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Spatial variation in herring gull traits and their potential as monitors of the coastal environment

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Summary

Coastal marine environments are important for biodiversity and ecosystem services; however human pressure on coastal ecosystems has increased markedly over the last several decades. In order to determine the state of coastal environments apex predators, in particularly seabirds, can be used to monitor these habitats. At the population level monitoring multiple populations of a species can be investigated to identify potential drivers of population changes. However, as many apex predators are long-lived with a low reproductive output there can be a time-lag before detecting changes in population abundance reflecting adverse environmental conditions. Therefore, instead traits which reflect environmental conditions during the breeding season may be useful in monitoring habitats over shorter time frames. Of several widespread seabird species associated with the coastal environment across the region of interest of south-west Scotland and Northern Ireland, the herring gull *Larus argentatus* was found to show the greatest potential as a monitoring species. Spatial variation in herring gull colony growth rate was observed across the region, potentially driven by the availability of local intertidal and terrestrial resources. I therefore investigate several herring gull traits from multiple colonies to determine whether these alternative traits can effectively be used to monitor the coastal marine environment. In particular I am interested in three features of these traits: (i) do they show spatial variation in the selected colonies across the region of interest; (ii) are these traits sensitive to local environmental conditions reflecting local resource availability and (iii) do the traits relate to a short- and long-term measure of the gulls' demography. Spatial variation between colonies was observed in all selected traits associated with eggs, the extent of marine and terrestrial resources consumed and with the gulls' foraging behaviour; albeit to differing extents. Firstly, I investigate the resource use of herring gulls as food resources are often an important limiting factor in seabird colonies. The resource use of gulls was estimated via two techniques, pellets and stable isotope analysis of chick feathers, which gave comparable results. Colonies located in sheltered coastlines, with more favourable intertidal habitats, were found to forage more on marine items; whilst colonies located nearer built-up areas foraged to a greater extent on terrestrial items. The resources the gulls predominantly consumed were found to influence their demography, with greater breeding success in colonies which consumed a higher proportion of marine resources. Traits associated with the herring gull's eggs showed different sensitivities to local conditions. Both egg colour and volume were found to be influenced by the ambient temperature prior to laying; with larger eggs and less brown eggs in colonies associated with higher ambient temperatures. In colonies with higher local SST and chlorophyll a concentrations, eggs were found to have greater maculation. Egg colour was also found to relate to the gulls' overall breeding success in 2014, with higher final brood sizes in colonies where eggs were less brown in colouration. Finally, investigating the gulls' foraging behaviours, nest attendance was higher in colonies with a higher amount of built-up area within the foraging range; and, during 2013, in colonies closer to farmland. In colonies with higher local SST and chlorophyll a concentrations, provisioning rates were higher and trip durations shorter; whilst provisioning rates were also higher in colonies located in areas of high wave fetch, along more exposed coastlines. Of the foraging behaviours trip duration was found to relate to the gulls overall breeding success; with shorter trip durations in colonies with higher breeding success. These results highlight that herring gull traits are sensitive to local environmental conditions during the breeding season, especially egg maculation, the extent of marine resources the gulls consume and the three foraging behaviours; and therefore may be effective in monitoring the coastal environment. In addition, it suggests that average egg colour, the extent of marine resources the gulls consume and trip duration of a colony, are useful in reflecting environmental conditions as well as reflecting the gulls' demography relating in breeding success. Investigating herring gull traits from multiple colonies, which reflect environmental conditions over shorter time periods than colony GR, may therefore be useful in monitoring the coastal environment. In addition, they may help establish why this species has experienced contrasting colony GR in recent years; leading it to be categorised as a red-listed bird on conservation concern in the UK.

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Author’s declaration

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1 General Introduction

The world's biological diversity is currently changing at an increasing rate due to natural and, predominantly, anthropogenic pressures acting upon it (Brooks *et al.* 2006). In order to document this change as well as to identify and prioritise what policy, management and conservation actions are needed to alleviate these pressures requires monitoring both of the environment and of the species that depend on it. This can be achieved by studying the interactions between species and their environment.

1.1 Monitoring

In the broadest sense monitoring is the observation of something of interest to check its progress or quality over time. Monitoring is therefore frequently used in ecology to detect changes in the environment; to assess the outcomes of management and conservation decisions; and to evaluate species populations over time, often over various temporal and spatial scales. This type of monitoring can be passive, where there are no pre-specified questions; mandatory, where data is collected as a requirement of legislation or a political directive; or question driven, which usually follows a strict protocol (Lindenmayer & Likens 2010).

In the context of this study monitoring was investigated to provide information on a species representing the state of a heavily impacted ecosystem in North-West Europe. European legislation requires that the state, or condition, of ecosystems need to be determined to establish whether they are in a good ecological or environmental state (EU 2008). This has been defined as 'the condition of a system that is self-maintaining, vigorous, resilient to externally imposed pressures, and able to sustain services to humans. It contains healthy organisms and populations, and adequate functional diversity and functional response diversity. All expected trophic levels are present and well interconnected, and there is good spatial connectivity amongst subsystems' (Tett *et al.* 2013). The importance of monitoring environmental change in order to provide an indication of ecological state, as well as how this can be achieved in terms of which species and traits to investigate, will be discussed; both broadly and in regards to the specific habitat and location this study covers.

1.1.1 Importance of ecological monitoring

The use of ecological monitoring in management and conservation is often used to provide a cost-effective way to assess the pressures acting on an ecosystem; providing a means of collecting information on a system which cannot be readily measured directly due to cost, logistical or technological reasons (Carignan & Villard 2002). In this sense, ecological monitoring can be defined simply as "the systematic collection of ecological data in a standardised manner at regular intervals over time" for a specific purpose (Spellerberg 2005). This can incorporate sampling, recording, mapping, surveying, inventories and long-term ecological research. Monitoring is a vital tool in ecosystem management and conservation as it can provide baseline information to determine the effectiveness of management decisions; long-term data sets can be acquired to identify possible causes of stress on ecosystems; and it can be used to detect, and provide a warning of, potential negative environmental changes (Spellerberg 2005; Durant *et al.* 2009). Frequently the purpose is to monitor the population abundance of species or the state of habitats of high conservation priority, for instance to determine whether management implementations are having the desired effect and to identify implications of 'threats' and environmental change on these species and habitats.

There are a number of long-term monitoring programmes which record information on specific species or habitats over long time periods (for example: Fox *et al.* 2011; Jewell *et al.* 2012; Sauer *et al.* 2013; Harris *et al.* 2014). These generally cover a wide range of taxonomic groups from across terrestrial, freshwater and marine ecosystems; with the data being used in a wide range of research to identify why changes in a species' population have occurred over time and space, and to identify which management and conservation actions may be required where declines are of concern (e.g. Thomas *et al.* 2004; Fox *et al.* 2010; Eglington & Pearce-Higgins 2012; Bennie *et al.* 2013). These long-term monitoring programmes are extremely valuable in investigating change over long time periods and indicating causal links between demographics and environmental change (Gregory *et al.* 2003). These datasets are also useful to answer questions that occur a priori to the data being collected. However, these monitoring programmes are relatively costly and labour intensive, largely relying on high numbers of volunteers and citizen scientists. In addition, they may not be able to answer all questions necessary about an ecosystem and therefore additional question-driven monitoring, where a strict protocol is adhered to in order to answer a priori predictions (Lindenmayer & Likens 2010), of specific habitats and species of interest over smaller scales may be required.

1.1.2 Monitoring environmental change

When monitoring an ecosystem it is important to consider the potential pressures that may impact upon the habitats and their associated species. Most species are influenced by multiple, often interacting, environmental factors such as food availability, weather conditions and habitat quality, as well as also biotic factors such as predation, parasitism, disease and inter- and intraspecific competition (Montevecchi 1993; Durant *et al.* 2009). The effects of these factors are often exacerbated as a result of anthropogenic activities resulting in habitat loss and degradation, over-exploitation of species and/or their prey, the introduction of non-native species, climate change and the input of contaminants into the environment (Butchart *et al.* 2010). These can then act as pressures on the populations of local species, driving their numbers down (Ceballos & Ehrlich 2002; Lemoine *et al.* 2007).

1.1.3 Which species to monitor?

There are numerous biological, chemical and physical attributes of an environment that could be monitored to provide information on that environment. However, measuring all these attributes would be extremely challenging and expensive. Instead biological species that inhabit a particular environment can be used as a proxy to indicate the state of an ecosystem (Koskimies 1989; Durant *et al.* 2009). In order to be a good proxy biological, or ecological, indicators need to be able to reflect the underlying processes affecting the populations, species and communities which best represent the ecosystem of interest; as well as reflecting the occurrence of ecological processes at the appropriate temporal and spatial scales (Angermeier & Karr 1993). All organisms have a tolerance range for specific environmental factors, which will vary between species as well as within a species depending on an individual's life stage, reproductive status and condition (Jarvis 1993). Changes in the environment will therefore impact upon an individual's physiology, morphology, behaviour and/or reproductive ability to different extents (Jarvis 1993), allowing the use ecological indicators to assess the condition of the environment it inhabits. Ecological indicators can then also provide a warning that environmental change is occurring and help diagnose the cause of an environmental issue (Cairns, McCormick & Niederlehner 1993).

To be effective, ecological indicators need to be easily monitored and modelled, whilst providing, ideally quantitative, information on the structure, function and composition of the ecosystem of interest (Dale & Beyeler 2001). Selected species therefore need to be sensitive to environmental change and relate information about a habitat through their presence, abundance or condition (Hollamby *et al.* 2006). However, it is often difficult to determine which species can achieve this. To facilitate the selection of appropriate species a range of criteria have been put forward (i.e. Hilty & Merenlender 2000; Dale & Beyeler 2001; Gregory *et al.* 2003). The list of criteria can be extensive (Table 1.1); however the most important criteria are arguably that indicator species should be easily measured, be cost-effective and be sensitive to stresses in the ecosystem, responding in a predictable way that provides a representative view of the ecological processes occurring in the environment.

Table 1-1. Criteria for selecting monitoring species

Criteria generally met by seabird species
Straight-forward to monitor with high accuracy/precision
Economical therefore inexpensive/cost-effective to measure
Anticipatory and signify an impending change in the ecosystem
Integrative, i.e. with social and economic goals
Low variability in response, i.e. low population fluctuations
Relatively easy to understand by non-scientists and decision makers
Easy to identify and be monitored by non-specialists
Consistent with theoretical studies
Long-term/historical data is available
Summarises and simplifies complex data
Technologically feasible
An interest to policy makers and the general public (socially desirable)
Taxonomic status clear
Biology and life history well known
Long-lived and therefore can be monitored over several seasons
The size, age and sex of individuals can be easily determined
The foraging range can be determined
Diet analysis can be undertaken
Criteria met to some extent by seabird species
Sensitive to anthropogenic stress but not to natural variation
Respond to stress in a predictable manner
Tightly linked with little time-lag
Indicates the cause of change rather than simply the existence of change
Reflects what is occurring at the species and population scale
Reflects the occurrence of ecological processes at the appropriate temporal and spatial scale
Representative/indicative of the habitat and other species within it
Provide a continuous assessment over a wide range and intensity of pressures
Concrete with units measurable in the real world and based on direct observations
Trends are detectable

Based on: Koskimies 1989; Hilty & Merenlender 2000; Dale & Beyeler 2001; Gregory *et al.* 2003; Rochet & Rice 2005; Hollamby *et al.* 2006; Borja & Dauer 2008.

When considering the listed criteria it is important to determine whether one or a panel of species should be used to monitor the ecosystem of interest. Many monitoring programmes use just one focal species as it is often more cost-effective and provides a simpler univaraite index (Borja *et al.* 2011). However, a single species may not provide a good representation of an ecosystem as it will only respond to a narrow range of ecological conditions (Koskimies 1989), and therefore be unlikely to detect all the pressures acting upon an ecosystem. Instead a panel of species with varying life-history traits could be selected to provide more representative information on the entire ecosystem (Piatt, Sydeman & Wiese 2007b; Mallory *et al.* 2010). Incorporating the responses of multiple species to a change in the environment can provide a better fit than the response of a single species (Reid *et al.* 2005). Integrating species with differing sensitivity to environmental change may also provide information on a broader range of environmental conditions and therefore potentially be a more informative indicator (Einoder 2009).

When deciding on an indicator it will also important to consider the question of what aspect of the environment is to be monitored. The species chosen may depend on whether short-term, potentially local, measures of the environment conditions are primarily of interest, for example associated with pollution events and disease although these can also be over much larger scales (Burger & Gochfeld 2004; Newman *et al.* 2007), or instead global pressures such as those associated with climate change (Croxall, Trathan & Murphy 2002; Durant *et al.* 2009). This will link to the scale of interest both temporally and spatially, which will best match the scale of the question being asked (Lindenmayer & Likens 2010). Different species will respond to environmental conditions over to different time periods and over different spatial scales depending on their life history. For instance, larger, longer-lived and mobile species are much more likely to respond over larger temporal and spatial scales than small, less mobile species (Diamond & Devlin 2003; Hollamby *et al.* 2006). The species traits selected will also vary over different temporal and spatial scales (see below).

There is no one ideal group of species which should be used as an ecological indicator; it will largely depend on the questions being asked and the habitat or ecosystem of interest. However, apex predators are often used as a cost-effective means of monitoring environmental change (Boyd, Wanless & Camphuysen 2006; Fossi *et al.* 2012). Apex predators can be defined as species which have a high trophic position and so are located at, or near, the top of the food web; therefore are likely responding to processes occurring at lower trophic levels, as well as potentially having an impact themselves through predation (Boyd *et al.* 2006; Wallach *et al.* 2015). Apex predators are also considered to be effective as indicator species as they generally exploit resources at a similar spatial and temporal scale as those used by humans and many have a high level of public interest, therefore monitoring programmes are generally supported long-term (Boyd *et al.* 2006). Of apex predators, bird species are considered to be good monitoring species and are widely used in long-term monitoring programmes (Furness & Greenwood 1993; Marchant, Forrest & Greenwood 1998). Compared to other specie groups birds are relatively easy to identify; they are well studied and therefore their ecology is generally well known; and there are many skilled individuals who record them (Greenwood *et al.* 2008) and, in Britain and Ireland, take part in long-term surveys set up to monitor terrestrial habitats through the Breeding Bird Survey (BBS) and aquatic habitats through the Wetland Bird Survey (WeBS) and the Seabird Monitoring Programme (SMP).

1.1.4 Which traits to monitor?

Once a suitable species or panel of species has been selected a range of traits can be measured to provide information on the environment over different spatial and temporal scales, and to aid in identifying the potential drivers acting upon the selected species (Furness & Greenwood 1993). Currently most monitoring programmes collect data on a species' population size, abundance or distribution, which provides useful information on long-term trends over years to decades (Einoder 2009). These may not however, be the traits that closely relate to immediate environmental change, particularly in long-lived species, due to the life-history-induced time lag between the factor being monitored and the response being measured (Wiens & Rotenberry 1985; Montevecchi 1993). In addition, detectable changes in population numbers are likely to be slow and therefore will be difficult to determine statistically (Maclean *et al.* 2013). A signal may also only be detectable when environmental conditions are particularly poor, with a threshold being reached when conditions are good, resulting in non-linear relationships (Cairns 1987a).

Instead, alternative traits which respond to environmental conditions over different, smaller temporal and spatial scales can be investigated (Cairns 1987a). Although the relationships for some of these traits may be non-linear, they are more likely to respond to moderate changes in environmental conditions over shorter temporal scales (Cairns

1987a). Therefore breeding traits, which portray information over a season, and behavioural and physiological traits, which portray information over hours and days, may provide much more useful information over the shorter time-scales required to advise on more immediate management and conservation decisions (Diamond & Devlin 2003).

The use of behaviour and physiology as a means of assessing the populations of species has frequently been identified as a potential monitoring tool (Cairns 1987a; Monaghan 1996; Wikelski & Cooke 2006; Piatt *et al.* 2007a; Wildermuth, Anadón & Gerber 2012). This is particularly relevant for long-lived species as behavioural and physiological traits will reflect environmental conditions over shorter time frames than demographic traits. There is debate over the effectiveness of using behaviours to infer population change, particularly in populations with large individual variation in behaviour (Caro 2007). Nevertheless, if changes in a species' behaviour and physiology has demographic consequences this may be valuable in providing a warning of changing environmental conditions (Wikelski & Cooke 2006; Wildermuth *et al.* 2012). In order for this to be useful the relationship between the species behaviour/physiology and demography need to be understood however, this is generally achievable, at least to the extent that meaningful inferences can be made (Wildermuth *et al.* 2012).

When determining which species and traits to monitor the size of the population to be investigated may also need to be considered; as small, and growing, populations may respond differently to local conditions than large, stable, or even declining populations, for instance due to density-dependent processes (Ashmole 1963; Matthysen 2005). In particular, in large populations there is likely to be higher levels of competition for limiting resources such as food, mates and breeding sites (Newton 1998); which may influence how a species responds to environmental change.

1.1.5 Monitoring the marine environment

Many current monitoring programs largely focus on terrestrial environments as monitoring the marine environment can be an even greater challenge due to the high costs involved and its relative inaccessibility (Furness & Camphuysen 1997). However monitoring of the marine environment is of particularly high priority as anthropogenic pressures on marine ecosystems has increased markedly over the last several decades (Costanza *et al.* 1998; Halpern *et al.* 2008; Sutherland *et al.* 2012; Boonstra *et al.* 2015). As a result of this increasing pressure the European Marine Strategy Framework Directive (MSFD, 2008/56/EC) was established, bringing together several already existing directives including the Habitats (19 92/43/EEC) and Birds (2009/147/EC) Directives and the Water Framework Directive (WFD, 2000/60/EC), with the main aim of restoring and protecting marine ecosystems through delivering "Good Environmental Status" to all European marine waters by 2020. To meet this objective the monitoring of marine ecosystems and the development of ecological indices have been identified as an important process in assessing the health and sustainability of marine habitats (Borja 2005; Jonge, Elliott & Brauer 2006; Rombouts *et al.* 2013). Within the marine environment, coastal habitats are particularly susceptible to anthropogenic and natural pressures due to their accessibility and their location at the coastal boundary, resulting in being impacted from pressures associated with both the marine and terrestrial environment (Thompson, Crowe & Hawkins 2002; Lopez y Royo *et al.* 2009). In the marine environment human impact has been identified as being most severe in coastal habitats especially in north-west Europe (Halpern *et al.* 2008). These coastal habitats are impacted by a wide range of pressures including the accumulation of contaminants from the land and sea, over-exploitation of resources, alien species, disturbance, habitat destruction, modified coastal processes and climate change (Crowe *et al.* 2000; Thompson *et al.* 2002; Halpern *et al.* 2008).

It is therefore important that the impacts of any pressures acting on coastal habitats are detected and monitored to assess the need for the restoration, conservation and sustainable management, and to ensure that they have "Good Environmental Status" under the Marine Stratergy Framework Directive. In order to help achieve the monitoring aspect of the MSFD funding from the European Union was provided to establish IBIS (Integrated Aquatic Resources Management Between Ireland, Northern Ireland and Scotland), a partnership between Loughs Agency, Queen's University Belfast, and the University of Glasgow, to carry out research on freshwater and marine ecosystems across this region (http://www.loughs-agency.org/ibis). As part of a larger programme, this specific project focuses on monitoring the coastal marine environment in south-west Scotland and Northern Ireland.

A number of species groups have been put forward to monitor coastal habitats in response to the Water Framework Directive (WFD) and Marine Strategy Framework Directive (MSFD) including phytoplankton, microalgae, benthic invertebrates and fish (i.e.

Borja 2005). Benthic invertebrates are known to be effective monitors particularly for contaminants and pollution as they are sessile, relatively easy to identify and survey, and their spatial scale is known (Atalah & Crowe 2012; Shirneshan & Riyahi 2012). However, they are arguably less sensitive to environmental change due to their mechanisms of tolerating the natural stresses of coastal habitats, which are also known to assist them in dealing with anthropogenic pressures such as pollutants (Elliott & Quintino 2007). Monitoring of phytoplankton, microalgae and fish has also been used, however, they can often be difficult and expensive to monitor making these lower trophic groups a less effective option (Scott *et al.* 2006). In addition, the distributions of many marine species, specifically fish, are unpredictable and patchy over large areas making them very difficult to monitor (Weimerskirch 2001b). In view of the criteria discussed above marine apex predators therefore provide a more practical alternative.

1.2 Seabirds as monitors of environmental change in marine coastal habitats

Of apex predators in the marine environment seabirds provide an attractive choice as indicator species as they are relatively large and conspicuous making them easy to observe, especially in comparison with predatory fish and marine mammals. Seabirds score highly against criteria on selecting monitor species and several review papers have discussed their suitability in monitoring the marine environment (Furness & Greenwood 1993; Rice & Rochet 2005; Piatt *et al.* 2007b; Durant *et al.* 2009); although they are not ideal indicator species in all situations (see Table 1.2). For the most part however, the authors agree that seabirds are effective monitors of environmental change (Montevecchi 1993; Frederiksen *et al.* 2004).

