Central place foraging drives niche partitioning in seabirds

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Abstract

When species coexist, it is expected that they will reduce competition through niche partitioning or spatial segregation. We investigated the importance of niche partitioning versus spatial segregation across a seabird community where food and foraging constraints vary seasonally. Spatial clustering of seabird density in the western Irish Sea occurred in both seasons, with hotspots of seabird occurrence significantly higher in summer (Moran's I: 0.29) than winter (Moran's I: 0.19). A positive correlation between seabird density and feeding guild richness suggested a role for niche partitioning in reducing competition. This correlation was significantly stronger in summer than winter (Z-test, $p<0.05$), suggesting that when foraging range is constrained during the breeding season, interspecific competition is reduced through increased niche partitioning. Reduced spatial clustering and weaker correlations between density and feeding guild richness in winter suggests that spatial segregation plays a greater role in reducing interspecific competition outside the breeding season. This study demonstrates the relative importance of niche partitioning and spatial segregation, highlighting niche partitioning as a response to constraints on foraging range during the breeding season.

Keywords: seabird, niche partitioning, spatial segregation, Irish Sea, ObSERVE, competition, aerial survey

Introduction

In marine ecosystems, prey is patchily distributed both in time and space (Humphries, et al. 2010, Russell, et al. 1992). In areas where species co-exist and share limited resources, one species may either outcompete others for food (Ballance, et al. 1997, Navarro, et al. 2013), aggressively prevent individuals from accessing the resources (Hudson and Furness 1989), or reduce competition by partitioning resources (Bodey, et al. 2014, Navarro, et al. 2013). Resource partitioning has been reported widely across individuals (Bolnick, et al. 2002, Estes, et al. 2003) and among sexes (Maxwell, et al. 2019), age-classes (Campioni, et al. 2015, Grecian, et al. 2018), and colonies (Bolton, et al. 2018). It is typically achieved either through the exploitation of different ecological niches such as depth (e.g. Wilson 2010) or diet (Croxall and Prince 1980), hereafter referred to as 'niche partitioning' (Schoener 1974, Schoener 1986), or through space, hereafter noted as 'spatial segregation' (Crowell 1962).

Seabirds represent a diverse group, consisting of 359 species worldwide (Dias, et al. 2019). Many seabird species exhibit a high degree of synchronous breeding (Gochfeld 1980, Keogan, et al. 2018), with the distribution of breeding colonies often limited by availability of nesting sites which need to be in proximity to food resources (Sandvik, et al. 2016). This results in large multispecies breeding aggregations where seabirds undertake foraging trips from a central place (Furness and Birkhead 1984), with many species limited to shorter foraging ranges (Phillips, et al. 2007) and a high dietary overlap (Forero, et al. 2004). Such seasonally varying food requirements and limitations on foraging ranges during chick-provisioning lead to seasonal peaks in resource competition.

Studies on resource partitioning as a means of reducing both intra- and inter-specific competition in seabirds have demonstrated the key roles of niche partitioning and spatial segregation. For example, Wilson (2010) and Linnebjerg et al. (2013) both reported sympatrically breeding seabirds foraging in overlapping areas, but targeting different water depths, while spatial segregation of sympatrically breeding shearwaters and auks was observed over the chick-rearing period, presumably because of the higher prey demand and limited resources during this period (Afán, et al. 2014, Pratte, et al. 2017). Density-dependent spatial segregation of foraging areas have been found between northern gannet (*Morus bassanus*) from different colonies around the British Isles (Wakefield, et al. 2013), hypothesised to be a response to high levels of inter-colony competition related to colony size and proximity (Bolton et al. 2018). There is less information on resource partitioning outside the breeding season. This is a period when winter conditions require seabirds to increase their metabolism (Bevan and Butler 1992), while the

abundance of seabird prey is reduced due to lower primary productivity (Crisp 1964). More frequent and intense winter storms can also reduce the foraging success of seabirds (Birkhead 1976), making mechanisms for reducing competition particularly important. There is evidence that dispersal enables seabirds to move to different areas of ocean productivity (Clay, et al. 2016, Edwards, et al. 2016, Fayet, et al. 2017, Guilford, et al. 2009) reducing competition from conspecifics. However, there are few studies demonstrating resource partitioning at the wider community level.

The western Irish sea is an important area for a range of breeding and migratory seabirds throughout the year (Cabot 1996, Mitchell, et al. 2004, Wakefield, et al. 2013), making it an ideal candidate site for investigating seasonal variation in competition leading to resource partitioning across the breeding and non-breeding seasons. We anticipate that:

1. During the breeding season, large aggregations of seabirds will be constrained to foraging near colonies, limiting the potential for spatial segregation. We hypothesise a negative correlation between the density of birds at sea and distance from colonies, high spatial clustering of seabird density, and a strong positive correlation between seabird density and feeding guild richness, indicative of increased reliance on niche partitioning;
2. The removal of central place foraging constraints for many seabirds outside the breeding season will enable seabirds to exploit areas further from colonies. We hypothesise a reduced correlation between seabird density at sea and distance from colonies, reduced spatial clustering of density, and reduced correlation between density and guild richness, indicative of spatial segregation;
3. Areas of higher productivity should be able to support higher densities of seabirds. We hypothesise a positive correlation between seabird density and ocean productivity irrespective of season.

Here, we investigate these hypotheses by modelling seabird densities from observations collected during aerial surveys conducted in the Irish Sea, whilst accounting for a range of environmental, spatial and temporal variables.

