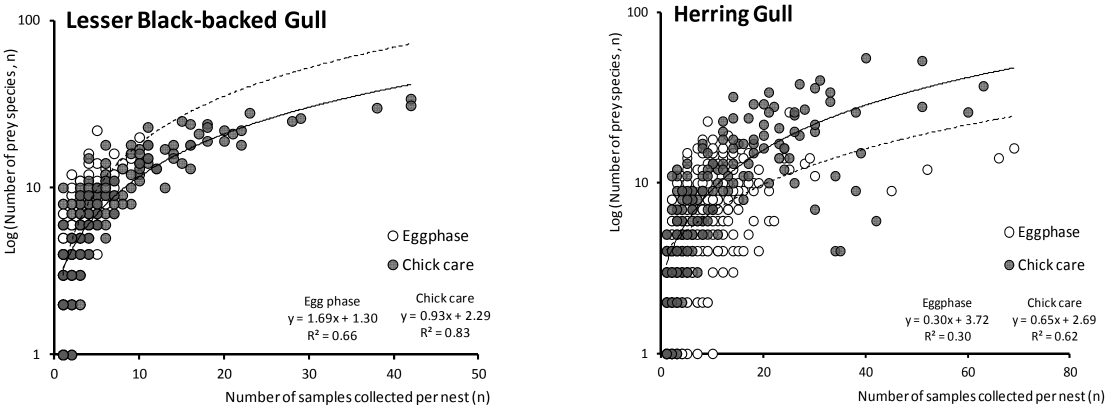


Fig. 7.2 Log(prey species) as a function of the number of samples collected at individual (marked) nests of Lesser Black-backed Gulls and Herring Gulls, Kelderhuispolder 2006-2011.

Size selection

In the absence of exact information on the exploited resources, it is difficult to meaningful evaluate prey size selection. Selection is likely to vary between species and with location, season, energetic requirements of adults and offspring, and prey availability. Predators should prefer the energetically most profitable prey, but must also forage in a cost-effective way. Herring Gulls are on average 11-12% heavier, 2-3% larger in size, with energetic requirements (FMR) that are 9-10% higher than Lesser Black-backed Gulls (Appendix 10). It may be expected that in mixed feeding flocks, on average, the slightly larger Herring Gull would select slightly larger prey than Lesser Black-backed Gulls. Consistent differences in size in samples of the same prey species could be indicative for species-specific differences in preferred size classes, or in the utilisation of different resources. A comparison of some of the most frequently taken marine prey (Whiting, Plaice and Swimming Crabs) by gulls nesting in the Kelderhuispolder shows that only the size differences in Swimming Crabs are according to the expectation based on differences in body size of the two predators (^{App}Table 7.5). It is clear that a meaningful selection of inter-specific differences in prey size selection should be conducted under controlled conditions (see sections on discards consumption based on experimental discarding). The results may indicate, however, that Lesser Black-backed Gulls and Herring Gull catch fish in different areas.

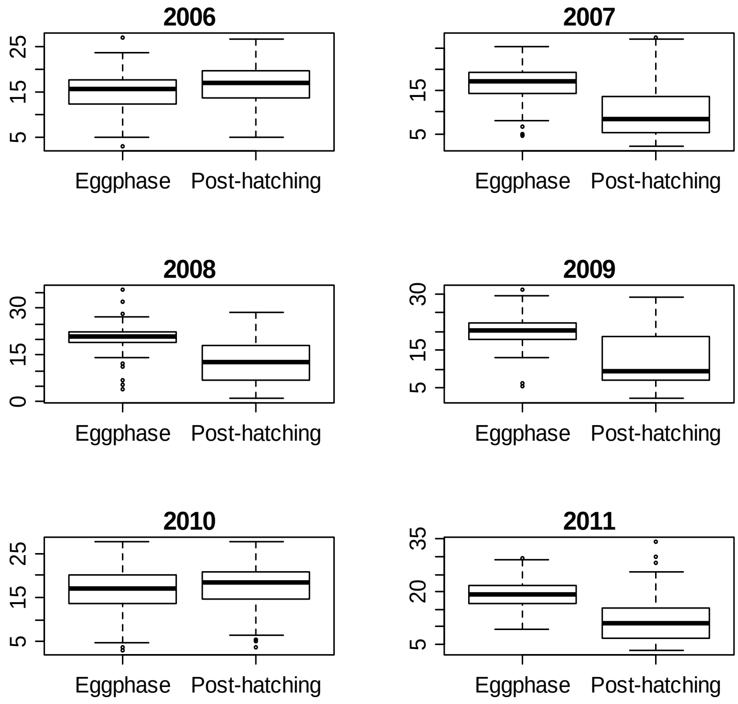


Fig. 7.3 Mussel size based on mean shell length (mm) per sample in Herring Gulls prior to hatching and during chick care, Kelderhuispolder 2006-2011. Further details and test results in ^{App}Table 7.6.

Prey size adjustments during chick care – During a breeding season, energetic requirements and likely prey selection for a pair of breeding gulls will change when the phase of chick care is entered. A dietary shift, but also a change in preferred prey size could be expected. In Herring

Table 7.5. Comparison of prey size based on prey body parts in Lesser Black-backed Gulls and Herring Gulls (pooled date for entire breeding season), Kelderhuispolder 2006-2011. VL = vertebra length, OW = otolith width, DL = dactylus length.

Prey species	**Lesser Bl.-b Gull**	**Herring Gull**	Difference	*t*	df	*P*
Whiting VL	3.1 ± 0.6 (1086)	2.8 ± 0.9 (224)	-9.7%	5.03	273.8	***
Whiting OW	3.8 ± 0.6 (908)	3.1 ± 0.9 (111)	-18.4%	7.76	121.4	***
Plaice VL	2.0 ± 0.6 (973)	1.5 ± 0.7 (197)	-25.0%	8.63	244.7	***
Swimming Crab DL	12.7 ± 2.4 (732)	13.5 ± 2.6 (209)	+5.9%	-4.36	322.0	***

Table 7.6. Mussel size (mean shell length, mm) in Herring Gulls prior to hatching and during chick care, Kelderhuispolder 2006-2011.

Mussel	**Egg phase**	**Chick care**	Change	*t*	df	*P*
2006	15.1 ± 4.7 (85)	16.2 ± 4.5 (95)	+6.8%	-1.63	174.1	n.s.
2007	16.8 ± 4.2 (112)	10.5 ± 6.6 (97)	-37.5%	8.09	158.5	***
2008	20.6 ± 3.8 (175)	12.8 ± 6.5 (157)	-37.9%	13.19	245.2	***
2009	19.9 ± 3.8 (111)	12.3 ± 6.6 (201)	-38.2%	12.94	309.2	***
2010	16.1 ± 5.5 (73)	17.4 ± 5.0 (146)	+7.5%	-1.70	133.8	n.s.
2011	19.6 ± 4.6 (41)	11.9 ± 5.8 (132)	-39.3%	8.80	83.4	***

Table 7.7 Prey size based on specific prey body parts in Herring Gulls prior to hatching and during chick care, Kelderhuispolder 2006-2011. VL = vertebra length, OW = otolith width, DL = dactylus length.

Prey species	**Egg phase**	**Chick care**	Change	t	df	P
Whiting VL	3.0 ± 0.5 (59)	2.7 ± 0.9 (165)	-10.0%	3.61	180.2	***
Whiting OW	3.8 ± 0.5 (37)	2.8 ± 0.9 (74)	-26.3%	8.16	109.0	***
Dab VL	2.1 ± 0.6 (42)	1.4 ± 0.7 (155)	-33.3%	7.30	70.0	***
Swimming Crab DL	12.8 ± 2.4 (36)	13.7 ± 2.6 (173)	+6.6%	-1.87	52.5	n.s.
Shore Crab DL	11.6 ± 2.6 (157)	10.8 ± 3.0 (196)	-6.9%	2.84	349.1	**

Table 7.8. Prey size based on prey body parts in Lesser Black-backed Gulls prior to hatching and during chick care, Kelderhuispolder 2006-2011. VL = vertebra length, OW = otolith width, DL = dactylus length.

Prey species	**Egg phase**	**Chick care**	Change	t	df	P
Whiting VL	3.1 ± 0.6 (603)	3.0 ± 0.7 (483)	-3.2%	3.75	926.6	***
Whiting OW	3.9 ± 0.5 (644)	3.6 ± 0.7 (264)	-7.7%	6.62	386.7	***
Hose Mackerel VL	6.9 ± 0.9 (357)	6.6 ± 0.8 (426)	-4.3%	4.66	731	***
Hose Mackerel OW	3.8 ± 0.4 (145)	3.8 ± 0.5(117)	0	1.21	221.8	n.s.
Plaice VL	2.1 ± 0.4 (554)	1.8 ± 0.6 (419)	-14.3%	9.54	679.1	***
Dab VL	2.3 ± 0.4 (446)	2.2 ± 0.5 (297)	-4.3%	2.94	530.3	**
Swimming Crab DL	11.9 ± 2.3 (331)	13.3 ± 2.3 (401)	+10.5%	-8.12	703.1	***

Gulls, the mean mussels size in the egg phase amounted to 18.0 ± 2.3 mm, which would be a considerable shell size for young chicks. The data show that in most years, Herring Gulls transported mussels into the colony that were some 38% smaller during chick care than in the eggphase (^{App}Fig. 7.3, ^{App}Table 7.6). There are two notable exceptions: in 2006 and 2010, mussel size increased 7% between the egg phase and chick care, suggesting that small mussels (mussel brood) may have been in short supply in these years. For all other abundant prey types, Herring Gulls tended to bring significantly smaller prey during chick care than in the egg phase, with the exception of Swimming Crabs (^{App}Table 7.7). The exact size difference was somewhat dependent on the proxies used for overall prey size (in fish otoliths and vertebrae were used here), and the exact size differences require a more complete analysis. The same tendencies for significantly smaller prey during chick care were found in the top-4 most frequently encountered fish prey in Lesser Black-backed Gulls, but again, not in Swimming Crabs (^{App}Table 7.8).

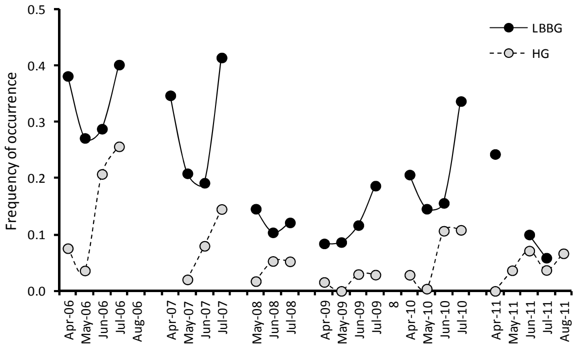


Fig. 7.4 Monthly variations in the frequency of occurrence of Swimming Crabs in prey samples of Lesser Black-backed Gulls and Herring Gulls, Kelderhuispolder, 2006-2011. A value is calculated if at least 10 prey samples were examined for that predator species in a given month

The absence of a size adjustment in Swimming Crabs transported into the colony is striking. In unpredictable resources, predators are perhaps more likely to simply take what is available. In the monthly representation of Swimming Crabs in prey samples collected in the Kelderhuispolder colony, rather strong fluctuations occurred, both between and within seasons (^{App}Fig. 7.4). Between the two species of gulls, the frequency of occurrence of Swimming Crabs as prey fluctuated more or less in concert, with Lesser Black-backed Gulls bringing consistently more of these prey in all seasons. Either Swimming Crabs have an invasive occurrence in Dutch coastal waters, or the resource has been exploited more intensely in some periods in the absence of other prey. The former explanation is the more likely of the two and is well in accordance with observations onshore (beached crabs on the tideline).

Lesser Black-backed Hulls and Herring Gulls as scavenging seabirds

Many of the data presented in this and earlier Appendices have indicated the importance of fisheries discards for both species of gulls in the Kelderhuispolder. It is exactly for that reason that some vital parts of more difficult to access final reports, produced in the 1990s in the course of a series of EC-funded research projects, have been reproduced here. These studies have greatly enhanced our understanding regarding spatial and temporal patterns in discards utilisation, prey and size selection under various circumstances and with different assemblages of seabirds attending the fishing vessels, dominance hierarchies at the trawl, the competitive strength of different species and the exact foraging techniques behind these vessels. The issue of size selection is further addressed in depth in Boxes 7.7-9 and in Camphuysen 1994 (see below), where under controlled conditions, scavenging seabirds at fishing vessels were offered the choice between species and size classes of discarded materials. In these studies onboard fishing vessels, the birds were anonymous; a link with certain breeding populations could not directly be established. In the current project in Kelderhuispolder, the reverse is true: we know our birds, but we have limited information on their feeding activities and interactions with other birds at sea. By elaborating on feeding strategies at the trawl from data gathered in the recent past and by combining these findings with currently collected data in the colony and during GPS tracking, it is hoped to complete the picture.

Camphuysen (1994b) reviewed the flatfish selection by scavenging Herring Gulls and Lesser Black-backed Gulls from discard experiments onboard a commercial beamtrawler in the southern North Sea. Dab (median total length 18 cm), Plaice (23 cm), Sole (22 cm) and Solenette (10 cm) dominated the flatfish discarded fraction of the catch and the overall consumption of flatfish by seabirds was 31%. Flatfish were selected on the basis of fish width rather than length or species, with low consumption rates (percentage consumed of number offered) of flatfish >8 cm width. All discarded Solenette, 98% of all Sole and 92% of all Dab were of suitable size for these gulls, whereas only 12% of all discarded Plaice were small enough to be consumed. Consumption rates of discarded flatfish of 'suitable size' for Herring Gulls and Lesser Black-backed Gulls (<8 cm width) ranged from 26% (Plaice) to 41% (Dab). Success indices and selected size classes of flatfish in the two scavenging gull species were similar, but Herring Gulls were more efficient than Lesser Black-backed Gulls and lost fewer flatfish as a consequence of kleptoparasitism.

Box 7.6 – Discarded biota in beamtrawl fisheries

Several research projects have demonstrated the importance of discards, 'undersized' fish and offal as a resource for seabirds. Unfortunately, these studies were confined to a small number of specific fisheries, and most were conducted in the northern North Sea or onboard fishery research vessels[1-5]. The significance for seabirds of commercial beamtrawl fisheries, one of the major fisheries in the southern North Sea, has received insufficient attention. The importance of discards for seabirds has been studied at NIOZ in the 1990s. Some results of studies in summer 1993 onboard a commercial beamtrawler are presented here. Observations were conducted onboard HD7 "6 Gebroeders", a 2000 Hp fishing vessel equipped with two 12m wide beamtrawls on either side. The ship targeted Dover Sole *Solea solea* in an area to the west of Helgoland (German Bight) and north of the Dutch Wadden Sea islands. The nets were set 47 times and the discards fraction was sampled in 34 of these hauls[1]. Added are assessments of the discards fraction in beamtrawlers and shrimpers from other published sources.

The mass of the total catch comprised 1-5% roundfish plus almost equal quantities of flatfish and benthic invertabrates (both <50%). After the trip, 7000 kg of fish was marketed of which (by mass) 40% were Plaice *Pleuronectes platessa*, 25% Dover Sole, 12.5% Dab *Limanda limanda*, 7% Cod *Gadus morhua*, 5% Red and Grey Gurnards (*Trigla lucerna* and *Eutrigla gurnardus*), 5% Turbot *Scophthalmus maximus* and Brill *(S. rhombus*), 4% Whiting *Merlangius merlangus*, and 1% Hake *Merluccius merluccius*). An estimate of the amount of discards produced would be 5-10kg undersized fish and invertebrates for each kg of fish marketed or *c.* 750-1500 kg per haul. For scavenging seabirds, some 40-60kg roundfish, 350-700kg flatfish, and 350-700kg benthic invertebrates would thus become available during each session of sorting and gutting. The amount of offal produced onboard has not been assessed. From published data, in gadoids, some 10-15% of total fish

Box 7.6 – Discarded biota in beamtrawl fisheries

mash landed is discarded as liver and guts, while 6-7% of flatfish mass is dumped[7-9]. Using these estimates, the amount of offal released into the sea per haul would be an additional 4kg from roundfish and 13kg from flatfish. Correcting for discarded animals that might escape predation and survive damage, Fonds[12] estimated a minimum of 9kg of dead fish (of which 0.1kg roundfish) and 4kg of dead invertebrates per kg marketable sole.

Discarded flatfish species included mostly Dab (75%), Plaice (20%) and a small fraction (5%) of a mix Dover Sole, Flounder *Platichthys flesus*, Solenette *Buglossidium luteum* and the occasional small Turbot, Brill or Lemon Sole *Microstomus kitt*. Most flatfish were less than 25cm in total length. Roundfish discarded were mainly gurnards (50%), Whiting (20%), Dragonet *Callionymus lyra* (10%), Cod (8%), and Scad *Trachurus trachurus* (3%) with small quantities of Ling *Molva molva*, Bib *Trisopterus luscus*, Hake, Bull-rout *Myoxocephalus scorpius*, Hooknose *Agonus cataphractus*, Lesser Weever *Echiichthys vipera*, Greater Sandeel *Hyperoplus lanceolatus* and Sand Goby *Pomatoschistus minutus*. Most discarded roundfish were less than 30cm in total length. Abundant discarded benthic invertebrates included Common Starfish *Asterias rubens*, Sand Star *Astropecten irregularis*, brittlestars *Ophiura* spp., Sea Potato *Echinocardium cordatum*, Common Sea Urchin *Psammechinus miliaris*, Masked Crab *Corystes cassivelaunus*, Hermit Crab *Pagurus bernhardus*, Common Swimming Crab *Liocarcinus holsatus*, Sea Mouse *Aphrodite aculeata*, Icelandic Cyprine *Arctica islandica*, Prickly Cockle *Acanthocardia echinata* and Whelk *Buccinuin undatum*. Small quantities of Edible Crab *Cancer pagurus*, Auger Shell *Turritella communis*, Dead man's Fingers *duim Alcyonium* digitatum and anemones *Actiniaria* spp were dumped.

From beamtrawl surveys using fisheries research vessels in the 1990s in the Southern and German Bights[12], the most abundant discarded benthic invertebrates were Common Starfish, Sand Star, the starfish *Luidia* sarsi, Brittlestar *Ophiura ophuria*, Sea Potato, Common Sea Urchin, Masked Crab, Hermit Crab, Common Swimming Crab, Edible Crab, Spider Crab *Hyas araneus,* Langoustine *Nephrops norvegicus,* the amphipod *Cirolana borealis*, the shrimps *Crangon allmanni and Processa canaliculata*, the mudlobster *Upogebia,* Sea Mouse, Icelandic Cyprine (or Quahog), Prickly Cockle, Queen Scallop *Chlamys opercularis, Dosinia lupines*, *Mya truncata*, *Gari fervensis*, Whelk, Alder's Necklace Shell *Polinices polianus*, *Aphorrhais pes-pelicanae*, and *Turritelaa* spp.

In studies onboard commercial shrimpers in the East Frisian part of the Wadden Sea, it appeared that 90% of the catch by mass was discarded. More than 60% of the catch consisted of undersized shrimps (all discarded), 20% represented fish (36 species) and invertebrates other than shrimps (23 species)[10]. The most important discarded species were: Common shore crab 18%, Common Swimming Crab 14%, Plaice (14%), Herring/Sprat (13%), Dab 7%, *Electra pilosa* (Bryozoa) 6%, Whiting 5%, jellyfish 5%, Sand Goby 4%, Smelt *Osmerus eperlanus* 4%, Hooknose 4%, Flounder 3%, Sole 1%, and Dragonet 1%, contributing to 92% of the discarded mass (undersized shrimps excluded). A sampling programme covering 103 hauls in 1992-93 revealed a catch composition (using frequency of occurrence) of Brown Shrimp$^{100\%}$, Plaice$^{100\%}$, Sand Goby$^{93\%}$, Nilsson's Pipefish *Syngnathus rostellatus*$^{90\%}$, Common Shore Crab$^{83\%}$, Common Swimming Crab$^{82\%}$, unident seaweeds$^{76\%}$, Herring$^{73\%}$, Smelt$^{69\%}$, Hooknose$^{68\%}$, Whiting$^{56\%}$, Flounder$^{49\%}$, Dab$^{48\%}$, Sprat$^{45\%}$, Five-bearded Rockling *Ciliata mustela*$^{39\%}$, Dover Sole$^{37\%}$, brittle stars$^{28\%}$, Electra pilosa$^{25\%}$, Sea Snail *Liparis liparis*$^{25\%}$, Dwarf Squid *Allotheutis subulata*$^{22\%}$, Common Starfish$^{21\%}$, Dragonet$^{21\%}$, Eelpout *Zoarces viviparus*$^{20\%}$, Hermit Crab$^{19\%}$, Bull-rout$^{18\%}$, Lesser Sandeel *Ammodytes tobianus*$^{17\%}$, Lemon Sole$^{15\%}$, anemones Actiniaria spp.$^{13\%}$, Butterfish *Pholis gunnellus*$^{13\%}$, Red Gurnards$^{12\%}$, and Horse Mackerels$^{10\%}$ (rarer species excluded)[11].

References: [1]Hudson & Furness 1988, [2]Berghahn & Rösner 1992, [3]Furness *et al.* 1992, [4]Garthe 1992, [5-6]Camphuysen *et al.* 1993, 1995, [7]Boswall 1960, [8]Bailey & Hislop 1978, [9]Furness *et al.* 1988, [10]Walter & Becker 1994, [11]Walter 1997, [12]Fonds 1994ab.; **Sources:** Camphuysen 1993b. Foerageermogelijkheden voor zeevogels in de boomkorvisserij: een verkennend onderzoek. Sula 7: 81-104.

Box 7.7 Consumption and size selection by gulls of discards in commercial beamtrawl fisheries

The significance for seabirds of commercial beamtrawl fisheries, one of the major fisheries in the southern North Sea, has been recognized in many earlier studies, but most research projects were conducted onboard fishery research vessels[1-6]. The consumption by seabirds of discarded bycatch (fish and marine invertebrates) was studied in summer 1993, onboard commercial beamtrawler HD7 "6 Gebroeders". The ship targeted Dover Sole *Solea solea* in an area to the west of Helgoland (German Bight) and north of the Dutch Wadden Sea islands. Discard experiments were conducted during 34 hauls of the net to assess prey selection and foraging success rates of the scavenging seabirds. During sorting, just before the first discards were dumped, a sample of discards and offal was collected to perform a discard experiment. Individual fish were identified, measured (cm total length), and thrown into the trickle of discards floating along at port side. The fate of each

Box 7.7 Consumption and size selection by gulls of discards in commercial beamtrawl fisheries

individual fish, invertebrate or morsel of offal was assessed (*i.e.* sinking, picked up but dropped, or picked up and consumed). Numbers of ship-associated seabirds were counted during hauling and sorting and the composition of the flock was used to evaluate individual and species-specific foraging success during the sessions of experimental discarding (number of prey swallowed by a species related to its relative abundance as a scavenger). Success indices (SI) were calculated by dividing the observed consumption of discards and offal with an expectation based on the numerical abundance of that species relative to the other scavengers. H_0 was an equal chance for all scavengers. SI <0 indicate consumption frequencies lower than expected, SI>0 are indicative for successful scavengers. See Box 7.10 for further details.

Offal consumption - Of 642 morsels of offal discarded, 93.6% were consumed by seabirds. Offal was normally picked up will still afloat at port side, few morsels floated on an reached turbulent waters over the ship's propellers. During sessions of discarding with high intensity feeding, not a single morsel was missed by seabirds, but the difference in feeding success between species was highly significant. The most successful scavengers feeding on offal were Black-legged Kittiwakes (SI 4.26) and Herring Gulls (SI 1.33). Lesser Black-backed Gulls (SI 0.73) and Great Black-backed Gulls (SI 0.00) consumed (far) less offal than expected based on their numerical abundance. Northern Fulmars performed according to expectation (SI 0.96; for all 5 species (X^2_4 = 107.6, $P < 0.001$).

Roundfish consumption – Most discarded roundfish were Red and Grey Gurnards of 16-22cm (median length resp. 19 (n= 266) and 21 cm (n=41)) and gadoids of 24-30 cm total length (median 27 (n= 112) and 29 cm (n= 54) for Whiting and Cod respectively). Dragonets were the smallest roundfish (median 17cm, n= 52), Horse Mackerels were relatively large (29 cm, n= 20). Of 642 experimentally discarded roundfish, 85.3% were consumed by seabirds. Consumption rates ranged from 58% in Dragonets, 73% in Cod and Horse Mackerel, 89% in Whiting and Red Gurnard to 93% in Grey Gurnards. Dragonets and Hooknose were relatively often rejected as prey and attempts to pick up these fish were often abandoned, apparently when the fish were recognised. Initially picked up Dragonets were often dropped and left to sink.

Roundfish were the second most wanted discards. Great Black-backed Gulls were most successful (SI 1.45) followed by Lesser Black-backed Gulls (SI 1.14), and Northern Fulmars (SI 1.07). Herring Gulls (SI 0.69) and particularly Black-legged Kittiwakes (SI 0.09) were rather less successful overall (for all five species X^2_4 = 27.6, $P < 0.001$). One reason for the lower overall success rate in Herring Gulls were the higher numbers of relatively numerous gurnards taken by Lesser Black-backed Gulls (SI Herring Gull 0.35, Lesser Black-backed Gull 1.27; for all five scavengers on gurnards X^2_4 = 38.2, $P < 0.001$). Herring Gulls were more successful picking up gadoids (SI Herring Gull 1.34, Lesser Black-backed Gull 0.87; for all five scavengers on gadoids X^2_4 = 11.4, $P < 0.05$). Great Black-backed Gulls and Northern Fulmars were particularly keen to feed on gadoids (SI respectively 2.12 and 2.38). Northern Fulmars were never seen to swallow entire fish, hoewver, but opened up the cavities of the fish and fed on guts and liver. The fate of opened carcasses could not be recorded, but most floated and were likely taken by scavengers at greater distances behind the ship.

Consumption rates fell below 80% in roundfish >28cm length. The median length of roundfish consumed for the most abundant scavengers following the ship was 19 cm in Lesser Black-backed Gulls (n= 346), 26 cm in Herring Gulls (n= 65) and 27 cm in Great Black-backed Gulls (n= 28). Black-legged Kittiwakes did not eat much apart from offal. The difference in median prey size between Herring Gulls and Lesser Black-backed Gulls is caused by the disproportionate consumption of (smaller) gurnards by the latter. There was only a small difference in median prey size between these two species if gurnards and gadoids are separated (gurnards 19cm in LBBG, n= 237; 19cm in HG, n= 21; 22cm in GBBG, n= 15 / gadoids 27cm in LBBG, n=71; 28cm in HG, n= 35, 29cm in GBBG, n= 11).

Flatfish consumption - During sessions of experimental discarding, 387 flatfish were presented (3 Flounder, 4 Solenette, 284 Dab, 72 Plaice, and 24 Dover Sole), of which 34.1% were consumed by seabirds. Consumption rates fell markedly in fish over 21 cm in length, probably because handling and swallowing is difficult and certainly time-consuming (high risk of failure). In Dab, rather many discarded individuals measured less than 21 cm in length, leading to higher consumption rates for that species (consumption rates Dab 38%, n= 284; Plaice 16%, n= 72, Dover Sole 48%, n= 24). Relatively high consumption rates in Dover Sole in comparison with Plaice of similar size may have been caused by the shape of the fish (softer bodies, more supple, smooth edges, less spines). The median length of consumed flatfish varied only slightly between gull species (17cm in LBBG, n= 86; 17cm in HG, n=30, 19cm in GBBG, n=9) and the observed success rates were in accordance with expectation (X^2_4 = 5.9, n.s.).

Consumption of benthic invertebrates - Only 0.3% of 1048 discarded benthic invertebrates were consumed by seabirds. Easily accessible flesh of broken Icelandic Cyprines and Prickly Cockles was taken occasionally, but otherwise, virtually nothing was picked up.

Box 7.7 Consumption and size selection by gulls of discards in commercial beamtrawl fisheries

For the five most numerous scavengers during the experiments, prey selection was remarkably different (prey specific SI values). Northern Fulmars, with their tendency to alight on the water to feed, experienced problems with the constantly moving beamtrawler and were outcompeted by the agile, aerial Kittiwakes and even by Herring Gulls. Lesser Black-backed Gulls had a preference for the (spiny) gurnards and were outcompeted on offal and gadoids by larger species. Great Black-backed Gulls were highly successful on flatfish and roundfish but had no access to particles of offal.

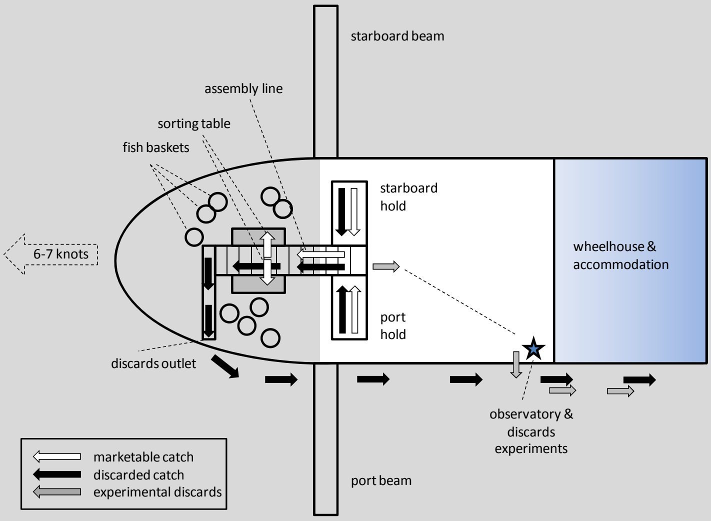
References: [1]Hudson & Furness 1988, [2]Berghahn & Rösner 1992, [3]Furness *et al.* 1992, [4]Garthe 1992, [5-6]Camphuysen *et al.* 1993, 1995; **Source:** Camphuysen 1993b. Foerageermogelijkheden voor zeevogels in de boomkorvisserij: een verkennend onderzoek. Sula 7: 81-104.

Box 7.8 – Foraging seabirds at a commercial beamtrawler

In summer 1993, scavenging seabirds were studied onboard commercial beamtrawler HD7 "6 Gebroeders", a 2000 Hp fishing vessel equipped with two 12m wide beamtrawls on either side. The ship targeted Dover Sole *Solea solea* in an area to the west of Helgoland (German Bight) and north of the Dutch Wadden Sea islands. The nets were set 47 times and discard experiments were conducted immediately following 34 of these hauls. The positioning of the different species of sea birds and their feeding techniques were described and the dominance hierarchy was reconstructed on the basis of kleptoparasitic interactions during discard experiments.

The duration of a single haul was approximately 1.5 hour (from setting to hauling). The catch was dumped into two holds on deck (Fig). When the nets were set for the next catch, the fish was transported in an assembly line towards two sorting tables, where marketable fish was selected, gutted and thrown into plastic baskets. The rest (discards, benthic invertebrates, and offal) was transported to a small opening on port side and dumped into the sea as a steady trickle of biota. The speed of the vessel during fishing (*i.e.* towing the net) and while the catch was sorted varied between 6 and 7 knots.

During sorting, just before the first discards were dumped, a sample of discards and offal was collected to perform a discard experiment. During these experiments, identified and individually measured fish (cm total length; TL) were thrown into the trickle of discards floating along at port side. The fate of each individual fish, invertebrate or morsel of offal was assessed (*i.e.* sinking, picked up but dropped, or picked up and consumed). When a bird failed to consume a prey item, for example when the prey was dropped again, or when prey were stolen by a competing bird, it was tried to assess the final consumer as well as each individual step between being picked up for the first time and final consumption (species and size of prey x species and age of each bird handling the prey item until ingestion by the final consumer). Feeding attempts were recorded as missed, picked up but dropped, picked up but lost as a result of kleptoparasitism, stolen from, picked up and swallowed whole or picked up and partially consumed. All results were tape-recorded and analysed later. Numbers of ship-associated seabirds were counted during hauling and sorting and the composition of the flock was used to evaluate individual and species-specific foraging success during the sessions of experimental discarding (number of prey swallowed by a species related to its relative abundance as a scavenger). Experiments were conducted on a safe zone onboard on port side (where the discards were normally produced), some 12m behind the opening where the trickle of discards was dumped (*Figure above*).