Table 1-2. Advantages and disadvantages of seabirds for monitoring the marine environment

Advantages
They are conspicuous in an environment where many other species are hidden
They are relatively easy to identify
They are relatively easy to observe and therefore survey
Their classification and systematics are well established
They are well studied with a vast amount of data available on their ecology and behaviour
There are long-term datasets available on their distribution, population and breeding success
There is a large availability of manpower through volunteers to carry out specific field work and provide monitoring data which would otherwise be extremely expensive
The colonial nature of these species also means that a large amount of data can be collected from one or a few sites in a short amount of time from multiple species
Different species feed at different trophic levels
As apex/top predators they are generally sensitive to factors affecting the food chain
Their mobility and longevity means they can monitor change over large scales and across systems which can otherwise be very difficult to survey/monitor
Disadvantages
Numbers are generally regulated by density dependant processes and therefore population sizes may be buffered against impacts of environmental change
Responses to food availability are non-linear therefore, there may be little change in predator populations and productivity up to a critical point, after which declines can be rapid.
Buffering can occur at the behavioural and physiological level therefore they may less readily reflect environmental stress
There may be large life history-induced time-lags between the factor being monitored and the response being measured
An individual in a population may respond to the environment differently therefore the impact of environmental change on a population may be influenced by the phenotypic plasticity of individuals to adjust their life history traits such as timing of reproduction and clutch size (Both *et al.* 2004)
Most research uses correlations to relate seabird parameters with environmental variables, however, significant correlations do not prove a cause and effect relationship (Votier, Heubeck & Furness 2008)
Although an explanatory variable, i.e. prey abundance, may strongly relate to and explain a species response the reverse may not necessarily be true (Inverse inference - Durant *et al*. 2009)
Migratory species may differ in their migrations to an uncertain extent making it difficult to determine the spatial scale they represent
Mobility may interact with temporal variation with populations of different origins passing through the same place at different times of year, potentially causing confusion where sampling is based at one site

Compiled from Furness & Greenwood 1993; Furness & Camphuysen 1997; Diamond & Devlin 2003; Boyd *et al.* 2006; Einoder 2009, unless stated.

The idea of seabirds as indicators mostly aims to demonstrate links between seabird traits, the response variable, and environmental parameters in a quantitative way (Wanless *et al.* 2007). To achieve this the relationships between the environmental parameters and seabird traits must be defined, predictable and well understood (Grémillet & Charmantier 2010). This can be problematic as in many cases the relationships between seabird traits and environmental variables are not fully understood and therefore it is difficult to identify traits which predictably reflect environmental conditions (Piatt *et al.* 2007b). In addition, the response of seabirds to specific environmental change varies across different temporal and spatial scales; with the issue exacerbated by individual variation in responses (Grémillet & Charmantier 2010). Furthermore, the relationships between biological traits and environmental parameters, such as food availability, can be complicated by the relationship not being linear (Cairns 1987a; Piatt *et al.* 2007a). However, even if the relationships between seabird traits and environmental parameters are not fully understood, and/or if the seabird traits are being monitored across different temporal and spatial scales than the environmental parameters, they are still of use as indicators; and can still reflect qualitative information on the state of environmental conditions (Piatt *et al.* 2007a; Grémillet & Charmantier 2010). This is demonstrated by their widespread use in the monitoring of fisheries management (Einoder 2009), food availability and fish stocks (Montevecchi 1993; Frederiksen *et al.* 2007), pollutants and contaminants (Furness & Camphuysen 1997; Burger & Gochfeld 2004), climate change (Thompson & Ollason 2001; Mesquita *et al.* 2015) and the impacts of oceanographic changes such as El Niño Southern Oscillation events (Schreiber & Schreiber 1984; Zipkin *et al.* 2010).

Different seabird species will respond differently to environmental change depending on their ecology, physiology and life-history traits (Einoder 2009). Traits such as potential foraging range, ability to dive, ability to switch diet, body size and foraging strategies will all have different constraints and therefore will influence a seabird's response to environmental change (Furness & Tasker 2000). These differences in the responses of seabirds are beneficial as they can help narrow down and identify the cause of environmental change through comparing species which respond in a similar way to species which display different responses (Greenwood *et al.* 1993). For example, factors that cause prey species to move into deeper water will impact shallow, surface feeders but not pursuit divers which are less constrained by depth (Baird 1990; Durant *et al.* 2009).

A seabird's response to environmental conditions will also depend on the spatial scale of consideration (Montevecchi & Myers 1993). The spatial scale over which a seabird species responds to environmental conditions is therefore also important to identify (Diamond & Devlin 2003). The majority of seabird monitoring occurs during the breeding season largely due to logistical reasons. During the breeding season a seabird's foraging range is constrained by the location of their breeding site and therefore the spatial scale of their foraging range is relatively small, with recent telemetry studies allowing the locality and extent of many foraging ranges to be established (Wanless, Harris & Morris 1991; Guilford *et al.* 2008). However, it should be noted that this is only one stage of a seabirds annual cycle with conditions outside of the breeding season also having an impact (Marra *et al.* 2015). However, despite advances in technology, there are challenges to studying seabirds over the non-breeding season. This study therefore focuses on the breeding season the area seabirds cover during this period is generally known, and individuals are more easily observed.

The spatial and or temporal scale of interest will also determine whether single or multiple colonies of a species should be monitored. Focusing on a single colony over long-term frames provide invaluable information on the responses of seabirds to changing environmental conditions over time and can provide useful details on within-population variation (for example: Frederiksen *et al.* 2004; Kadin *et al.* 2015). However, it could be argued that a single colony is not representative of all colonies within a region and therefore it is also useful to investigate between-colony variation (Frederiksen, Harris & Wanless 2005a). Where the monitored traits within the same region fluctuate synchronously it suggests that the colonies are experiencing similar environmental conditions (Liebhold, Koenig & Bjørnstad 2004; Bertram, Drever & Mcallister 2015). Alternatively, if they have differing responses it may indicates that they are experiencing different local conditions (Harris *et al.* 2005; Ens *et al.* 2009). Spatial similarity, or vairation, in traits can therefore be monitored to help narrow down and idenitfy factors influencing seabird populations.

1.2.1 Which seabird traits to monitor

The majority of current monitoring programmes directed at seabirds are focused on colony counts, as their colonial nature generally means they are readily counted (Walsh *et al.*

1995). These long-term counts provide invaluable information about large-scale temporal and spatial variation in seabird abundance and changing populations (i.e. JNCC 2012). However, in these long-lived species demographic traits are generally slow to respond to changes in their environment. Due largely to this longevity, many seabirds delay the onset of breeding and in some years may skip breeding altogether, and therefore the variation observed in colony numbers may only weakly reflect environmental influences on their population size (Erikstad *et al.* 1998). In addition, population numbers respond slowly to changes in breeding success, meaning that detectable effects are delayed (Montevecchi 1993); resulting in long-term datasets of around 25 years being required in some cases to detect changes as statistically significant (Maclean *et al.* 2013). Adult survival can also be investigated using unique marks on individual birds, which has also been found to be linked to local food availability (Davies, Nager & Furness 2005; Breton & Diamond 2013). However, this again generally reflects conditions over longer-time frames of at least a year and therefore is less sensitive to changes in the environment (Cairns 1987a). Survival is also less likely to reflect local conditions around the breeding colony with mortality often occurring during the non-breeding season, particularly associated with severe weather events (Votier *et al.* 2005; Wanless 2008; Cordes *et al.* 2015).

Seabird demographic parameters which reflect conditions over longer-time frames are therefore generally less responsive to environmental change, with little inter-annual variation observed in population size and adult survival, meaning that changes may only be detected when conditions are particularly poor (Cairns 1987a). In addition, when conditions are poor long-lived organisms like seabirds are more likely to invest in their own survival and ability to breed in future years rather than in their current breeding attempt (Montevecchi 1993 but see Johnsen *et al.* 1994; Golet *et al.* 1998). This may therefore introduce bias when looking at overall breeding success, which reflects environmental conditions over the entire breeding season; and which is also frequently used in monitoring seabirds, for example as part of the Seabird Monitoring Program (JNCC 2013).

Alternative seabird traits therefore need to be monitored to identify changes in seabird populations over shorter time frames, reflecting more moderate environmental changes than demographic traits can identify (Cairns 1987a). This is based on the assumption that these alternative traits are influenced by environmental conditions, which will, potentially after a time-delay, ultimately result in changes to the overall population growth of a colony. Therefore, to be useful in monitoring, there should ideally be a relationship between the trait being investigated and the species' overall demography. However, even if there is no detectable relationship between a trait and a species demography, if it relates to some aspect of the environment it may still be of use in monitoring; for instance using eggs to monitor contaminants can provide important information on the extent of contamination in the environment even if it doesn't; effect the species demography (Hanley & Doucet 2012).

There are a number of seabird traits that could also potentially be monitored and which have been associated with environmental variables including foraging behaviour, physiology and resource use (i.e. Cairns 1992; Montevecchi & Myers 1993; Croxall *et al.* 1999; Sydeman *et al.* 2001). In particular behavioural and physiological traits associated with breeding, may be effective, especially for larger seabirds (Temple & Wiens 1989; Durant *et al.* 2009). To use the full potential of seabirds as monitors it will be particularly valuable to investigate behavioural and physiological traits associated with breeding, which may be effective, especially for larger seabirds (Temple & Wiens 1989; Durant *et al.* 2009). To date, these traits have not been frequently investigated therefore this thesis aims to investigate the potential of these alternative traits to provide details on the marine environment. These associations are particularly strong for environmental conditions affecting food availability (Montevecchi 1993). Seabird traits which reflect changes in food availability are likely to provide a good overview of the biological and physical processes that are occurring at lower trophic levels; as the abundance and distribution of marine fish and invertebrates is strongly associated with ocean productivity, as well as weather conditions, sea surface temperature and salinity (Cury *et al.* 2008).

1.2.2 Breeding traits

Breeding traits which ultimately can effect overall breeding success and which are likely to reflect environmental conditions more closely and over medium time frames of weeks to months, include the timing of breeding, clutch size and traits associated with eggs (Cairns 1987a; Diamond & Devlin 2003). The timing of breeding, or phenology, can provide an indication of environmental conditions early in the season (Brouwer, Spaans & De Wit 1995; Monaghan 1996); as high quality adults, due to experience, size and condition, tend to establish favourable breeding territories and lay earlier (Brouwer *et al.* 1995; Catry, Ratcliffe & Furness 1998). However, in colonial breeders there can be a strong pressure on individuals to synchronise there breeding, which will therefore restrict variation in laying dates (Murphy & Schauer 1996; Reed *et al.* 2006). In many bird species, particularly those which lay large clutches, clutch size may provide an indication of the female's body condition and therefore local environmental conditions, specifically food availability (Hiom *et al.* 1991). The majority of seabirds, however, show very little variation in clutch size. In addition, during years where local environmental conditions are particularly poor only adults in the best condition may breed which may bias average breeding traits such as clutch size (Monaghan 1996). Another consideration is that establishing that a clutch size is reduced can be difficult as it can be confounded by partial clutch predation (Ost *et al.* 2008). Instead egg size, or volume, can be used to assess female condition and therefore local environmental conditions as eggs are costly to produce (Nager 2006). If local food availability is poor females may respond to this through laying smaller eggs (Coulson, Duncan & Thomas 1982; Hamer, Furness & Caldow 1991). In addition to size, eggshell colour, extent of maculation and shape may provide information on local environmental conditions. The level of pigmentation and patterning on eggshells can be highly variable; with this variability in some cases being associated with female condition (Hargitai *et al.* 2005; Siefferman, Navara & Hill 2006; Moreno *et al.* 2006a; Martinez-de la Puente *et al.* 2007) and environmental variables (Jagannath *et al.* 2007; Avilés *et al.* 2007; Hanley & Doucet 2012).

1.2.3 Physiological traits

Traits associated with physiology can portray information on environmental conditions over temporal scales of hours and days to weeks across the breeding season (Cairns 1987a; Diamond & Devlin 2003). Physiological traits associated with adult body condition have been found to relate to environmental conditions associated with habitat and resource use during the breeding season (Montevecchi 1993); with consequential negative impacts on breeding productivity, although not in all cases (Chastel, Weimerskirch & Jouventin 1995a; Robinson, Chiaradia & Hindell 2005). Poor body condition in adults may be attributed to consuming lower quality resources and/or to having higher energetic costs of foraging in areas of low food availability (Monaghan 1992; Harding *et al.* 2011; Cohen *et al.* 2014). Chick condition can also provide a reflection of local conditions as it will provide information on the quality of the chicks which are produced, which may influence their post-fledgling survival (Wanless *et al.* 2005). Low chick weights or growth rates generally suggest that the chicks are not receiving enough food and therefore may indicate low food availability within close vicinity of the colony (Cairns 1987b; Uttley *et al.* 1992). However, it can sometimes be difficult to attribute the condition of an individual to its environment rather than its intrinsic quality (Wilson & Nussey 2010).

Changes in local environmental conditions which cause poorer foraging conditions for seabirds can result in changes in the birds' physiological condition related to the release of corticosterone (CORT), the main stress hormone in birds. Several studies on seabirds suggest that there is a relationship between circulating CORT levels and food availability; with low baseline levels associated with good food availability, and elevated levels when availability is low, observed in both adults and chicks (Kitaysky *et al.* 1999, 2001, 2010; Benowitz-Fredericks, Shultz & Kitaysky 2008). This will then have consequences on productivity with high CORT levels being negatively related to breeding success (Buck, O'Reilly & Kildaw 2007; Kitaysky, Piatt & Wingfield 2007). However food availability may not be the only cause of stress in birds. Elevated levels of CORT may also be a result of disease and accumulated contaminants (Peakall *et al.* 1981; Lindström *et al.* 2005) or predation risk (Scheuerlein, Van't Hof & Gwinner 2001; Cockrem & Silverin 2002). For the purpose of this study I did not investigate body condition or stress levels as this generally requires catching and handling the birds, and therefore concentrated effort on single colonies, which in terms of both cost and logistics may not be the most effective way to monitor the coastal environment.

1.2.4 Foraging behaviour

Overall breeding success or productivity has frequently been found to be impacted upon by local changes in food availability during the breeding season (Baird 1990; Croxall *et al.* 1999; Furness & Tasker 2000; Cury *et al.* 2011); providing information on environmental change over temporal scales of months to weeks (Cairns 1987a; Diamond & Devlin 2003). However, over a certain threshold breeding success may no longer be impacted by environmental conditions (Cairns 1987a; Cury *et al.* 2011); although the extent to which environmental change is reflected in the breeding parameters may depend on the seabirds' time and energy budget (Cairns 1987a). The breeding parameters of small-bodied seabirds, such as terns, can be particularly sensitive to environmental change as they have tight time and energy budgets and a relatively expensive foraging strategy; therefore are unable to increase their foraging effort to compensate for reduced food availability

(Monaghan 1992). Conversely, larger seabird species generally have more flexibility in their time and energy budgets enabling them to buffer their breeding success during reduced prey availability by increasing their foraging rate; masking any effects of environmental change on their breeding population parameters (Aebischer & Wanless 1992; Piatt *et al.* 2007b). Which species to choose in regards to time and energy budgets will again depend on the question and temporal and spatial scale of interest; which may also influence which traits of that species to investigate.

As with physiological traits those associated with behaviour can also reflect environmental conditions over temporal scales of hours to weeks (Cairns 1987a; Diamond & Devlin 2003); with foraging behaviours in particular closely reflecting the status of prey populations (Monaghan 1996). Behaviours that can be readily observed and are likely to be impacted upon by environmental parameters include breeding, foraging and defence/anti-predator behaviours (Searle, Hobbs & Gordon 2007; Wildermuth *et al.* 2012; New *et al.* 2014). A better understanding of foraging behaviour can provide important insights into the status of the marine environment (Guilford *et al.* 2008; Wildermuth *et al.* 2012), as well as acting as potential drivers of seabirds' population numbers. Foraging behaviour is thought to be especially effective in reflecting local environmental conditions over relatively short time periods (Croll *et al.* 1998; Wilson *et al.* 2002; Austin *et al.* 2006; Lewis *et al.* 2008; Wildermuth *et al.* 2012). Foraging behaviours can be impacted upon by numerous factors, specifically by the availability, quality and distribution of food (Pyke 1984; Quintana 2008); as well as density-dependent competition (Birt *et al.* 1987) and environmental conditions such as weather (Finney, Wanless & Harris 1999; Bustnes, Barrett & Helberg 2010; Bustnes *et al.* 2013). Where these factors result in poorer foraging conditions birds are likely to spend longer foraging (Gaston & Nettleship 1982; Quintana 2008); with associated reduction in provisioning rates and nest attendance (Coulson & Johnson 1984; Cohen *et al.* 2014; Kadin *et al.* 2015). This can result in overall lower productivity due to higher chick starvation, predation and exposure risk (Uttley *et al.* 1992; Harding, Piatt & Schmutz 2007; Chivers *et al.* 2012).

1.2.5 Resources Use

The resources seabirds forage on can provide valuable information on interpreting the availability and relative abundance of local food resources, enabling seabirds to be used in monitoring local prey populations and environmental processes affecting low trophic levels in the ecosystem (Hislop & Harris 1983; Barrett *et al.* 2007). There are many different methods to assess the diet and resource use of seabirds (Cameron & Jackson 1986; Barrett *et al.* 2007); with the main techniques outlined in Table 1.3.

An abundance of high quality food being eaten can indicate good local environmental conditions and, due to the close relationship between seabirds and their prey species there are numerous studies which have found positive associations between seabird breeding success and prey abundance or availability (Davoren & Montevecchi 2003a; Davies *et al.* 2005; Bustnes *et al.* 2013; Goyert, Manne & Veit 2014). However, the response of a seabird may depend on whether it is a specialist whose diet is likely to respond rapidly to reductions in their preferred prey species (Montevecchi 1993), or a generalist, which will generally consume the most abundant food items from a range of trophic levels, providing details on a broader range of local food availability and their relative abundances (Martin 1989). Although generalist may still have a preferred resource, i.e. food sources of higher quality, and therefore changes in resource use can still be informative (Blight *et al.* 2015b).

The quality of food being consumed therefore is an important factor in determining diet/resource use (Österblom *et al.* 2006; Osterblom *et al.* 2008). Regime shifts resulting in increases of lipid-poor resources at the expense of lipid-rich prey can have negative consequences on seabird breeding success; particularly as a result of chick growth and condition being affected by the prey's nutrient content (Anderson & Piatt 1999; Wanless *et al.* 2005). Kadin *et al.* (2012) found that fledgling success was positively associated with food quality rather than food quantity. However, in reality both are likely to impact upon apex predators simultaneously and may affect different components of a species' reproduction and survival (Kadin *et al.* 2012).

Seabird traits associated with eggs (predominantly associated with egg size), diet and foraging behaviours have been investigated to various extents previously; however these have generally been at the single colony level. Of the studies which have looked at multiple colonies (Fox *et al.* 1990; Frederiksen *et al.* 2005b; Moreno *et al.* 2011a), in general only individual traits have been investigated; in comparison to this study which looks to focus on multiple traits from the same target colonies, and or the same time period. In addition, most studies have concentrated on either the environmental drivers influencing the trait or how variation in the trait relates to the birds' demography; however within this study I aim to identify what environmental conditions are causing variation in the seabird traits of influence and whether this has demographic consequences.

Table 1-3

Method	Advantages	Disadvantages
Sample locations where large numbers of seabirds are feeding	• Can determine the potential local prey availability • Can be sampled acoustically with echo sounders to reveal the locations and sizes of prey patches • In intertidal habitats can use bottom grabs, dredges, nets, SCUBA, and cameras on remotely operated vehicles to determine food availability	• May not know which colonies the foraging birds are from.
Regurgitated pellets and / or excrement	• It is simple and non-invasive • Large sample sizes can be collected • Time-series data can be gathered through repeated sampling • For pellets - can be used to provide a quantitative index if it is known that the consumer ejects only one pellet a day or meal (not always the case)	• Only contains the hard parts of prey so will under-represent soft food items. • Can over-represent less digestible matter such as molluscs • Cannot be assigned to particular consumer species when found in mixed colonies • Not all the hard parts may be found within the pellet or excrement therefore ideally both should be sampled to try and obtain all the hard parts • Pellets are generally restricted to roost sites
Observing feeding seabirds or adult carrying food back to chicks	• Large samples can be taken without disturbing the birds • The size of prey items can be estimated in relation to bill length • Returning birds can be filmed or photographed to improve identification and size measurements	• Prey may be misidentified • Numbers and sizes can be miscalculated • Only applicable to species which take relatively large prey and carry them in their bills
Catching birds carrying food before they reach the nest site	• Can get accurate quantitative data on prey composition as the prey items are whole and fresh	• Food items may easily be dropped in vegetation and crevices and be lost • May disturb the colony
Stomach flushing	• Prey items are generally only partially digested so may still be relatively easily identified and measured • The entire stomach is flushed to obtain all items consumed	• It is intrusive and may disturb the colony. • Some contents may already be heavily digested and therefore items may not be identifiable

Regurgitated meals for chicks from adults or regurgitations from chicks	• Prey items are generally only partially digested so may still be relatively easily identified and measured • Can be repeated during the breeding season	• Cannot be used as an estimate of meal size as the proportion of ingested items which are regurgitated varies • Some species may regurgitate more easily than others • Not all the stomach contents may be regurgitated • Some partially digested items may not be able to be identified or measured accurately • May disturb the colony
Staple isotope analysis	• Can provide information about diet over space and time • Can determine where in the trophic level prey foraging occurs • Can indicate broad foraging environment such as terrestrial and aquatic and if marine inshore vs offshore and pelagic vs benthic • Feathers can be used to determine diet over the entire year • Museum specimens can be used to obtain historic data	• Cannot be used to identify specific food items • Voucher samples from the hypothesised foraging areas are required • Trophic Enrichment Factors (TEFs) are required for the species and tissue of interest
Quantitative fatty acid signatures	• Can be sampled non-destructively using biopsy • Fatty acid composition of prey species is diverse between species and characteristic within species allowing them to be identified • Can be distinguished from the seabirds own fatty acids	• Is an invasive procedure • Is expensive
DNA of food items in faeces	• Can identify items which are too digested to be identified by visual methods	• More expensive option • Requires the DNA sequences of prey items to be known
Miniature digitised cameras	• Can determine underwater foraging behaviour • Some food items may be able to be identified and measured	• Relatively expensive

1.3 Study Design

1.3.1 Target region of south-west Scotland and Northern Ireland

The marine region of interest between south-west Scotland and Northern Ireland, as identified by the IBIS programme, covers two regional sea regions; the Irish Sea and the Minches and West Scotland (JNCC 2014, Figure 1.1). These regional sea regions have been categorised by JNCC based on the boundaries of the ICES fisheries sea areas and the OSPAR regional seas and are biogeographically distinct predominantly due to temperature, depth and currents (JNCC 2014). The Irish Sea region is strongly influenced by coastal processes with turbid waters attributed to the influx of water from the Celtic Sea and continental shelf current. Although stratification occurs in deep waters it does not in the coastal margins of interest, or in the north-east. This region has a varied seabed dominated by glacigenic deposits; with bottom water temperatures varying between 6 and 13°C (Turnbull 2000). The Minches and West Scotland region is part of the continental shelf current but is sheltered from the Atlantic swells by Northern Ireland and the Outer Hebrides so is mainly influenced by coastal processes. The seabed is largely muddy sand and mud containing more gravel to the south. The regions turbidity is moderate to low, with bottom temperatures between 8 and 10°C. In the summer months most of the waters stratify (Turnbull 2000). Stratification of marine waters is important as it can impact upon the extent and timing of phytoplankton blooms and therefore local marine productivity (Townsend *et al.* 1994; Sharples *et al.* 2006).