Methods

Aerial surveys

Aerial surveys were conducted in the western Irish Sea, covering an area of approximately 9,184 km^2, in summer and winter 2016. The Irish Sea is a semi-enclosed shelf area, with a channel, over 100m deep, running along the western side of the sea. The sea is close to resonance with the semi-diurnal tide, resulting in large tides and fast tidal streams. There is a region of weak tidal streams to the south-west of the Isle of Man which becomes thermally stratified in summer. The barocline pressure gradient caused by the stratification, combined with earth rotation, drives an anticlockwise gyre in this part of the Irish Sea (Hill et al. 1997). Surveys were conducted under target weather conditions of Beaufort sea state 3 or less and visibility ≥1km. Line transect surveys were carried out using a fixed high-wing, twin-engine Britten-Norman (BN-2) Islander fitted with bubble-windows to afford observers unrestricted views of the area beneath the aircraft. Flying speed was 90 knots (167 km/h) at an altitude of 76 m (250 feet) above the sea surface, consistent with other studies using aerial surveys for seabirds at sea (Bretagnolle, et al. 2004, Briggs, et al. 1985, Certain and Bretagnolle 2008). Fifty-five parallel survey transects spaced approximately two nautical miles (3.7 km) apart, and 20-30 nautical miles in length covered the east coast of Ireland in the Irish Sea. The parallel line design (Figure 1) sought to cover all the shallower sand banks on the east coast of Ireland which broadly run in a north-south direction.

Two observers sat at bubble windows on either side of the aircraft, relaying sightings to data loggers through a closed loop intercom. Due to the exceptionally high number of seabird sightings in the Irish Sea, distance band methodology extending to 1km either side of the aircraft as recommended by Camphuysen et al. (2004) was unfeasible. Instead, seabirds were recorded using a strip transect methodology (Briggs, et al. 1985, Certain and Bretagnolle 2008), with all sightings within 200 m of the trackline on each side of the plane recorded. Sightings were logged using a touchscreen tablet running a tailored data collection app '*buttons event recorder'* (https://itunes.apple.com/us/app/buttons-event-recorder/id955172667?mt=8) connected via Bluetooth to a GPS (BadElf GPS PRO) recording aircraft location every second. Beaufort sea state, glare intensity and cloud cover were recorded at the beginning of each transect and whenever conditions changed. When seabirds came abeam of the aircraft, a date/time stamped record was produced consisting of location (latitude, longitude), species (or species group if not identified to species level), group size, and behaviour. Species were identified to the lowest taxonomic level whenever possible. When individuals could not be identified to species level, they were grouped into higher categories of taxa (e.g. Razorbill/Guillemot, Cormorant/Shag, tern spp.), and numbers in these

categories indicate only those individuals that could not be identified to species level (e.g. 'tern species' only includes those individuals that could not be identified to species level, and will not include terns that were positively identified to species level). Seabird species/groups were also assigned to feeding guilds (Blondel 2003) based on foraging techniques following Ashmole (1971) and Shealer (2002) (Table 1).

Seabird density and feeding guild richness

As transects were approximately 4 km apart, a 4×4 km grid covering the entire survey area was generated using the 'create fishnet' tool in ArcGIS 10.2 and all seabird sightings were assigned to the corresponding grid cell they were observed in using ArcGIS spatial statistics tools. The density, species richness, and feeding guild richness were calculated for each grid cell. Species richness and feeding guild richness were determined by summing the number of unique species/species groups or unique feeding guilds occurring within each cell. Higher taxonomic groupings were only included if there were no species-specific observations present in the grid cell (i.e. 'large gull species' or 'small gull species' were only included if no other gull species had been recorded within the same grid cell) giving a conservative estimate of species richness. Seabird density (D, individuals per km^2) was calculated for each species and for each grid cell by dividing the total number of birds recorded in each grid cell by the area surveyed within the grid cell (distance travelled in km multiplied by 200 m strip width either side of the aircraft, accounting for any periods where observers were off effort due to glare or low cloud). Estimates of seabird abundance (N_{tot}) across the entire survey area for each season were determined by multiplying the density of seabirds in each grid cell by the grid cell area (16 km^2), to first get an estimate of cell abundance (N_{cell}), and then summing the N_{cell} across all grid cells. As an estimate of variability, coefficient of variation (CV), for the abundance was obtained by dividing the standard error of mean density by mean density across all grid cells. The resulting variability estimate, albeit large, is considered appropriate when assuming 100% detection within a 200 m strip width either side of the aircraft and given our inability to account for availability for detection (birds may be submerged) or detection bias resulting from differences in sighting conditions (sea state, glare). Upper and lower 95% confidence intervals were obtained for N_{tot} using the CV and assuming the estimates are log-normally distributed using the following equations:

$$c = e^{(1.96\times\sqrt{\log(1+CV^2)})}$$

$$lower\ 95\%\ CI = \frac{N}{c}$$

$$upper\ 95\%\ CI = N \times c$$

Differences in abundance, species richness and guild richness between seasons were each tested using a two-tailed Student's t-test.

Spatial analyses

Spatial clustering of seabird density and feeding guild richness were tested using Moran's I correlation coefficient, which measures here how related in space variables are to one another within seasons. Moran's I is typically used as a prerequisite to quantify the amount of spatial autocorrelation in data before further analyses, however, the test also allows inference to be made on the degree of spatial structuring across a distribution (Brown and Chung 2006, Poulsen, et al. 2011). Moran's I was calculated in the R package 'spdep' (v1.1-3 Bivand, et al. 2011) with weights using k nearest neighbours (k=8) through the functions 'knearneigh', 'knn2nb' and 'nb2listw'. While several methods of defining neighbourhood weight matrices are available, we applied the style "s" to compensate for potential bias from observations on the edges of our survey area. A high degree of spatial clustering accompanied by a high correlation between density and feeding guild richness would be indicative of an increased reliance on niche partitioning. In contrast, if seabirds were primarily reducing competition through spatial segregation, the degree of spatial clustering would be low, with a low correlation between density and feeding guild richness. Monte Carlo tests were carried out in 'spdep' to estimate the significance of the Moran's I values, and differences in spatial clustering between seasons tested using a Z-score.

To determine if environmental variables such as high primary productivity were influencing the observed distributions, we extracted seasonal composites of Chlorophyll-a (CHL, mg m^{-3}) and sea-surface temperature (SST, °C) from the Aqua-MODIS mission available in the NASA Ocean Colour Database (https://oceancolor.gsfc.nasa.gov/). CHL and SST values were extracted for the centre point of each grid cell. We used monthly averages for CHL in the summer (June) as all surveys were carried out within this month. A lack of suitable survey conditions in winter meant that surveys ran over multiple months (November-January) with cloud cover over the Irish Sea resulting in large gaps in monthly chlorophyll data. We therefore used the seasonal averages across the November – January survey period.