Processing fish onboard beamtrawler HD7. The catch is dumped into two holds on the foredeck. The fish is transported in an assembly line towards two tables, sorted, gutted and marketable fish was collected in plastic baskets. The rest (discards, benthic invertebrates, and offal) was transported to a small opening on port side and released as a steady trickle.

Box 7.8 – Foraging seabirds at a commercial beamtrawler

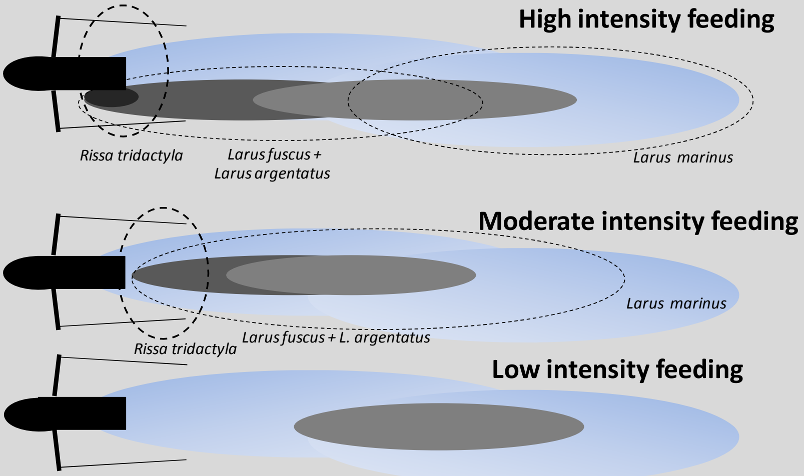
Numbers and age composition of seabirds attracted Eight species of seabirds were attracted by the vessel. Most abundant. in declining order of abundance, were Lesser Black-backed Gulls, Herring Gulls, Black-legged Kittiwakes, and Great Black-backed Gulls (Table 1). Nearly always present, but in small numbers, were Northern Fulmars *Fulmarus glacialis*. Northern Gannets *Morus bassanus*, Black-headed Gulls *Larus ridibundus*, and Common Gulls *Larus canus* occurred occasionally.

Lesser Black-backed Gulls were numerically dominant during all sessions of experimental discarding. During the first experiments, Herring Gulls were rather rare, but when the ship moved further away from the coast in a northerly and northwesterly direction, more and more Herring Gulls were attracted. The majority of both Herring Gulls and Lesser Black-backed Gulls were adult birds (*c.* 85%; *Table below*). Adult birds in the area had an intact plumage, with no signs of the onset of post-nuptial moult, and were as such not different from active breeders in this time of the year. In Great Black-backed Gull, a majority of the birds was immature, and the few adults present showed active primary moult. Black-legged Kittiwakes were all adult and with an intact plumage, as in active breeding birds. Northern Fulmars, however, judged from their ragged, worn plumage and active wing moult in 45 out of 94 individual birds, were mostly non-breeders or immatures.

Numbers of associated seabirds during discard experiments, HD 7, 28 June-2 July 1993 (frequency of occurrence, presence, total number observed, mean and SE, maximum, and proportion adult).

	N Fulmar	**Herring Gull**	**L Bl-b Gull**	**Gr Bl-b Gull**	**Kittiwake**
Frequency	29	29	30	29	30
Presence (%)	96.7	96.7	100	96.7	100
Total	172	3550	11095	704	792
Average	5.7	118.3	369.8	23.5	26.4
SE	0.7	19.2	46.1	4.9	4.9
Max	19	440	1000	130	150
% adult		86.1	85.1	4.4	100

Foraging behaviour, positioning around the ship and kleptoparasitism - Numbers of scavenging seabirds around the ship peaked during sorting and gutting of the catch, soon after the ship had resumed steaming (with nets lowered; max. *ca.* 1500 individual seabirds). The flock would concentrate at the stern on port side, but the exact positioning of the various species varied with the intensity of feeding. At high feeding densities, a dense flock of intensively competing individuals would be formed on the port side, with Black-legged Kittiwakes closest to hole where discards appeared, Herring Gulls and Lesser Black-backed Gulls in a dense pack to the side of the vessel, and lower densities (with most Great Black-backed Gulls) in the wake of the vessel (*Figure below*). With lower intensity feeding, few birds would assemble on port side, while most feeding occurred in turbulent waters in the wake. Different species had different tactics and the flock of scavengers appeared to have a rather typical constellation, depending on the intensity of feeding and the exact position at the stern of the different species. Herring Gulls and Lesser Black-backed Gulls tended to pack together in areas where feeding and fighting was most intense, either on port side (high intensity feeding) or in the wake of the vessel. Black-legged Kittiwakes were often much closer to the vessel than any other bird, pecking up small fish and smaller morsels, before it could float into the area with the highest concentrations if competing seabirds. Great Black-backed Gulls tended to linger around in the rear end of the following flock, taking whatever they wanted, often by kleptoparasitism.



Shape, position and constellation of the associated flock of scavenging seabirds with different feeding intensities.

Box 7.8 – Foraging seabirds at a commercial beamtrawler

Consumers of fish stolen from or simply picked up after being dropped incidentally by others, and expectations based on the relative abundance of scavengers at the trawl.

		Stolen by				Picked up by			
Lost by		LBBG	HG	GBBG	$X^2_{2=}$	LBBG	HG	GBBG	$X^2_{2=}$
LBBG	obs	54	37	13	10.1	65	16	5	0.75
	exp	75	24	5	**	62	20	4	n.s.
HG	obs	21	18	11	11.2	13	9	2	2.14
	exp	36	12	2	**	17	6	1	n.s.
GBBG	obs	0	0	5	-	3	0	0	-
	exp	4	1	0	-	2	1	0	-

Kleptoparasitism - 285 fish or morsels of offal that were picked up by one bird were lost and consumed by another. In 119 cases the prey was simply dropped, but 166 prey were stolen (kleptoparasitism). The Lesser Black-backed Gull lost 1.9x more prey to Herring Gulls and Great Black-backed Gulls than it managed to steal from these species (*Table below*). Apart from 54 prey items stolen by one Lesser Black-backed Gull from another, 37 prey were stolen by Herring Gulls and 13 by Great Black-backed Gulls. This ratio is significantly different from the expectation based on numerical abundance ($X^2_2 = 9.75$, $P< 0.01$), and suggests that Herring Gulls and Great Black-backed Gulls are superior over Lesser Black-backed Gulls in the inter-specific competition for prey at the stern. Of prey items that were dropped by Lesser Black-backed Gulls without an apparent reason, 65 were taken by conspecifics, 16 by a Herring Gull and 5 by Great Black-backed Gulls; in accordance with expectation based on numerical abundance ($X^2_2 = 5.70$, n.s.). Herring Gulls performed different. Fewer fish were stolen from Herring Gulls by Lesser Black-backed Gulls than expected, more prey were stolen by Great Black-backed Gulls (*Table below*; $X^2_2 = 11.38$, $P< 0.005$). Again, when considering fish that were simply dropped by Herring Gulls, fish were picked up by species according to the expectation based on their numerical abundance at the stern ($X^2_2 = 1.47$, n.s.).

The vessel as an attraction for seabirds – Sorting the catch took *c.* 30min and a complete haul 1.5hr. Sorting made the ship attractive for seabirds, and when the ship stopped towing to haul the nets in a stationary position seabirds would stream in from all directions. During the experiments 28-29 June, some 8-15 other beamtrawlers were active within a 3 nautical mile radius around the ship, on 30 June 5-8 beamtrawlers occurred within that range (mean 9.6 ± 4.5 fishing vessels within 3 miles, n= 23). Seabirds monitored ship-movements constantly and responded immediately on a vessels in which the nets were hauled. Associated numbers of birds were low during towing (in the absence of sorting).

Dominance hierarchy – The results of the discard experiments were indicative for a dominance hierarchy among scavengers with Great Black-backed Gulls at the top, Herring Gulls second, and Lesser Black-backed Gulls third in rank. The differences between Herring Gulls and Lesser Black-backed Gulls in foraging success were small, however. Herring Gulls took relatively many morsels of offal and gadoid roundfish in comparison with Lesser Black-backed Gulls (Box 7.8), suggesting that the former was most successful in getting easy (smooth) and attractive prey with a higher calorific value than the latter. Kittiwakes were more successful than expected from their numerical abundance in picking up offal by their strategic position at the trawl (close to the ship; *second Figure*), quicker response, and high manoeuvrability. There was no evidence that Lesser Black-backed Gulls outmanoeuvred Herring Gulls often (contra[1]). The poor performance of Northern Fulmars were largely due to their incapacity to deal with a constantly moving vessel, and the gradual trickle of discards (small quantities at the time), while facing a cloud of highly manoeuvrable gulls concentrating at the stern of the boat.

References: [1]Strann & Vader 1992; **Source:** Camphuysen 1993b. Foerageermogelijkheden voor zeevogels in de boomkorvisserij: een verkennend onderzoek. Sula 7: 81-104.

Box 7.9 – Lesser Black-backed Gulls and Herring Gulls as scavenging seabirds in the North Sea

EC funded projects in 1993 and 1994-95 were the first synoptic studies of discard utilisation by scavenging seabirds throughout the North Sea. Projects were designed to assess seasonal fluctuations in the distribution and overall numbers of scavenging seabirds and fisheries on a North Sea scale (51°-62°N, 4°W-12°E), to refine knowledge on the attraction of fishing vessels for seabirds, and to assess seasonal fluctuations in discards consumption. Basic questions were:

→ Which part of discards is utilised by seabirds and how do scavenging seabirds interact at the trawl ?
→ How large a proportion of discards and offal is consumed by scavenging seabirds ?

Box 7.9 – Lesser Black-backed Gulls and Herring Gulls as scavenging seabirds in the North Sea

→ How large are the amounts of discards and offal that are released into the North Sea ? and

→ How large a number of scavenging seabirds can potentially be supported by fishery waste in commercial fisheries in the North Sea ?

What has been reproduced here includes the results from discards experiments to reveal species-specific differences in prey selection, feeding efficiency, feeding strategy, and vulnerability to kleptoparasitism while scavenging at the trawl.

Material and methods Results are presented for the entire North Sea including the Skagerrak/Kattegat region (51-62°N, 4°W-12°E). The area was divided into 7 subregions on the basis of ICES areas IVa-c and IIIa (^{App}Fig. 8.5). The International Bottom Trawl Survey (IBTS) fisheries research vessels trawled for half an hour in each ICES square. Counts were made of birds attracted to the stern of the boats to determine the maximum number of scavenging seabirds present at each haul. To study prey preferences and consumption rates, a fresh sample of fish, offal and benthic invertebrates was taken from each haul to be used for experimental discarding. The intention was to discard roundfish, flatfish, offal and benthic invertebrates in a ratio of 2 : 2 : 1 : 1, but in practice this was not always possible. Flatfish and benthic invertebrates were under-represented in most catches and offal was not available on a regular basis. Items were identified, measured to the nearest cm in length and thrown overboard. Attempts by seabirds to pick up and swallow the item were recorded on tape, noting species and age and if an item was eaten, dropped or stolen. If it was dropped or stolen, the same notes were made for the second and subsequent birds, until the item was finally lost (sunk) or swallowed. Experimental discarding was usually carried out when vessels were stationary, during routine discarding of the ship if possible, but also steaming while sorting. When the number of scavengers was small, for example because they were attracted to nearby trawlers, experiments were discontinued. Results of experimental discarding were analysed by subregion and the relative abundance of scavengers was calculated using stern counts made during the discard experiment. Consumption rates for benthic invertebrates, flatfish, roundfish and offal were calculated for each subregion. The observed rates were compared with expected consumption rates calculated from the relative numerical abundance of each scavenger species during discard experiments. The percentages of all discarded items that were swallowed by a given seabird species divided by the percent of all birds present at the trawl that were this species were calculated and tabulated as success index (S.I.). The frequency with which experimentally discarded items were stolen by birds of one species from another were also calculated. Combining data from all experimental discarding sessions, the number of experimental discards stolen by birds of one species divided by the number of experimental discards stolen birds from this species from others was calculated and tabulated as the robbery index (R.I.). Quartiles and medians of roundfish length (cm) and flatfish width (0.5 cm) for the most abundant discards were calculated by subregion and differences between length distributions were tested by Kruskal-Wallis 1-way ANOVA. For roundfish discards, total length was used as a measurement of size, ignoring the fact that circumference or height varied between species. In flatfish, however, fish width was used for analysis, a measurement which was calculated from the total length assessed during experimental discarding (cf. Camphuysen (1994b). An analysis on the basis of width in flatfish appears to be more appropriate when dealing with gape-limited predators. Only fish species discarded in large quantities (over 250 offered) were analysed individually. For these species, length distributions (cm) of roundfish and width distributions (0.5 cm) of flatfish were tabulated for items that sunk or were consumed by one of the scavenging species. Minimum, median and maximum sizes of fish for the most abundant experimental discards were calculated and differences between common scavengers in size choices were compared by Kruskal-Wallis 1-way ANOVA.

Table 7.9.1. Flatfish selection by common scavenging seabirds (arranged by mass), expressed as median, minimum and maximum body width (0.5 cm) consumed during experimental discarding. All experiments combined (n= 2647 flatfish offered, 2414 of which with known fate). At least 400 flatfish of different size classes were offered in the presence of each species. Sample sizes refer to numbers of flatfish consumed by that species.

Species	body mass (g)	median length (cm)	range (cm)	sample (n)
Black-legged Kittiwake	300–500	3.5	0.5-6.5	28
Mew gull	300–500	-	-	1
Fulmar	700–900	3.5	1.0-6.0	57
Lesser black-backed gull	700–1000	4.5	2.5-9.0	80
Herring gull	800–1200	5.0	1.5-8.5	67
Great skua	1300–1800	-	-	-
Great black-backed gull	1100–2000	6.5	3.0-9.0	62
Northern Gannet	2800–3200	6.5	3.5-11.5	198

Lesser Black-backed Gulls as scavengers - In regions and seasons where Lesser Black-backed Gulls were common, the ship was often joined by at least a few of these birds which followed even if discards were not produced for a long time. During fishing, groups of associated Lesser Black-backed Gulls would gradually increase in size, while the birds followed at some distance or alighted in a concentration of birds somewhere in front (expected track) of the ship. When the net came up, all gulls would rush towards the ship and fly over the net and around the ship, generally at greater distances than the small gulls (Mew Gulls and Kittiwakes). From a trickle of discards, Lesser Black-backed Gulls would carefully select preferred items by eye and pick up fish and offal while still on the wing or with a shallow plunge dive. This species was apparently capable of diving up to half a metre or more, but seldom did so. Some of the fish was taken from other birds (robbery), but Lesser Black-backed Gulls seldom tried persistently to steal fish and rapidly gave up if its 'victim' did not drop the fish too rapidly. Lesser Black-backed Gulls took medium sized fish (BoxTables 7.9.1-2). The median width of 80 flatfish consumed by these gulls was 4.5 cm (range 2.5-9.0 cm), which is considerably less than the median width of flatfish offered in the presence of these birds (6.5 cm, n= 1279; BoxFig 7.9.1-2). Roundfish taken by Lesser Black-backed Gulls ranged in length from 6-32 cm (n= 1218). The median length of roundfish consumed by these birds was 18 cm, which equals the median length of roundfish offered in the presence of this species (18 cm, n= 12,088).

Lesser Black-backed Gulls were competitive and successful scavengers (S.I. >1; more fish obtained than expected from their numerical abundance during experiments) for Clupeids in spring in NW (S.I. 1.1), in NE (5.8), in CW (1.9), in C (1.4), and in CE (1.1), in summer in NW (1.8), in CW (2.4), and in S (1.3), in autumn in CW (92.2), and in S (1.2) (Tables 3-6). High foraging success, however, given the small numbers of Lesser Black-backed Gulls involved in certain subregions and seasons, did not always lead to high consumption rates (Tables 7-10). Considering gadoid fish, they were successful and competitive in autumn in NW (1.3), and in S (1.4), in spring in NW (1.1), in NE (2.2), in CE (1.6), in C (1.3), and in S (15.1), in summer in NE (3.6), in CW (9.1), in C (1.1), in CE (1.5), and in S (1.3), and even in winter in S (2.7). Again, high success indices did not always produce high consumption rates. With flatfish, Lesser Black-backed Gulls were successful in spring in NW (2.5), NE (5.0), CW (2.2), and in CE (2.1), in summer in NW (21.2), NE (3.5), C (16.2), CE (2.0), and in S (1.4), and in autumn in NE (32.0). High success indices while feeding on offal were obtained exclusively in spring, in NE (2.0), CW (4.2) and in CE (1.4).

Table 7.9.2. Roundfish selection by common scavenging seabirds (arranged by mass), expressed as median, minimum and maximum total length (cm) consumed during experimental discarding, all experiments combined (n= 25,016 roundfish offered, 23,389 of which with known fate). At least 4450 roundfish of different size classes were offered in the presence of each species. Sample sizes refer to numbers of roundfish consumed by that species.

Species	body mass (g)	median length (cm)	range (cm)	sample (n)
Black-legged Kittiwake	300–500	15	5-34	5675
Mew gull	300–500	14	6-22	71
Fulmar	700–900	16	6-33	4594
Lesser black-backed gull	700–1000	18	6-32	1218
Herring gull	800–1200	19	7-38	1813
Great skua	1300–1800	25	10-36	176
Great black-backed gull	1100–2000	24	6-38	1083
Northern Gannet	2800–3200	25	6-55	3083

Lesser Black-backed Gulls were the main consumers (≥ 50% of items) of experimentally discarded Clupeids in summer in subregion S (95) and in spring in NE (68%). Regarding Gadoids, Lesser Black-backed Gulls obtained the largest portion in spring in CE (68%) and in summer in S (95%) and CE (61%). They took all the flatfish in S in summer (100%), and high proportions in spring (88%) and summer (83%) in CE. Most flatfish in spring in NE was consumed by Lesser Black-backed Gulls (59%), whereas 50% of all flatfish in C was taken in summer (Tables 7-10). Offal is frequently taken by gulls, but not normally as an obvious preference. Yet, 60% of the offal discarded in CE in spring was taken by Lesser Black-backed Gulls. Lesser Black-backed Gulls were important consumers (10-50% of items) of experimentally discarded Clupeids in spring (47%) and summer (36%) in CE, in autumn in S (25%), and in spring in C (14%), of Gadoids in spring in S (40%), C (13%), and NE (25%), in summer in NE (10%) and in autumn in S (28%). Significant amounts of offal were taken in spring in NE (24%) and in summer in S (17%) and in CE (13%). Flatfish consumption by scavenging Lesser Black-backed Gulls was important in summer in NW (20%) and in NE (10%).

The robbery index of Lesser Black-backed Gulls was only slightly higher than that of Herring Gulls, but both species should be considered moderately vulnerable to kleptoparasitism. Of 108 fish stolen from Lesser Black-backed Gulls, 79 were taken by conspecifics, 29 by other seabirds. Many fish were simply dropped, but Lesser Black-backed Gulls obtained an equal amount of fish by picking up items dropped by others (mainly other Lesser Black-backed Gulls).

Herring Gulls as scavengers - Flocks of Herring Gulls at the stern, just as Lesser Black-backed Gulls, would gradually increase in size during fishing (towing), constantly flying at some distance or alighting in tight groups in the expected track of the moving ship. When the net came up and near the surface the gulls would rush towards the ship and fly over the net. As Lesser Black-backed Gulls, this species would usually operate at slightly greater distances than the small gulls (Mew Gulls and Kittiwakes). From a trickle of discards, items were selected by eye and fish and offal were picked up while still on the wing or with a shallow plunge dive. As the former species, Herring Gulls were seen to dive up to half a metre or more, but seldom did so. Occasionally, every fish which was not clear at the surface anymore was ignored by these gulls and only when

Box 7.9 – Lesser Black-backed Gulls and Herring Gulls as scavenging seabirds in the North Sea

another species picked it up there was an attempt to steal it. Herring Gulls were roughly equally successful as kleptoparasites of other species , but Herring Gulls were clearly more persistent to steal fish than Lesser Black-backed Gulls and did not easily gave up if its 'victim' did not drop the fish too rapidly. Herring Gulls, like the Lesser Black-backed Gull, took medium sized fish (Tables 1-2). The median width of 67 flatfish consumed by these gulls was 5 cm (range 1.5-8.5 cm), which is considerably less than the median width of 1312 flatfish offered in the presence of these birds (6.5 cm; Fig. 1). Roundfish taken by Herring Gulls ranged in length from 7-38 cm (n= 1813). The median length of roundfish consumed by these birds was 19 cm, making these fish slightly longer than roundfish consumed by Lesser Black-backed Gulls (median 18 cm), and which is 2 cm more than the median length of roundfish offered in the presence of this species (17 cm, n= 13,813).

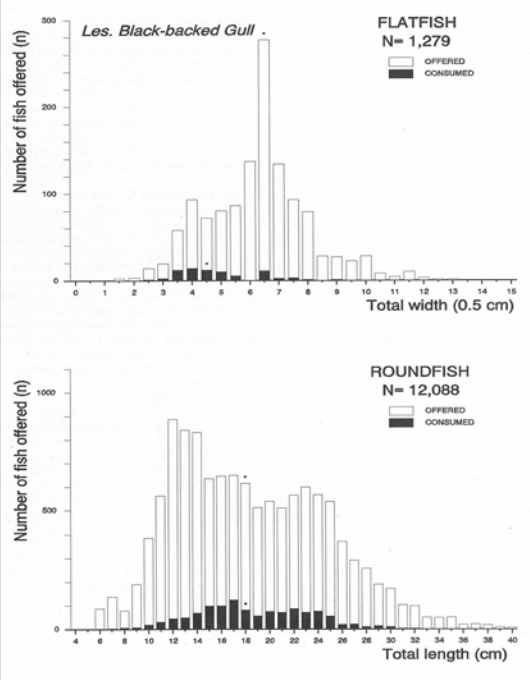


Fig. 7.9.1. Length distribution of flatfish and roundfish consumed by Lesser Black-backed Gulls in comparison with the length distribution of discards offered.

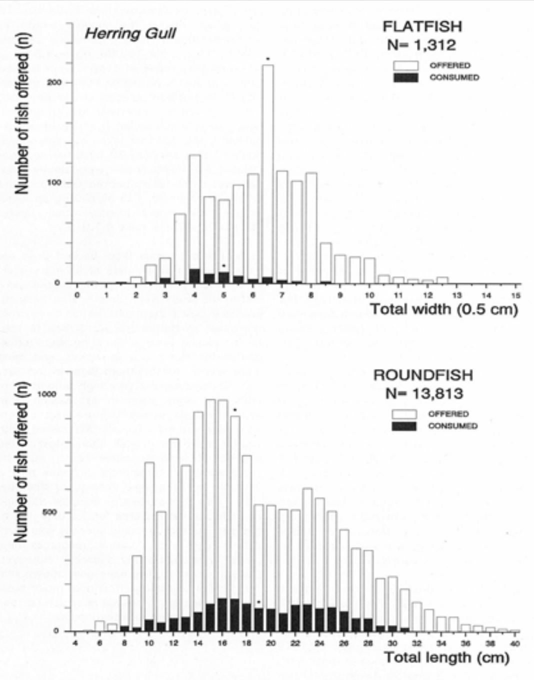


Fig. 7.9.2. Length distribution of flatfish and roundfish consumed by Herring Gulls in comparison with the length distribution of discards offered.

Herring Gulls were competitive and successful scavengers (S.I. >1; more fish obtained than expected from their numerical abundance during experiments) for Clupeids in spring in NW (S.I. 1.1), in NE (5.8), in CW (1.9), in C (1.4), and in CE (1.1), in summer in NW (1.8), in CW (2.4), and in S (1.3), in autumn in CW (92.2), and in S (1.2) in spring in NW (1.7), NE (48.6), CW (8.5), and in CE (1.1), in summer in NW (63.7), and in CW (6.3), in autumn in NE (2.9), CW (2.3), S (1.7), and in CE (1.4), and in winter in NW (1.3), and in NE (2.2) (^{Box}Tables 7.9.3-6). Considering gadoid fish, they were successful and competitive in spring in NW (2.8), NE (6.4), CW (19.4), C (5.1), and in CE (2.4), in summer in NW (10.6), CW (5.3), and in CE (2.4), in autumn in NW (1.2), NE (1.8), and in CW (2.7), and in winter in NE (2.0), C (1.6), CE (1.6), and in S (1.6). With flatfish, Herring Gulls were successful in spring in NW (3.5), and in NE (79.0), in autumn in NW (2.6), NE (2.3), C (3.0), and in CE (1.8), and in winter in NE (8.5), and in CW (2.1). High success indices while feeding on offal were obtained exclusively in in summer in NW (5.4; but a trivial amount given the small numbers of Herring Gulls in that region), in autumn in NE (2.1), and in winter in CW (5.4).

Herring Gulls were the main consumers (≥50% of items) of experimentally discarded Clupeids in autumn in CE (78%), NE (63%), and S (50%; ^{Box}Tables 7.9.7-10). Of Gadoids, Herring Gulls obtained the largest portion in autumn in CE (54%). They took all flatfish in autumn in CE (100%), and high proportions in NE (50%) and NW (64%). Half the flatfish discarded in winter in NE was consumed by Herring Gulls (50%). Of the offal discarded in winter in CW, 62% was taken by Herring Gulls. Herring Gulls were important consumers (10-50% of items) of experimentally discarded Clupeids in winter in CE (28%), in NW (16%), in NE (13%), in C (13%), in CW (12%), and in S (11%), in summer in CW (10%), and in autumn in NW (13%), of Gadoids in winter in NW (12%), in NE (12%), in CE (48%), in C (28%), in CW (12%), and in S (28%), in autumn in NE (39%), in NW (29%), and in CW (11%), of offal in autumn in NE (46%), and in winter in C (15%), and finally of Flatfish in autumn in C (30%), in winter in CW (24%) and in C (13%), and in spring in NE (12%).

Box 7.9 – Lesser Black-backed Gulls and Herring Gulls as scavenging seabirds in the North Sea

Table 7.2.3. Success indices (percent of all gadids that were consumed by a species divided by the percent of all birds present during experiments that were this species) of common scavenging seabirds with experimentally discarded gadids (haddock, whiting, cod, saithe, and Norway pout) in each of the subregions of the North Sea in February (winter), May (spring), August (summer) and November (autumn) [recalculated data from FRV cruises only].

Season	Subr	Fulmar	Gannet	GrSkua	MewG	LBbG	HG	GBbG	Kitt	Others
spring	NW	0.4	4.7	2.8	0.0	1.1	2.8	3.1	5.0	0.0
	NE	0.7	7.5	3.7		2.2	6.4	2.3	0.0	0.0
	CW	0.3	5.1	2.3		0.6	19.4	0.3	2.4	
	C	0.8	6.3	14.2	0.0	1.3	5.1	2.3	0.6	0.0
	CE	0.4	2.8	0.0	2.1	1.6	2.4	0.4	1.0	0.0
	S	1.3	0.0			15.1			0.5	
summer	NW	0.7	13.2	7.8	0.0	1.0	10.6	7.8	1.0	0.0
	NE	0.9	11.4	1.0	0.0	3.6	0.0	1.9	2.9	0.0
	CW	0.7	2.3	1.9	0.0	9.1	5.3	3.0	0.6	0.0
	C	1.0	2.1	0.9	0.0	1.1	0.0	0.8	0.4	0.0
	CE	0.2	0.0	0.0	2.4	1.5	2.4	0.9	1.3	0.0
	S	0.2	0.0	0.0	0.0	1.3		1.6	0.0	0.0
autumn	NW	0.3	5.5	0.0	4.6	1.3	1.2	1.4	1.6	1.2
	NE	0.4	1.7			0.0	1.8	0.6	2.3	0.0
	CW	0.2	4.6	0.0	0.0	0.0	2.7	0.7	1.2	0.0
	C	0.2	3.8	0.0	1.3	0.4	0.5	0.8	1.4	0.3
	CE	2.7	0.0		0.0	0.0	1.0	1.6	0.7	0.0
	S		4.7		0.0	1.4	0.0	0.6	0.0	
winter	NW	0.0	3.4				1.0	1.9	1.3	0.0
	NE	0.1	6.6				2.0	2.1	1.8	0.0
	CW	0.1	2.9	0.0	0.0		1.0	1.4	1.3	0.0
	C	0.1	5.5		0.0	0.0	1.6	1.0	1.0	0.0
	CE	0.0	0.0		0.1	0.0	1.6	2.1	1.1	
	S	0.0	7.2		0.0	2.7	1.6	1.2	1.3	

Table 7.9.4. Success indices (percent of all Clupeids that were consumed by a species divided by the percent of all birds present during experiments that were this species) of common scavenging seabirds with experimentally discarded Clupeids (Herring, Sprat) in each of the subregions of the North Sea in February (winter), May (spring), August (summer) and November (autumn) [recalculated data from FRV cruises only].

Season	Subr	Fulmar	Gannet	GrSkua	MewG	LBbG	HG	GBbG	Kitt	Others
spring	NW	0.5	5.4	7.6	0.0	1.1	1.7	4.8	1.3	0.0
	NE	0.1	8.2	0.0		5.8	48.6	1.4	0.0	0.0
	CW	0.4	4.4	0.0		1.9	8.5	0.0	2.7	
	C	0.8	2.3	0.0	0.0	1.4	1.0	0.4	1.3	0.0
	CE	0.6	1.3	0.0	1.0	1.1	1.1	0.0	2.0	0.2
	S	0.0	0.0			0.0			1.3	
summer	NW	0.5	11.7	21.6	0.0	1.8	63.7	12.3	0.0	0.0
	NE	0.8	38.7	31.0	0.0	0.8	0.0	19.4	2.7	0.0
	CW	0.4	2.9	0.0	0.0	2.4	6.3	0.6	3.6	0.0
	C	0.9	0.3	0.0	0.0	0.8	0.0	0.0	2.6	0.0
	CE	0.0	0.0	1.5	0.0	0.9	0.0	0.0	3.1	0.4
	S	0.3	0.0	0.0	0.0	1.3		0.0	0.0	0.0
autumn	NW	0.1	8.9	0.0	0.0	0.0	0.5	0.4	2.3	2.1
	NE	0.0	4.2			0.0	2.9	6.7	0.0	0.0
	CW	0.2	3.4	0.0	0.0	92.2	2.3	1.5	1.2	0.0
	C	0.1	2.1	0.0	0.0	0.0	0.3	0.1	1.8	0.0
	CE	0.0	0.0		0.0	0.0	1.4	0.1	0.8	0.0
	S		0.0		0.0	1.2	1.7	0.7	0.9	
winter	NW	0.1	3.9				1.3	0.3	1.4	0.0
	NE	0.0	1.9				2.2	0.4	2.4	0.0
	CW	0.0	0.7	0.0	0.0		1.0	0.4	1.6	0.0
	C	0.0	0.0		0.8	0.0	0.8	0.2	1.6	0.0
	CE	0.1	0.0		0.7	0.0	0.9	1.1	1.8	
	S	0.0	0.0		0.0	0.7	0.6	0.2	2.4	

Box 7.9 – Lesser Black-backed Gulls and Herring Gulls as scavenging seabirds in the North Sea

Table 7.9.5. Success indices (percent of all discarded flatfish that were consumed by a species divided by the percent of all birds present during experiments that were this species) of common scavenging seabirds with experimentally discarded flatfish (mostly plaice, dab, solenette, and sole) in each of the subregions of the North Sea in February (winter), May (spring), August (summer) and November (autumn) [recalculated data from FRV cruises only].