Figure 1-1. Study region, depicted by the grey areas, of south-west Scotland and Northern Ireland which covers two regional sea regions; the Minches and West Scotland (A) and the Irish Sea (B).

1.3.2 Potential study species

Coastal seabirds can be defined as species which forage within coastal marine waters and intertidal zones. They are therefore generally surface and benthic foraging species rather than diving species which exploit more pelagic, open marine waters. There are several seabird species that are closely associated with coastal habitats and which are common and widespread breeding birds across Northern Ireland and south-west Scotland (Table 1.4). These species have varied life-history traits enabling different information about that species' environment to be identified and can be classified into functional groups based on the similarity of their foraging behaviour and resource use. The species listed can be split into two main functional groups based largely on their foraging strategies; surface feeders, which include the four gull and two tern species, and the remaining four species which are surface diving and pursuit foragers. These two groups can be split further largely based on the resources they then exploit. Within the surface feeders the terns (*Sterna* spp.) are generally more specialist, predominantly feeding in marine waters within 9km of the coast (Rock, Leonard & Boyne 2007), whereas the gulls are more generalist and opportunistic foragers exploiting both marine and terrestrial resources. In marine environments herring gulls *Larus argentatus* are predominantly associated with intertidal habitats whilst the lesser *L. fuscus* and great black-backed gulls *L. marinus* forage more extensively out to sea (Camphuysen 1995). If these large gulls are increasingly foraging on terrestrial items it may suggest that there is not enough more typical, and higher quality, marine food available within close range of the breeding colony (Belant *et al.* 1993; Bukacińska, Bukaciński & Spaans 1996).

1.4 Thesis Aims

Within this study I aim to (i) investigate whether spatial variation exists in the colony growth rates of widespread coastal seabirds across south-west Scotland and Northern Ireland and identify suitable monitoring species that show spatial variation across the study region; (ii) investigate a suitable species from multiple colonies during the breeding season to determine whether spatial variation also exists in several 'alternative' monitoring traits; (iii) identify which local environmental conditions may be driving any spatial variation observed in traits; and (iv) determine whether spatial variation in the seabird traits has any influence on the colonies' overall demography, breeding success and colony growth rate (Figure 1.2).

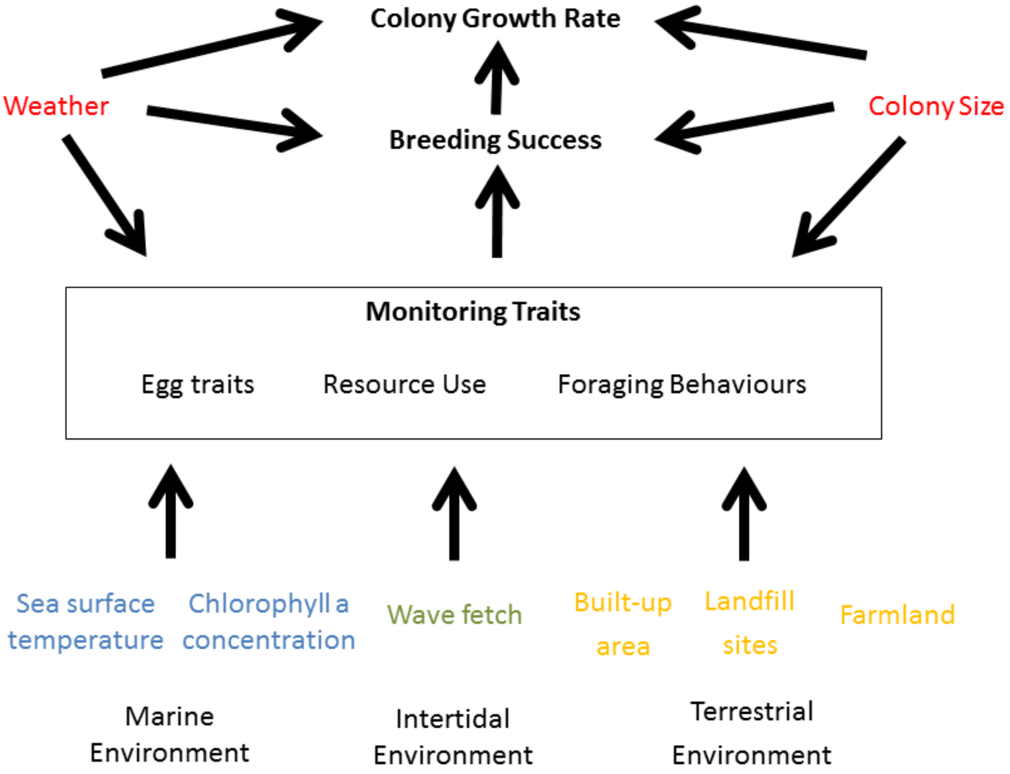
Environmental variables included in Figure 1.2 are those which will be investigated to determine which coastal seabird traits may be effective monitors of the coastal marine habitat. Sea surface temperature (SST) and chlorophyll concentration were included as proxies for marine productivity. SST influences marine processes associated with thermoclines and upwelling which in term will affect the distribution and abundance of potential prey species, whilst Chlorophyll a concentration acts as a proxy for primary productivity at the base of the marine food web (Huot *et al.* 2007). Wave fetch was included as a proxy for intertidal habitat, which is calculated based on the exposure of a coastline depending on topography and wind direction (Burrows 2009). Low wave fetch reflects a more sheltered intertidal habitat, whilst high wave fetch reflects an exposed coastline, and therefore intertidal habitat. Rocky shorelines with low wave fetch are thought to support a greater abundance of potential intertidal prey species (Burrows *et al.* 2012). Finally, three proxies of the terrestrial environment were included: built-up area, landfill sites and farmland (which incorporated agricultural land and improved grassland). The proxies for the marine and intertidal habitats are likely to be relevant to all the widespread coastal species listed in Table 1.4, whilst those associated with terrestrial habitats will only be relevant for the four gull species. Although not directly related to monitoring the coastal environment, weather conditions were also included in the analysis of certain traits as temperature and precipitation in particularly are known to affect seabirds (Becker, Finck & Anlauf 1985; Schreiber 2001). Colony size also needs to be taken into consideration as this may influence the response of a colony to environmental conditions/change attributed to density-dependent processes (Ashmole 1963; Matthysen 2005) or intra-specific competition for local resources (Furness & Birkhead 1984, Birt *et al.* 1987, Lewis *et al.* 2001).

Table 1-4. Life history and foraging characteristics of the coastal seabirds of Britain and Ireland

	Arctic tern	Black guillemot	Black-headed gull	Common eider	Common gull	Common tern	European shag	Great black-backed Gull	Great cormorant	Herring gull	Lesser black backed gull
Conservation Status[1,A]	Amber	Amber	Amber	Amber	Amber	Amber	Red	Amber	Green	Red	Amber
Dispersion[B]	Migratory	Resident	Resident	Resident	Resident	Migratory	Resident	Resident	Resident	Resident	Migratory
Breeding habitat[B]	Vegetated islands, remote beaches and coastal heath	Rocky islands and low-lying rocky coasts	Coast, wetlands, bogs, marshes and artificial water bodies	Rocky islands and low-lying rocky coasts	Coastal and inland sites	Coast and inland lakes, reservoirs and gravel pits	Coastal cliffs, ledges and boulders	Rocky coastlines with stacks and cliffs, occasionally inside	Mainly coastal on stacks, cliffs and rocky promontories but also inland	Rocky coastlines on cliffs, islets and islands, sand dunes, shingle banks and buildings	Offshore islands, coastal cliffs, sand dunes and saltmarshes
Foraging range	Mean: 9 km[D]	Mean range: 300m-10.5 km[E]	-	-	-	Mean: 9 km[D]	Mean: 7-12 km[J]	-	-	Mean maximum: 50 km[N]	Mean: 21.61±9.97 km[O]
Foraging stratergy	Surface / subsurface feeder	Pursuit diver	Surface feeder	Pursuit diver	Surface feeder	Surface / subsurface feeder	Pursuit diver	Surface feeder	Pursuit diver	Surface feeder	Surface feeder
Usual Clutch size[C]	1-2	1.75-1.92[F]	3	4-6	3	2-3	3	2-3	3-4	3	3
Incubation period (days) [M]	22 (20-24)	-	24 (23-26)	-	24-27 (22-28)	25 (21-29)	-	27-78	-	28-30 (26-32)	24-27
Fledgling period (days) [M]	21-24	30-32	*c*.35	-	*c*.35	28-30	-	35-42	-	35-40	30-40
Youngest age first breeds[C]	4	4	2	3	3	3	4	4	3	4	4
Diet[B,C]	Fish, crustaceans, invertebrates	Benthic zooplankton, crustaceans, fish, molluscs	Fish, crustaceans, invertebrates, fishery discards, refuse	Molluscs, crustaceans, fish[g]	Fish, bivalves, invertebrates, fishery discards	Fish, crustaceans	Fish, crustaceans	Fish, fishery discards, refuse	Fish, crustaceans	Fish, bivalves, crustaceans, fishery discards, refuse [L]	Fish, invertebrates, fishery discards, refuse
Survival[C]	Adult 0.900	Adult 0.870	Adult 0.900 Juvenile 0.447	Adult 0.820 Juvenile 0.330	Adult 0.860 Juvenile 0.250	Adult 0.900 Juvenile 0.470	Adult 0.878 Juvenile 0.380	-	Adult 0.880 Juvenile 0.580	Adult 0.880 Juvenile 0.630	Adult 0.913
Threats[B]	Food availability, weather, predation	Food availability, predation, drowning in nets	Food availability, predation	Predations, human disturbance, coastal oil pollution[G,H]	Predation, avian botulism	Food availability, tidal flooding, predation[I]	Food availability, weather, drowning in nets, shooting	Predation, culling, avian botulism	Food availability, shooting, contaminants, drowning in nets	Food availability, predation, avian botulism	Food availability, predation, culling, avian botulism

[1] Whether green, amber or red listed as a UK bird of conservation concern. References (Reference in the first colum for all species unless seperately stated overwise: [A] Eaton *et al*., 2015; [B] Mitchell *et al*. 2004; [C] Robinson 2005; [D] Rock *et al*., 2007; [E] Ronconi *et al*., 2002; [F] Ewins, 1989; [G] Keller, 1991; [H] Ost *et al*., 2008; [I] Uttley *et al*., 1989; [J] Wanless *et al*., 2000; [K] Andrews & Day, 1999; [L] Kubetzki & Garthe, 2003; [M] Walsh *et al*., 1995. [N] Birdlife International, 2015; [O] Thaxter *et al*. 2012 (offshore mean foraging range).

Figure 1-2. Relationships between the seabird traits to be investigated, environmental conditions and demographic traits.



In **Chapter 2** I investigate whether spatial variation exists in the long-term population growth rates of the widespread coastal seabird species present with the study region. Where it occurs this spatial variation can be exploited to help narrow down which local environmental variables are, or are not, driving observed differences in seabird population trends. The results from this analysis will be used to identify which coastal seabird species within the study region show spatial variation in the trends and which local environmental variables may drive this variation.

The species that reflected most information about their local coastal habitat, the herring gull, will be the focus of the rest of the thesis. A brief outline of its life history is described in **Chapter 3** as well as which colonies within the target region were selected to investigate herring gull traits in more detail.

In **Chapter 4** I used two complimentary approaches, pellet and stable isotope data, to determine whether spatial variation in marine and terrestrial resource use during the breeding season across the selected herring gull colonies in the study region is associated with environmental proxies of resource availability within the gulls' foraging range. I then investigate whether this variation in resource use has demographic consequences for the gulls.

In **Chapter 5** I investigated the usefulness of egg traits of herring gulls as a monitoring tool to reflect concurrent environmental conditions and proxies of resource availability. Specifically, whether spatial variation in egg colour, maculation, shape and/or shape reflects local environmental conditions early in the breeding season and whether there are any relationship with two measures of the herring gull's demography, breeding success and colony growth rate.

In **Chapter 6** I investigate spatial variation in herring gull foraging behaviours (nest non-attendance, provisioning rate and trip duration) to determine whether they are related to proxies of the availability of resources that were consumed by the gulls and whether that relate to the two measures of the gulls' demography.

In **Chapter 7** I bring together and summarise the results of the previous chapters to discuss the implications and limitations of this study.

Chapter 2

2 Identifying spatial variation in the population trends of coastal seabirds to explore drivers of change

2.1 Abstract

Populations can be affected by environmental factors that act over wider geographical scales so that nearby populations show more similar population trends than populations further apart. Monitoring multiple populations of one, or several species with different ecological requirements, may be a useful approach to identify potential drivers of population changes. Here I looked at spatial variation in population trends between the late 1960s and 2002 of seabirds using the coastal environment across south-west Scotland and Northern Ireland; a region where the coastal marine environment is under increasing anthropogenic pressure. Of the seven coastal seabird species investigated, spatial variation was found in the population trends of the herring gull *Larus argentatus*, lesser black-backed gull *L. fuscus*, great black-backed gull *L. marinus* and common gull *L. canus*, but not for the European shag *Phalacrocorax aristotelis*, Arctic tern *Sterna paradiseae* and common tern *S. hirundo*. I then related colony growth over three decades with spatially explicit environmental variables considered to be proxies of the foraging conditions in coastal habitats. Colonies of herring and lesser black-backed gulls located in more sheltered coastlines had more favourable growth than colonies in more exposed coastlines, possibly because exposure affects food availability and predictability in this habitat. In Herring gulls the greater the proportion of built-up area in their foraging range the more favourable the colony growth suggesting a positive effect of anthropogenic food available in built-up areas for this species. Therefore, monitoring spatial variation over multiple colonies helped identify variables influencing coastal populations of two gull species; highlighting the importance of natural intertidal habitats, as well as the potential of anthropogenic resources to buffer declining populations within the study region. These results demonstrate the potential of monitoring multiple populations within a region to identify candidate drivers for population changes.

2.2 Introduction

Animal population changes vary over time and space, with patterns often differing over different temporal and spatial scales (McArdle, Gastont & Lawtons 1990; Sutherland & Baillie 1992; Brown, Mehlman & Stevens 1995). Geographical variation in population trends is driven by spatial variation in environmental variables as well as by density-dependent processes, such as competition and predation (Furness & Birkhead 1984; Brown *et al.* 1995; Sibly & Hone 2002; Crespin *et al.* 2006). Regional differences in environmental variables, particularly climatic conditions and food availability, may therefore drive geographical variation in population trends. In recent decades, many ecosystems are also being impacted upon by anthropogenic influences; affecting population sizes through over-exploitation of resources, introduction of invasive species and habitat destruction/modification (Butchart *et al.* 2010). Spatial variation in animal population trends, however, is still poorly understood, partly because estimates of population sizes over wide geographic ranges are uncommon. Identifying the specific underlying drivers of population change is also challenging. Differences between different populations of the same species, or co-occurring populations of different species can provide a 'pseudo-experimental' approach that treats spatial contrasts in population trajectories as 'treatments' (Baum & Worm 2009), helping to identify factors that correlate with between-population differences. Therefore, comparing trends from multiple populations within a region may be used to narrow down potential drivers of change through investigating how spatial variation in population trends and local environmental variables interact (Frederiksen *et al.* 2005a, Robinson *et al*. 2013). However, this approach has rarely been used to explore its potential.

When multiple populations of the same, and potentially different, species fluctuate synchronously this may indicate that similar environmental conditions are occurring over the scale being measured (Harald *et al.* 2002, Liebhold *et al.* 2004). Contrasting trajectories between spatially distinct populations, however, may indicate that populations have experienced different local conditions (Ens *et al.* 2009); or that some populations are able to buffer themselves more effectively against adverse conditions (Burger & Piatt 1990). Different environmental variables are likely to impact populations over different scales; from predation and disturbance acting at a local level to severe or unusual weather events which typically act over larger spatial scales. Spatial variation in population trends may therefore be more likely in species which are affected by drivers acting over smaller spatial scales and in species which show higher site fidelity and move infrequently between different breeding sites (Erwin *et al*. 1981, Parsons *et al.* 2008). The extent to which spatial variation in populations occurs is likely therefore to depend on the species and habitats of interest.

Spatial variation, and similarities, in population trends have been found to exist in seabird populations across different scales with inter-population differences found in adult survival, productivity and population growth rate (Frederiksen *et al.* 2005a, Harris *et al.* 2005, Bertram *et al.* 2015, Cordes *et al.* 2015, Nager & O'Hanlon under review). However, this may not always be the case, with no spatial variation observed in the survival of Atlantic Puffin *Fratercula arctica* from multiple colonies despite variation in population growth, although this may suggest other traits such as breeding success may be responsible (Harris *et al.* 2005). Populations of apex predators, such as seabirds, are likely to reflect environmental conditions as being at a high trophic level they will integrate changes occurring at lower levels (Boyd *et al.* 2006; Fossi *et al.* 2012). The existence of spatial variation in the population trajectories of certain seabird species over different spatial scales does suggest that there is potential in investigating what variables are driving this variation.

Within the environments used by seabirds coastal habitats are particularly affected by anthropogenic and natural pressures due to their accessibility and location at a boundary between marine and terrestrial ecosystems, resulting in impact from both environments (Thompson *et al*. 2002, Lopez y Royo *et al.* 2009). Species utilising this coastal boundary have experienced declines in recent decades (Lotze *et al.* 2006, van Roomen *et al.* 2012). This study focuses on the coastal habitats of a region in north-west Europe which has experienced particularly high levels of anthropogenic pressure (Halpern *et al.* 2008). Within this region I am specifically interested in the environment at the boundary of the land and sea and how it affects the population growth of seabird species using these habitats. Within this study I aim to (i) identify whether spatial variation occurs in the population trends of a panel of seabird species breeding and foraging in coastal habitats. Where this spatial variation occurs I will (ii) identify any relationships between these population trends and spatially explicit environmental variables which relate to anthropogenic and natural resources; and therefore may affect seabirds at the boundary of terrestrial and marine habitats, to determine which factors may drive any spatial differences identified. Through this I can gain new insights into potential causes for the changing population trajectories of coastal seabird species across this region in recent decades.

2.3 Methods

2.3.1 Study region and study species

The study region incorporates a region of south-west Scotland and Northern Ireland covering an area of approximately 200 by 200 km (Figure 1.1). This area covers parts of two regional seas (JNCC 2014), the north Irish Sea and the south Minches and West Scotland Sea. Breeding seabirds within this region were counted as part of the three national censuses between 1969 and 2002: Operation Seafarer in 1969 (Cramp *et al*. 1974), Seabird Colony Register in 1985-1989 (Lloyd *et al*. 1991), and Seabird 2000 in 1998-2002 (Mitchell *et al.* 2004). Within the study region I selected seven common and widespread seabird species that are closely associated with coastal habitats and had sufficient population abundance data during the study period: Arctic tern *Sterna paradisaea*, common gull *Larus canus*, common tern *S. hirundo*, European shag *Phalacrocorax aristotelis*, great black-backed gull *L. marinus*, herring gull *L. argentatus* and lesser black-backed gull *L. fuscus*. These species have different ecological traits with the European shag being a surface diver and pursuit forager (Harris & Wanless 1993; Grémillet *et al.* 1998), whilst the other species are surface feeders; with the tern species having relatively specialist diets relative to the more generalist gull species (Pearson 1968; Götmark 1984). The cormorant *Phalacrocorax carbo* and black-headed gull *Chroicocephalus ridibundus* also breed in the study region, however, as they more frequently breed and forage inland than the other species, too few coastal colonies (i.e. colonies within 5 km of the coastline, Mitchell *et al*. 2004) were available for the analysis. The survey methodology for black guillemots *Cepphus grille* changed between the first two censuses (Mitchell *et al.* 2004), with the first census not being comparable with the following two, therefore I could not include this species in the analysis.

2.3.2 Population abundance data and growth rates

To estimate long-term population trends of the selected species I obtained counts of breeding colonies from the three national seabird censuses Operation Seafarer, Seabird Colony Register and Seabird 2000. All three censuses had a complete coverage of the study region and for each of the selected species used the same survey methodologies (Mitchell *et al*. 2004). Only coastal colonies within 5 km of the coast were included as I was interested in the interface between marine and terrestrial coastal habitats.