Variation in seabird density was modelled using generalized least squares (GLS) models fitted in the R-package '*nlme*' (Pinheiro, et al. 2012). Seabird density and guild richness data were spatially

autocorrelated, as indicated by significant Moran's I values, and GLS analyses have been shown to be an effective way to detect and include different spatial structures into models (Beale et al., 2010). This method models the spatial covariance structure in the variance-covariance matrix using parametric functions (Pinheiro, et al. 2012), and models were run with five different spatial structures: exponential, gaussian, spherical, linear and ratio. The best fitting spatial structure was selected using Akaike's information criterion (AIC) values. Data were not normally distributed, and were ln(x+1) transformed prior to analysis. Initially, all environmental variables were included in the models and a backward elimination of variables was carried out by comparing the AIC values of the candidate models. The distance from the nearest breeding colony using the JNCC Seabird Monitoring Programme Database (www.jncc.gov.uk/smp) was calculated for each species-level observation using the *gdist* function in the R-package 'Imap' (Wallace and Wallace 2010). Separate models were fitted using seabird density and feeding guild richness, allowing inference to be made on the relationships between the two response variables and covariates across seasons.

Dutilleul's modified t-test (Dutilleul 1993) was used to test for spatial correlations between density and feeding guild richness within seasons, as well as between the distribution of CHL between seasons. This method accounts for the degree of spatial autocorrelation in the data by blocking the data according to the level of autocorrelation present.

Results

Suitable weather conditions restricted aerial surveys to discrete periods within each season. Summer surveys were flown over four days in June-July, and winter surveys were flown over five days in November-January. In total, 4,498 km of survey track was surveyed over the two seasons. Ninety-eight percent (4,412 km) of all survey effort was conducted in Beaufort sea states of 0-3. Accounting for the 200 m strip width either side of the aircraft, visual surveys covered approximately 10% of the surface area for the entire survey area.

A total of 7,779 seabird sightings, representing 29 species or species groups and 18,834 individuals were recorded across summer and winter surveys. Frequently sighted and abundant species included Razorbill/Guillemot, Manx shearwater (*Puffinus puffinus*), Northern gannet, Arctic/Common tern (*Sterna spp.*), Black-legged kittiwake (*Rissa tridactyla*), Cormorant/Shag (*Phalacrocorax spp.*), Herring gull (*Larus argentatus*), Black-backed gull spp. (*Larus spp.*), and Northern fulmar (*Fulmaris glacialis*) (Appendix 1).

Removing all higher taxonomic groupings where species-specific records also occurred (e.g. 'small gull spp.', 'auk spp.' etc), total species richness was 16 species or species groups in summer, and 14 in winter. While summer had significantly higher mean abundance ($P<0.05$), species richness ($P<0.001$), and feeding guild richness ($P<0.0001$) across grid cells than winter, seabird density did not differ between seasons across grid cells ($P=0.31$) (Table 2). Regions of highest seabird density and feeding guild richness varied between seasons (Figure 2).

The distribution of seabird density varied across seasons. Spatial clustering was apparent in both seasons (summer Moran's I = 0.29, $P < 0.01$; winter Moran's I = 0.19, $P < 0.01$), and was significantly higher in summer (Z score = 5, $P < 0.01$). A similar relationship was evident for feeding guild richness (summer Moran's I = 0.51, $P < 0.01$; winter Moran's I = 0.22, $P < 0.01$), with the degree of clustering in feeding guild richness higher than that observed for density. Seabird density and feeding guild richness were significantly positively correlated in both summer (ρ 0.47, 61 d.f., $P < 0.001$), and winter (ρ 0.26, 296 d.f., $P < 0.001$). However, the strength of the correlation was significantly higher in summer compared to winter (Z test, Z = 1.727, $P < 0.05$).

Strong, significant positive correlations between seasons in the distribution of CHL (Dutilleul's modified t-test ρ 0.5, $P < 0.05$) suggest that patches of productivity were consistent over time. With the exception of feeding guild richness in winter, the GLS models including all environmental and spatial variables performed better compared to when models were run with fewer variables (Table 3). Higher seabird densities occurred with increasing CHL in both seasons (positive t-statistic), but the relationship was only significant in winter. Conversely, there was no association between CHL and feeding guild richness. The relationship between seabird density and SST varied with seasons; higher seabird densities occurred with increasing SST in summer, but not winter. Feeding guild richness increased with increasing SST in both seasons. Feeding guild richness decreased with the distance from the nearest colony in the breeding season (Table 3, significant negative t-statistic), but not in winter. In contrast to feeding guild richness, the density of birds decreased with distance from the nearest colony in both seasons, but this decrease was only statistically significant in winter (Table 3).

Discussion

Our results highlight a seasonal change in strategies for reducing interspecific competition in seabirds through increased use of spatial segregation in the non-breeding season, compared to a greater reliance on niche partitioning during the breeding season. A key component of resource partitioning theory is that stable strategies are required to reduce competition (MacArthur 1958). However, seabirds change from central place foraging during the breeding season to less spatially limited foraging strategies outside the breeding season. This seasonal effect is rarely considered in the context of resource partitioning, largely due to the difficulty of studying birds in the non-breeding season. By conducting aerial surveys in both summer and winter, we were able to examine the distribution of seabirds in response to the addition or removal of central place foraging constraints at the community level. While spatial segregation can be determined through aerial surveys, some measurement of resource use, either through direct observation, gut content, or stable isotope analysis is required to demonstrate niche partitioning. However, this would be impossible at the scale of the study area, and we therefore assume that feeding guild is a relevant measure of different foraging depths and diet, acknowledging that different species within each feeding guild may show further levels of dietary segregation.