Season	Subr	Fulmar	Gannet	GrSkua	MewG	LBbG	HG	GBbG	Kitt	Others
spring	NW	0.3	7.0	0.0	0.0	2.5	3.5	5.5	2.6	0.0
	NE	0.1	0.0	0.0		5.0	79.0	2.5	0.0	0.0
	CW	0.0	9.3	0.0		2.2	0.0	1.1	0.2	
	C	0.1	27.2	0.0	0.0	0.6	0.0	3.3	0.2	0.0
	CE	0.2	0.0	0.0	0.0	2.1	0.0	2.1	0.0	0.0
	S									
summer	NW	0.5	16.7	0.0	0.0	21.2		25.8	0.0	0.0
	NE	0.9	0.0	0.0	0.0	3.5	0.0	0.0	0.0	0.0
	CW	0.0	0.0	0.0	0.0	0.0	0.0	72.0	0.0	0.0
	C	0.3	0.0	0.0	0.0	16.2	0.0	49.0	0.0	0.0
	CE	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.9	0.0
	S	0.0	0.0	0.0	0.0	1.4		0.0	0.0	0.0
autumn	NW	0.0	0.0	0.0	239.8	0.0	2.6	2.0	0.6	0.0
	NE	0.5	3.9			32.0	2.3	1.9	0.0	0.0
	CW	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0
	C	0.0	5.0	0.0	0.0	0.0	3.0	0.0	0.9	0.0
	CE	0.0	0.0		0.0	0.0	1.8	0.0	0.0	0.0
	S									
winter	NW	0.0	7.2				0.4	1.7	0.1	0.0
	NE	0.2	17.0				8.5	2.0	0.0	0.0
	CW	0.0	13.4	0.0	0.0		2.1	2.5	0.0	0.0
	C	0.0	25.5		0.0	0.0	0.7	3.3	0.1	0.0
	CE	2.2	0.0		0.0	0.0	0.0	7.0	0.0	
	S									

Table 7.9.6 Success indices (percent of all offal particles that were consumed by a species divided by the percent of all birds present during experiments that were this species) of common scavenging seabirds with experimentally discarded offal (intestines and livers) in each of the subregions of the North Sea in February (winter), May (spring), August (summer) and November (autumn) [recalculated data from FRV cruises only].

Season	Subr	Fulmar	Gannet	GrSkua	MewG	LBbG	HG	GBbG	Kitt	Others
spring	NW	0.80	0.21	7.72	0.00	0.27	0.00	0.37	6.52	0.00
	NE	0.9	0.0	0.0		2.0	0.0	0.2	4.5	0.0
	CW	0.2	2.6	0.0		4.2	0.0	0.0	5.7	
	C	0.8	0.0	0.0	0.0	0.9	0.0	0.0	1.9	0.0
	CE	0.0	0.0	0.0	0.0	1.4	0.0	0.0	3.0	0.0
	S									
summer	NW	1.0	0.0	0.4	0.0	0.0	5.4	0.1	0.8	0.0
	NE	1.0	0.0	0.0	0.0	0.6	0.0	0.0	0.3	0.0
	CW	1.2	0.1	0.0	0.0	0.0	0.6	0.1	0.5	1.4
	C	1.1	0.0	0.0	1.9	0.6	0.0	0.0	0.3	0.0
	CE	2.4	0.0	0.0	0.0	0.3	0.0	0.5	1.0	0.8
	S	5.2	0.0	0.0	0.0	0.2		0.0	0.2	0.0
autumn	NW	0.6	0.0	0.0	0.0	0.0	0.3	0.2	2.3	1.9
	NE	0.3	0.0			0.0	2.1	0.4	2.3	1.1
	CW	0.2	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.0
	C	0.8	0.0	0.0	0.0	0.0	0.7	0.0	1.4	0.0
	CE									
	S									
winter	NW	1.4	0.1				0.4	0.0	1.4	0.0
	NE									
	CW	0.5	3.5	0.0	0.0		5.4	0.0	0.2	0.0
	C	2.8	0.0		0.0	0.0	0.9	0.6	0.5	0.0
	CE									
	S									

Box 7.9 – Lesser Black-backed Gulls and Herring Gulls as scavenging seabirds in the North Sea

Table 7.9.7. Consumption (%) of experimentally discarded gadids (haddock, whiting, cod, saithe, and Norway pout) in each of the subregions of the North Sea in February (winter), May (spring), August (summer) and November (autumn) [recalculated data from FRV cruises only].

Season	Subr	Fulmar	Gannet	GrSkua	MewG	LBbG	HG	GBbG	Kitt	Others
spring	NW	38	27	1	0	2	2	10	21	0
	NE	54	3	0		25	1	16	0	0
	CW	25	52	0		1	0	1	22	
	C	49	17	0	0	13	1	7	11	0
	CE	13	1	0	1	68	3	1	13	0
	S	20	0			40			40	
summer	NW	70	13	9	0	0	1	5	1	0
	NE	84	3	0	0	10	0	0	2	0
	CW	53	28	1	0	2	8	4	4	0
	C	90	3	0	0	3	0	0	3	0
	CE	5	0	0	1	61	1	6	25	0
	S	3	0	0	0	95		2	0	0
autumn	NW	10	7			0	29	6	47	0
	NE	24	3	0	0	0	39	3	31	0
	CW	7	31	0	0	0	11	2	49	0
	C	7	23	0	1	0	5	3	61	0
	CE	8	0		0	0	54	20	18	0
	S		61		0	28	0	11	0	
winter	NW	2	36				12	18	32	0
	NE	4	12				12	11	62	0
	CW	2	14	0	0		12	5	67	0
	C	3	12		0	0	28	9	48	0
	CE	0	0		3	0	48	23	28	
	S	1	8		0	3	28	14	46	

Table 7.9.8. Consumption (%) of experimentally discarded Clupeids (Herring and Sprat) in each of the subregions of the North Sea in February (winter), May (spring), August (summer) and November (autumn) [recalculated data from FRV cruises only].

Season	Subr	Fulmar	Gannet	GrSkua	MewG	LBbG	HG	GBbG	Kitt	Others
spring	NW	44	30	2	0	2	1	15	5	0
	NE	12	3	0		68	7	10	0	0
	CW	29	45	0		2	0	0	25	
	C	52	6	0	0	14	0	1	26	0
	CE	23	1	0	0	47	1	0	27	1
	S	0	0			0			100	
summer	NW	51	12	25	0	0	3	8	0	0
	NE	75	11	7	0	2	0	2	2	0
	CW	31	35	0	0	0	10	1	23	0
	C	81	0	0	0	2	0	0	16	0
	CE	0	0	2	0	36	0	0	60	2
	S	5	0	0	0	95		0	0	0
autumn	NW	4	11	0	0	0	13	2	70	1
	NE	0	6			0	63	31	0	0
	CW	9	23	0	0	5	9	5	50	0
	C	4	13	0	0	0	3	0	80	0
	CE	0	0		0	0	78	2	20	0
	S		0		0	25	50	13	13	
winter	NW	6	41				16	2	35	0
	NE	1	3				13	2	81	0
	CW	0	3	0	0		12	2	83	0
	C	0	0		1	0	13	2	83	0
	CE	1	0		15	0	28	12	44	
	S	0	0		0	1	11	2	86	

Box 7.9 – Lesser Black-backed Gulls and Herring Gulls as scavenging seabirds in the North Sea

Table 7.9.9. Consumption (%) of experimentally discarded flatfish (mostly plaice, dab and sole) in each of the subregions of the North Sea in February (winter), May (spring), August (summer) and November (autumn) [recalculated data from FRV cruises].

Season	Subr	Fulmar	Gannet	GrSkua	MewG	LBbG	HG	GBbG	Kitt	Others
spring	NW	26	39	0	0	4	2	17	11	0
	NE	12	0	0		59	12	18	0	0
	CW	0	95	0		2	0	2	2	
	C	4	75	0	0	6	0	10	4	0
	CE	8	0	0	0	88	0	4	0	0
	S									
summer	NW	46	17	0	0	20		17	0	0
	NE	90	0	0	0	10	0	0	0	0
	CW	0	0	0	0	0	0	100	0	0
	C	25	0	0	0	50	0	25	0	0
	CE	0	0	0	0	83	0	0	17	0
	S	0	0	0	0	100	0	0	0	0
autumn	NW	0	0	0	9	0	64	9	18	0
	NE	29	6	0	0	6	50	9	0	0
	CW	20	0	0	0	0	0	0	80	0
	C	0	30	0	0	0	30	0	40	0
	CE	0	0	0	0	0	100	0	0	0
	S									
winter	NW	0	77	0	0	0	5	15	3	0
	NE	10	30	0	0	0	50	10	0	0
	CW	0	67	0	0	0	24	10	0	0
	C	0	54	0	0	0	13	30	4	0
	CE	25	0	0	0	0	0	75	0	0
	S									

Table 7.9.10. Consumption (%) of experimentally discarded offal (intestines and livers) in each of the subregions of the North Sea in February (winter), May (spring), August (summer) and November (autumn) [recalculated data from FRV cruises only].

Season	Subr	Fulmar	Gannet	GrSkua	MewG	LBbG	HG	GBbG	Kitt	Others
spring	NW	68	1	2	0	0	0	1	27	0
	NE	74	0	0		24	0	2	1	0
	CW	17	27	0		3	0	0	53	0
	C	54	0	0	0	9	0	0	37	0
	CE	0	0	0	0	60	0	0	40	0
	S									
summer	NW	98	0	0	0	0	0	0	1	0
	NE	98	0	0	0	2	0	0	0	0
	CW	94	1	0	0	0	1	0	3	0
	C	96	0	0	0	2	0	0	2	0
	CE	63	0	0	0	13	0	3	19	3
	S	82	0	0	0	17	0	0	2	0
autumn	NW	22	0			0	6	1	70	1
	NE	20	0	0	0	0	46	2	31	0
	CW	6	0	0	0	0	0	0	94	0
	C	28	0	0	0	0	7	0	65	0
	CE									
	S									
winter	NW	60	1				4	0	34	0
	NE									
	CW	10	17	0	0		62	0	10	0
	C	54	0		0	0	15	6	25	0
	CE									
	S									

Source: Camphuysen C.J., Calvo B., Durinck J., Ensor K., Follestad A., Furness R.W., Garthe S., Leaper G., Skov H., Tasker M.L. & Winter C.J.N. 1995. Consumption of discards by seabirds in the North Sea. Final report to the European Comm., study contr. BIOECO/93/10, **NIOZ-Report 1995-5**, Netherlands Institute for Sea Research, Texel, 202+LVIIIpp.

Appendix 8. The utilisation of marine habitats

> *"Gulls are probably the best known of all sea-birds and those unacquainted with ornithology often call any bird seen at sea a Sea-Gull. In actual fact however gulls are pre-eminently birds of the coast. The flock of sea-gulls which usually follows a ship as it leaves harbour rapidly melts away as the land is behind."*
>
> W.B. Alexander 1928. Birds of the Ocean, A Handbook for Voyagers. G.P. Putnam's Sons, New York, London

It is since the mid-1980s that the marine distribution of Herring Gulls and Lesser Black-backed Gulls within the North Sea has been systematically studied, when first British and later also Dutch, German, Danish, Norwegian and Belgian ornithologists set out to sea (Blake *et al.* 1984). Early at-sea observers, such as Alexander (1928) and Wynne-Edwards (1935) had found that the offshore distribution of most gulls was in fact restricted to the nearshore zone (only Black-legged Kittiwakes *Rissa tridactyla* were considered 'true' seabirds), but it required more systematic survey techniques to properly analyse and describe the temporal and spatial patterns in the at-sea distribution. A standard observation protocol (Tasker *et al.* 1984), agreed upon by researchers around the North Sea, formed the basis of the European Seabirds at Sea database group (ESAS). Within a decade or so, distribution patterns were mapped for the first time (Stone *et al.* 1995, Skov *et al.* 1995) and systematic surveys have continued ever since. For Dutch waters, the first atlases presenting the distribution of seabirds were published in 1993 (based on aerial surveys, Baptist & Wolf 1993) and 1994 (based on ship-based surveys, Camphuysen & Leopold 1994).

Skov *et al.* (1995) concluded that Lesser Black-backed Gulls dispersed off the European Continental shelf coasts utilising virtually the entire North Sea, but densities along the British east coast were comparatively low. Numbers at sea were highest in March-Augugst, when *c.* 130,000 birds were estimated to occur (29% of the north-east Atlantic breeding population at the time). The Channel was used to enter and exit the North Sea and during spring migration (March-April). Some 95% of all Lesser Black-backed Gulls occurred in the eastern half of the North Sea. An area of international importance for Lesser Black-backed Gulls was identified between Vlieland and IJmuiden (i.e. off Texel) from May to October. In spring and early summer, both the Skagerrak (March-April) and Helgoland Bight (May-June) were also of international importance. In winter, the North Sea was largely abandoned, but some 15,000 birds were estimated to spend the winter in the Channel. Stone *et al.* (1995) further emphasised the importance of the Dutch sector of the North Sea, the German Bight and the Skagerrak within the North Sea as well as the fact that Lesser Black-backed Gulls were not common at sea along the east coast of Britain. Widespread low densities along the west coast of Scotland, in the Celtic Sea, the Irish Sea and the English Channel reflected the distribution of colonies along the western coast of Britain.

In winter (November-February), nearly one million Herring Gulls were found dispersed throughout the North Sea (Skov *et al.* 1995), while 157,000 individuals were estimated to winter in the Wadden Sea (Meltofte *et al.* 1994). Herring Gulls were found throughout the North Sea in winter, with the Dutch Bank (off SE Shetlands), North East Bank (off NE England), Brown Ridge (Southern Bight), the Dutch coast, and the eastern Kattegat/Skagerrak being areas of international importance. In March-April, a marked contraction occurred and most Herring Gulls were found in the Southern Bight and the German Bight, the Skagerrak/Kattegat, and in the northwest from north-east Scotland to Shetland. In summer and autumn (May-October) numbers of Herring Gulls at sea dropped markedly and not a single sea area is of particular importance for this species in this period. In the breeding season, Herring Gulls were widespread around most coastal regions (with the exception of the west coast of Norway), but the species was virtually absent from the offshore central and northern North Sea at this time (Stone *et al.* 1995). Highest densities were found along The Netherlands coast, near the Firths of Clyde and Forth, and in the Moray Firth. Herring Gull distribution was thus mainly coastal during spring and summer, but expanded to cover the whole North Sea in winter.

Lesser Black-backed Gulls in the Dutch sector of the North Sea

> *Excerpt from:* Camphuysen C.J. & M.F. Leopold 1994. Atlas of seabirds in the southern North Sea. **NIOZ-Report 1994-8**, Netherlands Institute for Sea Research, Texel, Institute for Forestry and Nature Research (IBN-DLO) & Dutch Seabird Group (NZG), 126pp.

Lesser Black-backed Gulls were the most numerous and widespread *Larus*-gull in the southern North Sea in summer, **June-July** (AppFig. 8.1a). 0ff the Wadden Sea islands, high densities were found near Terschelling, moderate to low densities elsewhere. Sightings were frequent at considerable distances from the coast and the Friese Front area and Terschellingerbank were regions where mature birds were common and often numerous. Large flocks of adult Lesser Black backed Gulls were seen to join commercial trawlers in these months (Camphuysen 1993ac). Moderate to high densities were also found occasionally along the mainland coast and in the Voordelta, and low densities occurred in a wide band off the coast. It was estimated that 20,200 Lesser Black-backed Gulls occurred in the coastal zone, plus another 37,200 individuals offshore (13.0% of the NE Atlantic population; AppTable 8.1; Rose & Scott 1994). Some 36,300 Lesser Black-backed Gulls were estimated to occur within the Dutch sector of the North Seaand . just over 90% were adults (AppTable 8.2). From coastal sites. Lesser Black backed Gulls were recorded as an abundant species, without any preferential direction of movement being observed (Camphuysen & Van Dijk 1983, Platteeuw *et al.* 1994). Apparently, most movements observed from the shore were feeding flights of mature birds towards and from the colonies. From aerial surveys, it was concluded that Lesser Black-backed Gulls occurred widespread in low densities south of 54°N, with moderate to high densities near the coast (Baptist & Wolf 1993). It was estimated that around 15,000 Lesser Black-backed Gulls were present in the Dutch sector during 1985-88, and over 25,000 individuals in 1989-92, a difference that remains unexplained.

Table 8.1 Estimated total numbers of birds in the southern North Sea (from birds in transect during ship-based surveys, corrected for individuals missed). Extrapolations were made per 30’Nx1°E rectangles (ICES squares) for the coastal zone (16,000 km²) and for the offshore zone (114,000 km²). Due to poor coverage north of 54°N in mid-winter (Dec-Jan), the offshore area for which numbers of birds were calculated was only 82,000 km² (ca. 70% of the total area). Estimates of the North Atlantic population following Rose & Scott (1994).

Species	**Area**	**Jun-Jul**	**Aug-Sep**	**Oct-Nov**	**Dec-Jan**	**Feb-Mar**	**Apr-May**
Lesser Bl-backed Gull	Coastal	20,200	16,200	19,600	700	2800	29,800
	Offshore	37,200	18,600	4900	500	9800	53,100
	Totals	57,400	34,800	24,500	1200	12,600	82,900
[NE Atlantic pop. 450,000]		12.8%	7.7%	5.4%	0.3%	2.8%	18.4%
Herring Gull	Coastal	14,500	3800	46,300	108,800	55,100	35,800
	Offshore	1600	3000	28,000	62,500	75,900	9500
	Totals	16,100	6800	74,300	171,300	131,000	45,300
[NE Atlantic pop. 1,400,000]		1.2%	0.5%	5.3%	12.2%	9.4%	3.2%

Table 8.2 Age composition in Lesser Black-backed Gulls (adult, immature, first year) in the southern North Sea, 1985-93.

Month	**Adult**	**Immature**	**First year**	**% adult**	**Sample**
Jan	103	5	16	83.1	124
Feb	78	9	22	71.6	109
Mar	1214	78	34	91.6	1326
Apr	2371	183	22	92.0	2576
May	3291	430	216	83.6	3937
Jun	2001	183	28	90.5	2212
Jul	3327	293	63	90.3	3683
Aug	2602	78	497	81.9	3177
Sep	1565	119	907	60.4	2591
Oct	910	72	369	67.4	1351
Nov	333	19	39	85.2	391
Dec	38	1	6	84.4	45
Totals	17833	1470	2219		21522

After fledging of the offspring, **August-September**, the proportion of adult Lesser Black-backed Gulls at sea declined gradually (81.9% adult in August, 60.4% in September; AppTable 8.2). The species was still numerous and widespread in a broad band off the coast, but fewer birds were found the reach the Friese Front area and larger numbers were found off the mainland coast (AppFig. 8.1b). It was estimated that around 16,200 Lesser Black-backed Gulls occurred the coastal zone in these months and another 18,600 offshore (24,600 in the Dutch sector). Hence, with nearly 8% of the NE Atlantic population of this species in the southern North Sea, these waters were still of international importance for Lesser Black-backed Gulls. Numbers of Lesser Black-backed Gulls seen from coastal sites increased sharply in these months and the dominant direction of flight (westward along the Wadden Sea islands and south-westward along the mainland coast) marked the departure of this species from Dutch waters. Many hundreds, up to a few thousands of Lesser Black-backed Gulls could be seen heading south on a single day in September (Camphuysen & Van Dijk 1983, Platteeuw *et al.* 1994). The distribution pattern derived from aerial surveys was similar to that described for ship-based surveys, with scattered moderate to high densities inshore and an broad band of low densities offshore (Baptist & Wolf 1993). Also, numbers estimated to occur in the Dutch sector (13,500) had declined compared to June-July.

Numbers declined rapidly in **October-November**, and the southward departure was clearly reflected in the distribution pattern found (AppFig. 8.1c). Moderate to high densities were mainly recorded in the Voordelta area, whereas off the Wadden Sea islands Lesser Black-backed Gulls were comparatively scarce. Immatures and juveniles were the first to leave the area, considering the proportion of adults which increased in November when total numbers became quite small (AppTable 8.2). It was estimated that 19,600 Lesser Black-backed Gulls occurred in coastal waters (while numbers in November were distinctly smaller than in October), plus some 4900 individuals offshore (AppTable 8.1). Of these, some 15,300 individuals were in the Dutch sector of the North Sea. Massive southward movements, as recorded from coastal sites, of Lesser Black-backed Gulls continued in early October, but numbers declined rapidly in November (Camphuysen & Van Dijk 1983, Platteeuw *et al.* 1994). Juveniles were comparatively scarce during these passages, perhaps because these birds are difficult to separate from juvenile Herring Gulls and therefore overlooked. The departure of Lesser Black-backed Gulls and the displacement of the zone with highest densities to the south was much less obviously recorded in aerial surveys (Baptist & Wolf 1993). From these counts, it was concluded that Lesser Black-backed occurred still in a wide band along the entire coast, in fact a similar distribution pattern as described for aerial surveys in June-September, but with lower densities near the coast. It was estimated that between 7000 and 10,000 Lesser Black-backed Gulls occurred in the Dutch sector.

Low densities were recorded in winter, **December-January**, with Lesser Black-backed Gulls being most frequently reported off Belgium (AppFig. 8.1d). Just over 80% of the gulls were adults (AppTable 8.2) and it was estimated that 700 Lesser Black-backed Gulls occurred in the coastal zone, plus another 500 offshore. The fact that the northern half of the offshore zone was poorly surveyed is not important for this species. Only 800 Lesser Black-backed Gulls were found in the Dutch sector. Numbers of Lesser Black-backed Gulls reported during seawatching were low, and most birds were seen along the coast of Zuid-Holland (Camphuysen & Van Dijk 1983, Platteeuw *et al.* 1994). Aerial surveys produced a pattern of scattered low densities, everywhere south of 54°N (Baptist & Wolf 1993) and an estimate of total numbers in the Dutch sector in the range of 2000 birds. The even distribution and the fact that estimates are now suddenly considerably higher than estimates from ship-based surveys make it tempting to speculate that Great Black-backed Gulls were frequently mistaken for its smaller lookalike, the Lesser Black-backed Gull (as already suggested in Baptist & Wolf 1993).

Lesser Black-backed Gulls returned in **February-March**, particularly in the Southern Bight (AppFig. 8.1e). Low densities were found off the Wadden Sea island and the Friese Front area was not of significance for the species in early spring. Some 90.0% of the gulls were adults (n = 1435; AppTable 8.2) and it was estimated that 2800 individuals occurred in the coastal zone, plus 9800 offshore (9300 in the Dutch sector). In fact, along the mainland coast Lesser Black-backed Gulls were most numerous at some distance away from the coast, as if it were a truly offshore species. Small numbers of Lesser Black-backed Gulls were recorded from coastal sites, but a gradual return was witnessed during late March, particularly along the coast of Zuid-Holland (Camphuysen & Van Dijk 1983, Platteeuw *et al.* 1994). Aerial surveys produced a similar distribution pattern, except that patches with higher densities did not occur (Baptist & Wolf 1993). Instead of a return of Lesser Black-backed Gulls, documented both in seawatching data and ship-based surveys, the estimate of 1500 individuals from aerial surveys, lower than in December/January, would indicate that numbers in Dutch waters had stabilized since early winter.

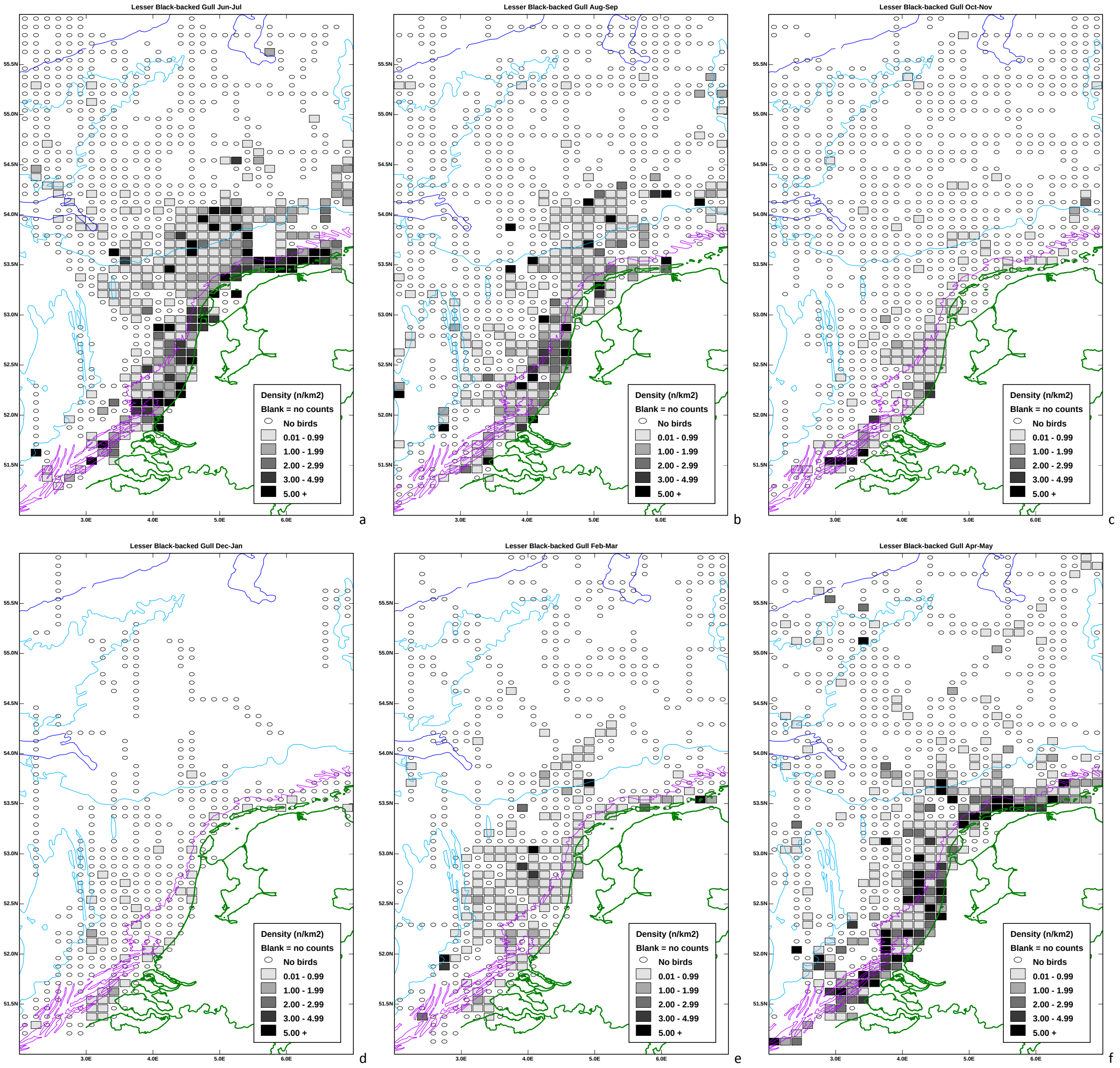


Fig. 8.1a-f Distribution of Lesser Black-backed Gulls (n km^{-2} per 5°Nx10°E rectangle) in the Dutch sector of the North Sea (based on SASBASE/ESAS data (NZG/NIOZ/IMARES), updated since Camphuysen & Leopold 1994 to include data collected between 1995 and 2012; Σ 88,000 counts, 48,475 km² surveyed).

High numbers were recorded in **April-May**, in the beginning of the breeding season. Highest densities were found around Terschelling, but moderate to high densities occurred everywhere along the coast. Offshore sightings were frequent, this obviously partly being caused by migrant birds (Doggersbank, Nordschillgrund, Outer Silver Pit), but also by birds frequenting the Friese Front and Terschellingerbank areas (^{App}Fig. 8.1f). It was estimated that 29,800 Lesser Black-backed Gulls occurred in the coastal zone, plus as many as 53,100 offshore (18.2% of the

NE Atlantic population; AppTable 8.1; Rose & Scott 1994). Of these gulls, 57,900 individuals were found in the Dutch sector of the North Sea. Adult gulls predominated (86.9%, n= 6513; AppTable 8.2). Numbers of Lesser Black-backed Gulls seen during seawatching increased rapidly during these months, and northward passages predominated (Camphuysen & Van Dijk 1983, Platteeuw *et al.* 1994). Aerial surveys produced a similar distribution pattern, except that moderate densities occurred seldom in the coastal strip and high densities were not found (Baptist & Wolf 1993). It was estimated from these counts that around 19,000 Lesser Black-backed Gulls occurred in the Dutch sector, indicating a sudden return of the species compared to the previous period.

Conclusions - Lesser Black-backed Gulls are the only truly marine species of gull breeding in The Netherlands. High densities occur red around colonies in the breeding season, but adults were found venturing out to sea over considerable distances. Peak numbers were found in April-July (over 80,000 individuals in the southern North Sea, some 58,000 of which within the Dutch sector), when the majority of these gulls were adults. Considering the Dutch breeding population (24,000 pairs in 1990), it is obvious that a substantial proportion of the food of this gull is obtained at sea. In April-May, over 18% of the NE Atlantic population was estimated to occur in the southern North Sea, indicating the international importance of this area for this species. Lesser Black-backed Gulls were frequent scavengers in the southern North Sea in summer (Camphuysen 1993a). This species was found dispersed at considerably larger distances from the shore than the Herring Gull, but it should still be considered a coastal species. As a dominating species (>50% of the birds behind a trawler), Lesser Black-backed Gulls were frequently encountered in a zone within 50 km from the coast. Off the mainland coast, Herring Gulls were always dominating over Lesser Black-backed Gulls within 20 km from the shore. Commercial fisheries were found to form an important source of food for Lesser Black-backed Gulls nesting on the Wadden Sea islands (Noordhuis & Spaans 1992, Camphuysen 1993c, Camphuysen 1994a).

From aerial surveys, changes in abundance and the spatial distribution of this species were not as obvious as ship-based data suggest. Considering the aggregations of Lesser Black-backed Gulls near fishing vessels, it is difficult to explain the lack of 'high density' squares in data from aerial surveys (Baptist & Wolf 1993). Estimates of total numbers ranged from figures well below those found in ship-based surveys in summer, to roughly equal numbers during spring and autumn migration and higher figures in winter. A wide band of low densities, nearly homogeneous over the entire southern half of the Dutch sector, only interrupted by patches of moderate to high densities in the coastal strip between April and September was found.

Herring Gulls in the Dutch sector of the North Sea

Excerpt from: Camphuysen C.J. & M.F. Leopold 1994. Atlas of seabirds in the southern North Sea. **NIOZ-Report 1994-8**, Netherlands Institute for Sea Research, Texel, Institute for Forestry and Nature Research (IBN-DLO) & Dutch Seabird Group (NZG), 126pp.

In summer, **June-July**, Herring Gulls were abundant at sea, but only near the coast (AppFig. 8.2a). Moderate to high densities were found off the Wadden Sea islands and off the mainland coast of Zuid-Holland. Large numbers of Herring Gulls, feeding at sea or associated with commercial trawlers, were almost exclusively found within 10km from the coast (Camphuysen 1993a). Over 90% of all Herring Gulls at sea were adults (AppTable 8.3) and some 14,500 individuals were estimated to occur in the coastal zone against only 1600 offshore (AppTable 8.1). Of these, 14,700 were in the Dutch sector of the North Sea. Aerial surveys produced a distribution pattern which was quite different from that described here (Baptist & Wolf 1993). Moderate to high densities were found in the coastal strip, but otherwise the species was found to be widespread over most of the Dutch sector, at least south of 54°N The Herring Gull thus seemed an equally offshore species as the Lesser Black-backed Gull, while the ship-based surveys showed it to be a much more inshore bird.