Count data for all selected species were available for individual species-specific colonies, based on the adjusted counts to specify Apparently Occupied Nests (AON) or Territories (AOT) (JNCC 2012, additional data for Operation Seafarer from JNCC (Roddy Mavor, pers. comm.)). I extracted counts for individual colonies for each of the selected species. During the seabird censuses grid references of all counted colonies were recorded. I matched counts from the same colony in different censuses by importing the grid references into ArcGIS (ArcMap ver.10. ESRI, USA) and extracted the location of all counts. Only where locations between censuses matched, by name or grid reference within 500m, I assumed successive counts for the same colony. Where there were multiple colony count data for small islands and sea-lochs (less than 5 km^2 in area) I summed all counts within such sites into one count as it could not be ruled out that there had been some small movement between these sub-sites.

Seabird count data are also given for unitary authority administration boundaries (hereafter administration areas) (Mitchell *et al*. 2004). Since birds can disperse between colonies, counts on a broader scale may provide more spatially integrated temporal trends taking into account movements of individuals between neighbouring colonies (Parsons *et al.* 2008). If there are spatial clusters of colonies that show similar population trends then I would expect differences in population trends between administration areas. Our study region included nine administration areas (Figure 1.1). However, it is unclear how biologically meaningful is the grouping in administration areas, so I therefore also compared those results with spatial autocorrelations of spatially explicit data on changes in size of individual colonies.

To quantify the population trends from 1969 to 2002 of our seven study species I calculated population growth rates for individual colonies and entire administration areas. For the colony-scale data, not all colonies were surveyed during all three seabird censuses. During the study period some colonies were newly established whilst others went extinct, which can be identified if their absence (a count of zero) was recorded. However, where no record of a zero count was made I could not be certain that the colony had been monitored.

Therefore, I included only colonies that reported a count, including a zero count, in Operation Seafarer (1969-1970) and in Seabird 2000 (1998-2002) ensuring that colony growth was estimated for all colonies over the same period of time, and therefore are comparable. The total number of individual colonies for each species within the study region, for which data was available in the first and last census, are displayed in Table 2.1. To estimate population growth at the level of administration areas I used the counts for each administration area in 1969-1970 and 1998-2002 as given in Mitchell *et al*. (2004). Count data was also available from the Seabird Colony Register (1985-1988) however, as not all colonies were surveyed during this census I only included the first and last census to maximise the sample size for the region of interest.

Table 2-1. Average coastal seabird population growth rates (GR) ± standard error (SE) based on individual colonies and on administration areas (Admin. Area) in the study region of south-west Scotland and Northern Ireland (Figure 2.1). Paired Wilcoxon Signed Rank tests compared the average GR of individual colonies per administration area included in the analysis and the administration area GR based on total counts of all colonies in that administration area.

Species	Spatial scale	GR ± SE	N[1]	Paired Wilcoxon test
Arctic tern	Colony	-0.086±0.18	17	
	Admin. Area	-0.396±0.32	6	*V*=3, *P*=0.28
Common gull	Colony	-0.229±0.13	32	
	Admin. Area	0.490±0.37	5	*V*=7, *P*=0.58
Common tern	Colony	-0.350±0.19	11	
	Admin. Area	0.013±0.20	5	*V*=13, *P*=0.19
Great black-backed gull	Colony	-0.098±0.09	48	
	Admin. Area	-0.002±0.29	6	*V*=13, *P*=0.69
Herring gull	Colony	**-0.228±0.09**[2]	68	
	Admin. Area	-0.216±0.31	6	*V*=11, *P*=0.99
Lesser black-backed gull	Colony	-0.032±0.14	33	
	Admin. Area	0.560±0.30	6	*V*=20, *P*=0.06
European shag	Colony	0.044±0.11	34	
	Admin. Area	0.311±0.25	5	*V*=12, *P*=0.31

[1] For colonies, N relates to number of individual colonies included within the analysis with population counts in Operation Seafarer (1969-1970) and Seabird 2000 (1998-2002). For Admin. Areas, N relates to the number of administration areas with colonies of that species. [2] Population trend significantly differed from zero (t = 2.53, df = 67, P = 0.014). Significant population trends are in bold.

The conventional calculation of population growth rate lambda, (N_{t+1}/N_t), is not defined for newly established colonies. I therefore calculated population growth rate (GR) using a formula based on Guillaumet *et al*. (2013):

$$GR = (N_t – N_{t-1})/\text{Maximum } [N_t, N_{t-1}]$$

where N_t is the count in Seabird 2000, N_{t-1} the count in Operation Seafarer, and Maximum [N_t, N_{t-1}] is the highest count from either Operation Seafarer or Seabird 2000. This calculation of GR avoids the issue of undefined growth rate for newly established colonies and GR=0 for extinct colonies (Guillaumet *et al.* 2013), both of which frequently occurred at the colony level. GR values were monotonically related to the calculated lambda with $r_s = 1.0$ in all species. For each species I calculated GR for individual colonies (colony GR) and for each administration area (administration area GR).

As the broad spatial pattern determined by administration area is biologically arbitrary, I also wanted to investigate the spatial variation in colony GR on a more objective basis using spatial autocorrelations. For each species I calculated a Moran's *I* Index, a measure of spatial autocorrelation, based on each species' colony GR and the colony's latitude and longitude. Moran's *I* Index ranges from -1 (spatially dispersed where neighbouring colonies have different values of GR) to +1 (spatially clustered where neighbouring colonies have similar values of GR) (Moran 1950, 1953, Legendre & Fortin 1989).

2.3.3 Environmental correlates of population growth rates

To determine whether environmental variables potentially reflecting food availability for at least some of the study species could explain any of the spatial variation observed in colony GR, three proxies for food availability in the coastal zone were obtained. These reflect different foraging habitats that could potentially influence coastal seabird numbers; wave fetch, built-up area and landfill sites. Variables were extracted for the foraging range of the focal species. For the common gull, terns and European shag I took a foraging range of 10 km from the colony whilst a foraging range of 50 km distance was used for the larger gulls (Pearson 1968, Götmark 1984, Wanless *et al*. 1991). Wave fetch, a measure of the exposure of the coastline that depends on topography and wind direction, was included as a proxy for potential intertidal foraging habitat quality; rocky shorelines with low wave fetch support a greater abundance of potential intertidal prey species, which is the predominant coastal habitat in the study region (Burrows *et al*. 2012). Average wave fetch (km) for each colony was calculated as the mean wave fetch across all quadrats of 200m^2 along the coastline (Burrows 2009) within that colony's foraging range. Due to the increased use of anthropogenic resources and habitats in recent decades by some species, in particular gulls (Pons 1992, Belant *et al.* 1993), two variables were considered as proxies for potential anthropogenic food resources; the amount of built-up area and the number of landfill sites within each foraging range. Amount of built-up area was taken from Landcover 2000, which uses computer classification of satellite images to quantify different land uses in the UK (Fuller *et al.* 2002). Built-up area is defined as the area covered by buildings and gardens in suburban/rural developed areas and continuous urban areas. For the analysis this was expressed as the amount of the total land area within each foraging range. The number of landfill sites for Scotland was obtained from SEPA (2015) and for Northern Ireland from NIEA (Eugene Kelly, pers. comm.).

For the purpose of the analysis I assumed that the colony GR reflects the average population trajectory across the study period, and therefore ideally the environmental variables included should reflect the same time frame. Average wave fetch as a proxy for food availability in the intertidal habitat is likely to reflect the entire study period, assuming that there have been no major changes in the prevailing wind direction between the late 1960s and 2002. The amount of built-up area and number of landfill sites, as a proxy for terrestrial anthropogenic food availability are based on information from 2000, at the end of the period of interest. Although the absolute values of these two variables have likely changed over time I assume that their levels relative to each other have remained largely the same, with areas with the greatest human impact in the late 1960s also being the areas with the greatest human impact in 2000. Landcover data was available for 1990 (Fuller *et al*. 1994) but it could not be included in the analysis as it did not cover Northern Ireland. However, for Scotland, there was a very positive, significant correlation between the amount of built-up area around the colonies during 1990 to that in 2000 ($r = 0.87$, $n = 241$, $P < 0.001$).

2.4 Statistical analysis

All statistical analyses were performed in R, Version 2.12.0 (R Development Core Team 2014). To check the representativeness of colonies included in our analysis I compared the mean GR of all included colonies per administration area with the administration area GR using paired Wilcoxon Signed Rank tests. To determine whether different species experienced similar GR across administration areas, and whether within the same administration area all species experienced similar GR, I used a two-way analysis of variance (ANOVA); with species and administration area and the interaction between the two as explanatory variables and colony GR as the response variable. To identify spatial auto-correlation in colony GR across the region Moran’s I Indexes were calculated for each species using the *ape* package (Paradis *et al*. 2004). A I value of zero indicates a random spatial pattern of GR. To statistically test whether Moran's I Index differs from 0 it can be transformed to Z-scores with values greater than 1.96 then $I > 0$ (spatially clustered) or smaller than −1.96 then $I < 1$ (spatially dispersed), indicating significant spatial autocorrelations at $P < 0.05$. To visualise the spatial variation in colony GR across the region for each species the locations of colonies were plotted in ArcMap 10.1 and shaded based on whether the GR had declined, increased or remained stable over the census period. A colony was classified as stable if its GR was within the 95% confidence interval of the mean GR across all species and colonies, calculated as 0.09; therefore all colonies with a GR between ±0.09 were classified as being stable over the census period.

To explore whether the colony GR was related to the characteristics of the coastal environment I considered proxies of food availability in the coastal zone (wave fetch, built-up area and number of landfill sites) as explanatory variables in a general linear model with colony GR as the response variable. I tested for multicollinerity between explanatory variable in the *car* package (Fox & Weisberg 2011) removing variables with a Variance Inflation Factor (VIF) greater than 3 (Zuur *et al*. 2010). Due to a high correlation between built-up area and number of landfill sites ($r = 0.87$, $n = 241$, $P < 0.001$) only built-up area was included in the statistical models. As the effect of the environment on population growth may vary with population density, and the same environmental value may be more limiting on colony GR when many birds compete for that resource, I also included colony size and its interaction with the environmental variables in the model. As I chose to consider the structure at the end of the census period for when I had reliable environmental information, I used colony size from Seabird 2000; to account for possible intra-specific competition occurring during the last census which might have influenced colony numbers and the relationship with environmental variables reflecting this later time period. Starting with the most complex model, including biologically relevant second-order interactions, model selection to determine the minimal adequate model was carried out using Likelihood Ratio tests to determine whether the exclusion of a term resulted in a significantly poorer fit of the model (Crawley 2007). Significance thresholds were set at $P < 0.05$, and only significant interaction terms are shown. Residual plots were inspected to ensure no deviations from homoscedasticity or normality occurred, and if necessary data were transformed (colony size was natural logarithm transformed). Residual spatial auto-correlation was also checked in the *spdep* package and residuals were independent (Bivand, Hauke & Kossowski 2013; Bivand & Piras 2015).

2.5 Results

2.5.1 Population growth rates

Across the seven coastal seabird species analysed there were no statistically significant differences in GR between the two spatial scales, colony and administration area (Table 2.1). Colony growth rates varied between species, but a statistically significant population trend for the study region was only found for the herring gull, and only at the level of individual colonies (Table 2.1). Colony GR differed between administration areas depending on species (two-way ANOVA, administration area: $F_{5,204} = 3.39$, $P = 0.009$; species: $F_{6,204} = 0.97$, $P = 0.491$; interaction between administration area and species: $F_{27,204} = 1.56$, $P = 0.045$; Table 2.2). Colony GR differed between administration areas only for great black-backed and herring gulls, with declining colonies in the east and the south (Antrim, Down, Wigtown) and increasing colonies in the west of the study region (Kyle & Carrick, Cunninghame). There were no differences between administration areas for the other five species.

Table 2-2. Colony GR ±SD (number of colonies in parenthesis) of the seven coastal seabird species for administration areas across south-west Scotland and Northern Ireland based on the population counts between Operation Seafarer (1969-1970) and Seabird 2000 (1998-2002). The last row compares GR between administration areas for each species separately using one-way ANOVAs.

Admin. Area	AT	CM	CN	GB	HG	LB	SA	All species[2]
Antrim	-0.40 (1)	0.93 (1)	-0.74 (1)	-0.58±0.70 (5)	-0.98±0.61 (5)	0.12±0.64 (2)	-0.08±0.62 (5)	-0.41±0.71 (20)
Argyll and Bute	-0.00±0.78 (10)	-0.34±0.74 (24)	-0.25±0.78 (6)	-0.01±0.64 (24)	-0.16±0.74 (40)	-0.17±0.85 (19)	0.07±0.66 (20)	-0.13±0.71 (143)
Cunninghame[1]	-0.93 (1)	0.02±0.76 (5)	-	0.36±0.76 (4)	0.46±0.73 (3)	0.45±0.84 (4)	0.8±0.67 (3)	-0.15±0.72 (20)
Down	0.89 (2)	0.84 (1)	0.13 (1)	-0.54±0.48 (8)	-0.84 (5)	0.19±0.80 (4)	-	-0.24±0.71 (21)
Kyle and Carrick	-0.75 (1)	-	-0.94 (1)	0.69±0.76 (4)	0.12±0.84 (4)	0.10±0.77 (3)	-0.24±0.80 (3)	0.07±0.72 (16)
Wigtown	-0.58±0.25 (2)	-0.97 (1)	-0.40±0.50 (2)	-0.54±0.44 (3)	-0.18±0.67 (11)	-0.88 (1)	-0.38±0.33 (3)	-0.37±0.72 (23)
Comparison between Admin. Areas	n.s	n.s	n.s	$F_{5,42}$ = 4.39, P = 0.003	$F_{5,62}$ = 2.99, P = 0.018	n.s	n.s	-

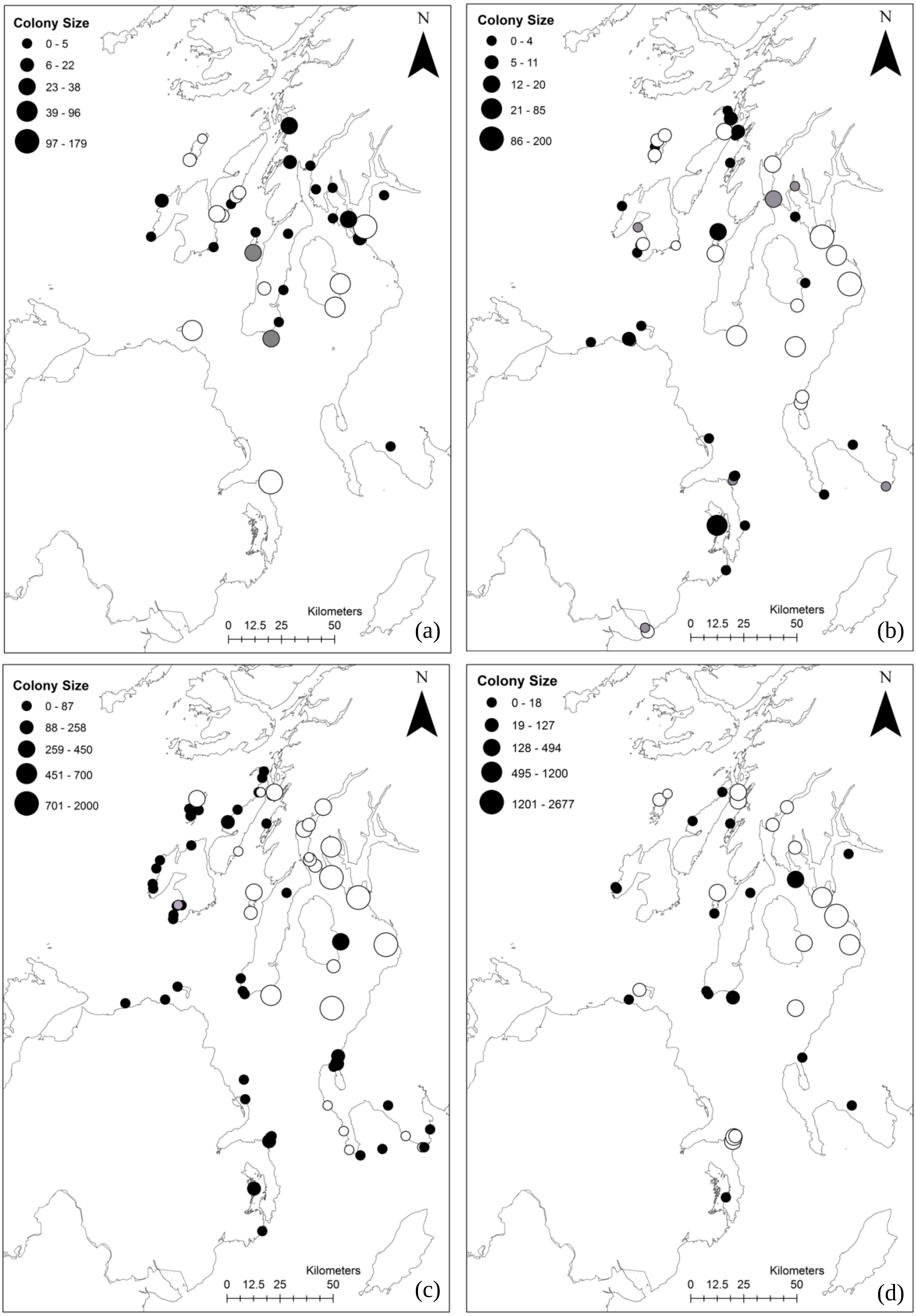
[1] As only two colonies (one Common Gull and one Lesser Black-backed Gull colony) were present within Inverclyde these were combined with Cunninghame in the analysis. Arctic Tern (AT), Common Gull (CM), Common Tern (CN) Great Black-backed Gull (GB), Herring Gull (HG), Lesser Black-backed Gull (LB) and Shag (SA). [2] Corresponds to the mean ± SD GR of all species per administration area. n.s – non significant difference in GR between administration areas.

The distribution of the colonies for the four gull species was spatially clustered with respect to colony GR (Moran's *I* Index > 0.07, Table 2.3); that is colonies with similar GR were nearby each other. On the other hand for European Shags and the two tern species the distribution of colony GR was spatially random (Moran's *I* Index close to 0; Table 2.3). The spatial distribution of colony GR for the seven species across the region of south-west Scotland and Northern Ireland are displayed in Figure 2.1. The three larger gull species (great black-backed, herring and lesser black-backed gull) showed a clustering of increasing populations around the Firth of Clyde whereas declining common gull colonies clustered in the northern part of the study region.

Table 2-3. Moran's *I* Index (measure of spatial autocorrelation) to determine the extent of spatial variation in colony population growth rates for seven coastal seabird species. Moran's *I* index values range from +1 (clustered) to -1 (dispersed) with values close to 0 indicating a random pattern.

Species	Moran's *I*	*Z* value	*SD*	*P*
Arctic tern	0.031	-0.063	0.091	0.306
Common gull	0.071	-0.032	0.042	**0.013**
Common tern	-0.024	-0.100	0.140	0.318
Great black-backed gull	0.104	-0.021	0.063	**0.046**
Herring gull	0.123	-0.015	0.045	**0.002**
Lesser black-backed gull	0.155	-0.031	0.079	**0.018**
European shag	0.068	-0.030	0.065	0.130

SD = standard deviation. Boldface indicates significance at $P < 0.05$.


Colony Size
0 - 5
6 - 22
23 - 38
39 - 96
97 - 179
N
Kilometers
0 12.5 25 50
(a)
Colony Size
0 - 4
5 - 11
12 - 20
21 - 85
86 - 200
N
Kilometers
0 12.5 25 50
(b)
Colony Size
0 - 87
88 - 258
259 - 450
451 - 700
701 - 2000
N
Kilometers
0 12.5 25 50
(c)
Colony Size
0 - 18
19 - 127
128 - 494
495 - 1200
1201 - 2677
N
Kilometers
0 12.5 25 50
(d)

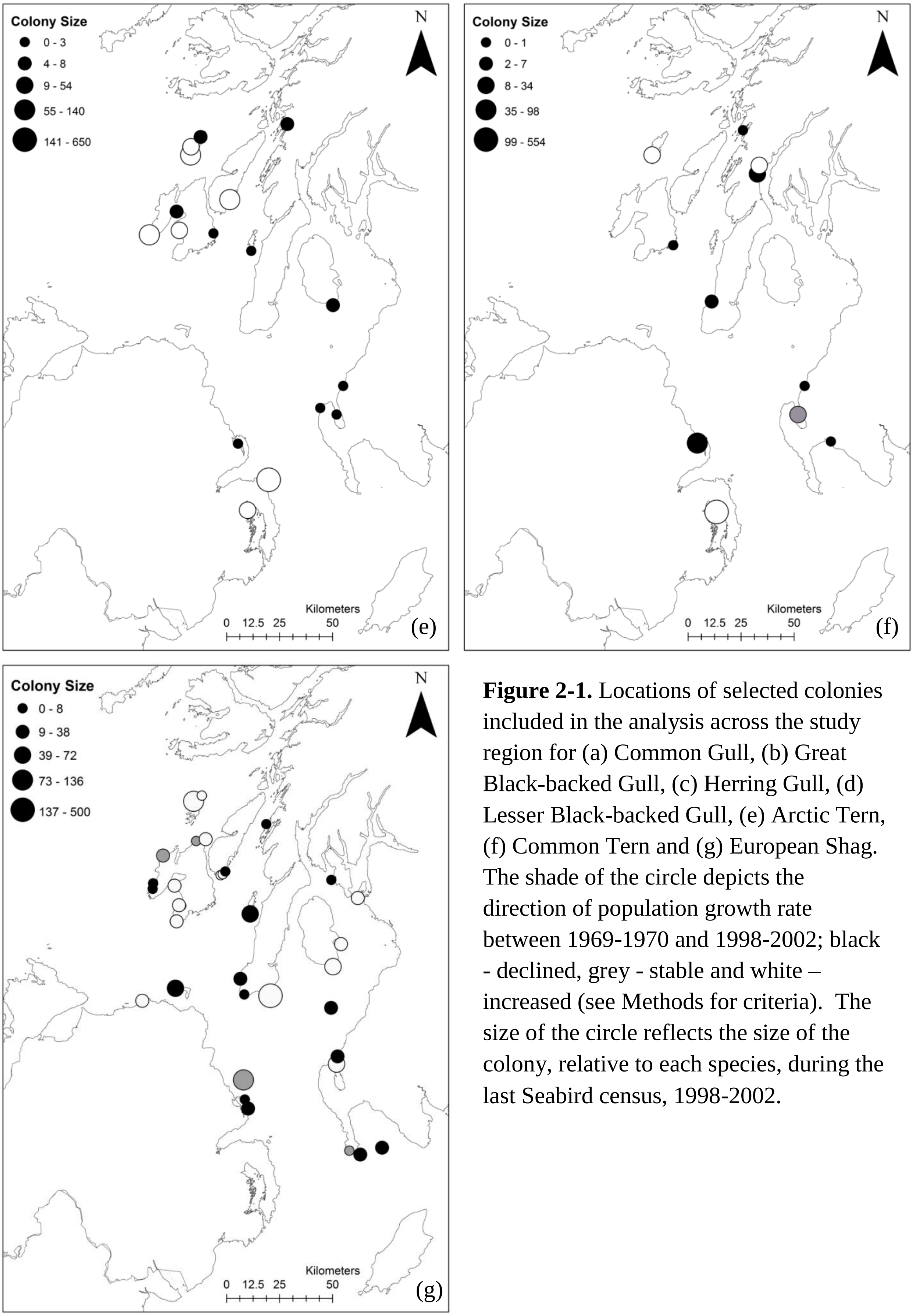


Figure 2-1. Locations of selected colonies included in the analysis across the study region for (a) Common Gull, (b) Great Black-backed Gull, (c) Herring Gull, (d) Lesser Black-backed Gull, (e) Arctic Tern, (f) Common Tern and (g) European Shag. The shade of the circle depicts the direction of population growth rate between 1969-1970 and 1998-2002; black - declined, grey - stable and white – increased (see Methods for criteria). The size of the circle reflects the size of the colony, relative to each species, during the last Seabird census, 1998-2002.