Environmental drivers of distribution

The Irish Sea is important for seabirds year-round, with similar mean densities and abundance in summer and winter. However, seabird distribution differed between seasons and was spatially clustered. High density areas may be partly explained by locally enhanced productivity supporting increased prey availability for predatorss (Bennison and Jessopp 2015, Haney 1986). Our results support this, as we found a positive effect of CHL on seabird density, but not on feeding guild richness, suggesting that in highly productive areas there is less need for niche partitioning to reduce competition. The strong positive correlation in the spatial distribution of chlorophyll-a between seasons also suggests that more productive regions are somewhat predictable over both time and space, at least in the Irish Sea which may explain its usefulness as a predictor of seabird distribution in some studies (e.g. Grémillet, et al. 2008, Suryan, et al. 2012, Vilchis, et al. 2006). Sea surface temperature was also determined to have a significant effect on seabird distributions with higher feeding guild richness in higher SSTs over both seasons. Within the western Irish Sea, a seasonal cyclonic gyre driven by the isolation of cold bottom water acts as a retention mechanism for larvae, pelagic juvenile crustaceans and fish (Dickey- Collas, et al. 1997, Phelps, et al. 2015). This could potentially cause stratification of prey species, enabling more efficient use of depth layers as a mechanism of niche partitioning. This gyre breaks down by August in most years (Olbert, et

al. 2011), which offers a possible explanation for the lack of relationship between seabird density and SST in winter.

Resource partitioning in summer

Summer is the period when many birds are less able to exploit foraging locations further afield due to the need to return to nests regularly to provision offspring (Croxall, et al. 1999). The east and southeast coasts of Ireland support numerous breeding colonies of guillemots, razorbills, puffins, gannets, kittiwakes, cormorants, fulmar, gulls and multiple tern species (Mitchell, et al. 2004). As expected, seabird density and feeding guild richness decreased with distance from the nearest colony in summer reflecting reduced foraging ranges. The high degree of spatial clustering in seabird density during the summer highlights the potential for interspecific competition, with large numbers of birds occurring in the same locations. The concurrent clustering of feeding guild richness, and strong positive correlation between density and guild richness in summer suggests that despite occupying the same space, interspecific competition is reduced through an increased reliance on niche partitioning. This process is ably demonstrated in sympatrically breeding seabirds in Greenland, that have overlapping foraging area, but segregated diet and dive depth during the breeding season (Linnebjerg, et al. 2013). Seabird prey species are understood to inhabit different depth layers of the water column, and although flexible, seabirds generally specialize in feeding at a particular depth range (Cherel, et al. 2014, Paiva, et al. 2010, Pettex, et al. 2012), such that competition for prey resources can be reduced. Feeding guilds recorded during the summer surveys included a range of surface feeders, shallow divers and deep divers, all able to exploit different prey or depths.

Resource partitioning in winter

The constraint of central place foraging is lifted at the end of the breeding season, enabling seabirds to utilise foraging opportunities further offshore (Frederiksen, et al. 2012, Jessopp, et al. 2013, McCutcheon, et al. 2011). We still saw a negative relationship between seabird density and distance from the colonies which is likely influenced by large numbers of auks and cormorants in the Irish sea, coupled with a high energetic cost of flight in auks (Elliott, et al. 2013) and wetting of plumage in *Phalacrophorax* spp. requiring regular roosting (Rijke 1968). A significant positive relationship between density and CHL in winter suggests that areas of higher productivity are able to support more foraging seabirds (Grecian, et al. 2016), and this is also reflected in the occurrence of spatial clustering in this season. However, the degree of spatial clustering was significantly reduced compared to summer, denoted by reduced Moran's

I. This reduced spatial clustering and more diffuse distribution of seabird density is consistent with increased spatial segregation, where the lifting of central place foraging constraints enables birds to forage over wider areas. The significant reduction in the correlation between density and feeding guild richness also supports this hypothesis.

Conclusion

Our study shows how interspecific competition can be reduced through flexible strategies to partition resources in different seasons. We noted an increased reliance on niche partitioning in the breeding season, and spatial segregation in the non-breeding season. However, it should be noted that neither strategy is used exclusively in either season. Furthermore, we suggest that the weaker correlation between density and feeding guild richness in winter compared to summer represents the degree to which niche partitioning is used to overcome central place foraging constraints in summer. While there are examples of similar changing patterns of resource partitioning across the annual cycle in studies which consider just a few species (Linnebjerg, et al. 2013), our results suggest that this seasonal change also occurs at the wider seabird community level. The interplay between the dynamic marine environment and adaptive mechanisms such as resource partitioning suggests that for species foraging on patchily distributed prey, spatial segregation may be optimal for reducing interspecific competition, and that niche partitioning is a likely response to central place foraging constraints where spatial segregation of foraging areas is less possible.

Data availability

All aerial survey data are available by request through the data holders, the Department of Communication, Climate Action and Environment.

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Competing Interests

The authors have no competing interests to declare.

References

Afán, I., J. Navarro, L. Cardador, F. Ramírez, A. Kato, B. Rodríguez, Y. Ropert-Coudert, and M. G. Forero. 2014. Foraging movements and habitat niche of two closely related seabirds breeding in sympatry. Marine Biology **161**:657-668.

Ashmole, N. P. 1971. Seabird ecology and the marine environment. Avian biology **1**:223-286.

Ballance, L. T., R. L. Pitman, and S. B. Reilly. 1997. Seabird community structure along a productivity gradient: Importance of competition and energetic constraint. Ecology **78**:1502-1518.

Bennison, A., and M. Jessopp. 2015. At-sea surveys confirm a North Atlantic biodiversity hotspot. Bird Study **62**:262-266.

Bevan, R., and P. Butler. 1992. The effects of temperature on the oxygen consumption, heart rate and deep body temperature during diving in the tufted duck Aythya fuligula. Journal of Experimental Biology **163**:139-151.

Birkhead, T. 1976. Effects of sea conditions on rates at which Guillemots feed chicks. British Birds **69**:490-492.

Blondel, J. 2003. Guilds or functional groups: does it matter? Oikos **100**:223-231.