Table 8.3 Age composition in Herring Gulls (adult, immature, first year) in the southern North Sea, 1985-93.

Month	Adult	Immature	First year	% adult	Sample
Jan	6345	959	1469	72.3	8773
Feb	4102	727	802	72.8	5631
Mar	3143	876	505	69.5	4524
Apr	1642	822	139	63.1	2603
May	1399	529	553	56.4	2481
Jun	1482	146	14	90.3	1642
Jul	1174	44	12	95.4	1230
Aug	370	31	151	67.0	552
Sep	109	117	431	16.6	657
Oct	877	345	1354	34.0	2576
Nov	1554	202	566	66.9	2322
Dec	699	198	207	63.3	1104
Totals	22896	4996	6203	67.2	34095

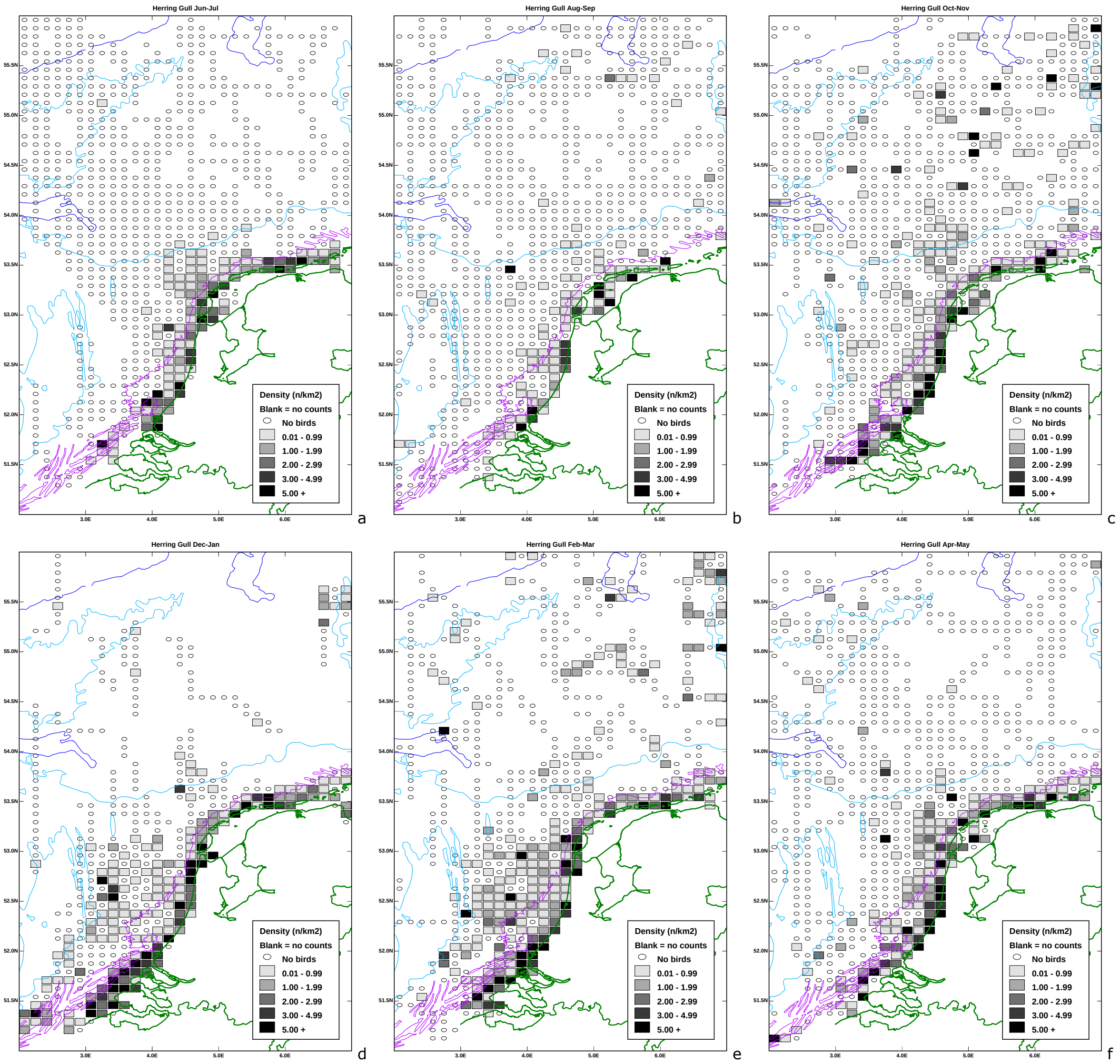


Fig. 8.2a-f Distribution of Herring Gulls (n km^{-2} per 5°Nx10°E rectangle) in the Dutch sector of the North Sea (based on SASBASE/ESAS data (NZG/NIOZ/IMARES), updated since Camphuysen & Leopold 1994 pooling all data collected between 1987 and 2012; Σ 88,000 counts, 48,475 km² surveyed).

In **August-September**, numbers of Herring Gulls in the coastal zone declined, whereas slightly more offshore sightings were reported (^{App}Fig. 8.2b). The drop in numbers along the coast was also obvious among scavengers associated with commercial trawlers (Camphuysen 1993a). The proportion of adult birds at sea fell sharply, to 67.0% (n= 552) in August and 16.6% in September (n = 657; ^{App}Table 8.3), indicating that most breeding birds had left the sea during the post-nuptial (primary) moult. Estimates of total numbers arrived at 3800 for the coastal zone and 3000 offshore (^{App}Table 8.1; only around 5000 in the Dutch sector). Numbers observed from the coast of Noord-Holland declined sharply in August, to a level of less than ten birds per hour in either direction during August and September (Platteeuw *et al.* 1994). Post-fledging mortality was frequently reported in these months and could occur on a large scale in all coastal provinces. Large numbers were found August 1979, September-October 1979, September 1981, 1982, 1983, 1984 and 1989 (Camphuysen 1989, NZG/NSO unpubl. data). Just as in June and July, aerial surveys produced a pattern of occurrence over a much wider area in the North Sea (Baptist & Wolf 1993). The estimated number on the basis of these surveys was 9750 individuals.

Herring Gulls suddenly became abundant at sea in autumn, **October-November**, particularly in the coastal zone and most notably in the Voordelta (^{App}Fig. 8.2c). Offshore sightings became more frequent and Herring Gulls could be seen everywhere in the study area during these months. Adults were still comparatively scarce, but the overall proportion increased from 34.0% in October (n= 2576) to 66.9% in November (n= 2322; ^{App}Table 8.3). It was estimated that some 46,300 Herring Gulls occurred in the coastal zone and 28,000 offshore in these months (^{App}Table 8.1; 51,900 within the Dutch sector of the North Sea). Numbers of Herring Gulls observed during seawatching in Noord-Holland remained rather low, but a remarkable increase in numbers was witnessed during late November/early December (Platteeuw *et al.* 1994). These data are not in agreement with the seasonal pattern described from ship-based surveys. Fewer juveniles were found dead on the coast, but densities increased gradually in November. Oil contamination of the feathers was a factor which was more important in Herring Gulls in winter than in late summer and early autumn (Camphuysen 1989). The increase in numbers was less dramatic in data from aerial surveys (Baptist & Wolf 1993). It was estimated that around 22,000 Herring Gulls occurred in the Dutch sector. Moderate to high densities were found near the coast, whereas low densities extended over a much wider area.

Numbers of Herring Gulls further increased in winter, **December-January**, and the lack of widespread surveys in the northern half of the study area is to be pitied here (^{App}Fig. 8.2d). An estimated 108,800 Herring Gulls were thought to occur in the coastal zone, apparently filling a niche which was just abandoned by Lesser Black-backed Gulls. A tentative estimate of 62,500 Herring Gulls offshore (over only 70% of the offshore area; ^{App}Table 8.1) indicates that at least 12% of the NE Atlantic population of Herring Gulls might occur in the southern North Sea in winter (cf. Rose & Scott 1994). The estimate for the Dutch sector of the North Sea is Ca. 117,500 individuals. Over two-thirds of the Herring Gulls wintering in the southern North Sea were adults (71.3%, n= 9877; ^{App}Table 8.3). Large numbers of Herring Gulls were observed from the coast of Noord-Holland in December, whereas numbers were quite small in January (Platteeuw *et al.* 1994) The fact that these data are only collected in one year make further comparisons superfluous Severe winters could produce large numbers of starved Herring Gulls on the beach Numbers of Herring Gulls coastal washing ashore were particularly large in 1979, 1982, 1985, 1987 (Camphuysen 1989) From aerial surveys it was estimated that around 56,000 Herring Gulls occurred within the Dutch sector Hence, the increase found in ship-based survey results was confirmed but seemed much less dramatic.

Herring Gulls were widespread, both inshore and offshore, in **February-March** (^{App}Fig. 8.2e) Moderate to high densities were found in most of the Southern Bight, along the coast and in places in the Nordschillgrund area. A North Sea wide survey in February 1993 showed that Herring Gulls were among the most abundant and numerous offshore species all over the North Sea (Camphuysen *et al.* 1993) Nearly half a million birds were thought to occur in the North Sea at large in February (ESAS unpubl. data) and estimates derived from ship-based surveys in the southern North Sea indicated that around 25% of these birds were found here (55,100 individuals in the zone, 75,900 offshore, ^{App}Table 8.1, just over 100,000 individuals in the Dutch sector). The proportion of adults in these months ranged from 69.5% in March (n= 4524) to 72 8% in February (n = 5631), a similar figure as found earlier in winter. Low to moderate numbers of Herring Gulls were recorded in Noord-Holland during seawatching, without any preferential direction (Platteeuw *et al.* 1994) Strandings of fresh, dead Herring Gulls declined in these months, but old corpses continued to wash ashore in substantial quantities (Camphuysen 1989) The distribution pattern deduced from aerial surveys (Baptist & Wolf 1993) was similar to that from ship-based work. The estimate of total numbers in the Dutch sector was again comparatively low (50,000 birds)

The early breeding season, **April-May** led to a major contraction of birds away from the offshore zone, into coastal waters (^{App}Fig. 8.2f). High densities were found inshore in the Voordelta and along the mainland coast of Zuid-Holland, moderate to high densities occurred elsewhere closely to the coast. Scattered sightings offshore occurred, mainly of immature gulls. It was estimated that 35,800 Herring Gulls occurred in the coastal zone in these months, plus another 9500 individuals offshore. Nearly 40,000 Herring Gulls occurred in the Dutch sector of the North Sea. Adult birds formed just over half of the Herring Gulls found at sea (63.1% in April, n= 2603, 56.4% in May, n = 2481), indicating that for breeding Herring Gulls, feeding areas other than the coastal zone were of great significance for this species (cf. Spaans 1971, Noordhuis 1987, Noordhuis & Spaans 1992). Low to moderate numbers of Herring Gulls were recorded in Noord-Holland during seawatching, flying in equal numbers in both directions (Platteeuw *et al.* 1994). The contraction towards the coast was also noticed during aerial surveys, but Herring Gulls were still also a widespread species in the offshore zone (Baptist & Wolf 1993). It was estimated that some 21,000 Herring Gulls occurred in the Dutch sector.

Conclusions - Herring Gulls were strictly confined to coastal waters during the breeding season and obviously obtained most of their food in these months on land, in the littoral zone or in the Wadden Sea (cf. Spaans 1971). Most gulls were found within 5 km of the nearest coast. Immediately after fledging of the young, the numbers of gulls at sea (and associated with commercial trawlers near the coast; Camphuysen 1993a), fell dramatically, indicating that the postnuptial wing moult was spent on or at least near land. In autumn, a rapid increase in numbers was witnessed leading to high numbers at sea in winter. Peak numbers were observed in winter (estimated over 170,000 individuals, or 12.2% of the NE Atlantic population, ^{App}Table 8.1; Rose & Scott 1994). In winter, Herring Gulls were more widespread and occurred scattered over the offshore zone. Substantial concentrations could be observed at trawlers or associated with offshore installations. Herring Gulls were the most numerous and most frequent scavengers behind commercial trawlers in the southern North Sea (287 records, 48.6% of all identified gulls, n= 63,523; Camphuysen 1993a). Herring Gulls have been observed as scavengers throughout the year, but least frequently in late summer (July- September). In summer, it was essentially a coastal species as a scavenger, while in winter this species appeared as a widespread and common scavenger offshore (Camphuysen *et al.* 1993). As a dominating species at trawlers, Herring Gulls were mainly found within 10 km from the coast off the Delta area and off the Wadden Sea islands and within 20 km from the shore off the mainland coast. Larger groups (>50 individuals) were most frequent from October through July (24-50% of all trawlers with scavenging seabirds), but remarkably absent in August and September (in total 9 flocks of scavenging Herring Gulls, 8 of which less than 10 individuals). Some large flocks of scavenging Herring Gulls were observed in July, while other large groups of scavenging Herring Gulls (>500 individuals), sometimes joined by Mew Gulls and/or Great Black-backed Gulls, were reported during January-March, usually within 10 km from the shore.

An apparent difference between results of aerial and ship-based surveys was the much wider area in which Herring Gulls were reported from the air, but this may be partly effort related. However, considering that vessels may attract these birds and, hence, overestimates are likely to occur, a wider distribution (a large 'grey' area on distribution maps) was more likely to be found from ship-based surveys. Abundance estimates were usually a lot lower than from ship-based surveys, except in summer and late summer when numbers at sea were relatively small.

Updated seasonal patterns in overall abundance (n km^{-1} steamed) and age composition (% juveniles, immature, and adults from all aged individuals), pooling all data collected during ship-based surveys between the mid-1980s and 2012 (from SASBASE) clearly show the peak in abundance of Lesser Black-backed Gulls at sea between April and August (^{App}Fig. 8.3). Juveniles are a significant proportion of the birds seen from August through January, but Lesser Black-backed Gulls are scarce during Nov-Feb. The late summer dip in overall abundance of Herring Gulls is clearly illustrated in this graph, but also the high proportion of adult birds at sea during the peak of the breeding season (^{App}Fig. 8.4). A June-July peak in overall abundance, as found by seawatchers observing seabirds from coastal vantage points (Box 4.2) and suggesting an increased use of marine resources during chick care, is virtually absent. A summer peak could have been partially "overlooked" by ship-based surveys, if the birds would stay close inshore (<5-10km).

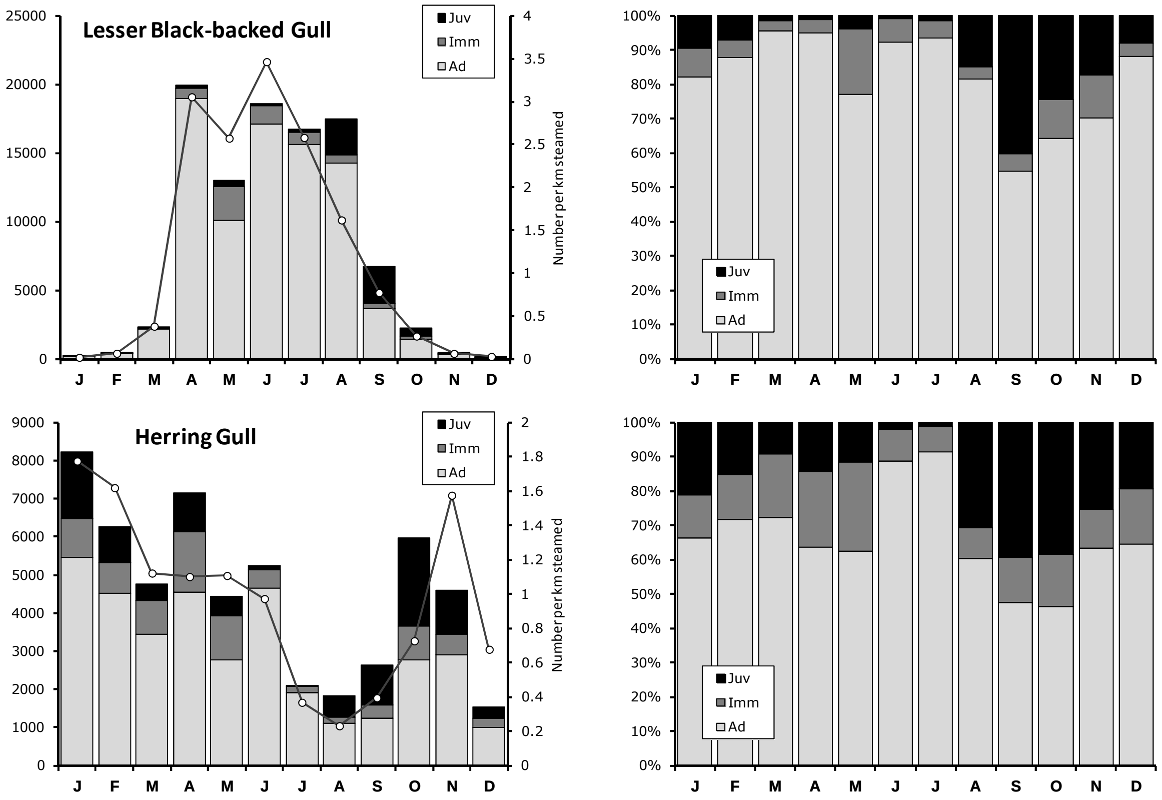


Fig. 8.4 Monthly abundance and age composition in Herring Gulls (adult, immature and first year) from ship-based surveys in the southern North Sea, 1985-2012. (^{App}Table 8.3 updated)

Seabirds and fisheries

It was quickly appreciated that fishing vessels had a profound effect on the distribution of gulls at sea (Skov *et al.* 1995, Stone *et al.* 1995), probably even more so than on most other seabirds, including notorious scavengers such as Northern Fulmars *Fulmarus glacialis* (Camphuysen & Garthe 1997). In two comprehensive studies of the scavenging behaviour and consumption rates of seabirds throughout the North Sea and through the year, it was concluded that Lesser Black-backed Gulls were important [abundant, locally dominant] scavengers at fishing vessels in summer, particularly in the southeastern half of the North Sea (Camphuysen *et al.* 1993, 1995). "*Considering the very high proportion of gulls that were seen in association with nearby trawlers* [relative to naturally feeding individuals] *during strip-transect counts and observations of gulls associated with nearby trawlers, higher than most other species of seabirds observed, it may be concluded that commercial fisheries play a key role in the pelagic ecology of this species.*"

(Camphuysen *et al.* 1995). Herring Gulls were important scavengers at fishing vessels in the winter half year, occurring in all subregions in substantial numbers and often with high feeding success rates when competing for prey with other scavengers at the trawl. Herring Gulls were rather scarce offshore in summer, particularly in August. While several studies have indicated that substantial numbers of Herring Gulls obtained at least part of their food at fishing vessels, it was evident that most birds stayed rather close inshore (mainly within 10km from land; Camphuysen 1995a, Camphuysen *et al.* 1995).

Relevant parts of the, EC funded discards studies (1993-1995) have been reproduced below, because these are still the most comprehensive studies ever conducted within the North Sea. From four cruises covering the entire North Sea in spring, summer, autumn and winter, seabird surveys coupled with discard experiments, the importance of discards for Lesser Black-backed Gulls and Herring Gulls throughout the year and throughout the North Sea was evaluated. The reports are often cited, worldwide, but the results have still only partly been published in refereed paper format. Within the context of this thesis, however, some unpublished results are important enough to warrant reproduction in a shortened format.

Lesser Black-backed Gulls and Herring Gulls as scavenging seabirds in the North Sea

Excerpt from: Camphuysen C.J., Calvo B., Durinck J., Ensor K., Follestad A., Furness R.W., Garthe S., Leaper G., Skov H., Tasker M.L. & Winter C.J.N. 1995. Consumption of discards by seabirds in the North Sea. Final report to the European Comm., study contr. BIOECO/93/10, **NIOZ-Report 1995-5**, Netherlands Institute for Sea Research, Texel, 202+LVIIIpp.

North Sea fisheries increased dramatically since the end of the 19th century and this has provided an increasing opportunity for scavenging seabirds to utilise foods that would otherwise not be available to them. Bycatch, often demersal roundfish and flatfish, and the intestines of gutted fish are discarded in enormous quantities and several species of seabirds which are incapable of diving to the seabed exploit this food resource with great success. The rapid increase in populations of Northern Fulmars, Northern Gannets and several species of gulls has often be attributed to this artificial source of food (Fisher 1952, Harris 1970, Goldbach & Hansen 1979, Croxall *et al.* 1984, Furness 1992).

Discarding bycatch, unmarketable fish and entrails of gutted fish is common practice, probably since fisheries began. It was in the late 19th century that fishery biologists became concerned about this spillage of valuable resources, when Weigelt (1891) investigated the nature, amount, use and exploitation of fishery waste produced by German fisheries. During the second half of this century, with a rapid increase in fishing effort, these concerns increased because large proportions of young fish of commercial species were killed as a result of the discarding practices (e.g. Sahrhage 1958, 1959). Meanwhile, the influence of fisheries is not only of interest for fishery science and the fishing industry but also for other biological and environmental sciences focussing on anthropogenic activities.

EC funded projects in 1993 and 1994-95 were the first synoptic studies of discard utilisation by scavenging seabirds throughout the North Sea. Projects were designed to assess seasonal fluctuations in the distribution and overall numbers of scavenging seabirds and fisheries on a North Sea scale (51°-62°N, 4°W-12°E), to refine knowledge on the attraction of fishing vessels for seabirds, and to assess seasonal fluctuations in discards consumption. Basic questions were:

→ Which seabirds are common scavengers at trawlers in the North Sea ?
→ How numerous are these birds in winter, spring, summer and autumn ?
→ How are these seabirds distributed in each season ?
→ How are North Sea fisheries distributed ?
→ Which fisheries attract most seabirds ?
→ Which part of discards is utilised by seabirds and how do scavenging seabirds interact at the trawl ?
→ How large a proportion of discards and offal is consumed by scavenging seabirds ?
→ How large are the amounts of discards and offal that are released into the North Sea ?

→ How large a number of scavenging seabirds can potentially be supported by fishery waste in commercial fisheries in the North Sea ?

The results of the studies that have been reproduced here include (1) a brief description of each species, including a summary of knowledge with respect to their status as a scavenger at commercial fishing vessels, (2) spatial distribution and relative abundance at sea on the basis of transect counts, and estimates of total numbers in the North Sea based on surveys during this project and the European Seabirds at Sea database, (3) occurrence as a scavengers at the stern of research vessels, and numbers associated with commercial fishing vessels. The results from discards experiments on prey selection, feeding efficiency, feeding strategy, and vulnerability to kleptoparasitism while scavenging at the trawl were presented in Appendix 7 (Box 7.7-9).

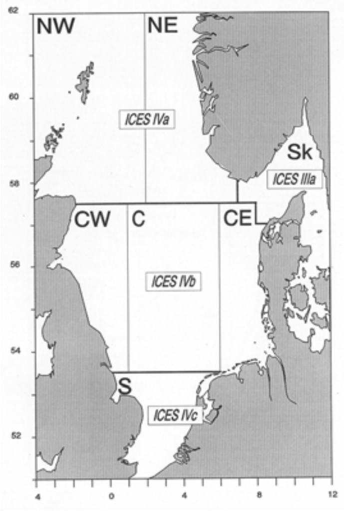
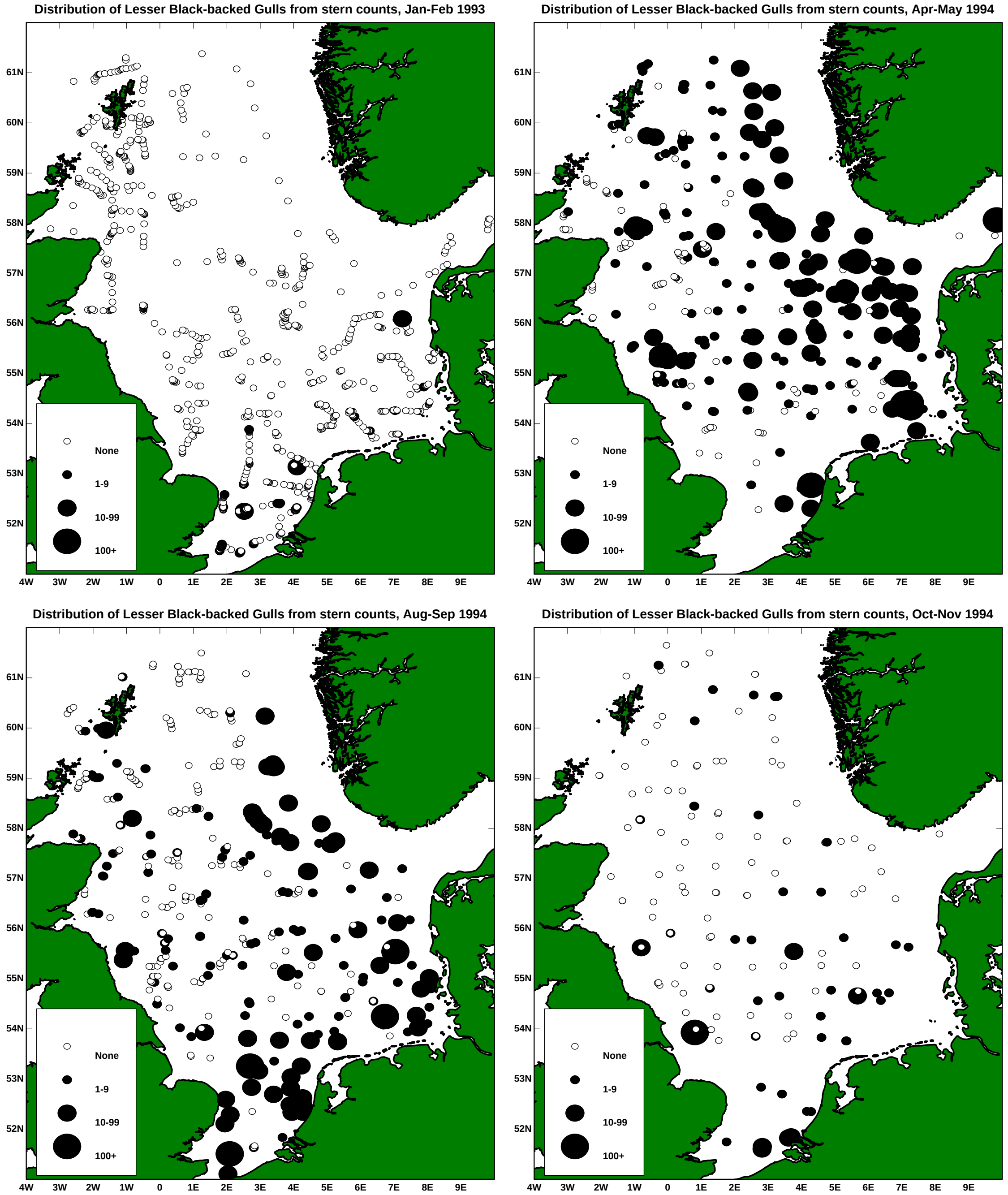


Fig. 8.5 Subregions in the North Sea and ICES fishing areas IVa-c and IIIa.

Material and methods Results are presented for the entire North Sea including the Skagerrak/Kattegat region (51-62°N, 4°W-12°E). The area was divided into 7 subregions on the basis of ICES areas IVa-c and IIIa (AppFig. 8.5). ICES area IVa, the northern part of the North Sea was split into two halves (subregions NW of 156,906 km²and NE of 97,271 km²), the central North Sea, ICES area IVb, was divided into three parts (subregions CW of 69,447 km², C of 140,933 km² and CE of 62,781 km² respectively), ICES area IVc, the Southern Bight, and area IIIa, the Skagerrak/Kattegat area, formed subregions S of 56,763 km² and Sk of 58,972 km² respectively. The total area was calculated as: 643,053 km². The fisheries research vessels engaged in the International Bottom Trawl Survey (IBTS) usually trawled for half an hour in each ICES square visited, steaming approximately 2-3 hours between fishing stations. Seabirds were counted in strip-transects only while steaming. Separate counts were made of the number of birds attracted at the stern of these vessels during fishing to determine the maximum number at each haul. Flocks of birds associated with nearby fishing vessels were identified and counted whenever possible (depending on distance and light conditions).

Lesser Black-backed Gulls were found as scavengers in the Irish Sea, but normally in small numbers (Boswall 1960, Hillis 1971, Verbeek 1977a, Watson 1981, Dare 1982). Dändliker & Mülhauser (1988) reported substantial numbers behind stern trawlers to the west of the Outer Hebrides, Furness *et al.* (1992) list this species among the 'common scavengers' for the Clyde area (southwest Scotland). Around Shetland, Lesser Black-backed Gulls are frequently reported in association with whitefish trawlers, but they were normally present in small numbers and absent during many hauls (Hudson & Furness 1989). In the southern and southeastern North Sea, in summer, the Lesser Black-backed Gull is one of the most numerous scavengers behind fishing vessels (Garthe 1993, Camphuysen 1993abc, 1994ab, Camphuysen 1995a). Coastal breeding Lesser Black-backed Gulls generally have a more marine diet than Herring Gulls and several studies have indicated the importance of fishery waste in the breeding season (Pearson 1968, Noordhuis 1987, Spaans *et al.* 1994). Structural food shortages, possibly related to declines in discard practices or fishing effort, negatively influenced the reproductive output in several breeding populations of Lesser Black-backed Gulls. Recent breeding failures on Skomer (Wales) have been attributed to a decline in fishery waste from Irish Sea trawlers (Walsh *et al.* 1990, Stone *et al.* 1992, Monaghan 1993). Experimental studies in the Bristol Channel and on Terschelling have shown that the provision of supplementary food raised the breeding success of Lesser Black-backed Gulls to normal levels (Hiom *et al.* 1991, Spaans *et al.* 1994).


Distribution of Lesser Black-backed Gulls from stern counts, Jan-Feb 1993

Distribution of Lesser Black-backed Gulls from stern counts, Apr-May 1994

Distribution of Lesser Black-backed Gulls from stern counts, Aug-Sep 1994

Distribution of Lesser Black-backed Gulls from stern counts, Oct-Nov 1994

Fig. 8.6 Seasonal variations in numbers of Lesser Black-backed Gulls at the stern of fisheries research vessels throughout the North Sea.