Interestingly, for the declining herring gull population, the declines were largest in what used to be the largest colonies (effect of colony size in 1969-1971 on the colony growth rate between 1969-1971 and 1998-2002 from linear regression: $F_{1,66} = 16.85$, $P < 0.001$). Similarly, there were also negative relationships between colony GR and the initial colony count during the late 1960s for common gulls ($F_{1,30} = 20.36$, $P < 0.001$), great black-backed gulls ($F_{1,46} = 10.34$, $P = 0.002$) and European shag ($F_{1,32} = 15.49$, $P < 0.001$), but not the other species ($P > 0.197$).

2.5.2 Environmental correlates of population growth rates

The amount of built-up area and wave fetch explained variation in colony GR, independent of current colony size, only for herring and lesser black-backed gulls (Table 2.4). Common and great black-backed gull colonies experiencing the highest GR also unsurprisingly had the largest colony counts in Seabird 2000, but neither environmental variables explained any of the remaining variation in colony GR (Table 2.4a, b). A positive relationship between colony GR and current colony size was also observed for the herring and lesser black-backed gulls; with wave fetch and built-up area explaining additional variation. For the herring and lesser black-backed gulls I found a significant negative relationship between GR and wave fetch (Table 2.4c, d); colonies declined more strongly at sites with higher average wave fetch within the foraging range of the colony (Figure 2.2a, b). Our results also showed a significant, positive relationship between Herring gull colony GR and the amount of built-up area within the foraging range (Table 2.4c; Figure 3.4); with faster growing colonies having more built-up area within their foraging range. Neither current colony size nor any of the environmental variables were associated with variation in colony GR of the European shag and the two tern species.

Table 2-4. Final models from general linear regression models relating colony GR to environmental variables (wave fetch, built-up area) and logged colony size in Seabird 2000 for the (a) common gull, (b) great black-backed gull, (c) herring gull and (d) lesser black-backed gull. Only significant variables are shown.

Species	Coefficients	Estimate	Std. Error	*z*	*P*	R^2
(a) Common gull	Intercept	-0.969	0.164	-5.922	**<0.001**	
	Colony Size	0.327	0.059	5.563	**<0.001**	0.49
(b) Great black-backed gull	Intercept	-0.633	0.110	-5.757	**<0.001**	
	Colony Size	0.322	0.051	6.288	**<0.001**	0.45
(c) Herring gull	Intercept	-0.4824	0.2095	-2.303	**0.025**	
	Colony Size	0.2236	0.0317	7.046	**<0.001**	
	Built-up area	-0.0015	0.0007	-2.189	**0.032**	
	Wave Fetch	-0.0004	0.0002	-2.946	**0.004**	0.52
(d) Lesser black-backed gull	Intercept	-0.4350	0.2118	-2.054	**0.049**	
	Colony Size	0.2417	0.0002	7.777	**<0.001**	
	Wave Fetch	-0.0004	0.0311	-2.242	**0.033**	0.71

All models started with all variables including interactions between each environmental variable and colony size. Final models were chosen using a model selection based on the lowest Akaike information criterion. Environmental variables were not found to explain any of the variation in Artic tern, common tern, or European shag.

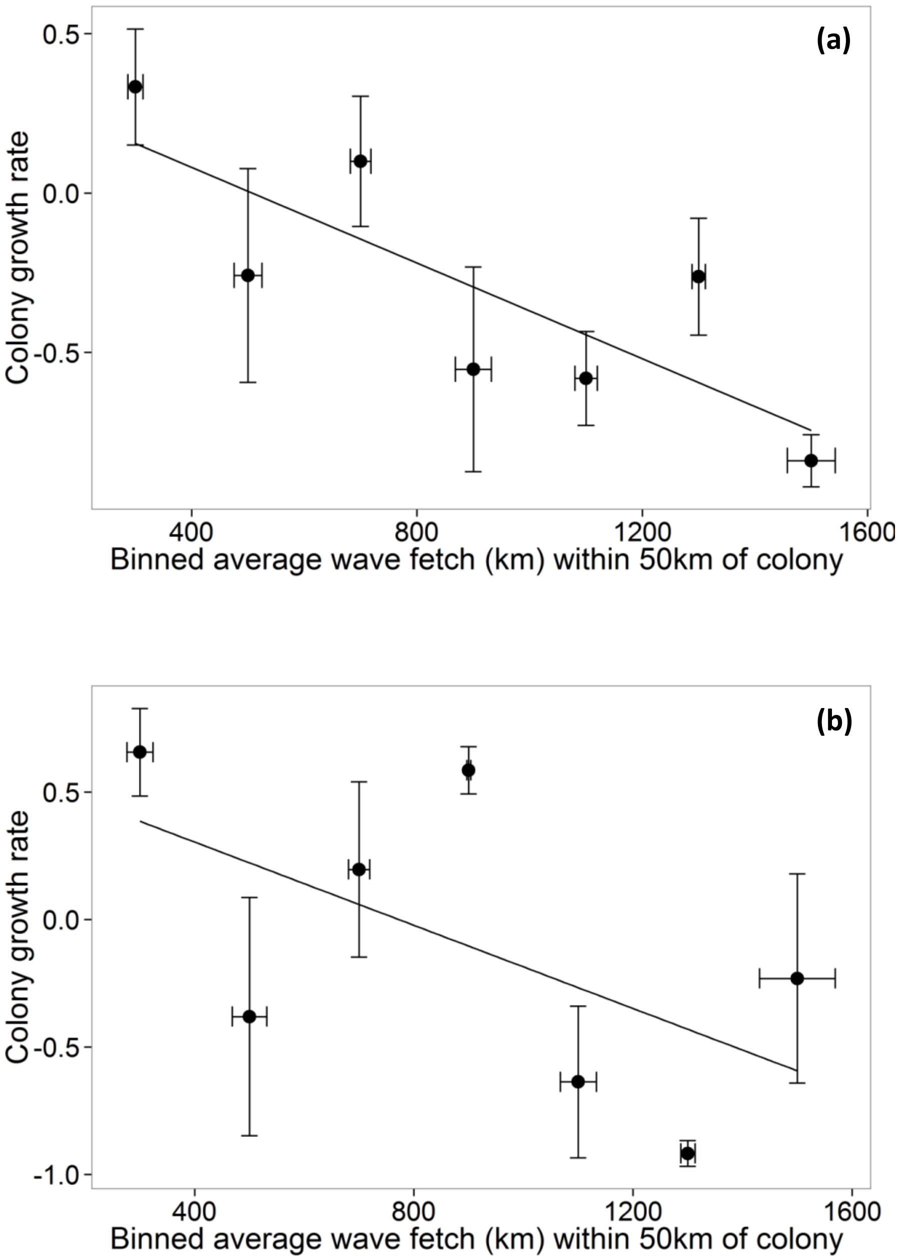


Figure 2-2. Relationship between average wave fetch (km) within the foraging range of the colony and colony growth rate, between 1969-1970 and 1998-2002 for (a) herring gull and (b) lesser black-backed gull. Data are binned for categories of 200 km wave fetch for illustration only.

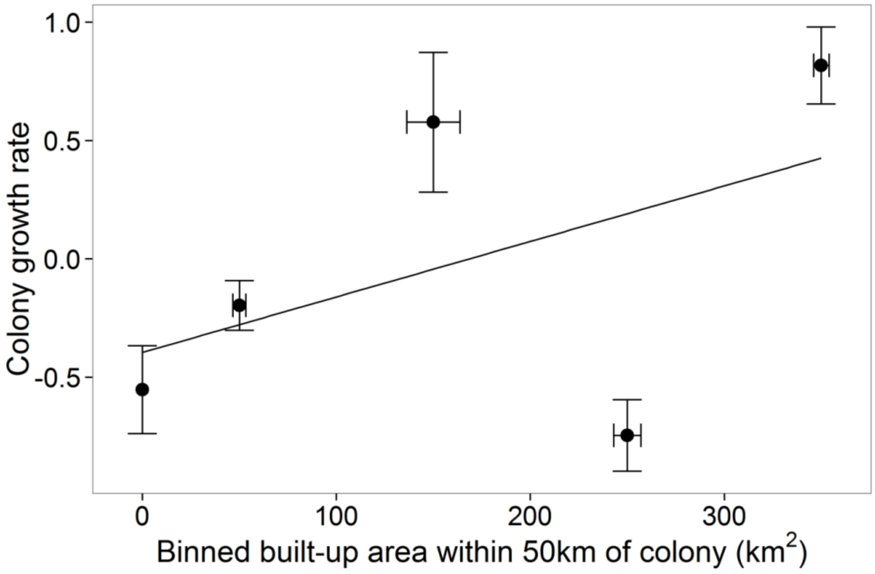


Figure 2-3. Relationship between amount of built-up area within the foraging range of the colony (km^2) and herring gull colony growth rate, between 1969-1970 and 1998-2002. Data are binned for categories of 100 km^2 built-up area for illustration only.

2.6 Discussion

Of the seven widespread coastal seabird species I investigated across south-west Scotland and Northern Ireland I found evidence for spatial clustering of colony growth in the common, great black-backed, herring and lesser black-backed gulls, but not in European shag, Arctic and common terns. This may indicate that nearby colonies of gulls experience similar environmental conditions which influenced their growth rate. Indeed for the herring and lesser black-backed gull I found that colony growth rate was related to the average wave fetch within their foraging range, a proxy for foraging conditions in the intertidal zone, with colonies declining more strongly in areas with exposed coast lines which have a high wave fetch. Herring gull colonies also had a higher growth rate when having a high amount of built-up area, a potential source of anthropogenic food, in their foraging range. I found no evidence that intra-specific competition for resources affected colony growth in any of the four gull species.

Not all monitored colonies within the study region could be included in the analysis due to incomplete records on colony size; which could be due to the colony not being counted or not being in existence at the time. When pooling all colonies into administration areas I get a spatially integrated measure accounting for some movement (Parsons *et al.* 2008) at least within administration areas. Comparisons between the growth rate at the level of administration area and the mean of the selected colonies in each administration area showed a very similar decline for the herring gull and similarly stable population trends in the great black-backed gull across the two scales. The herring gull was the only species showing a statistical significant population decline when considering the selected colonies For the remaining species there may be two potential reasons resulting in variation in population trends between the two scales, although not statistically significant. New colonies, or colonies missed during the first census could have resulted in apparently higher colony growth rates at the level of administration area than at the level of individual colonies, such as for the common gull, common tern, lesser black-backed gull and European shag. In contrast, colony extinctions since the first census could have resulted in the possibly lower growth at the level of administration area than at individual colonies, for example in the Arctic tern. Overall, I found no statistical evidence that the growth rate of selected colonies were not representative of the overall population growth, at least based on total counts at the scale of administration areas during the national censuses, despite that the administration areas represent a biologically arbitrary delimitation.

Across the study region I did find differences in colony GR between administration areas depending on species, indicating that colony growth rates differed between administration areas only for the herring gull and great black-backed Gull, but not for any of the other five species. At the scale of individual colonies, I found spatial variation in colony growth for all four gull species based on positive Moran *I* values, with clustering based on the direction and extent of colony growth rates. Great black-backed, herring and lesser black-backed gulls all showed a similar spatial clustering with colonies around the Firth of Clyde generally increasing whereas declining common gull colonies clustered in the northern part of the study region. Spatial synchrony in population trends have also been reported recently in another seabird, the marbled murrelet *Brachyramphus marmoratus* on a larger spatial scale (Bertram *et al.* 2015) and for herring gulls at the scale of the British Isles (Nager & O'Hanlon under review).

For the European shag and two tern species no spatial variation in colony growth was found on either scale, reflecting a random distribution pattern. One possible explanation is that the tern and European shag colonies were influenced more at the colony level by very local factors such as disturbance and predation. Terns are particularly susceptible to such local pressures during breeding (Craik 1997; Clode & Macdonald 2002; Nordstrom *et al.* 2004). Terns are also generally less site faithful than other seabird species (Whittam & Leonard 2000); therefore, if one colony experienced very local adverse conditions then individuals from this colony may have moved to another colony resulting in spatially asynchronous colony growth. In addition, a smaller number of colonies were included in the analysis for the two tern species which could be attributed to more colony extinctions or, more likely in this region, founding events during the census period (Balmer *et al.* 2013).

The lack of evidence for spatial variation between administration areas in the common gull and lesser black-backed gull, but spatial clustering confirmed by the Moran *I* values for these species, could be due to the arbitrary delimitation of administration areas, which may poorly reflect the actual spatial structuring that occurred across administration area boundaries. It is interesting to note that the administration areas nonetheless happened to be sufficiently sensitive to capture at least some of the spatial variation observed on the scale of individual colonies, and therefore spatial clustering may be at a smaller scale than administration area.

Geographic variation in colony growth, as found in the four gull species, could be due to spatial variation in deterministic processes such as strength of density dependence or spatial variation in environmental conditions that affect population growth (Brown *et al.* 1995; Williams, Ives & Applegate 2003). In four species, I found a significant negative relationship between colony growth and the size of the colony. Evidence for density-dependent population changes have also been found at the national level in the herring gull and the lesser black-backed gull (Nager & O'Hanlon, under review). However, Nager & O'Hanlon (under review) did not find evidence for spatial variation in density-dependence and therefore it is unlikely to explain the observed geographic variation in colony growth in gulls. Larger colonies may also deplete local food sources more strongly and experience higher levels of competition resulting in reduced population growth growth (e.g. Furness & Birkhead 1984, Birt *et al.* 1987, Lewis *et al.* 2001). Such processes would be indicated by interactive effects of colony size and environmental conditions on colony growth, however again I did not find any evidence in support of this. Deterministic processes are therefore unlikely to explain the observed spatial variation in the four gull species. Alternatively, spatially variable environmental conditions could be responsible for the geographic differences in population trends of the gulls.

To understand why within the study region some clusters of colonies did well whilst others less so, I looked at the relationship of the growth rate of individual colonies with relevant environmental variables that reflect food availability in some of the coastal foraging habitats used by at least some of the species included in our analyses. The absence of spatial clustering of colony GR in the European shag and the two tern species may explain why none of our environmental variables that act on a broad spatial scale were related to the colony growth, and environmental variables on a finer spatial scale may be required. It may also be that the environmental variables did not represent the main foraging habitats of these species. Although all three species do forage in the intertidal habitat, proxies reflecting the productivity of the marine environment, such as sea surface temperature and chlorophyll a concentration may have been more informative for these species. Fisheries data could have given additional information on availability of fisheries discards which can be an important food source for some seabirds (Garthe, Camphuysen &

Furness 1996; Oro *et al.* 2004; Votier *et al.* 2004). However, none of these variables were available for the spatial resolution and/or time period required for our study.

The similar spatial clustering of the three larger gull species suggests that they might have responded to similar environmental conditions, however common gulls most likely responded to different environmental variables. None of the included environmental variables was related to variation in colony growth rate of common gulls, possibly suggesting processes in the marine environment being the most relevant drivers for this species in our study region.

The two environmental variables, wave fetch and built-up area, included in the analysis as proxies of foraging conditions in the intertidal and terrestrial habitat, explained variation in colony growth rates of herring and lesser black-backed gulls. Faster growing colonies of herring and lesser black-backed gulls were associated with lower average wave fetch in their foraging range. Wave fetch can be used as a proxy of the composition of rocky shore communities due to the influence of wave exposure on these communities (Burrows *et al.* 2008). Low wave fetch reflects a more sheltered intertidal habitat that generally supports a greater abundance of intertidal prey species for gulls such as crabs and *Littorina* snails (Burrows *et al.* 2008; Burrows 2012). As both species do forage within intertidal habitats (Hunt & Hunt 1973; Kubetzki & Garthe 2003) the results suggest that colonies with sheltered intertidal habitats, with low wave fetch in their vicinity, have higher potential local food availability; potentially explaining why these colonies have higher colony GR and highlighting the importance of the natural intertidal habitat to these two gull species. Alternatively, gulls on more sheltered shorelines may breed more successfully possibly due to these colonies being more sheltered from adverse weather events which could impact upon egg and chick survival or forging ability (Schreiber 2001). I did not find a relationship between colony growth and wave fetch in the Great Black-backed Gull, possibly because among the larger gulls they are the most marine foraging species (McLellan & Shutler 2009, Washburn *et al.* 2013), and inclusion of information on marine productivity could be more informative.

In the herring gull, colony growth was also positively related to the amount of built-up area in the colony's foraging range. Built-up area may act as a proxy for terrestrial, anthropogenic resources; including the potential availability of landfill sites as the two variables were highly positively correlated. Several gull populations have been shown to exploit terrestrial, anthropogenic resources (Moreno *et al.* 2010, Ramos *et al.* 2011, Ramírez *et al.* 2012, Steigerwald *et al.* 2015) which could result in colony size being buffered from unfavourable marine conditions by alternative anthropogenic food resources. Belant *et al.* (1993) found that anthropogenic resources, specifically landfill sites, were less important to herring gulls where more natural food resources were available. On the other hand Blight *et al.* (2015) found that a decline in gull populations was most likely related to a shift in diet from marine to more terrestrial resources, whereas yellow-legged gull *Larus michahellis* colonies have been observed to increase in areas where anthropogenic resources in the vicinity of the colony have also increased (Duhem *et al.* 2008). It is therefore, arguable whether anthropogenic food is more beneficial to gulls than their more traditional marine diet (Pons 1992; Belant *et al.* 1993; Annett & Pierotti 1999; Duhem *et al.* 2008; Weiser & Powell 2010; Steigerwald *et al.* 2015). However, access to more predictable anthropogenic resources (Burger & Gochfeld 1983; Horton, Brough & Rochard 1983) compared to the typically more patchily distributed and temporally more variable distribution of food resources in the open sea (Weimerskirch 2007) or being constrained by the tides in intertidal habitats (Hunt & Hunt 1973) might help meet the demand of extra food required for chick provisioning (Hillstrom *et al.* 1994, Kilpi & Ost 1998). Alternatively, a high amount of built-up area in the foraging range may indicate potentially higher disturbance and higher levels of environmental pollution, both of which should negatively affect colony growth; however, I found a positive association between colony growth and built-up area. Our results may therefore suggest that the Herring gull's dependence on alternative, potentially poorer quality anthropogenic food resources signifies that local marine food conditions are poor and that they may have no choice but to seek alternative resources. This indicates that human activity in terrestrial habitats along the coast can impact the population growth of the large gull species although the exact mechanism needs further research.

The results from this study show that colony growth of herring and lesser black-backed gulls is sensitive to spatially variable environmental conditions at the interface of marine and terrestrial ecosystems. Identifying the environmental drivers of population changes is challenging and at the national scale there is no one overall cause of population change across the UK for any of the coastal seabird species monitored (Cramp *et al.* 1974, Lloyd *et al.* 1991, Mitchell *et al.* 2004).Depending on the species and location food availability, predation, disturbance, disease and weather/climatic conditions have all been cited as potential explanations for declines (Cramp *et al.* 1974, Lloyd *et al.* 1991, Mitchell *et al.* 2004). This study demonstrates that monitoring spatial variation in colony growth is a promising approach and highlights the potential of monitoring multiple colonies and identifying spatial variation in population trajectories to help investigate relevant environmental variables that drive spatial differences in population changes. This information is valuable in attempting to determine the status of coastal habitats at a local scale and may help in selecting suitable populations of species, or a panel of species, for monitoring programmes to most efficiently reflect what is occurring in the local environment. This will depend on the question being asked and what requires to be monitored; predation and disturbance may be very species- and colony-specific, whilst factors that reflect general marine productivity and food availability potentially have greater implications for the entire ecosystem.

Acknowledgements

The Seabird Colony Census data were extracted from the Seabird Monitoring Programme Database at www.jncc.gov.uk/smp and www.jncc.gov.uk/page-4460. Data have been provided to the SMP by the generous contributions of nature conservation and research organisations, and of many volunteers throughout the British Isles.