Bodey, T. W., E. J. Ward, R. A. Phillips, R. A. McGill, and S. Bearhop. 2014. Species versus guild level differentiation revealed across the annual cycle by isotopic niche examination. Journal of Animal Ecology **83**:470-478.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2002. The ecology of individuals: incidence and implications of individual specialization. The American naturalist **161**:1-28.

Bolton, M., G. Conolly, M. Carroll, E. D. Wakefield, and R. Caldow. 2018. A review of the occurrence of inter-colony segregation of seabird foraging areas and the implications for marine environmental impact assessment. Ibis **0**.

Bretagnolle, V., G. Certain, S. Houte, and M. Métais. 2004. Distribution maps and minimum abundance estimates for wintering auks in the Bay of Biscay, based on aerial surveys. Aquatic Living Resources **17**:353-360.

Briggs, K. T., W. B. Tyler, and D. B. Lewis. 1985. Aerial surveys for seabirds: methodological experiments. The Journal of Wildlife Management:412-417.

Brown, L. A., and S. Y. Chung. 2006. Spatial segregation, segregation indices and the geographical perspective. Population, space and place **12**:125-143.

Cabot, D. 1996. Performance of the Roseate Tern Population Breeding in North-West Europe: Ireland, Britain and France, 1960-94. Biology and Environment: Proceedings of the Royal Irish Academy **96B**:55-68.

Camphuysen, C., A. Fox, M. Leopold, and I. K. Petersen. 2004. Towards Standardised Seabirds at Sea Census Techniques in Connection with Environmental Impact Assessments for Offshore Wind Farms in the UK: a comparison of ship and aerial sampling methods for marine birds and their applicability to offshore wind farm assessments. Report commissioned by COWRIE Ltd., London. www. offshorewindfarms. co. uk.

Campioni, L., J. P. Granadeiro, and P. Catry. 2015. Niche segregation between immature and adult seabirds: does progressive maturation play a role? Behavioral Ecology **27**:426-433.

Certain, G., and V. Bretagnolle. 2008. Monitoring seabirds population in marine ecosystem: the use of strip-transect aerial surveys. Remote sensing of environment **112**:3314-3322.

Cherel, Y., M. Connan, A. Jaeger, and P. Richard. 2014. Seabird year-round and historical feeding ecology: blood and feather δ13C and δ15N values document foraging plasticity of small sympatric petrels. Marine Ecology Progress Series **505**:267-280.

Clay, T. A., A. Manica, P. G. Ryan, J. R. Silk, J. P. Croxall, L. Ireland, and R. A. Phillips. 2016. Proximate drivers of spatial segregation in non-breeding albatrosses. Scientific reports **6**:29932.

Crisp, D. 1964. The effects of the severe winter of 1962-63 on marine life in Britain. Journal of Animal Ecology **33**:165-210.

Crowell, K. L. 1962. Reduced interspecific competition among the birds of Bermuda. Ecology **43**:75-88.

Croxall, J., and P. Prince. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. Biological Journal of the Linnean Society **14**:103-131.

Croxall, J., K. Reid, and P. Prince. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Marine ecology. Progress series **177**:115-131.

Dias, M. P., R. Martin, E. J. Pearmain, I. J. Burfield, C. Small, R. A. Phillips, O. Yates, B. Lascelles, P. G. Borboroglu, and J. P. Croxall. 2019. Threats to seabirds: A global assessment. Biological Conservation.

Dickey- Collas, M., J. Brown, L. Fernand, A. Hill, K. Horsburgh, and R. Garvine. 1997. Does the western Irish Sea gyre influence the distribution of pelagic juvenile fish? Journal of Fish Biology **51**:206-229.

Dutilleul, P. 1993. Modifying the t test for assessing the correlation between two spatial processes. Biometrics **49**:305-314.

Edwards, E. W., L. R. Quinn, and P. M. Thompson. 2016. State- space modelling of geolocation data reveals sex differences in the use of management areas by breeding northern fulmars. Journal of Applied Ecology **53**:1880-1889.

Elliott, K. H., R. E. Ricklefs, A. J. Gaston, S. A. Hatch, J. R. Speakman, and G. K. Davoren. 2013. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. Proceedings of the National Academy of Sciences **110**:9380-9384.

Estes, J. A., M. L. Riedman, M. M. Staedler, M. T. Tinker, and B. E. Lyon. 2003. Individual variation in prey selection by sea otters: patterns, causes and implications. Journal of Animal Ecology **72**:144-155.

Fayet, A., R. Freeman, T. Anker-Nilssen, A. Diamond, K. E. Erikstad, D. Fifield, M. G. Fitzsimmons, E. S. Hansen, M. P. Harris, M. Jessopp, A. Kouwenberg, S. Kress, S. Mowat, C. M. Perrins, A. Petersen, I. K. Petersen, Þ. Þórarinsson, T. K. Reiertsen, G. J. Robertson, I. A. Sigurðsson, A. Shoji, S. Wanless, and T. Guilford. 2017. Ocean-wide drivers of migratory strategies and their influence on population breeding performance in an endangered seabird. Current Biology **27**:3871-3878.e3873.

Forero, M. G., G. R. Bortolotti, K. A. Hobson, J. A. Donazar, M. Bertelloti, and G. Blanco. 2004. High trophic overlap within the seabird community of

Argentinean Patagonia: a multiscale approach. Journal of Animal Ecology **73**:789–801.

Furness, R. W., and T. R. Birkhead. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature **311**:655.

Gochfeld, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. Pages 207-270 Behavior of marine animals. Springer.

Grecian, W. J., J. V. Lane, T. Michelot, H. M. Wade, and K. C. Hamer. 2018. Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. Journal of the Royal Society Interface **15**:p.20180084.

Grecian, W. J., M. J. Witt, M. J. Attrill, S. Bearhop, P. H. Becker, C. Egevang, R. W. Furness, B. J. Godley, J. González-Solís, and D. Grémillet. 2016a. Seabird diversity hotspot linked to ocean productivity in the Canary Current Large Marine Ecosystem. Biology Letters **12**:20160024.