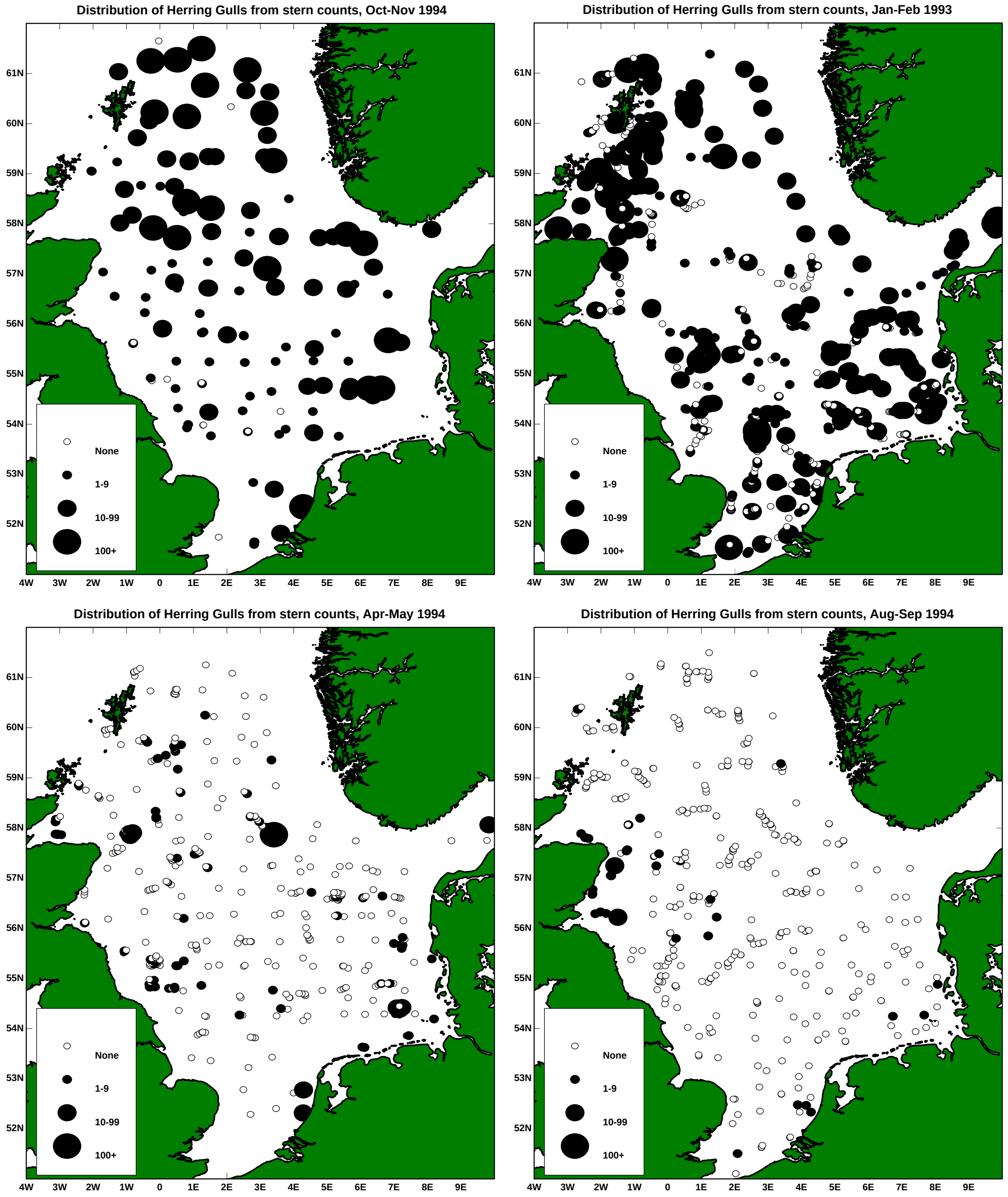
Occurrence and distribution in the North Sea - Lesser Black-backed Gulls were typically summer visitors in the North Sea. Most gulls were found in the southeastern half of the North Sea, frequently offshore, but particularly in coastal waters, and immediately after the breeding season juveniles moved to open sea. In February, Lesser Black-backed Gulls were scarce. In May, the situation had changed considerably. Scattered low to moderate and high densities occurred the eastern half of the North Sea and scattered low densities were found elsewhere. Adults predominated in all subregions (overall 81.4% adult, n= 1689). In August, just over two-thirds of the Lesser Black-backed Gulls observed were adult birds (68.3% adult, n= 1892), and recently fledged juveniles were frequently observed as far away from the coast as in the centre of the North Sea. Scattered moderate to high densities were observed in the southern North Sea (S, C and CE), and high densities were observed in the Norwegian sector in an area with extensive fishing activities. In November, overall numbers were strongly reduced and nearly three-quarters of the Lesser Black-backed gulls were adults (71.4% adult, n= 70), indicating that most immatures had already abandoned the North Sea for their more southerly wintering areas. Lesser Black-backed Gulls were most numerous during the May and August surveys (estimated at 100,000-200,000 individuals) and were otherwise rather scarce at sea. By far the largest numbers were observed in the southeastern half of the North Sea.

Associated with fishing vessels - Lesser Black-backed Gulls observed at the stern of fishing vessels were only common in summer, because most of the population had left the North Sea in November and February. Although this species breeds around the North Sea, the core of its North Sea distribution lies in the southeast and its distribution as a scavenger varied accordingly between subregions. In February, Lesser Black-backed Gulls, as offshore scavengers, were rare in most of the North Sea, except in the Southern Bight (^{App}Fig. 8.6). In May, this picture had changed completely and Lesser Black-backed Gulls were numerous and widespread in most subregions. In August, Lesser Black-backed Gulls had a more inshore distribution and the majority occurred in the southeastern half of the North Sea. Only half the birds aged in August were adults (50.0% adult, n= 2495) and it was obvious that many recently fledged juveniles had moved to sea, immediately after the breeding season. In November, numbers of scavenging Lesser Black-backed Gulls had fallen considerably and occasional large groups were attracted only in the southern half of the North Sea. In summer, 44-55% of the Lesser Black-backed Gulls recorded at sea were seen in association with fishing vessels, a higher percentage than in most other species, indicating the importance of fisheries for these birds.

It was concluded from these surveys that Lesser Black-backed Gulls are important scavengers at fishing vessels, particularly in the (south)eastern half of the study area, in spring and summer, less so in autumn but not in winter. Directly after fledging, juveniles joined mature birds as far away from the coast as the central North Sea to feed behind fishing vessels. Small numbers remained in the North Sea in winter, and most of those were seen in the Southern Bight. Considering the high proportion of gulls that were seen in association with fishing vessels during strip-transect counts and observations of gulls associated with nearby trawlers, higher than most other species of seabirds observed, it may be concluded that commercial fisheries play a key role in the pelagic ecology of this species. From diet studies in colonies, it could be deduced that discards formed only part of the diet and that breeding success was particularly high when 'natural' resources (Clupeids) were abundantly available. However, several recent studies have now shown that a reduction of fishing effort near major breeding colonies have resulted in structural food shortages and poor breeding results.

Herring Gulls are common scavengers at fishing vessels in the Irish Sea, off West Scotland, around Shetland and in the North Sea (Camphuysen 1993a). Hillis (1971) recorded Herring Gulls as the chief scavenging species in the Irish Sea, with up to 500 individuals at a fishing vessel. Of 21,500 scavengers at the trawl of northern Irish Sea Nephrops-trawlers, 65.9% were Herring Gulls (Watson 1981). In the open Atlantic, off Ireland and West Scotland, small numbers of Herring Gulls were reported (Dare 1982, Dändliker & Mülhauser 1988), but Herring Gulls occurred frequently off northern Norway (Strann & Vader 1992). Hudson & Furness (1989) found that proportions of Herring Gulls and Fulmars at fishing vessels interchanged at various distances from the nearest coast, with Herring Gulls becoming increasingly more numerous near land. In the southern North Sea the Herring Gull is one of the more important scavengers at fishing vessels, particularly close to the coast (Berghahn & Rösner 1992, Garthe 1992, Camphuysen 1993a). Near Helgoland, 58% of experimentally discarded offal was taken by Herring Gulls and at least in the offshore waters of the German Bight, these gulls were extremely dependent on fishery waste

(Hüppop & Garthe 1993). Over 60% of all scavenging Herring Gulls at commercial vessels off the Dutch coast were within 10km of the shore, which is significantly different from expected frequencies based on trawler distribution in five distance zones to the coast (G= 54.7, p< 0.001, df= 4; Camphuysen 1993a). Significant correlations between Herring Gull densities at sea and the presence of fishing vessels were found in February, April, November and December. Camphuysen (1993b) found that Herring Gulls were most numerous at fishing vessels in the southern North Sea between October and July, but were virtually absent in August and September (when breeding birds moult their primaries). In the southern North Sea, Herring Gulls were the most numerous (48.6% of all identified gulls at fishing vessels, n= 63,523) and frequent (presence 62.3%, n= 461 fishing vessels) scavengers.


Distribution of Herring Gulls from stern counts, Oct-Nov 1994

Distribution of Herring Gulls from stern counts, Jan-Feb 1993

Distribution of Herring Gulls from stern counts, Apr-May 1994

Distribution of Herring Gulls from stern counts, Aug-Sep 1994

Fig. 8.7 Seasonal variations in numbers of Herring Gulls with fisheries research vessels throughout the North Sea.

Occurrence and distribution in the North Sea - Herring Gulls were typically winter visitors in the North Sea, with high numbers offshore and inshore in November and February and low numbers offshore and low to moderate numbers in coastal waters in the breeding season. The Herring Gull is a common breeding species around the North Sea, but it is obvious that only coastal waters (particularly within 25 km from the nearest coast) are of significance for this species in the nesting season. In February, Herring Gulls were numerous and widespread in the North Sea. Nearly three-quarters of the Herring Gulls observed were mature birds (71.5% adult, n= 1595). In the pre-breeding season, in May, Herring Gulls disappeared almost completely. Small numbers were found in the German Bight and in the central North Sea, whereas Herring Gulls were quite rare elsewhere. In August, Herring Gulls were rare at sea, except off the east coast of Scotland, where moderate to high densities occurred. Nearly half the gulls off the Scottish coast were adults (47.3% adult, n= 207). In November, Herring Gulls had returned en masse into the North Sea after an absence of half a year. Just over half the Herring Gulls observed were mature birds (58.9% adult, n= 1449). Herring Gulls were widespread, with moderate to high densities in several areas. The overall picture, is of the greatest numbers and most frequent sightings in the northeastern two-thirds of the study area. Herring Gulls from northern Scandinavia and the Murmansk region move south after the breeding season to winter around the Norwegian south coast, in the North Sea and in Britain (Schüz 1933, Stanley *et al.* 1981, Cramp & Simmons 1983, Coulson *et al.* 1984). Herring Gulls breeding along the east coast of Britain, in southern Norway, Sweden and along the west coast of Denmark, Germany and The Netherlands are fairly sedentary. Outside the breeding season these birds occur dispersed along the coast, usually within 200 km from their natal colonies (Thomson 1924, Jørgensen 1973, Møller 1981). The observations during ship-based surveys strongly suggest that Herring Gulls enter the North Sea area from the NE, to become widespread and abundant both offshore and inshore during winter, and that the Herring Gull as a 'winter visitor' in the North Sea refers to its nordic populations. Herring Gulls were most numerous in winter with total numbers estimated for February at 0.3-1.0 million individuals and for November at 0.5-1.5 million individuals. In summer, overall numbers probably did not exceed 200,000 individuals. Estimates based on the cruises in 1993 and 1994 must be considered conservative, because the coastal zone was not well covered.

Associated with fishing vessels - As scavengers at the stern of fishing vessels, Herring Gulls were typically winter birds which then occurred widespread, both inshore and offshore (^{App}Fig. 8.7). Being abundant breeding species around the North Sea, it is remarkable to note how few scavenging Herring Gulls were reported in May and, particularly, in August. In February, Herring Gulls were numerous scavengers all over the North Sea, but particularly in coastal waters (up to 100 km away from the coast). Two-thirds of all scavenging Herring Gulls were adults (65.7% adult, n= 9312). In May, this had radically changed. Although occasionally up to 200 Herring Gulls assembled at a trawl (subregions NE and Sk), the species was rather scarce and occurred in less than 25% of the hauls in other subregions. As mentioned earlier, coverage in Dutch and German coastal waters was rather poor and earlier studies indicate that large numbers of scavenging Herring Gulls occur within 10 km from the coast in this region (Camphuysen 1993a, Garthe 1993, Garthe & Hüppop 1994, Camphuysen 1995a). In August, Herring Gull distribution and abundance had changed again. With the notable exception of coastal waters off East Scotland, Herring Gulls did not show up in significant numbers anywhere in the North Sea. Only a third of the Herring Gulls scavenging at the trawl were adults (37.5% adult, n= 816). The November cruises demonstrated a massive return of this species, particularly in the northern and eastern North Sea. Up to 1000 Herring Gulls assembled at a ship (subregion NW) and in most subregions at least at 8 out of 10 hauls Herring Gulls were attracted. Numbers were particularly large in the Fladengrund area (central northern North Sea) and off Shetland and Norway. Just less than half the Herring Gulls observed at the trawl were adults (41.7% adult, n= 2173). Of all Herring Gulls recorded at sea, up to 29% (February) and 83% (May) were observed in association with fishing vessels, indicating the importance of fisheries for this species.

It was concluded that Herring Gulls were important scavengers in the autumn and winter half year, when they occurred in all subregions in substantial numbers, often with high feeding success, certainly for discarded fish species. Herring Gulls were rather scarce offshore in spring and summer, however, particularly in August when only locally in CW and NW some Herring Gulls were found. Previous studies of the coastal waters of the south-eastern North Sea in summer have indicated that substantial numbers of Herring Gulls obtained at least part of their food at fishing vessels. Most birds stayed close inshore, mainly within 10 km from land (Camphuysen 1995a), which explains why during the surveys reported in this contribution (a project in which large, offshore fisheries research vessels were used) so few Herring Gulls were encountered.

Feeding on discards

The discards studies referred to earlier were conducted on fisheries research vessels; a potential flaw that is often mentioned in reviews. Within the southeastern North Sea, bottom trawl fisheries (beamtrawlers and shrimpers) are the most important fisheries providing huge amounts of discards for seabirds (Thiele 1994). While all research vessels used in the EC funded discards projects have used some kind of bottom gears (Camphuysen *et al.* 1993, 1995), it is important to know exactly how fishing operations onboard commercial boats attract seabirds and provide feeding opportunities. Fortunately, there are several published studies on the feeding activities of seabirds in Brown Shrimp *Crangon crangon* fisheries in the North Sea, notably in German waters (Berghahn & Rösner 1992, Walter & Becker 1994, Walter 1997, Walter & Becker 1997). Breeding Herring Gulls are strongly attracted to these fishing vessels for as long as the operations take place in coastal waters or within the Wadden Sea. Lesser Black-backed Gulls were assumed to move further out to sea to visit the off-shore, larger beamtrawlers. It is in a paper published in *Ardea* in 1995 that the differences between Lesser Black-backed Gulls and Herring Gulls as nearshore scavengers were emphasised (Chapter 11). The feeding range of Lesser Black-backed Gulls (95% of all birds within 135 km of the colonies) was considerably larger than that of Herring Gulls (95% within 54 km), reducing the potential for inter-specific competition at commercial trawlers. A more exact description of the fishing operations on board commercial, large, offshore beamtrawlers was based on observations on board a vessel of this kind operating north of the Wadden Sea islands in summer 1993 (Camphuysen 1993, 1994b and *unpubl. data*; Appendix 7). Seabird surveys in the Dutch sector of the North Sea have confirmed the strong attraction of fishing vessels (and other vessels) to seabirds. Of 323,050 recorded large gulls, 180,421 individuals (55.8%) were associated with (fishing) vessels ($^{\text{App}}$Table 8.4).

Table 8.4 Numbers of Lesser Black-backed Gulls and Herring Gulls in the Dutch sector of the North Sea and the numbers of birds associated with marine mammals, floating matter, vessels, platforms or land (1987-2009) and the number of birds observed in multi-species feeding associations (MSFAs). Source: based on SASBASE/ESAS data (NZG/NIOZ/IMARES)

Type of association	**LBBG**	**HG**
Associated with cetaceans	309	16
Associated with front or line in sea	2010	962
Sitting on or near floating wood	20	5
Associated with floating litter	81	477
Associated with oil slick	36	2
Associated with floating seaweed	256	6
Associated with observation base (ship)	15942	12520
Associated with other vessel	1376	855
Associated with or on buoy	229	176
Associated with offshore platform	3947	446
Associated with fishing vessel	80247	69481
Associated with land (e.g. colony)	33	1832
Total number observed	175451	147599
Vessel attracted (n)	97565	82856
% vessel attracted	55.6	56.1

Natural feeding

The evidence that seabirds, notably also Lesser Black-backed Gulls and Herring Gulls, exploit anthropogenic resources at sea and profit from commercial fisheries is overwhelming. Another likely positive effect of human fisheries, paradoxically, has been the overfishing of large predatory fish (Camphuysen & Garthe 2000, Christensen *et al.* 2003). It has been suggested that the gross overfishing of large predatory fish over the last century has led to increases in the survival and stocks of young fish. There is circumstantial evidence, but in fact few factual data, that seabirds have profited from this new situation.

'Naturally feeding seabirds' in the North Sea are a common sight, and the at-sea distribution patterns of seabirds usually match natural, species-specific foraging habitats at sea rather than simply the areas where the fishing fleets are (Garthe 1996, Garthe 1997, Camphuysen & Garthe 1997, Skov & Durinck 2001, Garthe *et al.* 2009). Only a partial overlap exists between the spatial distribution of fishing vessels and that of potentially scavenging seabirds in the North Sea (Skov & Durinck 2001). Gradients in the abundance of seabirds attracted to the ship indicate responses to hydrographic features such as upwelling zones and fronts, and gradients in the supply of natural foods such as fish schools, rather than responses to changes in the supply of discards from fishing vessels.

Not all prey taken at sea originates from fisheries discards (Appendix 7). Studies of the natural foraging behaviour and feeding distribution of the study species are important, given the declining fishing fleet size and planned reductions in discards production (Nerheim 2004, Gilman *et al.* 2006, Rijnsdorp *et al.* 2008, Schou 2011). Inter-specific interactions of seabirds in so-called multi-species foraging associations (MSFAs) have been described from studies at sea in the 1980s and 1990s (Camphuysen & Webb 1999). Based on numerous careful observations of feeding frenzies at sea, the exact role of the key players involved and dominance hierarchies in mixed feeding flocks could be assessed and described. Lesser Black-backed Gulls and Herring Gulls played an insignificant role in these studies, that were mainly conducted off the east coast of Scotland in summer. However, the principle of species-specific roles in feeding frenzies (a mix of interspecific competition and facilitation while feeding) is important, also in the southern North Sea where both gulls are relatively more abundant. The publication triggered the development of a coding system, so that seabird *behaviour* was recorded during at-sea, ship-based seabird studies more systematically after 2002 (Camphuysen & Garthe 2004, Camphuysen *et al.* 2004). The participation in MSFAs (^{App}Table 8.5) is thus an aspect that has been recorded and computer-coded only since 2002. Since that year, 3.0% of all recorded Lesser Black-backed Gulls and 0.9% of all Herring Gulls were seen to join MSFAs targeting 'natural' prey (2002-2009, n= 95,446 Lesser Black-backed Gulls recorded, 55,487 Herring Gulls). Associations with marine mammals have been recorded in all years of study (facilitated foraging; ^{App}Table 8.4). With few exceptions, gulls were following Harbour Porpoises *Phocoena phocoena* that were apparently chasing fish near the surface. Most sightings were in summer (May-Aug), when porpoises are in fact comparatively scarce in the Southern North Sea (Camphuysen 2011c).

Some 7% of the gulls during ship-based surveys in the Dutch sector of the North Sea were recorded as "foraging", but not associated with any obvious features as listed in ^{App}Table 8.4 (note that fronts and other hydrographic features may have been overlooked). Both gull species primarily used plunge diving techniques in which they rarely disappeared completely under water (^{App}Table 8.6). Surface pecking and surface seizing was more frequently seen in Lesser Black-backed Gulls (19% of the foraging individuals, n= 5612) than in Herring Gulls (4%, n= 2870). Concentrations of 'naturally foraging' Lesser Black-backed Gulls were most frequently encountered in two discrete areas: within the 20m depth contour off the mainland coast and off the Wadden Sea islands, and at the 30m depth contour separating thermally stratified central North Sea water and the mixed waters of the southern bight (including an area often mentioned as the Frisian Front; Chapter 13).

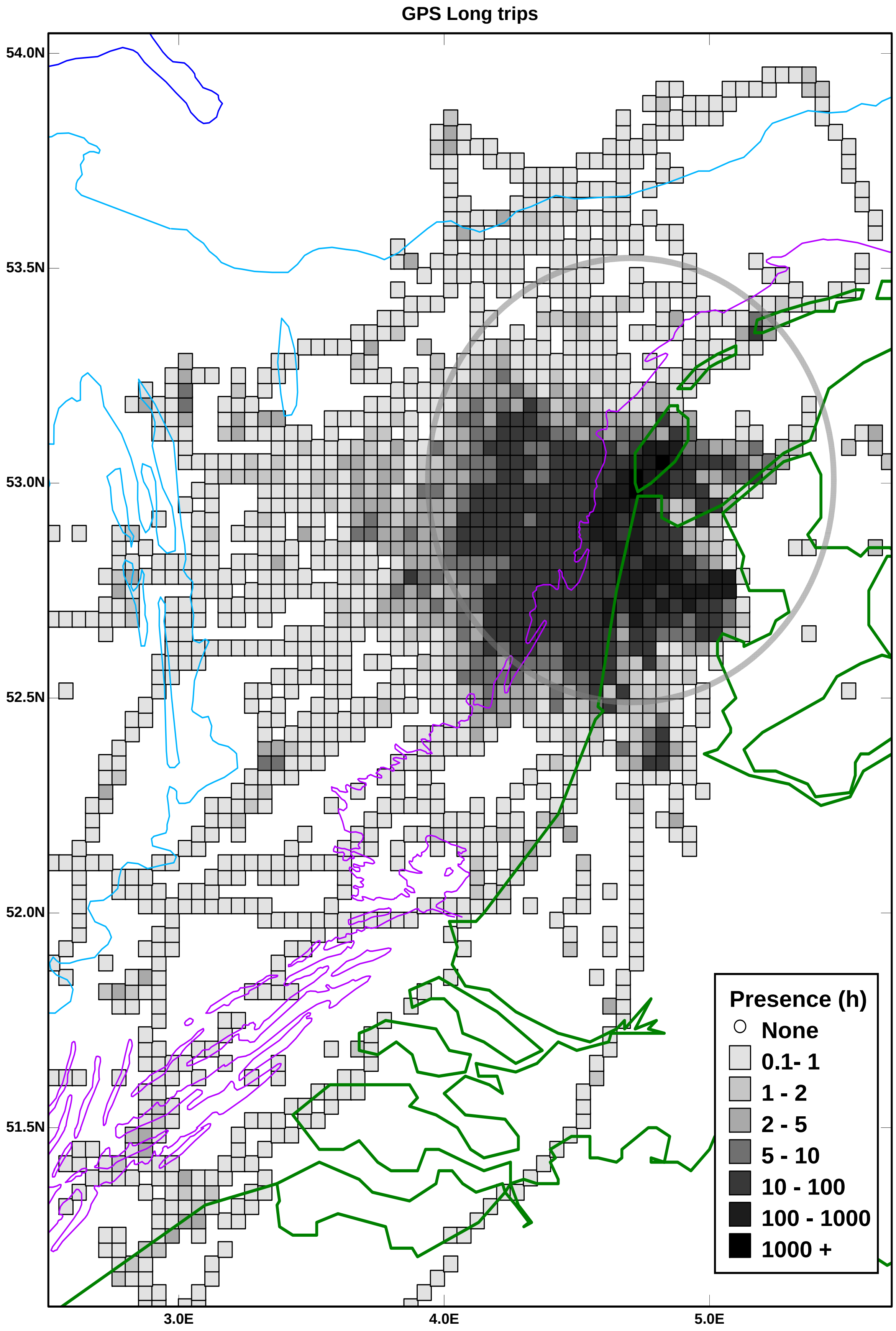


Fig. 8.8. Recorded long-trips of Lesser Black-backed Gulls carrying GPS loggers, 2008-2011. Shadings represent the total time spent within 2°Nx3°E/W rectangles around Texel. Active breeders and failed breeders are included in this map. The circle has a radius of *c.* 60km and is centred over the colony.

Participation in Multi-species feeding frenzies	**LBBG**	**HG**
MSFA participant, no further details	1877	241
MSFA initiator, joined by others	12	11
MSFA participant, joining flock	553	254
MSFA participant, scrounger type	20	
Type II MSFA participant	103	
Drive hunt MSFA participant	289	5
Total number observed	95446	55487
MSFA participation (n)	2854	511
% MSFA participation	3.0%	0.9%

Table 8.5 Numbers of Lesser Black-backed Gulls and Herring Gulls in the Dutch sector of the North Sea observed in multi-species feeding associateions (MSFAs), 2002-2009. Source: based on SASBASE/ESAS data (NZG/NIOZ/IMARES)

Foraging techniques	**LBBG**	**HG**
Holding or carrying prey	44	28
Feeding, method unspecified	2291	6079
Aerial pursuit[3]	116	355
Scavenging[2]	11	12
Dipping[1]	1532	1308
Surface seizing[2]	333	49
Surface pecking[2]	744	58
Deep plunging[1]	10	2
Shallow plunging[1]	2866	1086
Actively searching	4902	1491
	12849	10468
[1]Plunge diving & dipping	79%	84%
[2]Surface activities	19%	4%
[1-3]Total specified foraging	5612	2870

Table 8.6 Foraging techniques deployed by Lesser Black-backed Gulls and Herring Gulls in the Dutch sector of the North Sea, excluding birds that were associated with marine mammals, floating matter, vessels, platforms or land (1987-2009) and excluding birds in multi-species feeding associations (MSFAs, 2002-2009). Source: based on SASBASE/ESAS data (NZG/NIOZ/IMARES)

Modern techniques: the use of dataloggers

With modern tools, for the first time, we were able to follow individual birds with a known origin and nesting activity, into the open sea. GPS loggers deployed in 2008-2011 on **Lesser Black-backed Gulls** have revealed numerous unexpected aspects, many of which still await further analysis. An overwhelming majority of the recorded foraging trips of Lesser Black-backed Gulls (active and failed breeders included) were within 80 km from the nest (99%; ^{App}Fig. 8.8) with a mean trip duration 7.0 hours during incubation, 6.3 hours during chick care and 12.9 hours for failed breeders. Some were exceptionally distant trips, however, or of an unusually long duration and the characteristics of these so-called "freak-trips" have been addressed in Chapter 8.

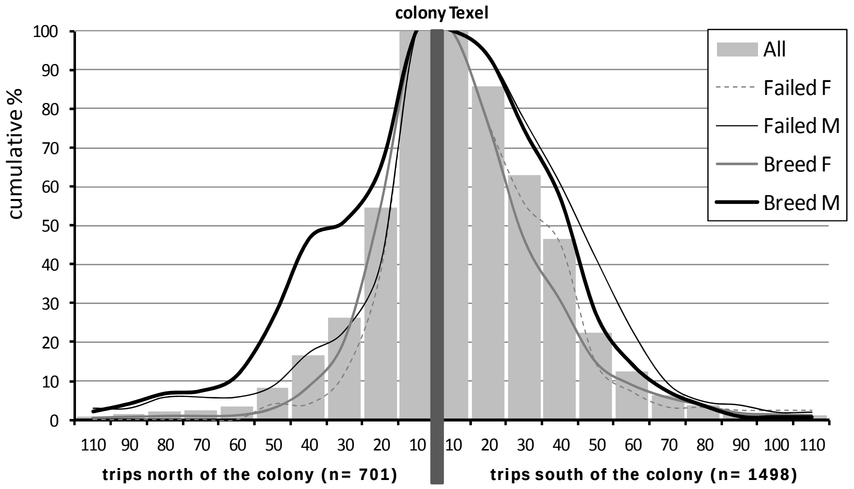


Fig. 8.9. Frequencies of maximal distances of long-trips of Lesser Black-backed Gulls carrying GPS loggers, 2008-2011 to the north (left) and to the south (right) of the colony at Texel. Shaded bars represent all individuals; lines reprensent active breeding males and females and failed males and females. Cumulative percentages to the north (n= 701 trips) and to the south (n= 1498 trips) in 10 km distance bands (110= >100km distance).

Most foraging trips were towards foraging areas to the southwest (North Sea), south (North Sea and Continental mainland), southeast (Wadden Sea and Continental mainland) and east of the colony on the island Texel (^{App}Fig. 8.8-9, details in Chapter 10). Nearshore waters along the mainland coast, south to IJmuiden, and the Southern Bight, were the most important offshore foraging areas for Lesser Black- backed Gulls from Texel. This zone was highlighted on the basis of ship-based surveys as an area with frequent observations of naturally foraging flocks of gulls (within the 20m depth contour). Dipping gulls (capturing Nereid worms *Nereis longissima*) and shallow-punge diving individuals (capturing swimming crabs) have been seen in these waters. The logger data indicated that trawlers were certainly targeted in this area, sometimes by birds that used roosts at the beach as a temporary base station. Few Lesser Black-backed Gulls foraged to the northwest of the breeding colony, a sea area that is actually packed with Lesser Black-backed Gulls in summer. Also the Frisian Front area was rarely utilised by tagged birds from Texel. The high densities of Lesser Black-backed Gulls in that area, and between the Frisian Front and the Wadden Sea islands, most likely comprised birds from colonies at Vlieland and Terschelling (see Chapter 11).

For **Herring Gulls**, there are no tracking data available from the Kelderhuispolder colonies. Studies of the diet composition, seawatching data, and offshore surveys all indicated that marine resources are scarcely used in the early breeding season, but more frequently during chick care. A restricted foraging range would lead to foraging concentrations around nearshore shrimpers in North Sea coastal waters and within the Wadden Sea rather than in association with the larger offshore beamtrawlers. The occurrence of juvenile flatfish and Brown Shrimps in may food samples collected in the period of chick care seem to confirm that. Large flocks of scavenging (adult) Herring Gulls (usually outnumbering Lesser Black-backed Gulls) behind shrimpers are indeed a common sight from coastal vantage points (www.trektellen.nl). Further offshore, scavenging Herring Gulls are scarce in summer (Chapter 11). SOVON fitted Argos PTTs on 11 adult Herring Gulls breeding at the nearby island Vlieland in 2007-8 (Box 5.1). None of the tagged birds from Vlieland were seen to target fishing vessels along the North Sea coast for any significant length of time, and few were recorded to spend significant amounts of time in the deeper gullies of the Wadden Sea where many shrimpers are working (http://www.sovon.nl/; ^{App}Fig. 5.3). Perhaps even more remarkable is that there is no evidence for a significant use of marine resources outside the breeding season (*i.e.* in winter) from Herring Gulls tracked with Argos PTTs, suggesting that the winter population offshore in the North Sea at large may be from an entirely different origin. Future tracking projects will be required to get a better idea of the utilisation of marine resources by Herring Gulls breeding at Texel.

Appendix 9 - Intertidal and terrestrial habitats

The significance of the Wadden Sea for Herring Gulls, both as a breeding and as a foraging area, is widely acknowledged (Smit & Wolff 1980, Van de Kam *et al.* 1999). Herring Gulls were listed among "the 32 most important estuarine birds species of the Wadden Sea" (Smit & Wolff 1980). The tideline and exposed mudflats in estuaries and in the Wadden Sea are important feeding areas for them (Spaans 1971, Smit & Wolff 1981). To turn this fact around, the numbers of carnivorous Herring Gulls in an area like the Wadden Sea are so large that this species must be a factor of importance in the regional ecosystem. The mean number of Herring Gulls in the Dutch part of the Wadden Sea (based on shore-based waterbird counts) in the 1970s ranged from 15,000 in February-March to 40,000 between September and December (Smit & Wolff 1981). Using an average of 15,000 individuals per day ("bird days") on tidal flats, deriving a BMR of 78 Kcal day^{-1} (~3.7W) from a mean body mass of 990g, assuming a FMR of 5BMR, Smit (in Smit & Wolff 1981) calculated the daily consumption by Herring Gulls of 5^6 Kcal (21^6 kJ). A similar consumption was expected in subtidal areas. With Black-headed and Mew Gulls, Herring Gulls were calculated to account for 17% of the total bird consumption (11% in subtidal areas and 6% on tidal flats). Cadée (1995) calculated that Herring Gulls, with Red Knots *Calidris canutus* and Common Eiders *Somateria mollissima*, are the most important avian shell-crushing predators that account for most of the shell fragments present in Wadden Sea sediments (leaving little room for physical factors).