Chapter 3

3 Study species and site selection

The results from Chapter 2 indicate that there are spatial differences in the population trajectories of some of the coastal seabird species across the study area. I therefore aim to exploit this spatial, rather than temporal, variation in population trajectories to investigate the usefulness of alternative traits to colony counts can be used to reflect what is occurring in seabird populations as well as in the wider environment. By selecting colonies which have undergone the greatest relative declines and increases it is hoped that spatial differences in seabird traits, due to reflecting environmental change over short time periods, across the study area can help explain the observed variation in how the colonies have fared historically. As at the national level there is unlikely one driver for the population changes observed in the seabird species monitored as part of the national seabird censuses it makes more sense to concentrate over a smaller region, in this case south-west Scotland and Northern Ireland, to determine if within this area the drivers of between colony differences in population changes can be identified.

Ideally all seven coastal species would be included in a multi-species panel, incorporating species with differing life history traits, would provide a much broader and representative assessment on the state of the marine coastal environment (Piatt *et al.* 2007b; Mallory *et al.* 2010). However, this is not feasible in the time frame and logistics of the project. Additionally, not all the coastal seabird species considered above show clear spatial clustering in their historic population trajectories, therefore it may be more informative to select those that did to understand what is occurring within the local environment. For the region of south-west Scotland and Northern Ireland it appears that the herring gull will be a useful monitor of the coastal marine environment as it is widespread, spatial variation does exist in population growth rates across the region, and shows evidence to be relatively sensitive to the local environmental conditions for which data is available. In addition, any conclusions about what is driving the changes in herring gull population growth rates may also relate to the other coastal seabird species. The extremes observed in population growth rates across the regions also provides an excellent opportunity to investigate in more detail what may be driving these differences at these contracting colonies. In addition, the herring gull is red listed as a UK bird of conservation concern (Eaton *et al.* 2009, 2015), therefore as well as monitors of the coastal marine environment it is also of interest to understand more on this species ecology.

It would also be unfeasible to monitor all the coastal colonies present across the study region for these two species. Instead a selection of colonies, included in the above analysis, with contrasting population trajectories were identified to represent the wider region based on the results of the colony population growth trends and cluster analysis. From examining the cluster maps for the herring gull as well as considering the logistics of accessing and monitoring colonies, several colonies which have experienced contrasting extremes of population trajectory over the census period were selected to investigate this species in more detail (Table 3.1). The chosen colonies also provide a good spatial coverage of the study area across south west Scotland and Northern Ireland (Figure 3.1).

Table 3-1. Colony GR for selected herring gull colonies between the three seabird censuses and the most recent count (year given in parenthesis)

Colony	Latitude	Longitude	Seafarer-S2000[1]	Seafarer-SCR[2]	SCR-S2000	S2000-recent	
Isle of Muck	54.85	-5.72	-0.986	-0.608	-0.965	-0.556	(2013)
Copelands	54.69	-5.52	-0.891	0.536	-0.949	0. 480	(2012)
Strangford Lough	54.43	-5.57	-0.875	-0.140	-0.854	0.685	(2013)
Coul Point, Islay	55.80	-6.48	-0.824	-0.465	-0.671	0.000	(2013)
Oronsay	56.02	-6.22	0.522	0.736	-0.447	-0.301	(2012)
Portpatrick	54.84	-5.13	0.867	-0.333	0.606	-0.197	(2013)
An Dunan, Jura	55.98	-5.87	0.900	0.663	0.933	-0.700	(2013)
Lady Isle, Clyde	55.53	-4.73	0.980	0.967	0.733	-0.446	(2013)
Pladda, Arran	55.43	-5.12	0.988	0.989	-0.074	-0.400	(2012)

[1] S2000 – Seabird 2000 between 1998 and 2002. [2] SCR – Seabird Colony Register between 1985 and 1989.

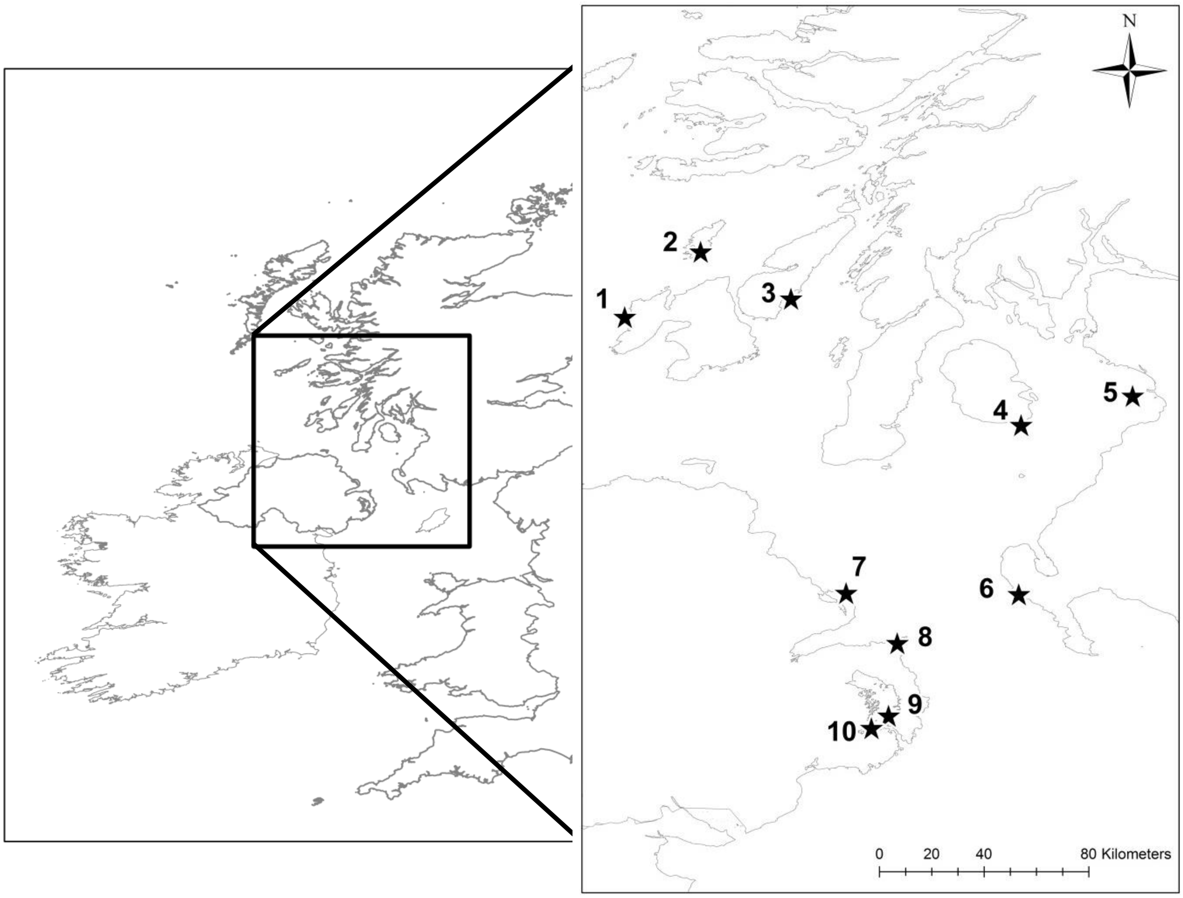


Figure 3-1. Study region and location of the eight herring gull breeding colonies across south-western Scotland and Northern Ireland. 1 Islay, 2 Oronsay, 3 Jura, 4 Pladda, 5 Lady Isle, 6 Portpatrick, 7 Isle of Muck, 8 Copeland Islands, 9 Green Island, 10 Round Island. These colonies within the region can be sub-divided into three separate geographic areas: 1, 2 & 3 – Inner Hebrides; 4 & 5 – Clyde; 6, 7, 8, 9 & 10 – North Channel of the Irish Sea.

The selection of the colonies was based on the population growth rate between the first seabird census in the late 1960’s, Operation Seafarer, and the last seabird census around the year 2000, Seabird 2000, using a single count for each colony from each census. However, these population numbers represent the colonies over a decade ago and it is possible that the population trajectories for these colonies have since changed. For all of the target colonies there are additional counts available during this three censuses period as well as more recent counts from local bird reports, organisations and the Seabird Monitoring Programme (JNCC 2013). The population growth rates were therefore also calculated using the most recent population counts to determine whether the population trajectory had changed since Seabird 2000. For the target herring gull colonies the year of the most recent counts varied from 2005 to 2013 (Table 3.1). As individual count data was not available for Green Island and Round Island total counts of all herring gulls within Strangford Lough are used. Green and Round Island were chosen to represent the breeding gulls in Strangford Lough as they are two of the largest colonies and had more recent count data available due to being managed by the National Trust for Northern Ireland. For Oronsay all counts across the island were combined into one count. To determine whether the population growth rates were similar over the national seabird censuses over 1969 to 2002 and between Seabird 2000 and the most recent count of the target colonies Pearson's product-moment correlations were performed.

For the herring gull there was a positive, but not statistically significant correlation between the population growth rates between Operation Seafarer and Seabird Colony Register and between Seabird Colony Register and Seabird 2000 ($r_{(8)} = 0.49$, $p = 0.15$) indicating that the population trajectories across the target colonies were not consistent between Operation Seafarer and Seabird Colony Register and between Seabird Colony Register and Seabird 2000. There was a negative, but again not statistically significant correlation between the population growth rates between Seabird Colony Register and Seabird 2000 and between Seabird 2000 and the most recent count ($r_{(8)} = -0.42$, $p = 0.23$); indicating inversions of the population trajectories in the most recent decade. Looking at the population growth rate values from Table 3.1, the five Scottish colonies which historically experienced increases have, since Seabird 2000, been in decline; whilst the Coul Point colony on Islay remained stable. In Northern Ireland, the Ile of Muck has continued to experience declines since Seabird 2000, whilst the Copeland and Strangford Lough colonies have seen some recovery over the past decade. The drivers behind these population growth rates are not known. In Scotland, the former observed increase may have coincided with an increase in anthropogenic resources, specifically discards and landfill; however the availability of these resources has declined over the past few decade (Pons 1992; Votier *et al.* 2004); which may have started to have an effect on the herring gulls at the population level. In Northern Ireland the increase of aquaculture in Strangford Lough may have benefited colonies there. Due to missing census counts I was unable to repeat this analysis for the shags.

In order to establish whether I can use alternative traits to colony counts to monitor colonies across this region the above target colonies will be investigated in more detail, as well as determining how these traits reflect the gulls demography. In order to achieve this, gaps in the knowledge of herring gull traits associated with the gulls' eggs, resource use and foraging behaviours will be filled through further fieldwork.

3.1 Herring gull biology

Herring gulls are widespread breeding and non-breeding residents in the UK and Ireland. The most recent breeding population of herring gulls in the UK is estimated at 139,200 apparently occupied nests (AON), with 50% of these breeding in Scotland (Mitchell *et al.* 2004); with a UK wintering population estimated at 729,801 individuals, with 37% recorded in Scotland (Banks, Calladine & Austin 2007). However, over the past 25 years UK herring gulls have experienced severe breeding and non-breeding population declines, resulting in the species being included on the UK's red list of birds of conservation concern (Eaton *et al.* 2009, 2015). There is no one distinct cause for the recorded declines and it is likely that a number of different factors are responsible, especially given that there is spatial variation in population trends across the UK at the regional level (Nager & O'Hanlon, In press). Declines have been attributed to changes in waste processing at landfill sites, reductions in fishery discards as well as natural food sources, American mink *Neovison vison* predation of eggs and chicks, mortality from botulism and culling (Mitchell *et al.* 2004, Coulson 2015, Nager & O'Hanlon, In press).

Herring gulls breed in a wide variety of habitats including rocky shores, outcrops and islands, sandy beaches and dunes, salt marshes, gravel bars, and in more recent times, man-made structures particularly buildings (Monaghan & Coulson 1977; Raven & Coulson 2001). Nests within these colonies are generally a depression in mounds of vegetation on the ground or flat areas of cliffs or rocky areas. Site fidelity is strong with individuals not only coming back to the same colony but to the same location within the colony generally with the same mate (Tinbergen 1961; Ludwig 1963).

Eggs are typically laid in May with timing of breeding being fairly synchronous within colonies (Madden & Newton 2004). Most herring gulls lay a clutch of three eggs though infrequently one, two or four eggs are laid; with two eggs being more frequent when environmental conditions are poor (Parsons 1976; Hiom *et al.* 1991). Incubation is undertaken by both the male and female over 28-30 days (Parsons 1972). Chicks are semi-precocial and downy when hatching and they fledge 35-40 days after hatching (Tinbergen 1961; Parsons 1975). Once fledged the survival of juvenile to immature bird, up to four years when it attains full adult plumage and breed for the first time is 0.630; once they reach sexual maturity, adult survival is 0.880 (Robinson 2005).

Herring gulls traditionally forage in coastal and near-coastal habitats specifically intertidal areas but they will also forage inland on lakes and reservoirs, fields and agricultural land. Being opportunistic species they will also exploit rubbish tips, sewage outfalls, and urban areas as well as by-catch from fishing vessels and landing areas (Pons 1992; Camphuysen 1995). Herring gulls have a very generalist diet foraging on fish, marine invertebrates, terrestrial insects and earthworms, vegetation, the eggs and chicks of bird species including their own and small rodents (Hunt & Hunt 1973; Kubetzki & Garthe 2003; Washburn *et al.* 2013). The gulls' foraging range is typically within 25 km of the coast and within approximately 50 km of the colony during the breeding season when attending an active nest (Camphuysen 1995).

Chapter 4

4 Influence of spatial variation in resource availability and use on herring gull demography

4.1 Abstract

Animal population numbers are often very closely linked to factors associated with resource availability. Food resources in particular can be an important limiting factor in many animal populations. To understand this relationship it is therefore necessary to determine how species use their environment with regards to these food resources. If environmental conditions result in species using less favourable resources, or resources that are of poorer quality, this may adversely affect their demographic traits and therefore population trends. Determining how resource use impacts on a species' demography is especially important in habitats which are being altered by anthropogenic land-use change. Generalists are useful when investigating the consequences of changes in resource availability as, although they are likely to have a preferred food if this becomes unavailable, they can switch to alternatives. However, it is often not known whether consuming alternative food has a negative effect on that species. One widespread generalist that opportunistically forages within coastal habitats, which are increasingly altered by humans, is the herring gull *Larus argentatus*. Herring gulls make use of abundant and predictable terrestrial/anthropogenic food resources, but that may be of poorer quality than their traditional marine resources. The extent of marine and terrestrial resources the gulls used across these colonies was determined by two methods: regurgitated pellets and stable isotope analysis of chick feathers, which gave comparable results. In this study I investigated whether differential resource use of the herring gull during the breeding season has demographic consequences. I studied eight colonies over two years across south-west Scotland and Northern Ireland that differed in resource use. Herring gulls mainly foraged in the habitat most readily available in their foraging range. Birds from colonies which were located in areas with sheltered coastlines, that offer abundant and diverse marine food from the intertidal zone, foraged more on marine food resources. In contrast, colonies closer to built-up areas used terrestrial food sources to a larger extent. The extent of the use of marine resources across colonies was associated with breeding success, with colonies consuming more marine resources raising larger

broods in both years. However, colonies with a higher use of marine resource did not have greater growth rates over the past 15 years, suggesting factors other than breeding productivity may drive the growth of herring gull colonies. This suggests that herring gulls benefit from consuming a higher proportion of their traditional marine resources and that terrestrial/anthropogenic food resources, despite potentially high and predictable availability, have negative effects on the birds breeding success, at least in areas where sufficient alternative food resources are still available.

4.2 Introduction

In order to understand causes of population change it is important to determine how species use their environment specifically with regards to the habitats they occupy and the resources they utilise (Johnson 1980). Food is an important resource which can be a limiting factor in many animal populations (White 2008). Both availability and quality of food can directly impact upon various aspect of a species' demography, particularly on its breeding success and survival which determine population abundance (Boggs 1992; McNab 1994; Weimerskirch 2001a). In bottom-up-controlled populations, demographic traits can inform on local environmental conditions which might be occurring in that species' foraging range affecting their food resource (Koskimies 1989; Furness & Greenwood 1993). Understanding the resource use of a species can therefore help to determine factors influencing population numbers (Davoren & Montevecchi 2003b) as well as identifying particular prey or foraging areas that need protection (Hooker & Gerber 2004; Louzao *et al.* 2008). If the individuals cannot meet their required resources, for example due to unfavourable environmental conditions, then this will adversely affect their demographic traits and ultimately population trends; either across years or spatially between different populations (Frederiksen *et al.* 2005b; Bustnes *et al.* 2013).

Foraging theory predicts that consumers prefer prey that benefits their individual fitness and key demographic traits (Schoener 1971; Pyke, Pulliam & Charnov 1977), and hence variation in resource utilisation can affect population dynamics (Vucetich & Peterson 2004; Millon & Bretagnolle 2008). Foragers will consume resources from what is available within their foraging range depending on the abundance and quality of the available resources (Osterblom *et al.* 2008; White 2008). If their preferred prey is abundant, consumers will forage most efficiently by specialising on a narrow range of preferred, high quality prey items (specialists). On the other hand, if preferred food is scarce, foragers are likely to expand their range of food and include less-preferred prey items into their diet (generalists) (Emlen 1966; Futuyma & Moreno 1988; Ceia & Ramos 2015). As specialists can be sensitive to changes in the environment which affect their preferred prey their demographic traits will respond rapidly to changes in the availability of these preferred prey species (Montevecchi 1993; Barrett *et al.* 2007). In comparison, generalists exploit a larger range of resources (Martin 1989; Whitfield *et al.* 2009) either at the individual level or the population level; with some populations of generalists being made up of individual specialists (Bolnick *et al.* 2003; Vander Zanden *et al.* 2010; Ceia & Ramos 2015). As generalists may buffer against changes in one resource by consuming alternative resources, and thereby mask potential effects of the availability of the preferred prey on the consumer population, their demographic traits might not be informative for particular environmental factors as it would be for a specialist. However, investigating the diet of generalists is thought to reflect the availability of local food sources as they will forage on what is most abundant (Barrett *et al.* 2007). Therefore measures of diet diversity and niche width, acting as a proxy of resource use strategies, can provide information on local resource availability in generalist foragers (Bearhop *et al.* 2004).

In addition to food availability, food quality can also be important (Österblom *et al.* 2008). When the preferred food is scarce foragers may be forced to consume alternative food (Schoener 1971; Pyke *et al.* 1977). If the alternative food returns less energy or nutrients per foraging expenditure, either because of higher acquisition costs or poorer food quality, this can adversely affect the forager's demographic traits – junk-food hypothesis (Alverson 1992; Grémillet *et al.* 2008; Osterblom *et al.* 2008). The type of resources a forager consumes have been found to be closely related to numerous traits related to demography, including egg quality (Hiom *et al.* 1991; Christians 2002; Gasparini *et al.* 2007), offspring condition (Wanless *et al.* 2005; Velando *et al.* 2005; Kitaysky *et al.* 2006) and breeding success (Uttley, Monaghan & White 1989; van Heezik 1990; Pierotti & Annett 1990; Ratcliffe 1997; Romano, Piatt & Roby 2006; Österblom *et al.* 2008). However, other studies have found no evidence that changes in prey quality do affect reproductive output (Jodice *et al.* 2006; Hjernquist & Hjernquist 2010), and possibly high prey abundance may compensate for its low quality.

A particular situation where foragers are increasingly forced to change their resource use arises through land use changes from a natural to an anthropogenic habitat, resulting in an increased presence of anthropogenic resources in their diet (Fedriani, Fuller & Sauvajot 2001; Weiser & Powell 2010). In many instances the impact of this land-use change is negative due to habitat and foraging area losses (Andrén & Andren 1994; Jetz, Wilcove & Dobson 2007; Lemoine *et al.* 2007). In other cases the impact is largely unknown although some animal species adapt to changes in their environment and manage to exploit anthropogenic, often poorer-quality resources, however the consequences of these change on the species involved is often difficult to determine (Ditchkoff, Saalfeld & Gibson 2006).

Resource use may also vary through the annual cycle. An individual's resource requirements can be particularly high during specific time periods such as during breeding and moulting (Drent & Daan 1980; Lindström, Visser & Daan 1993; Ydenberg *et al.* 1994; Perrins 1996). In addition, when provisioning dependent young in a nest, individuals forage from a central place which constrains the available resources to within a limited foraging range. Central place foraging will have the added effect of local depletion of the preferred prey and increased intra- and inter-specific competition, especially for colonial breeders (Furness & Birkhead 1984; Hunt *et al.* 1986; Birt *et al.* 1987; Lewis *et al.* 2001; Ainley *et al.* 2003). During times of high energy expenditure the quality of resources is also particularly important (Kadin *et al.* 2012) with many species depending on energy-rich food items for successful reproduction (Wanless *et al.* 2005; Österblom *et al.* 2008; Kadin *et al.* 2012). Therefore resource use may vary between different stages of the annual cycle due to the consumers' changing resource requirements and seasonal variation in food availability (Lindsay & Meathrel 2008). Specifically, birds for example will require protein and calcium for egg formation (Niebuhr 1983; Pierotti & Annett 1990; Williams 2005), whilst during chick rearing they require high levels of protein and fat for chick development and growth (Golet *et al.* 2000; Romano *et al.* 2006; Kadin *et al.* 2012).