Grecian, W. J., M. J. Witt, M. J. Attrill, S. Bearhop, P. H. Becker, C. Egevang, R. W. Furness, B. J. Godley, J. González-Solís, D. Grémillet, M. Kopp, A. Lescroël, J. Matthiopoulos, S. C. Patrick, H.-U. Peter, R. A. Phillips, I. J. Stenhouse, and S. C. Votier. 2016b. Seabird diversity hotspot linked to ocean productivity in the Canary Current Large Marine Ecosystem. Biology letters **12**:20160024.

Grémillet, D., S. Lewis, L. Drapeau, C. D. van Der Lingen, J. A. Huggett, J. C. Coetzee, H. M. Verheye, F. Daunt, S. Wanless, and P. G. Ryan. 2008. Spatial match–mismatch in the Benguela upwelling zone: should we expect chlorophyll and sea- surface temperature to predict marine predator distributions? Journal of Applied Ecology **45**:610-621.

Guilford, T., J. Meade, J. Willis, R. A. Phillips, D. Boyle, S. Roberts, M. Collett, R. Freeman, and C. M. Perrins. 2009. Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. Proceedings of the Royal Society B: Biological Sciences **276**:1215-1223.

Haney, J. C. 1986. Seabird affinities for Gulf Stream frontal eddies: Responses of mobile marine consumers to episodic upwelling. Journal of Marine Research **44**:361-384.

Hudson, A., and R. Furness. 1989. The behaviour of seabirds foraging at fishing boats around Shetland. Ibis **131**:225-237.

Humphries, N. E., N. Queiroz, J. R. Dyer, N. G. Pade, M. K. Musyl, K. M. Schaefer, D. W. Fuller, J. M. Brunnschweiler, T. K. Doyle, J. Houghton, and G. C. Hays. 2010. Environmental context explains Lévy and Brownian movement patterns of marine predators. Nature **465**:1066.

Keogan, K., F. Daunt, S. Wanless, R. A. Phillips, C. A. Walling, P. Agnew, D. G. Ainley, T. Anker-Nilssen, G. Ballard, and R. T. Barrett. 2018. Global phenological insensitivity to shifting ocean temperatures among seabirds. Nature Climate Change **8**:313.

Linnebjerg, J. F., J. Fort, T. Guilford, A. Reuleaux, A. Mosbech, and M. Frederiksen. 2013. Sympatric breeding auks shift between dietary and spatial resource partitioning across the annual cycle. PLOS ONE **8**:e72987.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology **39**:599-619.

Maxwell, S. M., K. L. Scales, S. J. Bograd, D. K. Briscoe, H. Dewar, E. L. Hazen, R. L. Lewison, H. Welch, and L. B. Crowder. 2019. Seasonal spatial segregation in

blue sharks (Prionace glauca) by sex and size class in the Northeast Pacific Ocean. Diversity and Distributions.

Mitchell, P. E., S. F. Newton, N. Ratcliffe, and T. E. Dun. 2004. Seabird populations of Britain and Ireland. Results of the Seabird 2000 census (1998-2002). A&C Black publishers Ltd, London.

Navarro, J., S. C. Votier, J. Aguzzi, J. J. Chiesa, M. G. Forero, and R. A. Phillips. 2013. Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. PloS one **8**:e62897.

Olbert, A. I., M. Hartnett, T. Dabrowski, and U. Mikolajewicz. 2011. Long-term inter-annual variability of a cyclonic gyre in the western Irish Sea. Continental Shelf Research **31**:1343-1356.

Paiva, V. H., P. Geraldes, I. Ramírez, A. Meirinho, S. Garthe, and J. A. Ramos. 2010. Foraging plasticity in a pelagic seabird species along a marine productivity gradient. Marine Ecology Progress Series **398**:259-274.

Pettex, E., S.-H. Lorentsen, D. Grémillet, O. Gimenez, R. T. Barrett, J.-B. Pons, C. Le Bohec, and F. Bonadonna. 2012. Multi-scale foraging variability in Northern gannet (*Morus bassanus*) fuels potential foraging plasticity. Marine Biology **159**:2743-2756.

Phelps, J. J., J. A. Polton, A. J. Souza, and L. A. Robinson. 2015. Behaviour influences larval dispersal in shelf sea gyres: Nephrops norvegicus in the Irish Sea. Marine Ecology Progress Series **518**:177-191.

Phillips, R., J. Croxall, J. Silk, and D. Briggs. 2007. Foraging ecology of albatrosses and petrels from South Georgia: two decades of insights from tracking technologies. Aquatic Conservation: Marine and Freshwater Ecosystems **17**.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. C. Team. 2012. nlme: Linear and nonlinear mixed effects models. R package version **3**.

Poulsen, M., R. Johnston, and J. Forrest. 2011. Using local statistics and neighbourhood classifications to portray ethnic residential segregation: a London example. Environment and Planning B: Planning and Design **38**:636-658.

Pratte, I., G. J. Robertson, and M. L. Mallory. 2017. Four sympatrically nesting auks show clear resource segregation in their foraging environment. Marine Ecology Progress Series **572**:243-254.

Rijke, A. M. 1968. The water repellency and feather structure of cormorants, Phalacrocoracidae. Journal of Experimental Biology **48**:185-189.

Russell, R. W., G. L. Hunt, K. O. Coyle, and R. T. Cooney. 1992. Foraging in a fractal environment: spatial patterns in a marine predator-prey system. Landscape Ecology **7**:195-209.

Sandvik, H., R. T. Barrett, K. E. Erikstad, M. S. Myksvoll, F. Vikebø, N. G. Yoccoz, T. Anker-Nilssen, S.-H. Lorentsen, T. K. Reiertsen, and J. Skarðhamar. 2016. Modelled drift patterns of fish larvae link coastal morphology to seabird colony distribution. Nature communications **7**.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science **185**:27-39.

Schoener, T. W. 1986. Resource partitioning. Pages 91-126 *in* J. Kikkawa and D. J. Anderson, editors. Community Ecology. Blackwell Scientific, Oxford, UK. .