Recent waterbird counts by SOVON in the Wadden Sea produced higher numbers of Herring Gulls in the late 1970s and 1980s (annual mean *c.* 60,000) than Smit & Wolff (1981), but indicated gradual declines in numbers since the early 1990s (Hustings *et al.* 2009, Hornman *et al.* 2011). Currently, peaks in abundance are observed directly after the breeding season (August-September; *c.* 80,000 individuals) and in mid-winter (January-February; *c.* 100-120,000); relatively low numbers occur in November (*c.* 30,000) and May (*c.* 25,000). The energetic requirements during breeding (modern calculations such as in Box 7.2 arrived at *ca.* 30% higher values during breeding than those assumed by Smit & Wolff 1981) are such that Herring Gulls must still be considered a highly significant component of the Wadden Sea ecosystem.

High numbers of Lesser Black-backed Gulls breed on Wadden Sea islands of The Netherlands, Germany and Denmark (Fleet *et al.* 1994, Olsen 1992, Hälterlein 1998, Garthe *et al.* 2000, Koffijberg *et al.* 2006). Three Natura 2000 areas within the Wadden Sea have been designated, with the high numbers of breeding Lesser Black-backed Gulls as important conservation issues (Janssen & Schaminée 2009). The importance of the Wadden Sea as a foraging area for this species is less well understood, however. Lesser Black-backed Gulls were not listed among "the 32 most important estuarine birds species of the Wadden Sea" (Smit & Wolff 1980). Van de Kam *et al.* (1999) do acknowledge the substantial breeding population, but do not provide information on the foraging ecology other than that Lesser Black-backed Gulls capture fish in the North Sea. The Lesser Black-backed Gull is not even mentioned as a species in a recent overview on migratory waterbirds in the (international) Wadden Sea (Laursen *et al.* 2010). Recent reports on waterbird counts in The Netherlands failed to specify numbers of Lesser Black-backed Gulls for the Wadden Sea area or to produce substantial species accounts in the text (Hustings *et al.* 2009, Hornman *et al.* 2011, 2012).

The occurrence inland - The gulls in this thesis are regarded as coastal seabirds, but they also frequently utilise terrestrial resources (Furness & Monaghan 1987). Their inland presence (at roosts or in bathing places) and terrestrial foraging activities are well known, but relatively little studied ecological aspects (but see Andersson 1970, Spaans 1971, Demuth 1983, Horton *et al.* 1983, SOVON 1987, Vauk & Prüter 1987, Voslamber 1991, Hüppop & Hüppop 1999, Vercruijsse 1999, Camphuysen *et al.* 2006, Coulson & Coulson 2008). During strong winds and in heavy rains, much higher numbers of gulls (including at least Herring, Lesser Black-backed, Black-headed and Mew Gulls) are visible in compact flocks on land than during fine conditions (SOVON 1987).

Regarding inland foraging opportunities, Spaans (1971) showed that food from refuse dumps was important for Herring Gulls in the late 1960s, but particularly in winter. From inland water bird counts in winter in the 1980s, Herring Gull concentrations were reported to occur at sites with ample supplies of (anthropogenic) waste such as landfill areas, industrial areas, harbours, large cities (SOVON 1987). Violent storms could make nearly the entire population to seek refuge at inland roosts and foraging areas (mainly in Nov-Apr, much less so in May-Jul). In mild winters, Herring Gulls were seen throughout the country. Important areas in winter were the Wadden Sea, fishing harbours of Den Helder and IJmuiden, in Amsterdam and surrounding urban areas, on the Maasvlakte and in the Delta area. The large demostic refuse dump at Wijster (Drente) was attraction number one deeper inland. Large numbers of Herring Gulls could be seen in central Friesland and along the coast of the entire IJsselmeer, especially in January. Cold winters could lead to concentrations in the Delta area, along the larger rivers and in cities and larger villages. After the breeding season, Herring Gulls were found to disperse to rich feeding areas in the Delta area and within the Wadden Sea. Later in autumn, inland sites gain popularity and peak numbers at Wijster were found only in November (c. 20 000). Along the larger rivers, the highest numbers were recorded in Dec-Feb. The utilisation by large gulls of human waste as a food supply, particularly sewage and refuse emanating from our towns and cities, coupled with their habits of roosting on agricultural land and water storage reservoirs and of breeding on inhabited buildings, gave rise to concern over the role of these birds in the spread of disease to man and domestic animals (Girdwood *et al.* 1985, Whelan *et al.* 1988).

The same analysis by SOVON published in the late 1980s indicated that Lesser Black-backed Gulls could be seen year-round within The Netherlands, but mainly in coastal provinces and along the larger rivers (SOVON 1987). Numbers recorded deep inland were often rather small; higher numbers occurred in the IJsselmeer and in the Delta area. From March on, numbers of Lesser Black-backed Gulls along the rivers declined and concentrations around the major (coastal) colonies grew substantially. From June on, small numbers re-appear along the major rivers and these birds were probably mainly immatures, non-breeding adults or failed breeders. Larger flocks were formed in some areas (Waal, Rijn, southern Maas), in other parts gulls were scarce (IJssel, northern Maas). Numbers were higher in August and September, with migratory movements of Lesser Black-backed Gulls throughout the country. After October, the remaining birds concentrate along the coast and larger rivers, with low numbers elswhere at inland locations and low numbers in the Wadden Sea district.

Many ornithologists claim that the numbers of Lesser Black-backed Gulls foraging inland have increased markedly in recent years. Confronted with the fact that the Dutch breeding population has increased exponentially between the 1970s and late 20th century, few of them dare to claim that this has been the result of a change in foraging behaviour and feeding habitat rather than simply a higher overall abundance. Data compilations based on sightings stored in www.trektellen.nl and certainly www.waarneming.nl are inconclusive in this respect, and cannot be compared directly with the atlas produced in the late 1980s (SOVON 1987). In Appendix 2 has been shown how changes in waste management over the past three decades have reduced access to domestic refuse, but there are still opportunities. In this Appendix it is explored how important domestic refuse still is and where the birds currently might obtain it.

Inland breeding - The occurrence of inland breeding and roof-nesting has been reported since the mid-20th century (Strijbos 1942ab), but is increasing in recent decades (de Jong 1984, Vegelin 1989, van der Helm 1992, Anon. 1994a, Cottaar 1994, Anon. 1995, Poot 2008, Roobeek 2010). The same has been witnessed in surrounding countries (François 2003, Rock 2005) and roof-nesting as well as inland feeding large gulls were quickly disqualified as being a nuisance and a formidable health and safety issue (Butterfield *et al.* 1983, Coulson *et al.* 1983a, Rock 2003). Several coastal cities, notably Leiden, Den Haag (Zuid-Holland), IJmuiden, and Alkmaar (Noord-Holland) currently have well-established roof-nesting breeding populations (http://www.meeuwenoverlast.nl) that seemingly reproduce at rather high rates and with relatively many recruits in immature plumage (both indicative for expanding, growing colonies; impressions from personal observations; no accurate data available). Inland breeding large gulls still concentrate in cities that are relatively close to the coast, and marine foraging opportunities are therefore still available. Hüppop & Hüppop (1999) suggested that the inland breeding distribution of Herring Gulls was limited by the availability of fish during the breeding season rather than by the availability of human refuse or by the lack of breeding. Exactly how important the foraging conditions on land (and within cities) are for these city-dwelling, roof-nesting gulls is often unclear and an aspect that is certainly understudied. This thesis will not evaluate the foraging ecology of birds breeding in cities, but the data collected at Texel indicate that some birds breeding on the island explore resources of food that are typical for large cities.

This Appendix and Chapter 14 report on the intertidal and inland foraging opportunities of the two species of gulls breeding in the western Wadden Sea. As a starting point, dietary information is examined: which (common) prey items occur that are certainly not marine. A second set of data is the information obtained from colour-ringed individuals (Box 4.1). It is clear that these data need to be treated with care, given the unevenness in observer effort and the bias towards areas where ring-readers can successfully collect data. Finally, the tracking data will be explored to shed more light on the exact foraging areas and habitats of both species of gulls.

Dietary information

From dietary information collected in the Kelderhuispolder colony (Appendix 7), prey items from the marine habitats (offshore) occurred in nearly 90% of all 5256 prey samples collected from Lesser Black-backed Gulls during breeding (^{App}Table 9.1). Prey from intertidal habitats occurred in three quarters of 5542 prey samples collected from Herring Gulls. Prey from terrestrial sources (ignoring human waste materials categorised under Anthropogenic) was slightly more prominently represented in Lesser Black-backed Gulls (32%) than in Herring Gulls (23%). Human waste was more frequently found in Herring Gulls (13%), than in Lesser Black-backed Gulls (6%).

Table 9.1. Frequency of occurrence (n, %) of prey items from different habitats in Lesser Black-backed Gulls (n= 5256 food samples) and Herring Gulls (n= 5542 samples), Kelderhuispolder colony, 2006-2011. Waste materials classified under "Anthropogenic" originated probably all from land.

Origin of prey	Lesser Black-backed Gull		Herring Gull	
Marine[1]	4593	87.4%	1268	22.9%
Intertidal[2]	131	2.5%	4122	74.4%
Terrestrial[3]	1691	32.2%	1299	23.4%
Anthropogenic[4]	297	5.7%	710	12.8%
Undetermined	155	2.9%	891	16.1%
Sample size (n)	5256		5542	

[1] **Marine:** polychaetes, sponges, echinoderms, gastropods, bivalves, cephalopods, crustaceans, roundfish, and flatfish; [2] **Intertidal:** polychaetes, echinoderms, gastropods, bivalves, and crustaceans; [3] **Terrestrial:** insects, oligochaetes, snails, crustaceans, freshwater fish, amphibians, non-passerine birds, passerine birds, mammals, and plants; [4] **Antropogenic:** human waste.

Intertidal prey species - At least 40 prey types and species found in the Kelderhuispolder studies were most likely taken in the intertidal zone (the North Sea beach included; Appendix 7). In total 37 of these prey could be identified at least to genus level, including:

marine polychaetes *Lanice conchilega, Alitta virens, Nereis diversicolor*, echinoderm *Asterias rubens*, gastropods *Littorina littorea, Hydrobia ulvae, Polinices catenus, Littorina saxatilis*, bivalves *Mytilus edulis, Cerastoderma edule, Spisula subtruncata, Macoma balthica, Ensis directus, Spisula solida, Venerupis senegalensis, Scrobicularia plana, Mya arenaria, Crassostrea gigas, Petricola pholadiformis, Mya truncata, Donax vittatus, Abra tenuis, Chamelea striatula*, barnacles *Balanus crenatus, Balanus spp*, isopods *Idotea balthica, Idotea pelagica*, amphipods *Gammarus spp, Jassa marmorata*, decapods *Carcinus maenas, Hemigrapsus sanguineus, Hemigrapsus pensillatus, Portunus latipes*, marine plants *Enteromorpha spp, Ceramium rubrum, Ulva lactuca*, *Sargassum muticum*.

Between 2006 and 2011, 19 of these species were found in 142 prey samples (2.6%, n= 5361) of Lesser Black-backed Gulls. The most frequently found prey species were *Alitta virens* (63x; possibly taken while foraging over the surf along a North Sea beach), unidentified *Carcinus*/*Liocarcinus* (47x[1]), and *Ensis directus* (11x; exclusively encountered as flesh to provision the chicks, from moribund shells washed ashore on the North Sea beach). The dietary data suggest that Lesser Black-backed Gulls from Texel do forage (at least occasionally) along the North Sea shoreline, but rarely on mudflats or in shallower gullies of the western Wadden Sea. At least 34 of these intertidal species were found in 4122 prey samples (74.4%, n= 5543) of Herring Gulls with *Mytilus edulis* (3493x), *Carcinus maenas* (540x), *Ensis directus* (376x), *Cerastoderma edule* (140x), and *Asterias rubens* (86x) as most commonly encountered prey items. Within a radius of *c.* 30km around the colony, access to these commoner prey types is available in a number of locations (AppFig. 9.1).

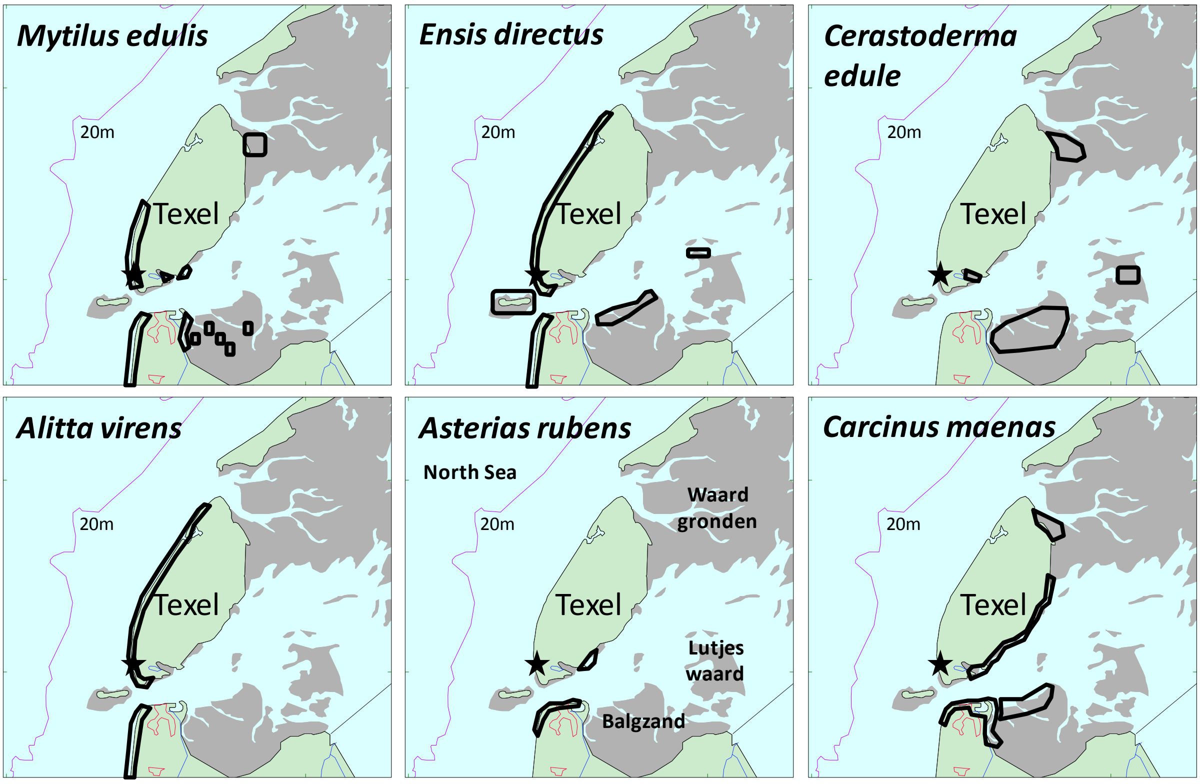


Fig. 9.1 Likely areas to access common intertidal prey species for Herring Gulls: **mussels** *Mytilus edulis* on hard substrate (breakwaters) along the North Sea coastline, and localized mussel banks in Mokbaai, near 't Horntje, and De Cocksdorp at Texel, mussel beds in the Balgzand area); **American razorclam** *Ensis directus*, moribund washed ashore on sandy beaches (with and without breakwaters) including Noorderhaaks, or (difficult to access) in situ in more exposed mudflats of the Balgzand area; **common cockles** *Cerastoderma edule* in Mokbaai at Texel and in cockle beds on mudflats of Balgzand, Lutjeswaard, and off Cocksdorp**; king ragworm** *Alitta virens* as free-swimming (spawning?) worms in the surf, **common starfish** *Asterias rubens* and **common shore crabs** *Carcinus maenas during* receding tides in shallow waters off dikes and in harbours or in gullies in the northern Balgzand area.

Mussels are plentiful available on breakwaters (hard substrate) that occur perpendicular of sandy beaches between De Koog (Texel) and Schoorl (mainland Noord-Holland). These mussels are exposed to rough seas, have relatively heavy (thick) shells, and are sometimes overgrown with barnacles *Balanus* spp. Since smaller mussels have to be pulled loose and are often ingested in small clumps, breakwater mussels encountered in pellets are often polluted with grit and fossil

---

[1] no evidence for *Carcinus* taken by Lesser Black-backed Gulls otherwise, so these may all have been swimming crabs taken at sea

(sea) shell fragments. Alternative sites are mussel beds (some of which currently overgrown by Pacific Oysters) in the Mokbaai at Texel, in the Balgzand area and off De Cocksdorp in the north of the island. These mussel bed mussels are often overgrown with barnacles. In the deeper gullies of the Malzwin (Gat van de Stier, immediately to the east of the major inlet Marsdiep), floating contraptions been constructed to catch mussel seed from the water column (settlement of seed on nets; "*Mosselzaadinvanginstallaties*" MZI). The mussels in these installations will not be readily available for foraging gulls, but during harvesting or transports they might be. These subtidal mussels are typically clean (no barnacles) and thin-shelled.

Box 9.1 - Bizarre prey items

Unusual or even bizarre prey was sometimes found in the course of the ecological study of Herring Gulls and Lesser Black-backed Gulls nesting at Texel. The diet of these omnivorous species is spectacularly varied, but most individuals simply feed on energy rich, natural prey such as bivalves, fish and crustaceans. Bizarre prey and junk food are the exception rather than the rule. All prey were examined in considerable detail, because it could point at foraging locations that were either unexpected or otherwise unknown. A rare (aquarium) fish, plastic dolls and soldiers, a mobile phone and a medal are examples of bizarre or at least unusual prey. Some of the junkfood was accompanied with plastics, foils and paper indicating hasty meals. Some gulls produced pellets that almost entirely consisted of glass, plastic, aluminum foil, and other rubbish.

More traditional prey items (domestic refuse), including selection of sausages, cheese spread and other plastics plus a wooden float for angling (15cm long).

Mobile phone, food remains are scraped off, now defunct (except the memory card)

A plastic and paper pellet.

A plastic doll (legs) filled with onion rings and fish vertebrae (bottom).

Medal on ribbon

Plastic soldiers (all in one pellet)

Source: Camphuysen C.J., S. Boekhout, A. Gronert, V. Hunt, T. van Nus & J. Ouwehand 2008. Bizarre prooien: vreemd voedsel opgepikt door Zilvermeeuwen en Kleine Mantelmeeuwen. Sula 21: 49-61.

Terrestrial prey - Appendix 7 provided evidence for 114 terrestrial prey species or types, plus 92 "anthropogenic" types, many of which probably came from terrestrial sources (see also Box 9.1). Several of these prey, including some mammals and particular types of domestic refuse, showed that at least some of this must have been taken somewhere on the Continental mainland. Many of the observed terrestrial prey items could have been obtained just about anywhere. Common prey items that cannot be easily pin-pointed to a certain resource were:

> Coleoptera (frequency of occurrence, two gull species combined, 2006-2011; 570x), unident insects (396x), bread (137x), bread seeds (120x), plastic fragments (119x), plastic line or thread (108x), unidentified plant seeds (108x), Carabidae (77x), Elateridae (67x), Rabbit *Oryctolagus cuniculus* (65x), terrestrial snails (55x), Plantae (50x), Formicidae (48x), wood (43x), plastic pellets (41x), polystyreen (40x).

From the colony itself were:

> large gull pullus (589x) or eggs (494x).

From nearby dunes on Texel:

> Berries of Crowberry *Empetrum nigrum* (145x).

From freshwater reservoirs either on Texel or on the mainland:

> Roach *Rutilus rutilus* (139x).

From grasslands either on Texel or on the mainland:

> grassland *Lumbricus terrestris* setae (255x) and the crystalline calcite that is excreted by these worms(88x), unidentified grass seed (70x), unidentified Poaceae leaves (47x).

From grasslands on Texel:

> Zea mays from sheep feeders (192x).

From refuse dumps or urban areas on Texel or on the mainland:

> plastic packaging (168x), chicken (160x), plastic foil (108x), pork (82x), paper (76x), aluminium foil (52x), pieces of broken glass (48x), vegetables (48x).

The occurrence of mammalian prey in the diet of Herring Gulls and Lesser Black-backed Gulls breeding at Texel was analysed in order to quantify and compare the predation on mammals from coastal and inland colony sites (Chapter 14). Specialised coastal nesting birds and a majority of individuals in an inland colony were found to frequently feed on mammals (hedgehogs, shrews, voles, mice, moles, rats, rabbits and hares). Most mammalian prey may have been obtained on inland fields, perhaps during ploughing or other activities of farmers, some may have been captured within the colony, and some will have been scavenged at roadsides. The presence of moles *Talpa europaea* in pellets found on Texel (where this species does not exist) was further evidence for foraging activities on mainland grasslands.

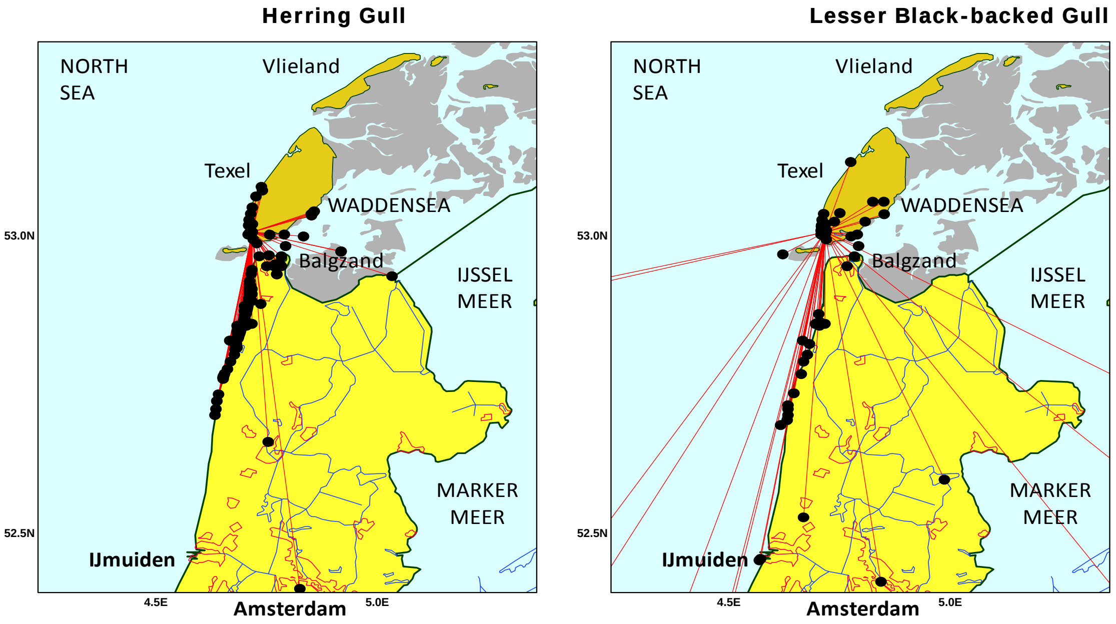


Fig. 9.2 Re-sightings of adult Herring Gulls (n= 952) and Lesser Black-backed Gulls (n= 174) colour-ringed as adult breeding birds in summer around the Kelderhuispolder colonies on the south tip of Texel.

Foraging distribution (1) colour-ring sightings

The just over 1300 colour-ringed gulls from the Kelderhuispolder colonies have generated more than 6000 re-sigthings$^{\text{Oct 2012}}$ outside the colony. A selection of sightings of adult birds within the breeding season would give at least some idea of the foraging range of these birds and hopefully also of the most important foraging habitats ($^{\text{App}}$Fig. 9.2). At first glance, the re-sightings locations of the two species are rather similar: mostly on the southern half of Texel, with frequent re-sightings along the mainland coast of Noord-Holland and in Den Helder. A more detailed analysis would show the differences between the species. Herring Gull re-sightings at Texel were mostly confined to the three harbours (Oudeschild, NIOZ and ferry harbours), the Mokbaai (usually resting), and breakwaters along the coast (foraging on mussels). Lesser Black-backed Gulls were more frequently seen in grasslands, on beaches off the colony rather than on any of the breakwaters, on bathing places to the northeast of the colony and in the ferry harbour. Many more Herring Gulls than Lesser Black-backed Gulls were reported from Den Helder city, just opposite to the colony on the mainland. From the ferry between Texel and Den Helder, both species were reported (foraging on bread and other food provided by tourists).

Table 9.2 Observed activities of colour-ringed Herring Gulls and Lesser Black-backed Gulls along the North Sea coast of Noord-Holland, between Schoorl and Den Helder (2006-2012; only sightings by Arnold Gronert).

	Herring Gull				**Lesser Black-backed Gull**			
	Adult	Immature	Juvenile	%	Adult	Immature	Juvenile	%
Foraging breakwater	379x	268x	119x	43.7%	1x	1x	1x	7%
Foraging tideline	25x	13x	11x	2.8%				0%
Preening	190x	92x	30x	17.8%	7x	3x	4x	33%
Resting	348x	202x	75x	35.7%	18x	2x	6x	60%
Total re-sightings	942	575	235	(n= 1752)	26	6	11	(n= 43)

Most re-sightings originate from the North Sea coastline of Noord-Holland, all the way down to Schoorl aan Zee (36km south of the breeding colonies, 52°41'N, 04°38'E). This coastal area is of significance as a resting area (beach roosts and roosts on agricultural land just inland, behind the dunes and dikes), and as a feeding area, notably for Herring Gulls. It is important to realise, however, that this stretch is also the '*hunting terrain*' of two keen ring-readers, Arnold Gronert (7492 re-sightings$^{\text{Oct 2012}}$ of birds ringed by Arie Spaans 1986-88, at Texel since 2006, Vlieland since 2007 and in IJmuiden since 2008) and Ruud Costers (3972 re-sightings$^{\text{Oct 2012}}$) who aimed at carefully documenting each and every colour-ringed gull on the coastal stretch between Schoorl and Callantsoog for more than 25 years. From these documented sightings, however, it can be calculated that of 1752 Herring Gulls from Texel seen in the area (any age, anytime), some 45% were actively foraging and mostly on the coastal breakwaters (hard-substrate mussels). Of the only 43 Lesser Black-backed Gulls, only a small fraction was seemingly foraging, while nearly 95% of the birds were preening or resting on roosts ($^{\text{App}}$Table 9.2).

The mudflats of the Balgzand area were visited only once by observers (March 2012), but that visit produced sightings of five colour-ringed birds from Texel (resting at low tide on the exposed flats), suggesting that this area may in fact be rather important. Few people have access to this intertidal area, and ring-reading is extremely hard because the birds are shy.

The absence of sightings in the northern part of Texel could be an observer-effect, but the frequent sightings of colour-ringed birds from Vlieland in that part of Texel (and the confirmation of the utilisation of resources at Texel by the birds carrying Argos PTTs, see below), suggest that the scarcity of Kelderhuispolder birds in that area is a genuine aspect of their foraging distribution.

The most distant re-sightings of adult breeding birds were Herring Gulls and Lesser Black-backed Gulls foraging in Amsterdam (ICOVA refuse processing plant and Amsterdam city; 60-70km south of the breeding colony).

Foraging distribution (2) information from dataloggers

Herring Gulls - At Vlieland, SOVON and partners colour-ringed 12 Herring Guls and instrumented these birds with Argos PTT's (SOVON 2012, Box 5.1). Five of these birds have produced data only for 2007 (the year of deployment), but the other seven instruments have generated data for a number of years (max 2007-2011). With regard to the utilisation of marine, intertidal and terrestrial resources, these devices have produced unique data (see also Appendices 5 and 7). The main foraging areas for Herring Gulls in summer were mudflats south and southeast of Vlieland, the breakwaters at Vlieland and Texel, Eyerlandsche Gat (gullies between Texel and Vlieland), Texel grasslands (F.AFF^{41816}), and a refuse processing plant near Medemblik in Noord-Holland ("*Afvalverwerking Wieringermeer*"). All birds frequently foraged on the mudflats south of Vlieland, and/or on breakwaters at Vlieland or Texel, indicating the importance of intertidal resources for this population. In autumn, one bird foraged at the Attero refuse processing plant (formerly Essent Milieu, earlier VAM refuse dump) in Wijster (Drente), several birds moved to the mudflats near Griend, but most birds were wintering in Noord- and Zuid-Holland (mostly between Amsterdam and Hoek van Holland), utilising foraging opportunities inland (and in cities) or on beaches.

From radio tags deployed on Herring Gulls breeding on Texel (^{App}Table 3.1), information on the presence/absence within the colony could be derived and the influence of the tidal cycle could be examined. Given the dietary switch in Herring Gulls from incubation to chick care (Appendix 7, Box 7.3), which led to a decline in the utilisation of mussel resources, a more substantial "low-tide effect" on colony attendance was expected to occur in the egg phase than during chick care. In active breeding birds, but not in failed breeders, males spent on average more time within the colony than females and colony presence (% of total time recorded) was only marginally higher during the egg phase than during chick care in both sexes (mean ± SD, number of individuals monitored):

	Females	**Males**	**Bird days**
Egg phase	46.9±17.7% (8)	57.0±14.6% (11)	260
Chick care	43.9±23.0% (5)	48.7±17.3% (9)	230
Failed	58.1± 31.8% (3)	40.3±27.9% (3)	272

In active breeding birds (failed breeders excluded from the analysis), both females and males spent on average proportionally more time within the colony at night (22:00-05:00) than during the day (05:00-22:00), but the differences were again small:

	Females	**Males**	**Bird days**
Daytime	39.8±18.7% (10)	52.5±11.4% (11)	490
Nighttime	48.6±29.0% (10)	56.6±21.2% (11)	490

Though overall nests attendance in active breeders was lowest at low tide (females 42.4±19.7%, males 49.3±19.4%), the individual variation was considerable. Between the two main phases of breeding (from the egg phase to chick care), the differences in nest attendance were small and though the low-tide effect was even less conspicuous during chick care, the differences were smaller than expected from the dietary shift:

Egg phase	**High**	**Falling**	**Low**	**Rising**
Females	46.8±23.2%	47.2±17.7%	43.0±20.1%	48.6±24.1%
Males	59.9±19.3%	56.4±17.1%	52.5±20.6%	57.6±16.8%
Chick care				
Females	41.0±21.4%	45.3±24.1%	41.6±21.5%	47.9±29.7%
Males	44.6±24.4%	50.9±21.4%	45.3±18.1%	55.9±19.3%

As in many earlier studies, from bird counts in the colony the effect of low tide was clear: clubs were empty and densities within the colony are usually lower than during high tide. Nesting birds, however, maintained a certain level of nest attendance and radio-tagged partners “negotiated” a presence/absence scheme in which both birds could profit from at least part of the time available with low water (^{App}Fig. 9.3). The Texel birds also foraged at considerable distances from the colony, profiting from a low water phase that was up to several hours different from the tidal phase nearer the colony. The result is a rather diffuse pattern, and the effect of low-tide on the foraging activities of the birds (there are no tracking data available and, hence, no exact foraging site information) is largely obscured.

Lesser Black-backed Gulls - Fourteen Lesser Black-backed Gulls colour-ringed and instrumented with Argos PTT’s at Vlieland (SOVON 2012, Box 5.1) have produced data indicating the importance of inland foraging opportunities, but also on the utilisation of mudflats to the south of the island in summer. The breeding status of (most) these birds was uncertain, but “central place foraging” (from the colony) was obvious for several individuals in a series of years (2007-2011). Three i (21%) were frequently present, and apparently foraging, at mudflats to the south of Vlieland (colour-rings$^{PTT\#}$: M.AFA^{41745}, M.AFM^{41749}, and F.AFL^{41780}; SOVON 2012). Three other birds were commonly utilising inland resources in Friesland (up to *c.* 80km to the southeast of the breeding colony; M.AFR^{41752}, M.AFP^{41764}, and F.AFA^{41771}). One bird spent most of its time inland at the island Texel (M.AFT^{41762}), the rest (50%) had a more marine orientation or a more variable foraging distribution pattern, including visits to mainland sites in Noord-Holland, Flevoland and Utrecht.