Changes in resource availability will have a varied impact on generalist foragers depending on the type and number of resources available within their foraging range. One group of generalists that are widespread and opportunistic foragers, and therefore exploit a wide range of resources which has consequences for their breeding success, are gulls (Hunt & Hunt 1973). Gulls are increasingly foraging in terrestrial habitats, in particular on anthropogenic foods (Belant *et al.* 1993; Smith & Carlile 1993; Brousseau, Lefebvre & Giroux 1996; Weiser & Powell 2010; Yoda *et al.* 2012; Steigerwald *et al.* 2015), presumably due to changes to their natural prey base in the marine environment. There is conflicting evidence currently in the literature on the consequences to gulls of consuming terrestrial/anthropogenic items rather than their more traditional intertidal/marine resources. Although terrestrial/anthropogenic food resources can be more predictable and therefore available to the gulls than more traditional marine resources (Burger & Gochfeld 1983; Horton *et al.* 1983), it has also been argued that terrestrial resources are of poorer quality and therefore individuals or populations that forage on these resources will be less successful than those foraging on the higher quality marine resources (Pierotti & Annett 1991; Annett & Pierotti 1999). For instance the long-term decline in the glaucous-winged gull *Larus glaucescens* has been attributed to a dietary shift from marine to more terrestrial resources (Hobson, Blight & Arcese 2015; Blight, Drever & Arcese 2015a). However, in the glaucous gull *Larus hyperboreus* colonies which consumed a higher proportion of refuse also had a higher breeding success (Weiser & Powell 2010), whilst the availability of anthropogenic food in the vicinity of a colony has been linked to an increase in yellow-legged gull *Larus michahellis* numbers (Duhem *et al.* 2008). A particular anthropogenic food source that gulls use are landfills; closure or change in management of landfill sites have resulted in declines in gull productivity and adult condition (Pons 1992; Pons & Migot 1995; Steigerwald *et al.* 2015). However, it is not clear whether anthropogenic resources resulted in the previously observed higher levels of condition and productivity or whether there were no alternative i.e. more traditional marine resources for the gulls to exploit (Pons 1992; Alonso *et al.* 2015).

In this study I investigate the resource use of a widespread, generalist gull species, the herring gull *Larus argentatus* (Hunt & Hunt 1973; Götmark 1984). During the breeding season herring gulls are central place foragers and are constrained by the distance over which they can forage from the breeding colony. This means that during this time they can, like other colonial generalist consumers, be particularly sensitive to changes in food availability within their foraging range, and therefore reflect food availability over this spatial scale (Orians & Pearson 1979; Pinaud & Weimerskirch 2005). Therefore, variation in resource use between colonies can reflect differences in local food availability, and therefore potentially environmental conditions (Fox *et al.* 1990; Ainley *et al.* 1996, 2003; Anderson *et al.* 2014). Here I investigated whether resource use differed between eight colonies with contrasting long-term colony trends across south-west Scotland and Northern Ireland over two breeding seasons using pellets and stable isotope analysis of feathers. I predict that (i) the gulls within each colony will exploit the resources most readily available within their foraging range; and (ii) that the predominant resources used, especially in regards to marine and terrestrial resources, will influence the gulls' demography. This will provide insights into whether consuming more traditional intertidal/marine resources is beneficial to a generalist seabird's demography and whether this could be an important driver of gull populations.

4.3 Methods

The herring gull is a widespread colonial seabird which nests in relatively accessible locations. They are generalist, opportunistic foragers (Götmark 1984) which traditionally forage primarily in intertidal habitats, but are now increasingly foraging on terrestrial and anthropogenic resources (Hunt & Hunt 1976; Götmark 1984; Pons 1992; Kubetzki & Garthe 2003). My study investigates resource use and breeding success of herring gulls across eight colonies during 2013 and 2014 over south-west Scotland and Northern Ireland (Figure 3.1); a region covering an approximate area of 200 by 250 km. I selected colonies which had experienced contrasting population trajectories based on population trends calculated between the first national seabird census, Operation Seafarer, 1969-1970 (Cramp *et al.* 1974) and the currently last census, Seabird 2000, 1998-2002 (Mitchell *et al.* 2004). Resource use information was obtained from pellets, for which I had 14 colony years of data, and feather samples, which were analysed for stable isotope ratios, collected from seven colonies in 2014. The use of pellets and stable isotopes can result in biases when estimating resources use. Using pellets to infer information about diet can over-represent food items with hard parts, whilst under-representing easily digested items, as well as only providing a snapshot of the birds' diet (Votier *et al.* 2003; Barrett *et al.* 2007; Lindsay & Meathrel 2008). Stable isotopes provide a more integrated representation of resource use for a longer period of time over which the sampled tissue is formed, however inferring resource use form these values can be difficult where a population consumes a variety of foods with similar stable isotope signatures (Bond & Jones 2009; Phillips *et al.* 2014). Therefore, combining both methods should provide a more accurate indication of resource use (Barrett *et al.* 2007). Demographic variables were determined for all colonies and years.

4.3.1 Pellets analysis

Each colony was visited one to six times over the breeding season during the pre- and post-hatching period; between 17/05/2013-12/07/2013 and 02/05/2014-13/07/2014. At each visit complete pellets were collected from as many nests as possible. In the majority of cases one pellet was collected per nest; when several pellets were collected from the same nest on the same visit they were combined into one pellet sample. I collected a total of 300 pellet samples from six colonies in 2013 and 481 from eight colonies in 2014 (Table 4.1).

Table 4-1. Number of pellet and feather samples collected from eight herring gull colonies during the 2013 and 2014 breeding seasons for resource use analyses. All feather samples were collected during the 2014 breeding season.

Colony	Pellet samples				Pellet Total	Feather samples		
	2013		2014			Chicks		
	Pre-hatching	Post-hatching	Pre-hatching	Post-hatching		Down	Feathers	Total
Copeland[1]	1*	20	27	79	127	22	25	47
Islay	21	66	36	4	127	11	0	11
Jura	16	7	25	0	48	-	-	-
Lady Isle	-	-	31	39	70	28	28	56
Oronsay	13	49	0	30	92	33	15	48
Pladda	40	62	81	30	213	24	31	55
Portpatrick	0	0	43	6	49	2*	14	16
Strangford[2]	0	5	24	26	55	13	13	26
Total	91	209	265	216	781	133	126	259

[1] All samples collected from Lighthouse Island however, colony size is for the three Copeland Islands combined due to their close proximity. [2] Pellet samples at Strangford were collected from two different sites (Round Island in 2013, Green Island in 2014) that are within 7km of each other and treated as a single colony. Colony size is the average of Green Island (115) and Round Island (265). *Not included in the analysis to investigate the early breeding season due to small sample sizes < 5.

Pellet samples were stored frozen until dissection and identification of food types in the laboratory, using a binocular microscope where necessary. Food items were identified to the lowest taxonomic level possible and then assigned to one of three broad resource categories; terrestrial, intertidal or offshore (Table 4.2). To determine the abundance of food types within pellets, the amount of each food item found in each pellet was scored based on its abundance within the pellet as making up more or less than 25% of the pellets bulk. For each food type I calculated the frequency of occurrence for each food type as the number of pellet samples where that food type was scored as over 25% of the pellet's bulk divided by the total number of pellets (Duffy, Jackson & Cameron 1986). For 120 pellets (15% of total) both marine and terrestrial food types were scored as above 25% and therefore were included in the proportions of both categories. Frequency of occurrence was calculated separately for each colony for each breeding season and whether collected during incubation (pre-hatching: 02/05 - 31/05) or chick rearing (post-hatching: 01/06 – 13/07); by 01/06 the majority of clutches had hatched.

Table 4-2. Food items or items that indicate the foraging habitat, and broad food category assigned, identified from herring gull pellets collected during the 2013 and 2014 breeding season from eight colonies. Mean frequency of occurrence (FO%) of items making up at least 25% of each pellet sample across all 924 dissected individual pellets from 781 territories (pellet samples). Individual pellet samples may contain multiple food items.

Foraging habitat	Food type	FO (%)	Indicator of foraging habitat	FO (%)
Terrestrial	Grain	65.30	**Terrestrial vegetation** (exc. grain)	16.26
	Invertebrates	41.35	**Anthropogenic items**:	
	Mammal bone/fur	2.31	Plastic	3.20
	Bird bone/feathers	1.66	Paper	1.54
			Glass	0.90
			Man-made fibre	0.90
			Metal/tin foil	0.51
			Unknown anthropogenic	0.26
Intertidal	**Crab species**	16.01		
	Marine shells	1.79		
	Mytilus edulis	1.66		
	Marine snails	0.51		
	Starfish	0.13		
Offshore	**Fish species**	6.40		
	Nethrops norvegicus	2.82		

Categories in bold are those which were used to calculate Shannon-Wiener diversity values (*H*) to investigate trophic diversity.

4.3.2 Feather samples for stable isotope analysis

In 2014, during colony visits I took samples of feather material from accessible broods known to be herring gulls from visual observations. In mixed-species colonies herring gull nests were identified by direct observations of who attended the nest. Recognisable down feathers were collected from recently hatched chicks, whilst chick feathers, which the chick had grown since hatching, were collected from older chicks. Small amounts of feather material were cut from several feathers on the back, head and underside of the body in order to obtain a representative sample. In chicks older than 1 week I avoided the tips of feathers as these could still contain down material. All sampled material from the same chick, and from the same brood where more than chick were sampled, was homogenised. I collected a total of 259 samples (Table 4.1): 133 down samples from chicks less than 1 week old from seven colonies which, reflect the resource use of adult female's during egg formation with nutrients passed into the egg being incorporated into the chicks down, and 126 feather samples of chick feathers older than 1 week from six colonies, which reflects the resources the adults bring back during chick rearing (Klaassen *et al.* 2004). These samples were analysed for their stable isotope ratios in order to identify the gulls' broad resource use (Hobson 1987).

Stable isotope ratios $^{12}C/^{13}C$ ($\delta^{13}C$) and $^{14}N/^{15}N$ ($\delta^{15}N$) vary along a gradient between terrestrial and marine habitats and between low and high trophic levels, respectively (Hobson 1987; Hobson & Clark 1992a; Hobson *et al.* 1994; Connolly *et al.* 2004). The carbon isotope ratio $\delta^{13}C$ reflects the sources of primary production and distinguishes between marine and terrestrial/freshwater-derived food sources (Hobson 1987; Hobson *et al.* 1994; Forero & Hobson 2003; Connolly *et al.* 2004). The heavier ^{15}N isotope accumulates through the food chain and therefore higher $\delta^{15}N$ are found in species at higher trophic levels, providing an indication of the trophic level at which the consumer forages (DeNiro & Epstein 1978; Minagawa & Wada 1984; Hobson *et al.* 1994; Hobson & Wassenaar 1999). In addition, the isotopic variability amongst sampled consumers within a population can be used as an estimation of its trophic niche width (Bearhop *et al.* 2004). In order to relate stable isotope ratios more specifically to the foraging habitats the herring gulls used I also collected samples of potential prey herring gulls are known to consume during the breeding season from our study area (Table 4.3). This provided a reference dataset for Bayesian multi-source stable isotope mixing models (Parnell *et al.* 2013; Stock & Semmens 2013).

Table 4-3. Stable isotope values of marine and terrestrial food sources obtained during the 2014 breeding season to use as reference values in the stable isotope mixing models.

Food Item	Category	Samples	δ13C ±SD	δ15N ±SD
Grain	Terrestrial	1	-28.62	9.38
Invertebrates	Terrestrial	5	-27.73 ± 0.34	7.08 ± 1.81
Rodent species	Terrestrial	1	-29.41	8.64
Refuse	Terrestrial	2	-23.93 ± 2.52	5.13 ± 3.66
Crab species	Intertidal	15	-16.17 ± 1.52	11.20 ± 2.09
Coelopidae larvae	Intertidal	1	-20.04	8.05
Marine fish	Offshore	11	-17.62 ± 0.65	14.46 ± 0.83
Blenidae spp.		2	-17.88 ±0.14	13.79 ±088
Pollachius pollachius		1	-17.57	16.00
Trisopterus minutus		5	-17.99 ±0.26	13.63 ±0.23
Gaidropsarus spp.		1	-15.96	14.03
Unidentified spp.[1]		2	-17.29 ±0.37	15.13 ±0.13
Nephrops norvegicus	Offshore	6	-17.41 ± 0.36	13.08 ± 2.08

[1] Unidentified fish from chick regurgitates.

Prior to stable isotope analyses all feather material was cleaned to remove impurities from the feather surface by washing in liquid detergent (Ecover^{TM}) diluted with deionised water (approximate 1:99 dilution), and then in a 2:1 mixture of chloroform: methanol (Cherel, Hobson & Hassani 2005). As high lipid concentrations in a sample may result in apparently depleted ^{13}C levels (Post *et al.* 2007) I extracted lipids from half of the tissue samples of potential gull prey using a Soxhlet apparatus with a 2:1 chloroform:methanol mixture until the solvent ran clear indicating all lipids were extracted. δ^{13}C values were therefore taken from these lipid-extracted samples whilst δ^{15}N values were taken from the non-lipid extracted samples, so as not to use potentially altered δ^{15}N from the lipid extraction (Yurkowski *et al.* 2015). Dried feather and potential food samples were cut, homogenized and weighed (mass between 0.7-0.8mg) into tin capsules before being combusted and analysed by continuous-flow isotope ratio mass spectrometry (Costech Elemental Analyser, Milan Italy linked to a Thermo Finnigan Delta Plus XP Mass Spectrometer, Bremen Germany) at NERC Life Sciences Mass Spectrometry Facility, East Kilbride. Stable isotope ratios δ are expressed as parts per thousand (‰) relative to the international references PeeDee belemnite marine fossil limestone for carbon and atmospheric N_2 for nitrogen. Measurement precision, calculated as the standard deviation of repeated analyses of an internal standard (tryptophan), was ±0.09 ‰ for δ^{13}C and ±0.12 ‰ for δ^{15}N.

As the herring gull feather samples for stable isotope analysis were collected from multiple colonies and background levels of stable isotope may vary between colonies I also collected and analysed down feathers from nests of common eiders *Somateria mollissima* from five colonies during the 2013 and 2014 breeding seasons (Copeland, Isle of Muck, Lady Isle, Oronsay and Pladda, 1-8 nests per colony). Common eider are specialised mussel feeders and are relatively residential (Player 1971; Guillemette, Ydenberg & Himmelman 1992) therefore should reflect local stable isotope ratios at a low trophic level in the marine coastal environment the herring gulls also forage in and were considered a proxy of the stable isotope baseline level of the gulls' preferred foraging habitat. Stable isotope ratios of common eider down feather as a proxy for local baseline levels did not vary between colonies for δ^{13}C ($F_{5,15} = 0.34$, $P = 0.88$). For δ^{15}N I did find spatial variation ($F_{5,15} = 4.78$, $P = 0.008$); however this was only attributed to a lower δ^{15}N value for Oronsay than Copeland and Lady Isle ($P > 0.004$), which could lead to an under-estimate of the trophic position of resources in Oronsay. I decided to assume that the marine baseline level did not vary within the study region, in agreement with other work in this region (Jennings & Cogan 2015), therefore I did not correct for spatial variation in the baseline level.

To estimate the contribution of different resources to the gulls’ diet from the stable isotope ratios of the feathers samples I carried out Bayesian multi-source stable isotope mixing models in the MixSIAR GUI package in R (Stock & Semmens 2013). δ^{13}C and δ^{15}N values for chick down and feathers were included in the analysis for each feather sample as well as the mean and standard deviation of sampled food sources. As the δ^{13}C values of food sources only differed between terrestrial and marine food sources but not between the two marine food sources, intertidal and offshore (ANOVA: $F_{2,5} = 38.21$, $P < 0.001$; post-hoc Tukey HSD pair-wise comparisons between offshore and intertidal $P = 0.93$; both were significantly different from terrestrial items $P < 0.003$), therefore offshore and intertidal food sources were pooled into one marine category. Average values of δ^{13}C and δ^{15}N values for marine and terrestrial food sources were then entered into the Bayesian multi-source stable isotope mixing model. Trophic Enrichment Factors (TEFs) were not available for herring gull feathers therefore I used known values for ring-billed gull *Larus delawarensis* feathers providing an enrichment factor of 0.2 ± 1.3 ‰ for carbon and 3 ± 0.2 ‰ for nitrogen (Hobson & Clark 1992b). The output of the Bayesian multi-source stable isotope mixing model provided estimates of the contribution of marine and terrestrial resources to the gulls’ diet for each colony as well as for each individual sample.

4.3.3 Potential environmental variables influencing variation in resource use

To determine whether between-colony variation in resource use was driven by variation in the local availability of resources I obtained data on environmental variables which potentially reflect the different resources the gulls utilised. Environmental variables were extracted for an area of 50 km around each study colony corresponding to the foraging range of herring gulls (Spaans 1971; Götmark 1984).

The intertidal habitat is an important foraging area of the herring gull (Götmark 1984; Kubetzki & Garthe 2003). Evidence from Chapter 2 suggests that in this study region, wave fetch is an important driver of changes in herring gull colony size. This may be as it provides a proxy of the abundance of invertebrate prey in the intertidal area of rocky shores (Burrows *et al.* 2008) which is the main shore habitat in my study region. I calculated in ArcMap 10.1 the average wave fetch (km) of the shoreline in each colony’s foraging range based on wave fetch data obtained from Burrows (2009).

As herring gulls can also forage in terrestrial habitats, and in particular on landfill sites and in built-up areas and on farmland (e.g. Pons 1992; Belant *et al.* 1993), I also included the extent of built-up area and farmland, the nearest distance to the nearest built-up area and to farmland and number of landfill sites within each colony’s foraging range as a proxy for the potential availability of terrestrial/anthropogenic food. I obtained the amount of built-up area and farmland within the colonies’ foraging ranges from Landsat 2007 (Fuller *et al.* 2002); calculated, along with the nearest distance, in ArcMap 10.1. For this analysis I classified farmland as agricultural land and improved grassland (Fuller *et al.* 2002). The number of landfill sites within each colony’s foraging range was obtained for Scotland from SEPA (2015) and for Northern Ireland from NIEA (Eugene Kelly, pers. comm.).

As a proxy for marine productivity, and therefore for marine resources, sea surface temperature (SST, 11µ night-time) and chlorophyll concentration (mg/m^3) composites were extracted from Aqua MODIS at 4 km resolution (http://oceancolor.gsfc.nasa.gov/cgi/l3) separately for May (pre-hatching period) and June (post-hatching period) in each year.

4.3.4 Relationship of resource use with demography

To determine whether variation in resource use was associated with differences in demographic traits I investigated the relationships between resource use and final brood size, as a short-term measure of annual breeding success, and colony growth, as a long-term measure of colony success. Final brood size was defined as the number of chicks of at least three weeks old, and therefore likely to successfully fledge (Bolton, Monaghan & Houston 1991) observed from nest watches, for each colony (mean of 16±9 nests, range 4-33, n = 7, no data on final brood size was available for Jura in 2014; see table 4.4). Colony growth rate (GR) was calculated for the period between the last seabird census N_{t-1} in 1998-2002 (Mitchell *et al.* 2004) and the most recent available count N_t (Table 4.4) using the formula: $GR = (N_t – N_{t-1})/\text{Maximum}\ [N_t, N_{t-1}]$ as explained in Nager & O’Hanlon (in press).

Table 4-4. Demographic information for target herring gull colonies during 2013 and 2014

Colony	Colony Size[2]	Growth Rate[3]	Year	Final brood size	Number of nests[4]	
Copeland[1]	683 (2012)	0.55	2013	1.5	8	(0.01)
			2014	2.27	15	(0.02)
Islay	25 (2013)	0.00	2013	1.43	7	(0.28)
			2014	1.75	4	(0.16)
Jura	15 (2013)	-0.70	2013	1.83	6	(0.40)
			2014	-	-	-
Lady Isle	830 (2012)	-0.45	2013	-	-	-
			2014	2.13	15	(0.02)
Isle of Muck	40 (2013)	0.90	2013	-	-	-
			2014	-	-	-
Oronsay	95 (2013)	-0.30	2013	1.65	20	(0.21)
			2014	1.75	24	(0.25)
Pladda	150 (2013)	-0.40	2013	1.78	23	(0.13)
			2014	1.77	13	(0.09)
Portpatrick	175 (2013)	-0.20	2013	1.64	11	(0.06)
			2014	1.71	31	(0.18)
Green Island, Strangford	115 (2013)	0.69	2013	2.2	5	(0.04)
			2014	2.39	33	(0.29)
Round Island, Strangford	265 (2013)	0.69	2013	2.08	13	(0.05)
			2014	-	-	-

[1] Colony size is that of three Copeland islands due to their close proximity. [2] Colony size from the most recent colony count (year of count in parenthesis) – Apparently Occupied Nests (AON). [3] Colony growth rate between 2002 and the most recent count. [4] Number of nests final chick brood size was estimated from; with the proportion of total nests with known final chick brood sizes from the total apparently occupied nests (AON) of each colony in parenthesis.

4.4 Statistical analysis

All statistical analyses were performed in R, Version 3.2.1 (R Development Core Team 2015). Diagnostic plots were checked to ensure all model assumptions were met. In all models colony size was natural logarithm transformed.

To validate the estimates of the proportion of marine resources taken up by chicks from pellet data I compared the results from the pellets with the proportion of marine resources based on the output from the Bayesian multi-source stable isotope mixing models, using linear mixed effect multivariate models (GLMM) in R's *lme4* package (Bates *et al.* 2014). The proportion of pellets containing marine items was included as the response variable with the contribution of marine sources estimated from MixSIAR and breeding stage as explanatory variables, and colony as a random effect to account for samples taken in both the early and late stage of the breeding season from each colony. Breeding stage was classified as either pre-hatching (stable isotope ratios of down feathers, sampling the egg formation period, and pellets collected during incubation) or post-hatching (stable isotope ratios of chick feathers and pellets collected during the chick rearing period).