Shealer, D. A. 2002. Foraging behaviour and food of seabirds. Pages 137-177 *in* E. A. Schreiber and J. Burger, editors. Biology of marine birds. CRC Press, London.

Suryan, R. M., J. A. Santora, and W. J. Sydeman. 2012. New approach for using remotely sensed chlorophyll a to identify seabird hotspots. Marine Ecology Progress Series **451**:213.

Vilchis, L. I., L. T. Ballance, and P. C. Fiedler. 2006. Pelagic habitat of seabirds in the eastern tropical Pacific: effects of foraging ecology on habitat selection. Marine Ecology Progress Series **315**:279-292.

Wakefield, E. D., T. W. Bodey, S. Bearhop, J. Blackburn, K. Colhoun, R. Davies, R. G. Dwyer, J. Green, D. Grémillet, A. L. Jackson, M. J. Jessopp, A. Kane, R. H. W. Langston, A. Lescroël, S. Murray, M. Le Nuz, S. C. Patrick, C. Péron, L. Soanes, S. Wanless, S. C. Votier, and K. C. Hamer. 2013. Space Partitioning Without Territoriality in Gannets. Science **341**:68-70.

Wallace, J. R., and M. J. R. Wallace. 2010. Package 'Imap'.

Wilson, R. P. 2010. Resource partitioning and niche hyper- volume overlap in free-living Pygoscelid penguins. Functional Ecology **24**:646-657.

Appendix 1. Seabird sightings summary for low level aerial surveys for seabirds in the Irish Sea in summer and winter 2016. Sight. indicates the number of sightings, Indivs. indicates the total number of individuals counted.

	summer		winter	
Species	**Sight.**	**Indivs.**	**Sight.**	**Indivs.**
Northern gannet	194	331	27	33
Cormorant/shag	53	255	71	106
Northern fulmar	41	59	75	137
Great skua			1	1
Herring/common gull	207	568	412	1268
Black-headed gull	6	17	79	214
Lesser black-backed gull			8	8
Greater black-backed gull			34	48
Black-backed gull species	55	77	72	171
Little gull			37	80
Black-legged kittiwake	309	499	310	567
Large gull spp.	9	43	62	579
Small gull spp.	38	63	97	144
Manx shearwater	790	3669	2	5
Shearwater spp.	3	7	2	4
Petrel spp.	1	1		
Atlantic puffin	23	26		
Black guillemot	5	6		
Razorbill/Guillemot	1800	3849	2245	4470
Auk spp.	20	135		
Arctic/Common tern	299	498		
Roseate tern	66	131		
Sandwich tern	39	60		
Little tern	52	72		
Tern spp.	7	8		
Common scoter			41	328
Velvet scoter			9	30
Scoter spp.			4	11
Diver spp.	4	4	170	252

Figure Legends

Figure 1. Study area off the east coast of Ireland showing parallel transects flown during aerial surveys in summer and winter 2016. The transects are spaced approximately 4 km apart and were flown at an altitude of 76 m.

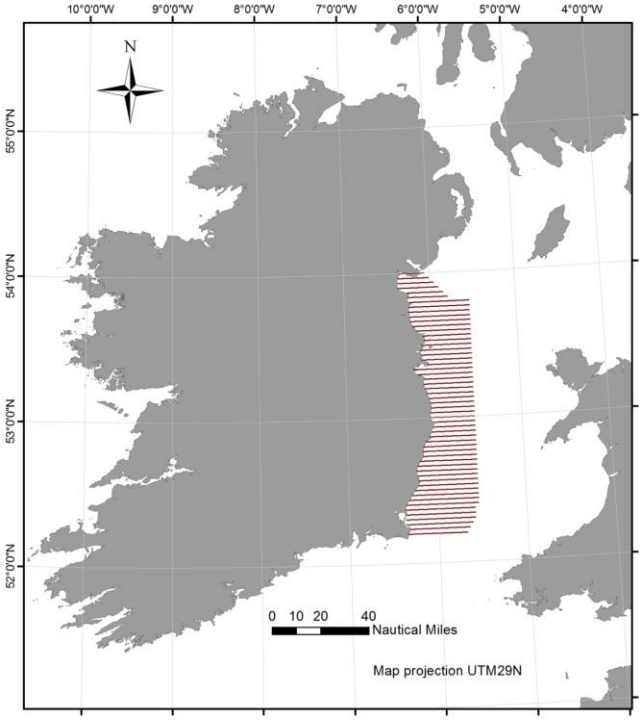

Figure 2. Seabird density (top) and guild richness (bottom) in 4×4 km grid cells across the survey area during summer and winter 2016.