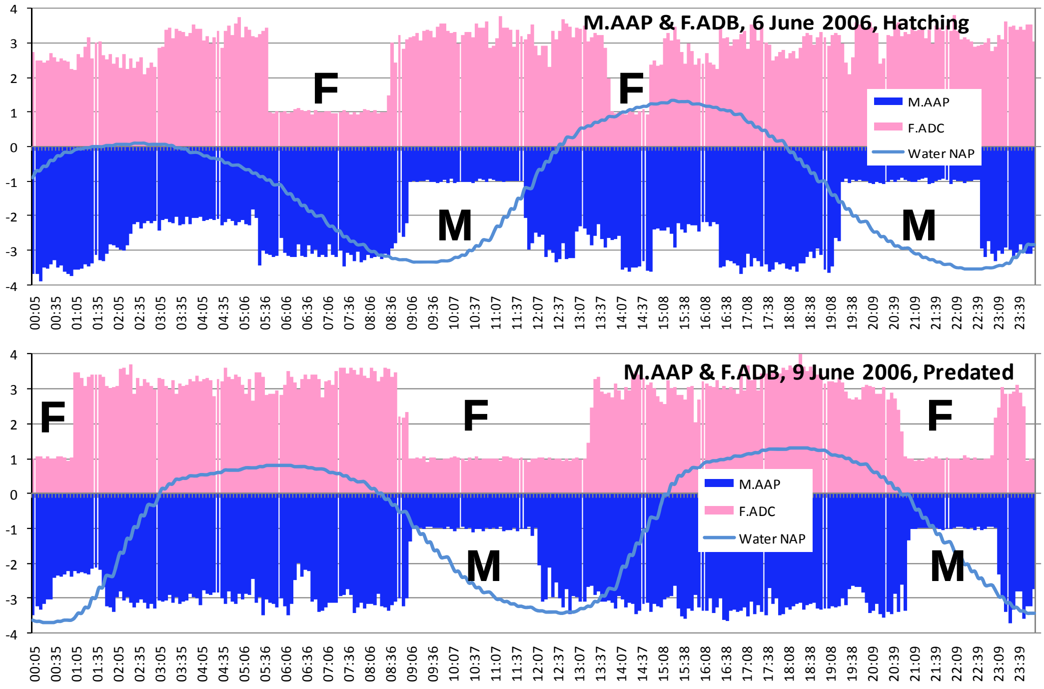


Fig. 9.3 Radio tag information on the presence and absence of a Herring Gull pair (2x 24h period; male M.AAP below, female F.ADB above the x-axis) combined with local sea water levels (Water NAP; line). Absences are indicated by capital letters, showing absences one after the other (during hatching; top), and joined absences when the chicks were predated (bottom). On the y-axis left: A/B ratios of signal strength: values >1 (or <-1 in the mirrored image) indicate presence (reception of a signal), values around 1 (-1) indicate absences. On the right y-axis: water level (cm) relative to new Amsterdam level (NAP). X-axis: time of day.

Lesser Black-backed Gulls from Texel were tracked with GPS loggers (Box 5.2) and their presence in coastal and terrestrial habitats was monitored during 2199 long-trips (short excursions towards colonies and bathing places around the colony excluded; Chapter 10) in 34 individual birds. Substantial differences in habitat choice between the sexes were found and the time spent at sea or on land was different during incubation and chick care. Male Lesser Black-backed Gulls with active nests at Texel during incubation and hatching spent 14% of the on feeding trips in terrestrial habitats on the mainland, 4.5% of the trip time at Texel, and 3.5% within the Wadden Sea (the rest, some 78% of the time over the North Sea). Females in that same condition spent on average a rather higher 21% of their time on the mainland, 29% on Texel, and 21% within the Wadden Sea (only 29% over the North Sea). During chick care, males on average nearly doubled their time on the mainland (25%), but still kept away from Texel (4.5%) and the Wadden Sea (5%). Females slightly increased their sea time at the expense of foraging time on the mainland (halved, now 14%), but maintained a genuine interest in resources on Texel (24%) and the Wadden Sea (25%). When breeding attempts failed, the time budgets within each of the prime habitats changed markedly in females: the time spent over sea fell to 23%, while the time spent on the Continental mainland increased to 56%. Less time was also spent within the Wadden Sea, now less than 10%. Males spent slightly more time at Texel (9%), but continued to focus on marine resources (66%). The Wadden Sea remained an area of secondary interest only with 3% of the time on foraging trips within that area.

The variation between individuals in time allocation to each habitat was considerable (Chapter 10). On the one extreme end, some male birds, spent virtually all their foraging time at sea, on the other extreme, one female barely left the island Texel. A consistent difference between the sexes was the utilisation of the Wadden Sea area: <5% of the time in males (including time "on transit" towards other feeding grounds), against 20-25% in actively breeding females. When plotting all GPS positions of all (actively breeding, non-failed) females on a map of the western Wadden Sea, it is evident that these birds circumnavigate tidal flats and exclusively forage over deeper gullies (AppFig. 9.4). The deeper waters most frequently visited by these gulls are the exact same locations as where the commercial fisheries occur, trawling for shrimps (black box data; AppFig. 9.4). Incidentally, the results confirm the relative unimportance of the northern half of Texel for birds breeding in Kelderhuispolder colony, as was reported from colour-ring data; even for the females that spent most or much of their foraging time on the island.

Several trips were deep inland and some individual birds, mostly females, had apparently specialised on terrestrial resources. Refuse processing and sewage treatment plants provided occasionally used foraging opportunities for Lesser Black-backed Gulls. Some grasslands and agricultural areas were preferred over others. By combining tracking data and detailed descriptions of the diet from collected food samples, it will be tried to assess the importance of inland foraging opportunities for Lesser Black-backed Gulls in the near future. Trips towards Amsterdam by active breeding birds were confirmed with logger data and Chapter 8 reports on extremely long trips by adult birds, which fell out of the regular pattern and are not further discussed here.

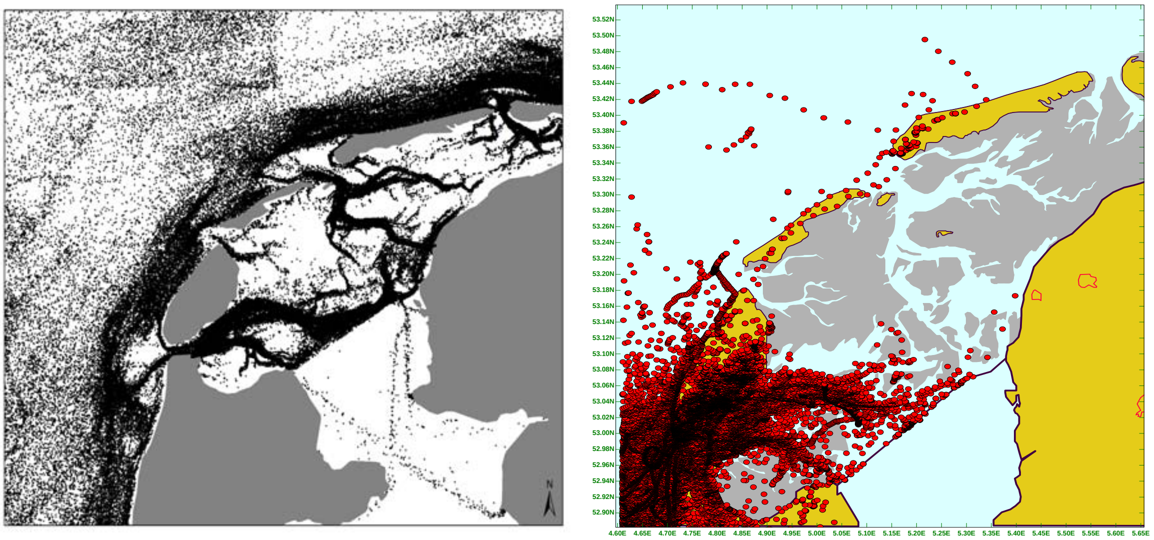


Fig. 9.4 Black-box information on fisheries distribution in the western Wadden Sea and off Noord-Holland, Texel, Vlieland and Terschelling in de North Sea (left) and all GPS positions of female Lesser Black-backed Gulls, 2008-2011, in the western Wadden Sea.

Combining dietary information with foraging whereabouts

Shallow tidal waters – At receding or rising tide, solitary Herring Gulls commonly swim in shallow waters along dikes and breakwaters of Texel and near Den Helder to capture Common Starfish and Common Shore Crabs. Colour-ringed individuals have been recorded feeding as far north as Oudeschild on Texel and Herring Gulls utilising this resource on the northern half of the island originate likely from either Vlieland or from some of the other (smaller) colonies at Texel. Some specialised individuals exploit Pacific Oysters in the same area (dumping shells on the dike and roads to crack their shells).

Soft substrate intertidal areas – Herring Gulls from Vlieland carrying Argos PTT's confirmed the utilisation of breakwaters on Vlieland itself, as well as on Texel. Colour-ring sightings from that same population had provided similar info. The much more widespread and consistent use of the mudflats to the south of Vlieland and the exploitation of resources around the island Griend (between the island Terschelling and mainland Friesland) and along the Wadden Sea coast of Friesland had not been revealed with colour-ring data. Important (demonstrated) prey for these Herring Gulls have been Cockles, Sand Mason Worms *Lanice conchilega* and Balthic Tellins, perhaps also Brown Shrimps and Common Shore Crabs (from prey samples provided by Peter de Boer, SOVON). Herring Gulls from the Kelderhuispolder at Texel may have exploited resources on tidal flats in the Mokbaai or elsewhere in the western Wadden Sea (Balgzand included). In the absence of ring-readers in these areas, tracking data would be required to quantify the importance of these feeding grounds. The cockles taken by some Herring Gulls at Texel, however, most likely originate from cockle beds in the Balgzand area, a region that is well within the likely foraging range for this species and where high densities of cockles occur in favourable years (Boer *et al.* 1970, Dekker 2011).

Lesser Black-backed Gulls from Texel are currently not known to utilise soft substrate intertidal areas other than the beach. By contrast, three out of 14 Lesser Black-backed Gulls carrying Argos PTTs from Vlieland spent considerable time on intertidal mudflats to the south of the island, right in the middle of prime Herring Gull foraging habitats (SOVON 2012, this Appendix). The tracking results suggest that these birds were feeding on intertidal resources and the data are radically different from any GPS tracking data of birds tagged at Texel, where evidence was provided that mudflats were actually circumnavigated (even during high tide) and where the deeper gullies of the Wadden Sea were the prime foraging areas. Even more striking regarding the utilization of intertidal resources by Lesser Black-backed Gulls, were results reported by Garthe *et al.* (1999a). They studied diet, colony attendance, breeding success and behaviour in 1994 and 1995 in a mixed-colony on Amrum (German Wadden Sea). During incubation Lesser Black-backed Gulls fed mainly upon crustaceans and molluscs which were taken from the intertidal zone. During chick-rearing, they took mainly crustaceans and fish which were gathered mostly as trawler discards. Numbers of Lesser Black-backed Gulls in the colony mainly varied with season and time of day, while only those of Herring Gulls varied with tide and season. A marked dietary shift towards fish prey during chick-rearing occurred in Lesser Black-backed Gulls, but not in Herring Gulls. During incubation, the diet of the two species (predominantly prey from intertidal areas) was largely overlapping.

Also in other parts of the world have Lesser Black-backed Gulls been recorded as foraging birds on tidal mudflats. Swennen (1990), studying Oystercatchers *Haematopus ostralegus* feeding on Giant Bloody Cockles *Anadara senilis* on the Banc d'Arguin (NW Africa), described Lesser Black-backed Gulls as effective kleptoparasites of Oystercatchers. During daytime low tides, Oystercatchers that were feeding on (difficult to open) Giant Bloody Cockles were frequently robbed by Lesser Black-backed Gulls. On average 2.5 of these gulls were present in the observation area (0.4 birds ha^{-1}). The gulls were territorial, each keeping control on 10-15 Oystercatchers, and they apparently obtained all their food from 'their' Oystercatchers. The gulls could not open the shells or reach for the flesh in the deep shells on their own. The gulls therefore kept a good eye on their workers and waited until an Oystercatcher had a piece of flesh in the bill before attacking. Coulson & Coulson (2008) studied the diet and foraging habitats of Lesser Black-backed Gulls breeding on buildings in Dumfries (Scotland, UK, *c.* 15km from open sea). Some 14% of the examined pellets contained marine prey, including shore crabs *Carcinus maenas* and bivalve mollusc shells *Tellina* sp. Bones and otoliths from fish were absent from all samples, indicating that these gulls had fed at intertidal areas, and not over the open sea. Hence, while Lesser Black-backed Gulls breeding on Texel have not been found to forage on intertidal mudflats at all (a combination of tracking data, colour-ring sightings, dietary information), they might utilise these resources when either the opportunities were there or when they would need to.

Hard substrate intertidal areas – Numerous re-sightings of colour-ringed Herring Gulls from Texel have indicated that the breakwaters off the sandy beaches and dikes of the mainland coast of Noord-Holland and the southern half of Texel are important feeding grounds for Herring Gulls nesting in the Kelderhuispolder (^{App}Fig. 9.1-2). Throughout the breeding season, adults have been seen foraging on breakwaters spanning an area of nearly 50km of coastline packed with mussels. Low tide at the southernmost foraging opportunities can be up to 2-3 hours earlier than at the northern edge of this feeding area. Alternative hard-substrate foraging areas for mussels are the numerous buoys in the waterways around the southern tip of Texel. Flying to or from these hard substrate intertidal foraging areas can be at low cost in favourable winds by soaring along the dunes. There was a distinct seasonal pattern in numerical abundance of foraging gulls from Texel on the mainland coast breakwaters (^{App}Fig. 9.5). Based on year-round ring-reading effort, the coastal breakwaters between Schoorl and Callantsoog (the prime research area for ring-reading activities throughout the project) were found to attract relatively few colour-ringed individuals from Texel in winter (Dec-Mar), a marked increase occurred in Apr-May, a slight dip in Jun-Jul, followed by a peak period from late July through September (^{App}Fig. 9.5). Colour-ring effort in IJmuiden since 2008 has demonstrated that adult birds from that colony also utilise the breakwaters of Noord-Holland, but almost exclusively after the breeding season, after the young have fledged (^{App}Fig. 9.6).

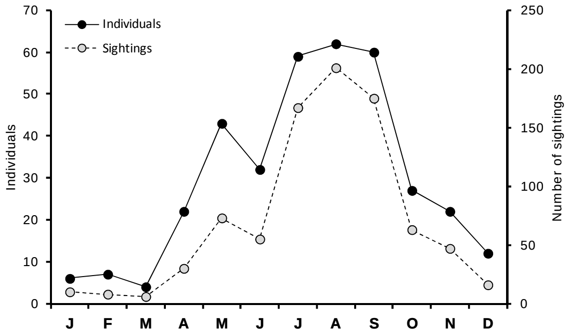


Fig. 9.5 Sightings (n) and individual birds (n) ringed as adults at Texel (2006-2012) foraging on mussels at breakwaters along the mainland coast of Noord-Holland (Schoorl-Den Helder) through the year. Numbers peak in the late breeding season and early autumn when roosts are formed on the Hondsbossche Zeewering, on the beach and in the hinterland of this feeding area (agricultural areas).

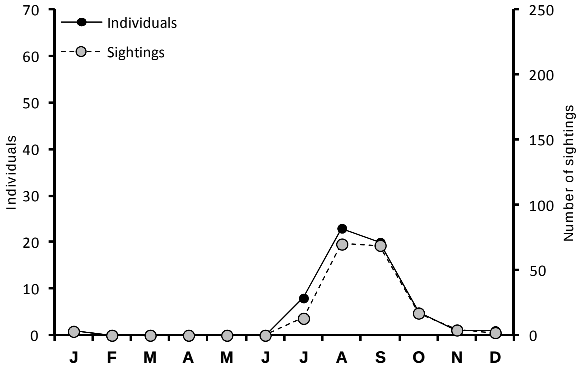


Fig. 9.6 Sightings (n) and individual birds (n) ringed as adults in IJmuiden (2008-2012) foraging on mussels at breakwaters along the mainland coast of Noord-Holland (Schoorl-Den Helder) through the year. Numbers peak after the breeding season and in early autumn.

In the mid- and late-1980s, thousands of fledglings of Herring Gulls have been colour-ringed in 14 Dutch colonies (Rottum-Saeftinghe; Box 4.1, Chapter 6). The presence of these colour-ringed Herring Gulls along the mainland coast area with breakwaters has been intensively studied since the late 1980s (A. Gronert & R. Costers *unpubl. data*). These studies revealed not only how local populations frequently used the hard-substrate shoreline in mainland Noord-Holland, but also how Herring Gulls from virtually all major colonies within The Netherlands shared this foraging area with breakwaters during different parts of the year. The project yielded 15,816 sightings of colour ringed Herring Gulls originating from all 14 colonies where birds were ringed in the 1980s. The numbers of adults and immatures (both the number of sightings and the number of different individuals involved) consistently peaked just after the expected peak in mussel quality ($^{\text{App}}$Table 9.4). It is clear that Herring Gulls from around the country are attracted to this area, suggesting that the breakwater defended coast of Noord-Holland is an important post-breeding staging area.

This mainland hard substrate resource is now at risk. Major works to strengthen this Noord-Holland shoreline will be executed in years to come (project “Zwakke Schakels”), altering the foraging conditions for many shorebirds dramatically. The baseline study included in this thesis may serve as a point of reference to allow a future evaluation of the effects of what could be seen as a major field experiment. Typically, the presence of Herring Gulls did not play any role in the decisions to modify these habitats. It could well be, however, that the planned destruction of a major resource may have unwanted and unappreciated side-effects, for example if thousands of gulls have to seek alternative resources deeper inland or in cities and townships.

Table 9.4 Monthly variations in the number of colour-ringed Herring Gulls (number of colonies of origin (Cols, max 14), total number of sightings and different individuals), recorded as adults (left) or as immatures (right) along the coast of Noord-Holland, 1986-2012 (A Gronert & R Costers *unpubl. data*) versus the seasonality in body mass index of intertidal mussels (mean gAFDM mm^{-3} 10^{6} ± SE) in the Marsdiep area (NIOZ jetty), as deduced from measurements in 2011-2011 (R Dekker *unpubl. data*). Peak periods in **bold**. The percentage of individuals observed per month was calculated on the basis of the total number of individuals recorded as adults (n= 407) or immatures (n= 997) within the area.

	Adults				**Immatures**				**mussel**
	Cols	Sightings	Indiv	%Ind	Cols	Sightings	Indiv	%Ind	**BMI**
J	7	264	74	18.2	11	234	99	9.9	4.2 ± 0.2
F	5	204	71	17.4	8	120	54	5.4	4.1 ± 0.2
M	5	99	41	10.1	9	217	84	8.4	3.7 ± 0.2
A	5	94	51	12.5	12	619	183	18.4	6.8 ± 0.2
M	5	129	84	20.6	13	988	305	30.6	**8.0 ± 0.4**
J	6	151	95	23.3	13	1054	296	29.7	**7.7 ± 0.3**
J	7	432	153	37.6	14	1415	349	35.0	**8.1 ± 0.3**
A	**8**	**934**	**221**	**54.3**	**14**	**2483**	**621**	**62.3**	6.4 ± 0.2
S	**10**	**1179**	**243**	**59.7**	**14**	**1899**	**491**	**49.2**	5.9 ± 0.2
O	8	803	182	44.7	12	845	284	28.5	5.5 ± 0.2
N	10	541	122	30.0	13	477	198	19.9	5.1 ± 0.2
D	8	382	91	22.4	10	253	107	10.7	5.3 ± 0.2
Totals	10	5212	407		14	10604	997		

Mussel body mass index - From a recent study in the Marsdiep area (mussels settled on a jetty on the south tip of Texel), a seasonal pattern in body mass index (BMI, gAFDM mm^{-3} 10^{6}) could be deduced with a peak in ‘mussel quality’ in May-July (*c.* 8 gAFDM mm^{-3} 10^{6}) and a distinct dip in Jan-Mar (*c.* 4 gAFDM mm^{-3} 10^{6}). A rapid increase in mussel BMI in spring coincided with rapidly increasing exploitation rates of the Noord-Holland breakwater mussels by adult Herring Gulls from the Texel colonies ($^{\text{App}}$Fig. 9.11). A gradual decline in BMI in late summer (post-breeding season; Aug-Sep), however, coincided with a further increase in numbers of foragers (now including birds from IJmuiden $^{\text{App}}$Fig. 9.6) before numbers of foragers fell to winter levels following the continuing decline in mussel BMI in autumn and early winter. So, while the utilisation of the breakwaters by adult Herring Gulls from Texel was positively correlated with mussel quality (assuming that the recent measurements in the Marsdiep area would be representative for a similar seasonality in mussel condition on breakwaters along the mainland coast), a peak in numerical abundance of adult Herring Gulls (Aug-Sep) occurred just *after* the peak in mussel condition (^{App}Fig. 9.11). An explanation for this "mis-match" is that this sector of mainland coast is attractive for Herring Gulls for more reasons than just the availability or quality of mussels. Large roosts are formed in the area on beaches, on the dikes, and in the hinterland (arable land and grasslands with limited human disturbance). Aug-Sep is a phase during which large gulls undergo a complete (post-nuptial) moult and the easy and nearby access to mussels (of still rather high quality) could be an attractive bonus for these birds.

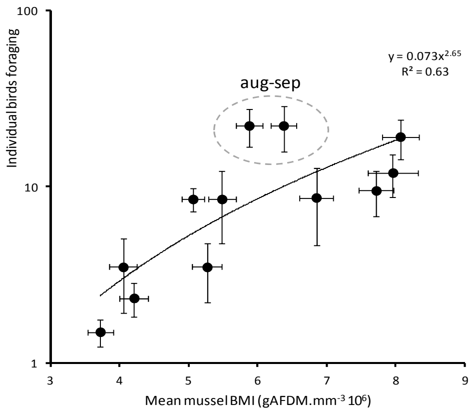


Fig. 9.11 Monthly (Jan-Dec) body mass index of intertidal mussels (mean ± SE) in the Marsdiep area (NIOZ jetty) based on measurements in 2011-2012 (R Dekker *unpubl. data*) versus monthly variations in the log(number) of colour-ringed adult individuals from Texel, foraging as on hard-substrate mussels on breakwaters along the coast of Noord-Holland (immediately south of the Marsdiep area), 2006-2012 (mean ± SE).

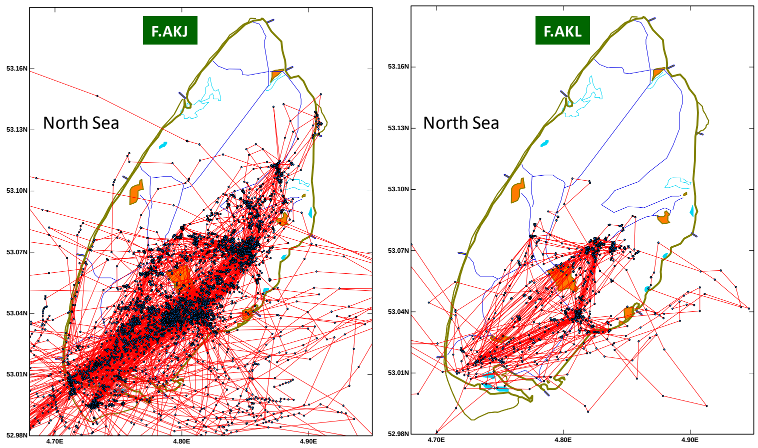
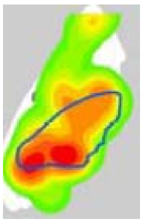


Fig. 9.7 Foraging trips of two female Lesser Black-backed Gulls tracked with IBED GPS loggers on Texel: Left: F.AKJ: 61% of total trip time on the island Texel, n= 270 trips (3.1h trip^{-1}); Right: F.AKL: 87% of trip time on Texel, n= 58 trips (3.8h trip^{-1}).



Sheep densities Texel

Texel grasslands – Not all encountered prey items were easy to identify and numerous prey samples contained shredded fibres (grains, maize) that were difficult to interpret until GPS logger data revealed the origin (^{App}Fig. 9.7). Land use on the island Texel includes agriculture (66%), forest and nature (26%), tourism (3%), urban areas (1%), industry (1%), roads (2%) and waterways (1%). Ringing data and GPS loggers suggest that most feeding is concentrated in the southern half of the island Texel. The island Texel is packed with grazing sheep that receive supplementary food in the form of food pellets. The food is provided in open sheep-feeders of which many hundreds are found in the Texel country side, often next to small circular drinking pools (traditional Texel countryside features; Van der Goes & Hartog 2011). A quick ground-truthing study to validate GPS logger results in 2010 revealed that and nearly all sheep feeders and ponds were attended by small flocks of Lesser Black-backed Gulls (rarely Herring Gulls) and the tracks overlapped the highest density areas of sheep farming (Kuhlman *et al.* 2009; ^{App}Fig. 9.7^{inset}). Several thousands of birds must exploit this resource. The ponds were used for drinking and bathing. The GPS data indicated that foraging trips to sheep-feeders roughly took 3-4 hours to complete. Given the short distance to the colony this would imply low flying costs and considerable "standing around" time (waiting for the sheep to be fed).

Grasslands and arable land on the mainland – Both species of gulls are commonly seen to forage on grasslands or while following ploughs working arable land. Land use in the NW part of mainland Noord-Holland (the key area for foraging Lesser Black-backed Gulls) includes agriculture (80%), forest and nature (4%), tourism (2%), urban areas (4%), industry (3%), roads (3%) and waterways (4%) (Kuhlman *et al.* 2009). Ringing data and GPS loggers would suggest that most feeding is concentrated in the north-western part of Noord-Holland (between Den Helder, Alkmaar, and Hoorn; ^{App}Fig. 9.8). This roughly 625 km^2 area is a mosaic landscape with relatively young polders in the east as well as older grasslands in the centre and in the south, and flower beds mostly in the north (notably on relatively sandy grounds behind the dunes). Several moderate cities are within this area, a sewage treatment plant that is frequently visited by tagged gulls, but no major landfill sites. The ‘historical’ landfill area near Medemblik, the ‘Wieringermeer refuse tip’ is just east of the preference area and this site does not provide the foraging opportunities that it did some decades ago (Chapter 6, ^{App}Table 6.11).

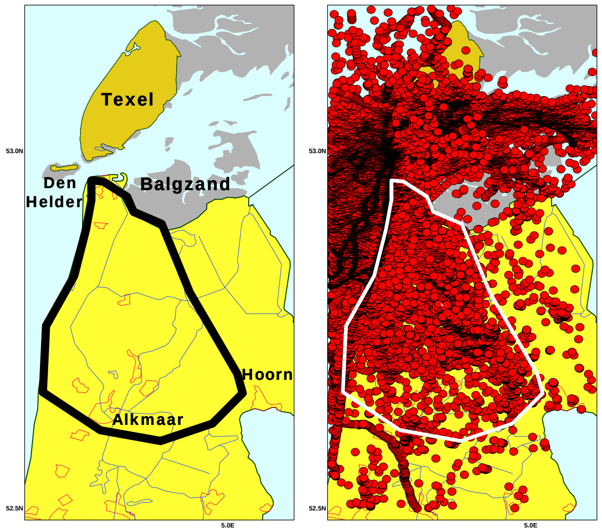


Fig. 9.8 Exact positions of male and female Lesser Black-backed Gulls nesting in the Kelderhuispolder on Texel during incubation or chick care and the prime search area for inland foraging in the NW part of Noord-Holland (polygon).

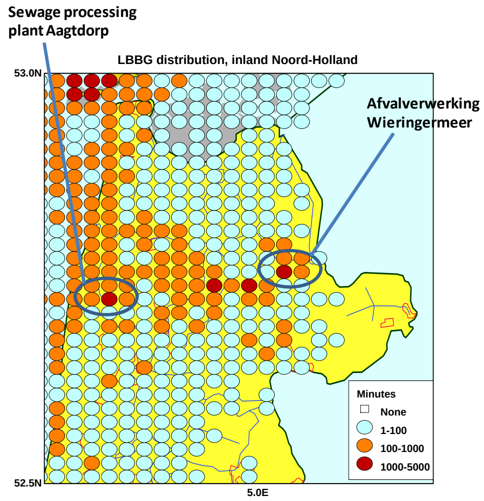


Fig. 9.9 Time spent (minutes) by male and female Lesser Black-backed Gulls nesting in the Kelderhuispolder on Texel during incubation or chick care in the NW part of Noord-Holland, summarised per 1’x2’ rectangle. A sewage plot near Aagtdorp and a former domestic refuse dump (now a processing plant) near Medemblik (Afvalverwerking Wieringermeer) were prime attractions for some specialised individuals. Relatively frequent and prolonged occurrences (darker shadings) were found along the west coast (including roosts) and in areas of mixed use (older grasslands and arable land).

The relatively young Wieringermeer polder (dry ground since 1930) was more or less avoided by foraging Lesser Black-backed Gulls, but also the old island Wieringen was rarely visited as a foraging ground. Older polders with a mosaic landscape (grasslands mixed with arable lands for vegetables near urban areas) were preferred habitats. These areas must provide a variety of foraging opportunities, throughout the breeding season. Some arable areas for flower production in Noord-Holland are favourite roosting sites (extensive agricultural use, relatively distant from human activities) that were also frequently used by failed breeders.

Utilisation of refuse dumps

In 1958, M.F. Mörzer Bruyns of the Institute for Nature Conservation and Research (RIVON) wrote an essay on “*Gulls which are a menace to other species*” and remarked that a population of 10,000 pairs breeding in The Netherlands should be seen an upper population limit.*”The surplus population is able to survive largely because summer conditions along the coast are particularly favourable, while in autumn and winter rubbish dumps and refuse from fishery factories etc. provide enough food to keep the gull population as a whole in quite good condition.”* Spaans (1971) presented the results of systematic counts of gulls at 13 dumps in Friesland (1967-1969), showing that indeed the lowest numbers were present during the breeding season. The number of scavengers increased from August to October (when “winter levels” were reached) and remained high until April. During the winter months, numbers of scavengers at the refuse dumps showed marked fluctuations and there appeared to be a negative correlation between the feeding conditions on the mudflats of the Wadden Sea and the number of gulls present at dumps. In December 1967, a census of gulls at all 100 refuse dumps in the three northern provinces resulted in 26,097 (range 20,000 -39,000) Herring Gulls. There was a positive correlation between the number of inhabitants of the relevant municipalities and the number of gulls at associated dumps, indicating that the distribution of the gulls over the refuse dumps was closely related to the quantities of food locally released.

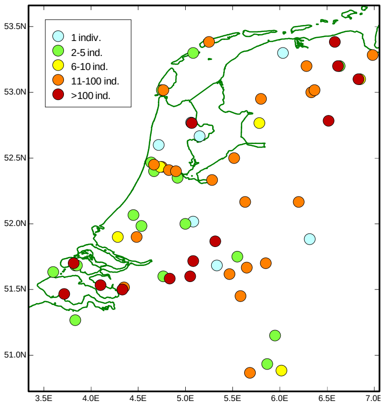
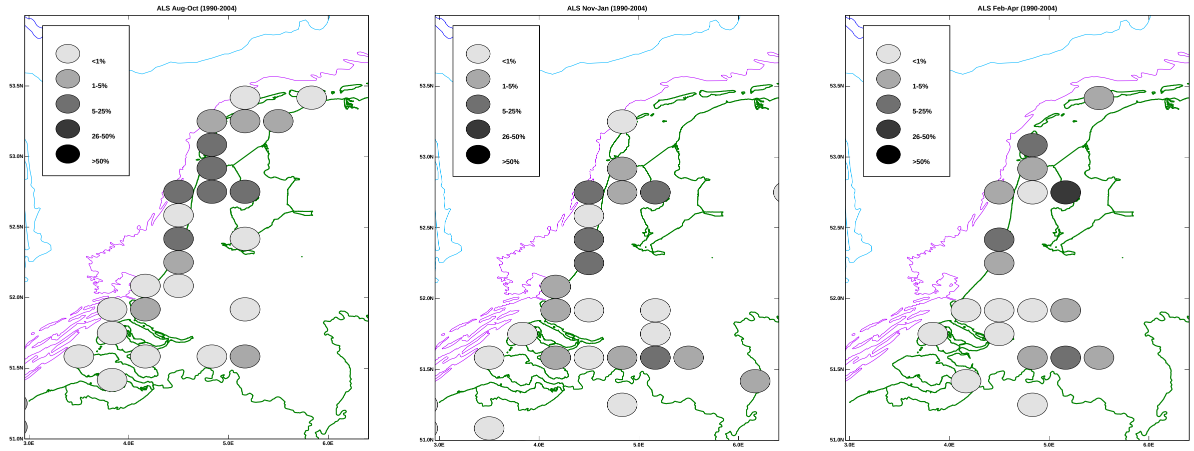


Fig. 9.10 Sightings (number of different individuals per site) of colour-ringed large gulls at landfill sites, 1985-2011. Note that many of these sites closed down between the early 1990s and 2011.

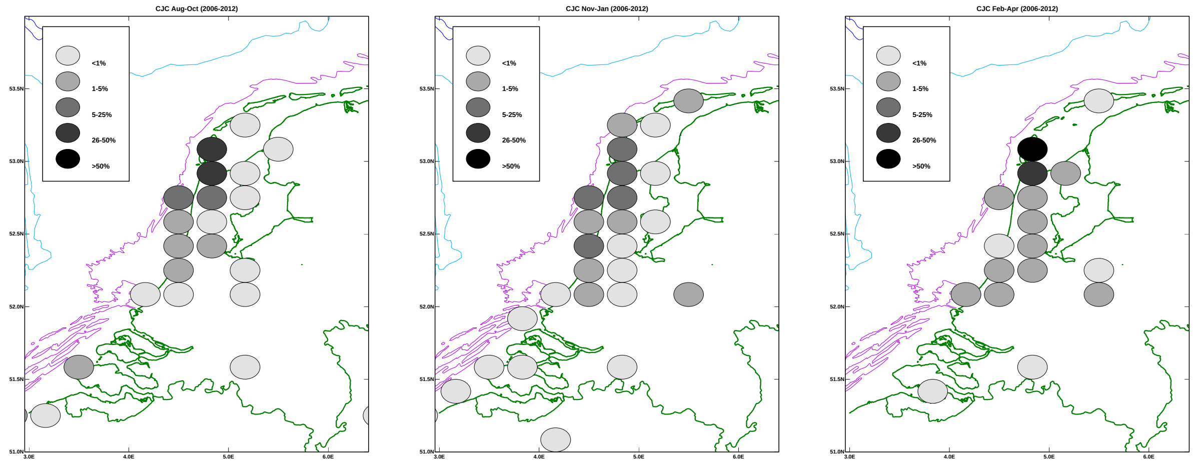
Table 9.3. Observed and expected numbers of Herring Gulls and Lesser Black-backed Gulls in summer on dump locations and near household refuse incinerators, 1985-2011. Numbers refer to unique rings (individual birds) newly ringed, seen alive anywhere in The Netherlands, observed on dumps and the expected number on dumps based on the overall number of sightings and ringing effort.

				On dumps		**on dump**
		Ringed	**Sightings**	Obs	Exp	**%**
1985-1989	Lesser Black-backed Gull	132	28	0	10	0%
	Herring Gull	4301	2561	881	871	34%
1990s	Lesser Black-backed Gull	367	252	15	130	6%
	Herring Gull	50	1486	879	764	59%
2000s	Lesser Black-backed Gull	1124	476	9	26	2%
	Herring Gull	544	475	43	26	9%

While the use of refuse dumps by Herring Gulls was obvious (Spaans 1971, Chapter 6), there is much less information on the historical presence of Lesser Black-backed Gulls utilising human waste materials on landfill areas. Of 4891 Herring Gulls colour-ringed in The Netherlands since 1985, 2251 individuals (46.0%) were seen at least once at one of 70 dump sites regularly visited by colour-ring readers (AppFig. 9.10). In contrast, of 1611 colour-ringed Lesser Black-backed Gulls, only 28 (1.7%) have been observed at dump sites (including 6 specialised birds that were recorded frequently at dumps). This difference is partly caused by the fact that most Herring Gulls were ringed in the 1980s, when refuse dumps were still available in large numbers, and the majority of Lesser Black-backed Gulls was ringed in later years. A decadal comparison, however, using only sightings in summer (Apr-Sep) of colour-ringed gulls foraging or roosting away from the colonies, shows that Lesser Black-backed Gulls were consistently 'under-represented' at dump sites (AppTable 9.3). The absence or scarcity of Lesser Black-backed Gulls at visited refuse dumps is remarkable given the representation of human waste materials in 6% of the food samples collected in recent years at Texel (Appendix 7). Part of the packaging materials and other domestic refuse found in the Kelderhuispolder colony may have originated from waste bins or bags on the mainland or on Texel. Some labels strongly suggested a mainland origin (specific restaurant names, and halal food that originated from moslim communities) and some species of prey confirmed mainland foraging trips (Chapter 14).



Aug-Oct 1990-2004 **Nov-Jan 1990-2004** **Feb-Apr 1990-2004**



Aug-Oct 2006-2012 **Nov-Jan 2006-2012** **Feb-Apr 2006-2012**

Fig. 9.11 Herring Gulls colour-ringed as juveniles at Texel in 1986-1988 (ALS programme) and as juveniles or adults at Texel in 2006-2012 (Kelderhuispolder programme), recorded as adults per 10' latitude x 20'longitude rectangles within The Netherlands. Shown are percentages of all birds ever recorded as adults since ringing (n= 119 for the early period, n= 180 for the more recent period) per rectangle (depicted as a circle to be able to see the underlying map) in autumn (Aug-Oct), winter (Nov-Jan), and spring (Feb-Apr),. For the older dataset, only sightings prior to 2005 were included (1990-2005).

In recent years, most of the *c.* 4000 open refuse dumps in The Netherlands were covered up (van Vossen 2001, in 't Veld & Krol 2005ab, Moerke 2008; Appendix 2). Only a few dozens of landfill sites are currently accessible for foraging birds: 50 in 1995, 36 in 2000, 22 in 2009 (CBS, PBL, Wageningen UR 2011). Around Texel the nearest plants of any significance are near Amsterdam and some actively breeding adult Herring Gulls are known to forage there occasionally. An effect on wintering distribution is not unlikely, given the suggestion by Spaans (1971) and other authors that landfill food is particularly important during winter. The winter dispersal of Herring Gulls is addressed in Chapter 6, based on Herring Gulls ringed in the mid 1980s, and several of the dumps currently closed featured in this study as key wintering (and key ring-reading) sites. For Herring Gulls breeding at Texel, Vlieland and in Noord-Holland, landfill sites in Zeeland and Brabant formed important attractions in winter. The SOVON tagging data suggested that few (tagged) Herring Gulls ever moved south of Hoek van Holland, which was not in agreement with the findings on wintering areas in the paper on colour-rings deployed in the 1980s. A combination of strong population growth of Herring Gulls in Zeeland and Zuid-Holland, coupled with a reduced number and restricted access to these domestic refuse dumps could have led to a shift in wintering distribution in recent years. Herring Gulls from Texel stayed closer to the breeding grounds recent winters winter, mostly in Noord-Holland and Zuid-Holland (^{App}Fig. 9.11). Overall, adult Herring Gulls from Texel wintered on average *c.* 30km further to the north (*i.e.* nearer the breeding grounds) than in the 1980s and 1990s (Dec-Jan 1990-2005 mean (±SD) wintering latitude 52.11±0.7°N, 2006-2012 52.27±0.8°N; t_{349}= -1.89, P= 0.03). A small subset from Texel ringed since 2006, 21 adult Herring Gulls, were found in winter on still existing refuse dumps in northern France: Blaringhem, Nord (50°40'N, 02°25'E), Dannes, Pas de Calais (50°35'N, 01°38'E), Lewarde (50°20'N, 03°10'E), and Nurlu, Somme (49°59'N, 03°00'E).

Inland foraging opportunities – The inland feeding opportunities for omnivorous species such as large gulls are notoriously diverse and include freshwater (fish, insects), air (hawking for insects), fields (both natural fields with low vegetation and cultivated, arable lands with or without a covering of vegetation; insects, grains, earthworms, mammals, birds, etcetera), dunes (insects, berries), cities (domestic refuse and human food), dumps (terrestrial solid-waste-disposal grounds or processing plants; domestic refuse), and effluent (liquid wastes within or discharged from sewers, including discharge outlets; a variety of waste materials). Many of these resources are ephemeral and a substantial degree of opportunism is required to forage with success. Aspects that influence foraging opportunities are highly diverse and include all kinds of human activities (tourism included), weather, flowering and seed-setting processes of the vegetation, seasonal and annual cycles in the abundance of mammalian prey and insects, migratory movements of birds and insects, harvests and transports of harvested crops. Marked seasonal variations in the diet may therefore be expected Andersson 1970).

The GPS tracking data suggested that inland foraging Lesser Black-backed Gulls concentrated on older pastures rather than arable land and younger grasslands in more recent polders, preferably in mosaic landscapes. Several studies have shown positive correlations with pasture age and earthworm density. Likely explanations are (1) as pastures mature, there is a gradual accumulation of dead organic material on which worms feed, and (2) old pastures are generally grazed by cattle or sheep for a greater part of the year and therefore have a higher organic input from dung (Barnard & Thompson 1985). Earthworms are an important food for several species of gulls (Sibly & McCleery 1983b, Kubetzki 1997, Coulson & Coulson 2008, this study), and although their availability is generally weather dependent, a preference for grasslands rich in invertebrate fauna would be quite understandable. In a Swedish study, waste grain, refuse and earthworms were found to be the most important food groups of terrestrial origin (Andersson 1970). While insects were eaten frequently, this was always in small quantities. The same seems to be true for gulls nesting at Texel (Appendix 7). Perhaps a more significant factor than the quality of a grassland area is a certain level of variety in land use (mosaic landscapes). Mosaic landscapes will obviously provide more diverse foraging opportunities, possibly requiring only short distances of flight, than monocultures.

The intensively farmed coastal lowland landscape of Germany, adjacent to the North Sea, provides important foraging opportunities for gulls (Schwemmer *et al.* 2008). Spatial and temporal patterns in the utilisation of the landscape mosaic as well as behavioural traits and the utilisation of prey types were expected to differ between the four closely related species foraging in the area, facilitating niche segregation. Numbers of LBBGs were small and this species was therefore not considered to play an important ecological role in the study area. Black-headed Gulls preferred bare fields with recently prepared soils and were often associated with tractors in the fields, Mew Gulls and Herring Gulls were most often found on pastures, fallows and fields with crops. Black-headed gulls were shown to have a higher ability to exploit ephemeral, food sources associated with human activities whereas the other species preferred habitats with low human activity and with naturally distributed prey. While the findings of this study emphasised the importance of terrestrial (nearshore) agricultural habitats for the two smaller gull species, inland feeding was considered less important for the two larger species that occurred in much lower numbers. The larger species used the farmland habitats only partly for foraging, given that high proportions of individuals were inactive and resting during these studies.

Tinbergen (1953) observed how remarkable differently different populations of Herring Gulls behaved. Hunt & Hunt (1973) found striking differences in the usage of certain habitats (substrates) between areas studied in Maine (USA) and Europe. No gulls were recorded foraging in fields in Maine, while fields in Europe were a major foraging substrate for Mew Gulls and Black-headed Gulls. In Maine Herring Gulls were the principal users of mudflats, but in Europe [at the time!] they were disproportionately scarce on this substrate. While Herring Gulls exploited intertidal flats in Holland (Spaans 1971) and southern England (Harris 1965), but they appeared to have been replaced on the mud flats of Scotland and Norway by the Black-headed Gull. In Maine foraging activity on the water was dominated by Herring Gulls, while in Europe Herring Gulls shared this substrate with large numbers of Black-headed and Mew Gulls. In aerial foraging Herring Gulls played a less significant role in Europe than in Maine. The studies at Texel and Vlieland reported in this thesis seem to suggest that terrestrial foraging opportunities are more important for Herring Gulls and Lesser Black-backed Gulls than indicated by Schemmer *et al.* (2008) for populations in Germany.

Domestic waste - For several bird species domestic waste on refuse dumps forms an important anthropogenic food which is clumped subject to human activities like bulldozer operations or diurnal patterns in the timing of deliveries (Coulson *et al.* 1987). Feeding on refuse by large flocks of gulls is a conspicuous example and also known to be highly competitive (Monaghan 1980, Greig *et al.* 1983, 1985; Bellebaum 2005). Belant *et al.* (1989) found that, overall, female Herring Gulls visited landfills more frequently and stayed longer than males. Pons (1994) studied male and female foraging strategies during a transition phase from the use of landfill areas (open access) to domestic waste incineration. During the first period, most of breeders intensively used a refuse tip which was the main feeding site of the colony. In the second period, an incinerator was running that reduced the amount of dumped food by 80%. Females disappeared from the tip, whereas the numbers of males did not change. It is suggested that the differences between the foraging strategies of the two sexes was linked to the higher levels of aggression at the tip when the incinerator became active. Bellebaum (2005) studied flock composition and dominance hierarchies in Black-headed Gulls and Herring Gulls at an inland refuse dump in Germany. Herring Gulls were the dominant species and forced the more numerous Black-headed Gulls to forage close to operating bulldozers. This supported the hypothesis that social dominance governs the relationship between gulls feeding on refuse dumps. Verbeek (1977b) studied interactions among Lesser Black-backed Gulls and Herring Gulls while feeding on a refuse dump near Walney Island (England). Herring Gulls were more aggressive than Lesser Black-backed Gulls toward Lesser Black-backs and to conspecifics. Lesser Black-backs were more timid than Herring Gulls, but were effective kleptoparasites. Most Herring Gulls (77%) found their own food, 95% of the Lesser Black-backs stole theirs, mostly from Herring Gulls.

Within a radius of *c.* 80 km around the Texel colonies, the availability of domestic refuse has changed considerably. The most important landfill area (“Afvalverwerking Wieringermeer”) is now a waste processing plant with limited feeding opportunities. The numbers of gulls visiting the area have declined accordingly, but some specialised individuals still forage there. Waste incinerators became established (Alkmaar, Amsterdam) rather than open dumps and the foraging opportunities for gulls have declined throughout the country (Appendix 2). In comparison with the studies of Spaans (1971) on Herring Gulls breeding at Terschelling in the late 1960s, the utilisation of domestic waste by Herring Gulls has seemingly declined. Belant *et al.* (1989) concluded that landfills are unimportant to nesting Herring Gulls when alternate, higher quality food is available. In these American studies, the occurrence of garbage in the diet of adults and chicks remained low through chick-rearing but increased after fledging. Similar patterns were found in Yellow-legged Gulls in Spain and in wintering gulls in Scandinavia, Germany, the UK, and the USA (Kihlman & Larsson 1974, Horton *et al.* 1983, Lüttringhaus & Vauk-Hentzelt 1983, Patton 1988, Blanco & Marchamalo 1999).

Early authors in The Netherlands observed that immature Herring Gulls were more abundant than adults on refuse dumps in summer (Binsbergen 1935) and overall numbers of gulls were higher in winter (now including many adults) than in summer. Since the late 1960s, large numbers of gulls breeding in The Netherlands were found to winter in the Ruhr district, a highly industrialised inland urban landscape in Germany, where gulls foraged mainly on refuse dumps (Camphuysen & Spaans 2005). While refuse production rose in the 1980s, numbers of wintering Herring Gulls increased, but after 1992, several refuse dumps were decommissioned. Gull roosts and flight lanes subsequently lost their importance (Bellebaum *et al.* 2000) and few Dutch colour-ringed Herring Gulls were reported from German sites in recent years (CJC database, unpubl. data; Appendix 5). Changes in Wallonia were thus far rather small, but Lesser Black-backed Gulls increasingly used pastures as if driven off the remaining belts (Deflorenne & Ellis 2012). The possible consequences of reduced access to domestic refuse for the overwinter survival of Herring Gulls is discussed in Chapter 15.

Mammalian prey - In coastal colonies only few (specialised) individuals were found to feed on mammalian prey. By contrast, a majority of the individuals in an inland colony were found to frequently feed on mammals (hedgehogs, shrews, voles, mice, moles, rats, rabbits and hares). Most mammalian prey must have been obtained on inland fields or on roadside (roadkills), although some may have been captured within the colonies. The discussion in Chapter 14 points at the possibility that an increasing scarcity of food (discards and refuse dumps) could force increasing numbers of gulls to increasingly focus on alternative inland foraging habitats and prey species, mammals included. Further information on the utilisation of inland foraging behaviour is expected when tag data are analysed in more depth, using accelerometer information, so that [prey] strike rates can be coupled with exact habitat type and weather conditions. Technology is now so far advanced, that this is possible. In case of the Texel birds, much of the required info is in fact already available in the collected data, just awaiting analysis.

Appendix 10 - Species comparisons

Currently, Herring Gulls and Lesser Black-backed Gulls both have a breeding distribution within the sub-polar and temperate zones, nesting on the ground in colonies, where they normally incubate a clutch of three eggs for a period of *c.* 28 days. Chicks take a further 40 days of bi-parental care prior to fledging. They are rather long-lived (sea-)birds with a life-expectancy of some 10-20 years (records known being >30y of age in both taxa; annual adult survival in many studies around *c.* 90%). Both species utilise both marine (offshore and inshore), intertidal and terrestrial resources, including domestic refuse. First breeding occurs at an age of 4-5 years in most colonies, but few recruits of that age have been recorded at Texel.

Herring Gulls, certainly those in the temperate zone, are semi-residents that disperse in winter (range several hundreds of kilometres at most), while Lesser Black-backed Gulls are truly migratory, travelling thousands of kilometres to wintering grounds in Spain, Portugal or NW Africa. Some winter further north (France, southern England), but all leave the breeding grounds in autumn and return in March. Hybridisation is uncommon, except in newly established colonies. Herring Gulls are on average larger, heavier and relatively shorter-winged than Lesser Black-backed Gulls. In both species, males are on average larger than females. The energetic requirements (BMR) of females are *c.* 87% that of males in both species.

Summary of characteristics of Lesser Black-backed Gulls and Herring Gulls at Texel from multiple sources, with emphasis on data collected in this study. See remarks and footnotes.

English name	**European Herring Gull**	**Lesser Black-backed Gull**
Dutch name	Zilvermeeuw	Kleine Mantelmeeuw
Class	← Aves →	
Order	← Charadriiformes →	
Family	← Laridae →	
Genus	← *Larus* →	
Species	*argentatus*	*fuscus*
Subspecies	*argenteus*	*intermedius / graellsii*
Authority	Pontoppidan, 1763	Linnaeus, 1758
Breeding distribution[6]	Sub polar-temperate	Sub polar-temperate
Faunal type[12]	Nearctic	Palaearctic
Nesting, laying	**European Herring Gull**	**Lesser Black-backed Gull**
Nest location[1]	ground-nesting, dune tops and slopes	ground-nesting, flat ground, valleys
Nesting density (nests ha^{-1})	136 ± 44 (60-190)	266 ± 169 (50-530)
First eggs[1]	26 Apr ± 2.9 d (23 Apr-2 May)	1 May ± 2.1 d (29 Apr-4 May)
Mean laying date[1]	6 May ± 2.0 d (4-10 May)	13 May ± 2.9 (10-18 May)
Median laying date[1]	6 May ± 2.0 d (4-9 May)	12 May ± 3.3 d (9-19 May)
Clutch size[1]	2.72 ± 0.09 (1-4) eggs	2.76 ± 0.08 (1-5) eggs*
1-egg clutches[Freq, 1]	5.4% (n= 407)	5.4% (n= 594)
2-egg clutches	17.2% (n= 407)	14.8% (n= 594)
3-egg clutches	77.1% (n= 407)	79.8% (n= 594)
4-egg clutches	0.2% (n= 407)	none (n=594)
A-egg size (mm, mean ± SD)[1]	71.3 ± 3.0 x 48.6 ± 1.9 (n= 270)	67.5 ± 2.7 x 47.2 ± 1.4 (n= 313)
volume (cc, mean ± SD)[1]	85.0 ± 7.9 (n= 270)	75.9 ± 6.0 (n= 313)
B-egg size (mm, mean ± SD)[1]	69.8 ± 2.9 x 48.3 ± 1.7 (n= 217)	67.2 ± 2.7 x 47.3 ± 1.4 (n= 244)
volume (cc, mean ± SD[1])	82.2 ± 7.8 (n= 216)	76.0 ± 5.9 (n= 244)
C-egg size (mm, mean ± SD)[1]	68.1 ± 2.9 x 47.5 ± 1.7 (n= 205)	66.2 ± 2.8 x 46.5 ± 1.3 (n= 297)
volume (cc, mean ± SD)[1]	77.6 ± 7.5 (n= 205)	72.2 ± 5.9 (n= 297)
Clutch volume (cc, 3-eggs)[1]	245.7 ± 3.0	223.4 ± 3.2
Egg predation (%)[1]	17.9 ± 5.3	18.2 ± 6.7
Addled eggs (%)[1]	10.5 ± 6.3	8.0 ± 2.2
Hatching eggs (%)[1]	71.3 ± 7.0	73.2 ± 7.3
Incubation period (d)[1]	27.9 ± 0.9	27.6 ± 1.1

Chick care	**European Herring Gull**	**Lesser Black-backed Gull**
Hatching type[6]	semi-precocial	semi-precocial
Mean hatching date[1]	2 Jun ± 1.9 d (31 May-6 Jun)	8 Jun ± 2.9 d (5-14 Jun)
Median hatching date[1]	2 Jun ± 1.8 d (31 May-5 Jun)	8 Jun ± 2.9 d (5-14 Jun)
Growth rate at 5-20d, fledging chicks[1]		
Bill (mm d^{-1})	1.9 ± 0.7 (n= 104)	1.7 ± 0.6 (n= 143)
Head (mm d^{-1})	0.8 ± 0.6 (n= 104)	0.9 ± 0.6 (n= 143)
Wing (mm d^{-1})	7.3 ± 3.5 (n= 104)	8.2 ± 2.7 (n= 143)
Tarsus (mm d^{-1})	1.5 ± 0.6 (n= 92)	1.5 ± 0.7 (n= 133)
Mass (g d^{-1})	29.6 ± 13.9 (n= 104)	24.3 ± 13.5 (n= 143)
Chick predation (%)[1]	30.9 ± 11.8	56.9 ± 10.9
Chick mortality (%)[1]	24.3 ± 15.3	19.6 ± 8.2
Chicks fledged (%)[1]	44.4 ± 11.6	22.4 ± 6.7
Fledging period (%)[6]	40-50 d	35-45 d
Fledging rates (chicks $pair^{-1}$)	0.88 ± 0.3	0.49 ± 0.2
Post-fledging care[6]	45+ d	yes

Survival and recruitment	**European Herring Gull**	**Lesser Black-backed Gull**
First year survival (%)[guesstimate]	25 ± 6%	31 ± 8%
Age of first breeding[6, 1]	4-6 yrs	5-6 yrs
Immature survival (2-5yr, %) [guesstimate]	70 ± 6%	83 ± 5%
Recruitment (%)[guesstimate]	6%	14%
Maximum age (longevity)	34 yrs[4]	33 yrs[5]
Adult annual survival[1]	♀ 79%, ♂ 86%[1]	91%[1]

Migratory movements, wintering	**European Herring Gull**	**Lesser Black-backed Gull**
Migratory movements	resident, dispersive	seasonal migrant
Migratory range ($adult^{mean}$, Dec-Jan)	99 ± 109 km[7]	1367 ± 206 km[8]
Migratory range ($adult^{max}$, Dec-Jan)	333 km[7]	2049 km[8]
Migratory range ($adult^{mean}$, Dec-Jan	52.3 ± 0.8°N[7]	42.1 ± 5.1°N[8]
Migratory direction ($adult^{mean}$, Dec-Jan)	173 ± 57° (min 50.4°N)[7]	206 ± 14°(min 36.5°N)[8]
Migratory range (juv^{mean}, Dec-Jan)	68 ± 72 km[7]	1861 ± 201 km[8]
Migratory range (juv^{max}, Dec-Jan)	382 km[7]	2780 km[8]
Migratory range (juv^{mean}, Dec-Jan)	52.5 ± 0.6°N (min 50.1°N)[7]	37.9 ± 4.5°N (min 30.4°N)[8]
Migratory direction (juv^{mean}, Dec-Jan)	157 ± 51° [7]	201 ± 8° [8]
Main wintering area	Netherlands, Belgium, N France[7]	NW Africa, Spain, Portugal[8]

Principal resources during breeding	**European Herring Gull**	**Lesser Black-backed Gull**
Foraging habitat[1]	nearshore, intertidal, inland	offshore, inland
Foraging distance (km)	20-30 km[13]	40-80 km[9]
Marine prey (freq occ)[1]	23% discards, pelagic fish, shrimps, (Σ 65 species)	**90%** **discards, pelagic fish, crustaceans, Nereid worms** (Σ 69 species)
Intertidal prey (freq occ)[1]	**75%** **mussels, cockles, razor clams, starfish, crustaceans** (Σ 34 species)	3% razor clams, Nereid worms (Σ 18 species)
Terrestrial prey (freq occ)[1]	23% cannibalistic prey, mammals, grains (Σ 86 species)	31% cannibalistic prey, insects, earthworms, cattle feed, berries (Σ 86 species)
Domestic refuse (freq occ)[1]	13% plastics, chick, bread, meat (Σ 80 types)	6% plastics, chick, bread, meat (Σ 51 types)

Biometrics	**European Herring Gull**	**Lesser Black-backed Gull**
Adult mass ♂[1]	1032 ± 73.1, max 1295 g (n= 86)	910 ± 76.3, max 1065 g (n= 105)
Adult mass ♀[1]	862 ± 56.8, max 1005 g (n= 84)	745 ± 52.1, max 880 g (n= 121)
Wing span, ♂ (mean ± SE)[10]	140.9 ± 6.5 cm	140.8 ± 6.2 cm
Wing span, ♀[10]	132.5 ± 7.0 cm	133.2 ± 5.7 cm
Wing area, ♂ (mean ± SE)[10]	210.6 ± 23.4 cm²	205.3 ± 20.3 cm²
Wing area, ♀[10]	183.8 ± 21.7 cm²	184.8 ± 16.8 cm²

Biometrics	**European Herring Gull**	**Lesser Black-backed Gull**
Bill, tip to feathers, ♂[1]	55.7 ± 2.3, 49.8-60.3 mm (n= 86)	56.2 ± 2.3, 51.0-61.8 mm (n= 105)
Bill, tip to feathers, ♀[1]	50.2 ± 2.0, 46.0-54.7 mm (n= 85)	50.7 ± 1.9, 46.4-55.0 mm (n= 122)
Bill depth base, ♂[1]	20.1± 0.9, 17.6-22.3 mm (n= 86)	19.3± 1.1, 16.5-22.5 mm (n= 105)
Bill depth base, ♀[1]	17.5 ± 0.7, 15.8-19.9 mm (n= 85)	17.1 ± 0.7, 14.6-19.1 mm (n= 122)
Bill depth gonys, ♂[1]	20.7 ± 0.8, 19.1-22.7 mm (n= 86)	19.0 ± 0.9, 16.3-21.6 mm (n= 105)
Bill depth gonys, ♀[1]	18.4 ± 0.7, 16.5-20.6 mm (n= 85)	16.9 ± 0.7, 14.0-19.0 mm (n= 122)
Head length, ♂[1]	124.6 ± 2.7, 119-130 mm (n= 86)	122.0 ± 3.2, 113-128 mm (n= 105)
Head length, ♀[1]	114.1 ± 2.2, 109-119 mm (n= 85)	110.9 ± 2.2, 103-117 mm (n= 122)
Tarsus length, ♂[1]	67.7 ± 2.1, 63-74 mm (n= 86)	66.3 ± 2.7, 59-72 mm (n= 105)
Tarsus length, ♀[1]	62.8 ± 2.1, 57-68 mm (n= 85)	61.5 ± 2.2, 55-67 mm (n= 122)
Wing length, ♂[1]	435.4 ± 11.7, 415-458 mm (n= 84)	437.6 ± 11.1, 409-458 mm (n= 105)
Wing length, ♀[1]	413.7 ± 8.9, 393-439 mm (n= 83)	416.2 ± 9.0, 392-436 mm (n= 122)

Energetic requirements	**European Herring Gull**	**Lesser Black-backed Gull**
Energetic req., ♂ (BMR)[2]	312 kJ (3.6W)	285 kJ (3.3W)
Energetic req., ♀ (BMR)[2]	273 kJ (3.2W)	247 kJ (2.9W)
Daily req., ♂ (FMR)[3]	1560 kJ (18.1W)	1427 kJ (16.5W)
Daily req., ♀ (FMR)[3]	1365 kJ (15.8W)	1236 kJ (14.3W)

[1] own data, Kelderhuispolder 2006-2012, adult birds sexed on head-length, chicks unsexed, biometrics as mean ± SD, range or max and sample size, [2] *cf.* Aschoff & Pohl 1970 (relationship between *BMR* (kJ) and mass (W in kg): $BMR = 307.6 \cdot W^{0.734}$), [3] *cf.* Drent & Daan 1980, Ellis 1984 (seabirds from high latitudes have a greater BMR than tropical seabirds (assumed 1.25 BMR for 53°N); energy requirements adults during breeding estimated at 4(1.25 BMR), [4] Vogeltrekstation Heteren 2008, ring report 5054793, [5] Staav & Fransson 2006, [6] Schreiber & Burger 2002, [7] colour ring sightings, Dec-Jan, [8] colour ring sightings Dec-Jan, [9] own GPS loggers 2008-2012, (exceptional trips excluded), [10] Verbeek 1977, [11] BWP*i*, [12] Voous 1960, [13] colour ring sightings adults, Apr-Aug, (n=287), exceptional 34km, 68km. "Guesstimates" are based on confirmed resightings at Texel and elsewhere within their flyways, rather than proper modelling, and following a proper MARK analysis, after corrections for re-sighting probabilities, these values are bound to rise slightly. *) 4 and 5-egg clutches in Lesser Black-backed Gulls at Texel only found during wide-ranging density assessments.

Annual cycle (Appendices 3-4, $^{\mathrm{App}}$Tabs 3.3-4 & $^{\mathrm{App}}$Figs. 4.1-2)

European Herring Gull		**Lesser Black-backed Gull**	
Wintering period	Nov-Feb	Wintering period	Nov-Feb
Pre-nuptial moult completed	Feb-Mar	Pre-nuptial moult completed	Feb-Mar
Adult return migration	Feb-Apr	Adult return migration	Feb-Apr
Earliest colony returns	21-28 Mar	Earliest colony returns	22-29 Mar
Prospecting phase	Apr	Prospecting phase	Apr
First eggs	23 Apr-2 May	First eggs	29 Apr-4 May
Median laying	4-9 May	Median laying	9-19 May
Start primary moult	early May	First hatchlings	22 May-1 Jun
First hatchlings	20-29 May	Start primary moult	mid-Jun/Jul
Median hatching	31 May-5 Jun	Median hatching	5-14 Jun
Chick care	4 Jun-19 Jul	Chick care	12 Jun-26 Jul
First fledglings	2-12 Jul	First fledglings	10-17 Jul
Colony departure	Aug	Colony departure	Jul-Aug
Autumn dispersal	Aug-Oct	Autumn migration, 1st leg	Aug-Oct
Winter plumage attained	Oct	Winter plumage attained	Sep-Oct
Post-nuptial moult completed	Oct-Nov	Autumn migration final leg	Oct-Nov
		Post-nuptial moult completed	Nov-Dec?

Subject index