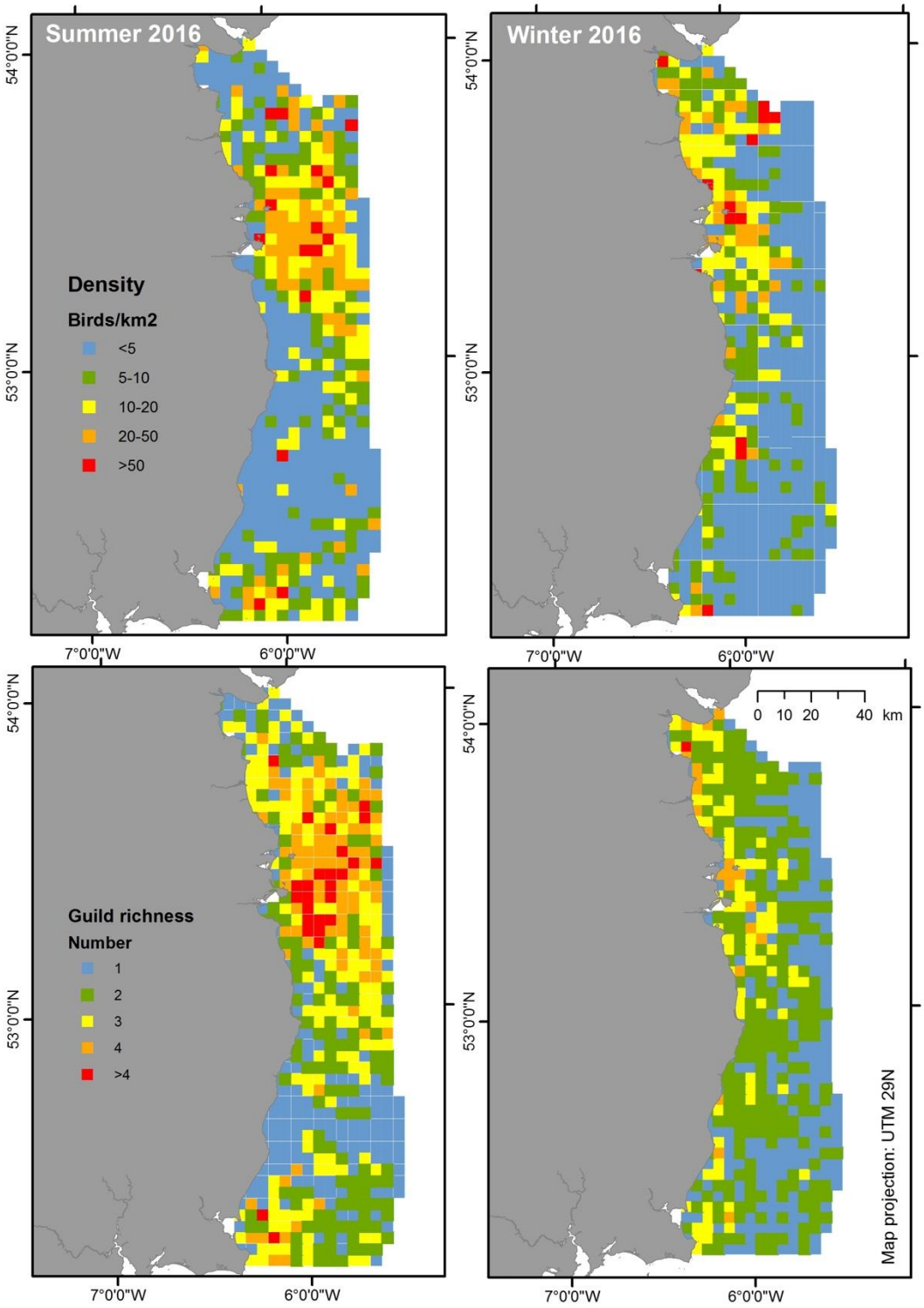

Table Legends

Table 1. Feeding guilds of seabirds based on foraging style following Shealer (2002) and Ashmole (1971).

Species/ species group	Feeding guild
Arctic/Common tern, *Sterna spp.*	dipping
Roseate tern, *Sterna dougallii*	dipping
Sandwich tern, *Thalasseus sandvicensis*	dipping
Little tern, *Sternula albifrons*	dipping
Tern spp.	dipping
Cormorant/Shag, *Phalacrocorax carbo/P. aristotelis*	pursuit dive shallow
Fulmar, *Fulmaris glacialis*	surface
Kittiwake, *Rissa tridactyla*	surface
Greater black-backed gull, *Larus marinus*	surface
Lesser black-backed gull, *Larus fuscus*	surface
Black-backed gull spp., *Larus marinus/ L. fuscus*	surface
Herring/Common gull, *Larus spp.*	surface
Black-headed gull, *Chroicocephalus ridibundus*	surface
Little gull, *Hydrocoloeus minutus*	surface
Small gull spp.	surface
Large gull spp.	surface
Common scoter, *Melanitta nigra*	bottom feeder
Velvet scoter, *Melanitta fusca*	bottom feeder
Scoter spp., *Melanitta spp.*	bottom feeder
Diver spp.	bottom feeder
Great skua, *Stercorarius skua*	kleptoparasite
Manx shearwater, *Puffinus puffinus*	pursuit plunge
Shearwater spp.	pursuit plunge
Northern gannet, *Morus bassanus*	plunge
Petrel spp.	surface
Atlantic Puffin, *Fratercula arctica*	pursuit dive deep
Black guillemot, *Cepphus grylle*	pursuit dive deep
Razorbill/Guillemot, *Alca torda/Uria aalge*	pursuit dive deep
Auk spp.	pursuit dive deep

Table 2. Summary data from aerial surveys in the Irish Sea summer and winter 2016. S = species richness (removing higher taxonomic groupings if species-specific sightings occurred), D = density of seabirds per grid cell (number of seabirds sighted divided by total area surveyed), F = feeding guild richness, N_{tot} = estimated total abundance (with 95% CI) across the survey area.

Season	**Total S**	**Mean S / grid cell**	**Mean F / grid cell**	**Mean D /grid cell (Individuals/km^2)**	**N_{tot} (individuals)**
Summer	16	2.65	2.24	10.62	97,326 (90,292-104,908)
Winter	14	2.18	1.74	9.51	87,179 (77,160-98,499)

Table 3. Relationship between seabird density (D) and feeding guild richness (F) with environmental covariates; sea surface temperature (SST), distance from the nearest breeding colony (Dist), and chlorophyll-a (CHL). To account for spatial autocorrelation, models included a spatial correlation structure (XY). Test t-statistic (t-stat) is included to indicate the direction of the effect. Significant effects and corresponding *P*-values are highlighted in bold.

	Model	**CHL**		**SST**		**Dist**		**Spatial correlation structure**
		t-stat	***P***	**t-stat**	***P***	**t-stat**	***P***	
Summer	F ~ CHL + Dist + SST + XY	-0.28	0.7792	**2.75**	**0.0060**	**-2.18**	**0.0294**	Spherical
	D ~ CHL + Dist + SST + XY	1.16	0.2450	**2.52**	**0.0118**	-0.24	0.8048	Spherical
Winter	F ~ CHL + SST + XY	0.51	0.6080	**2.86**	**0.0044**	-	-	Ratio
	D ~ CHL + Dist + SST + XY	**2.67**	**0.0078**	0.55	0.5800	**-2.72**	**0.0067**	Spherical