Spatial variation in the proportion of pellets containing offshore, intertidal and terrestrial food resources was analysed using a two-way analysis of variance (ANOVA) for frequency of occurrence of food items from each of the three foraging habitats separately as response variable and with colony, year and breeding stage (pre- versus post- hatching) included as main effects as well as second-order interactions between colony and year, and between colony and breeding stage. To identify where differences occurred post-hoc multiple comparisons were carried out using the *glht* function in R's *multcomp* package (Hothorn, T., Bretz & Westfall 2008). To determine the repeatability of resource use within colonies, estimated from the pellet data, between the two years and breeding stages I calculated the consistency repeatability (*Rc*) according to Biro & Stamps (2015) using the *rptR* package in R (Nakagawa & Schielzeth 2010) (see Chapter 2 for more details).

The trophic diversity based on the pellet data was investigated using Shannon-Wiener diversity values (*H*) (Shannon 1948). *H* values were calculated for each colony for the pre- and post- hatching stage and for the two breeding seasons; based on the food categories in bold in Table 3.2 (with terrestrial vegetation including grain). Alternatively trophic diversity was also estimated using isotopic niche widths calculated from Stable Isotope Bayesian Ellipses in R: SIBER (Jackson *et al.* 2011). Bayesian ellipses include 40% of the δ^{13}C and δ^{15}N values, representing the core isotope niche, and provide a mean and estimate of error of niche width based on the size of this ellipse. The area of Bayesian ellipses (SEA_B) were calculated in the R package *SIAR* (Parnell *et al.* 2010) for each colony and feather type to identify which colonies and breeding stages differed from each other; with probabilities > 0.95 indicating that the niche width differed between two groups (Jackson *et al.* 2011). To compare the estimates of trophic diversity from the two techniques I carried out a linear mixed effect multivariate model with the Shannon diversity values (*H*) estimated from the pellet data as the response variable, the isotopic niche widths and breeding stage as explanatory variables and colony as a random effect. To investigate variation in trophic diversity *H* and SEA_B values were included, separately, as the response variable in linear models with colony and breeding stage as explanatory variables; as well as year for model with trophic diversity *H* estimated from the pellet data.

To determine whether the local environment may influence the gulls' resource use during the breeding season I carried out mixed effect multivariate models in the *lme4* package (Bates *et al.* 2014) with the proportion of pellets containing marine and intertidal items as the response variable. Colony was included as a random effect to account for pellets being collected from the same colony in multiple years and during the incubation and chick-rearing stage. Environmental variables reflecting local food availability were included as main effects. As the colonies sampled varied between 15 and 830 apparently occupied nests (AON) I included colony size in the analysis to account for potential higher levels of competition and local resource depletion in the proximity to larger colonies (Furness & Birkhead 1984; Birt *et al.* 1987; Lewis *et al.* 2001). Due to the number of environmental variables being too large for one model two separate model were run; the first including variables reflecting marine resources (chlorophyll a concentration, sea surface temperature and wave fetch) and the second including variables reflecting terrestrial resources (distance to and the extent of built-up area and farmland, and number of landfill sites). For the marine model chlorophyll a concentration was removed from the model to avoid issues with collinearity due to being correlated with colony size ($r = 0.56$, $P = 0.004$); with this relationship assumed to be related to the location of the colonies rather than a biological relationship. For the terrestrial model colony size was correlated to the extent of built-up area and farmland within the gulls foraging range and number of landfill sites ($r > 0.80$, $P < 0.001$). With larger colonies having a greater amount of built-up area and farmland and a higher number of landfill sites within 50km of the colony. Distance to the nearest built-up area and landfill site was also significantly correlated ($r > 0.62$, $P = 0.001$). Therefore only distance to the nearest built-up area and distance to nearest farmland were included in the terrestrial model; along with year, colony size and breeding stage. To estimate the variance explained by the models R^2_{GLMM} was calculated in the R package *MuMIn* (Barton 2012). R^2 is the "marginal" R^2 value ($R^2_{\mathrm{GLMM(m)}}$) which is the proportion of the variance in the dependant variable that is explained by the fixed variables. The "conditional" R^2 value ($R^2_{\mathrm{GLMM}(c)}$) is also calculated which is the proportion of the variance in the dependant variable explained by the fixed and random variables (Johnson 2014).

Investigating any potential effect of resource use on the herring gulls' demography I carried out mixed effect multivariate models using the *lme4* package with a normal error distribution (Bates *et al.* 2014). In a first analysis average final brood size was analysed as the response variable with the proportion of pellets containing marine items, year and colony size as main effects, including second-order interactions, and colony as a random effect to account for the non-independence of broods from the same colony. Separate models were run for pellets collected during incubation and chick rearing to determine whether the resource use during both stages of the breeding season influences the gulls' productivity. To investigate relationships with colony growth rate, I used the average proportion of pellets containing marine items across the two years and breeding stage for each colony as explanatory variables in a linear model.

Starting with the most complex model, including biologically relevant second-order interactions, model selection to determine the minimal adequate model was carried out using Likelihood Ratio tests to determine whether the exclusion of a term resulted in a significantly poorer fit of the model (Crawley 2007). Main effects that are part of significant interaction terms were not tested as they could not be removed from the model in isolation. Significance thresholds were set at two-tailed $P < 0.05$.

4.5 Results

4.5.1 Spatio-temporal variation in resource use during the breeding season

The two methods, pellet analysis and the MixSIAR model using δ^{13}C and δ^{15}N values of down and chick feathers, gave very similar results for the proportions of diet comprised by marine (GLMM: $\chi^2_1 = 25.22$, $P < 0.001$, $R^2_{\mathrm{GLMM(m)}} = 0.88$, Figure 4.1) and terrestrial sources ($\chi^2 = 30.43$, $P < 0.001$, $R^2_{\mathrm{GLMM(m)}} = 0.86$) for the 2014 breeding season when results from both methods were available for the same colonies. Breeding stage was not found to be significant in the marine model ($\chi^2 = 2.77$, $P = 0.10$), however it was found to be significant in the terrestrial model ($\chi^2 = 6.15$, $P = 0.01$); suggesting the pellets may have underestimated the proportion of terrestrial food consumed during the post-hatching stage compared to the pre-breeding stage.

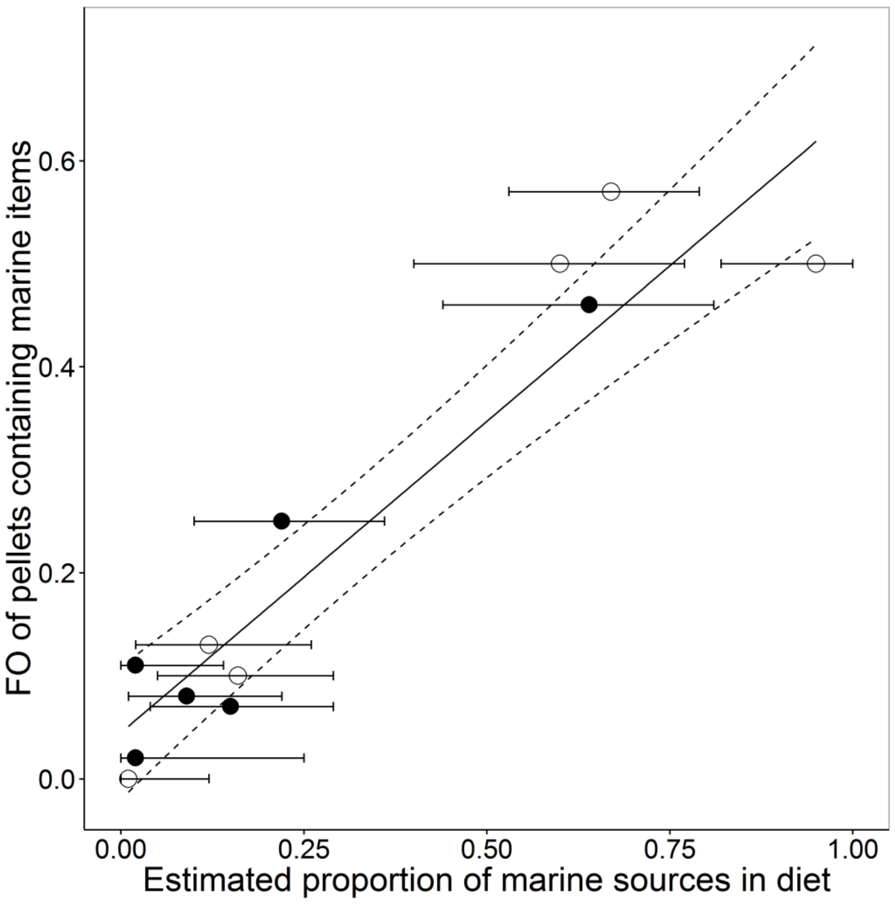


Figure 4-1. Relationship between the proportion of use of marine (intertidal and offshore) sources by herring gulls in 2014 estimated from pellets and stable isotope analysis of feather samples. The horizontal axis shows median and 95% Bayesian credible intervals given by MixSIAR run with marine and terrestrial sources for δ^{13}C and δ^{15}N. Closed symbols show the pre-hatching period from pellets collected during the incubation period and from stable isotopes of down feathers. Open symbols show the post-hatching period from pellets collected during chick rearing and from stable isotopes of chick feathers. Each point represents a colony (see Table 4.1). Solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

The frequencies of occurrence of food items in pellets from the three foraging habitats offshore, intertidal and terrestrial differed across colonies (Table 4.5a-c; Figure 4.2), but not between years and breeding stages. Colonies differed in the proportion of offshore food items with birds from Pladda using significantly more offshore resources than all other colonies (post-hoc multiple comparisons: $P < 0.002$). Intertidal food items were more common on Oronsay, Jura and Strangford than all other colonies (post-hoc multiple comparisons: $P < 0.005$). However, in all colonies, except Jura, the most consumed resources come from terrestrial foraging habitats with Jura having significantly lower use of terrestrial resources than all other colonies (post-hoc multiple comparisons: $P < 0.03$).

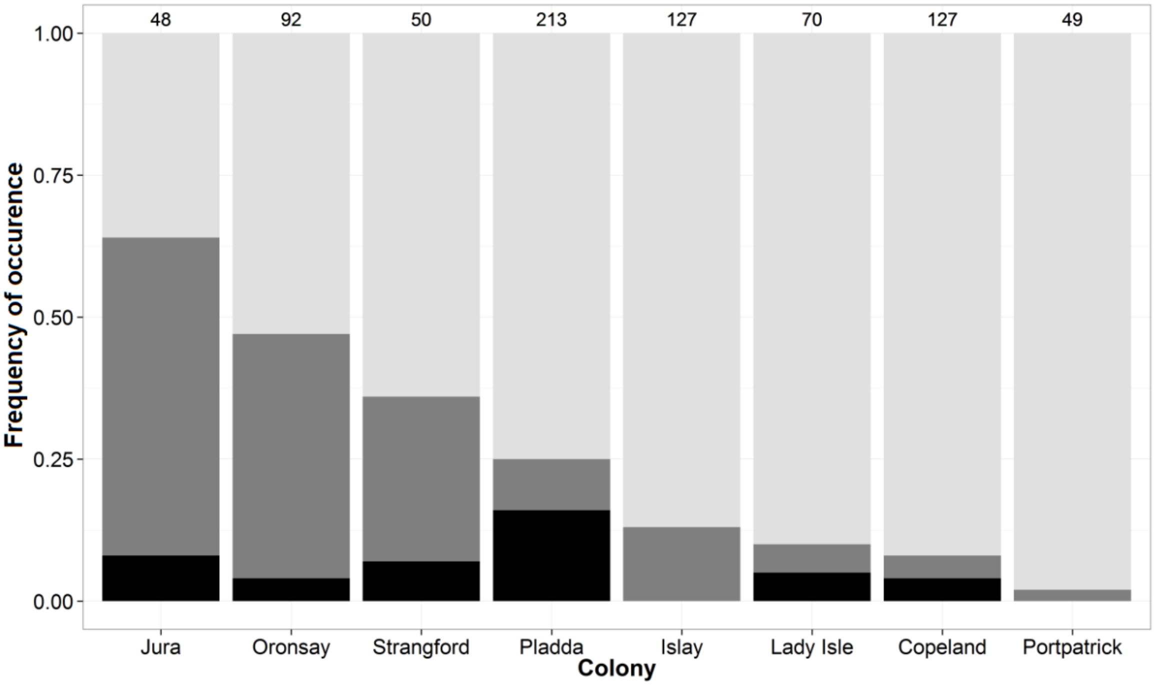


Figure 4-2. Frequency of occurrence of pellets containing offshore (black), intertidal (dark grey) and terrestrial (light grey) items making up at least 25% of each pellet sample for the sampled colonies pooled for year and breeding stage. Pellets from the pre- and post-hatching period for both 2013 and 2014 were pooled as no difference between years or breeding stage was found. Number of pellet samples above bars. Colonies are ordered from left to right in increasing frequency of occurrence of terrestrial food items.

Table 4-5. Two-way ANOVA analysing variation in (a) offshore, (b) intertidal, and (c) terrestrial resource use of herring gulls based on pellets found on the breeding territory, and (d) the proportion of marine resources contributing to the diet from MixSIAR results in relation to colony, breeding stage (pre- and post-hatching) and the interaction between colony and breeding stage, and with year for models a-c.

Response variable	Explanatory variable	Sum sq.	Mean sq.	*df*	Residual *df*	*F*	*P*	R^2
(a) FO of offshore items	Colony	0.10	0.01	7	15	7.53	<0.001	0.68
(b) FO of intertidal items	Colony	1.18	0.17	7	5	18.29	<0.001	0.85
(c) FO of terrestrial items	Colony	0.59	0.08	7	15	3.19	0.028	0.41
(d) Marine contribution from MixSiar model	Colony	12.48	2.08	6		123.36	<0.001	
	Breeding Period	2.22	2.22	1		131.65	<0.001	
	Colony * Breeding Period	2.66	0.53	5	246	31.51	<0.001	0.80

FO – Frequency of occurrence. *df* = degrees of freedom. Non-significant main effects and interactions were dropped from the models ($P > 0.10$). R^2 is the proportion of the variance explained by the explanatory variables.

I also found spatial variation in the utilisation of marine sources by gulls in 2014 estimated for individual feather samples from the MixSIAR model, although this was dependent on the breeding stage (Table 4.5d, Figure 4.3); with the contribution of marine sources being higher in the post- than in the pre- hatching stage for two colonies, Oronsay and Pladda (post-hoc multiple comparisons: *P* < 0.001).

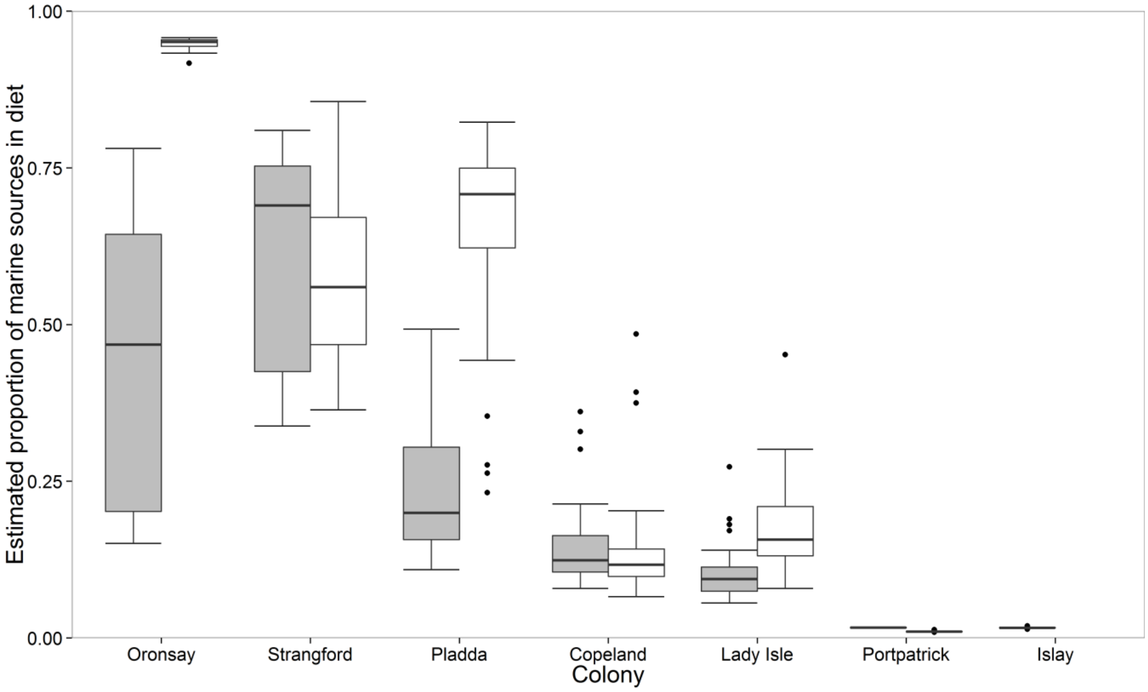


Figure 4-3. Estimated proportion of herring gull diet comprised by marine sources (offshore and intertidal resources combined) during the pre- (grey) and post-hatching period (white) during the 2014 breeding season. Colonies ordered from the highest proportion of marine sources.

Trophic diversity H based on the pellet data from 2013 and 2014 differed between colonies but not breeding stages or years (linear model, colony: $F_{7,16} = 3.07$, $P = 0.03$; breeding stage: $F_{1,22} = 0.03$, $P = 0.86$; Year: $F_{1,22} = 0.22$, $P = 0.64$). The difference in H between colonies was driven only by Pladda having a significantly greater trophic diversity than Copeland (post-hoc multiple comparisons: $P = 0.046$). For 2014, trophic diversity SEA_B based on stable isotope analyses of feather samples did not differ between colonies and breeding stages (linear model, colony: $F_{7,5} = 1.68$, $P = 0.36$; breeding stage: $F_{1,5} = 0.19$, $P = 0.69$). I found no relationship between estimates of trophic diversity H, from the pellets data, and SEA_B, from the feather stable isotope analysis were unrelated ($\chi^2_1 = 0.01$, $P = 0.93$, Figure 4.4).

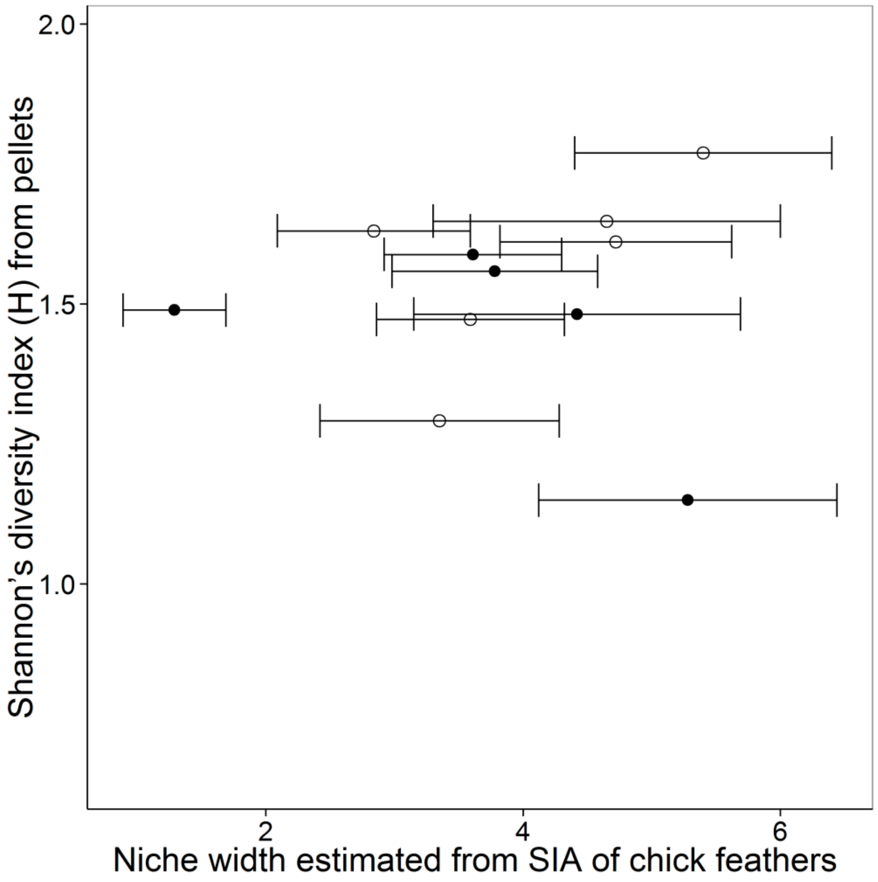


Figure 4-4. Relationship between the niche widths of herring gulls in 2014 estimated from pellets and stable isotope analysis of feather samples. The horizontal axis shows Bayesian Ellipse Areas (SEA) ± standard deviation based on δ^{13}C and δ^{15}N. The vertical axis shows the Shannon's diversity index (*H*) of items identified from pellets. Closed symbols show the pre-hatching period from pellets collected during the incubation period and from stable isotopes of down feathers. Open symbols show the post-hatching period from pellets collected during chick rearing and from stable isotopes of chick feathers.

Due to the high correlation between the estimated use of marine resources by herring gulls from both the pellets and stable isotope analysis I used proportion of marine (offshore and intertidal pooled) and terrestrial sources from the pellet data for the remaining analyses because they provided a larger sample size. The within-colony repeatabilities (*Rc*) of the proportion of marine and terrestrial food types found in the pellets of the eight colonies sampled during both breeding stages of 2013 and 2014 was high (marine food types: $Rc = 0.87$, 95% CI: 0.54 – 0.96, $P = 0.002$; but less so for terrestrial food types: $Rc = 0.39$, 95% CI: 0.00 – 0.76, $P = 0.05$). As would be expected there was a negative correlation between the proportion of marine and terrestrial items in the diet estimated by pellets ($r = -0.85$, $P < 0.001$) therefore for the rest of the analysis I also just used the proportion of marine resources (combining the offshore and intertidal categories) to reflect the gulls' resource use.

4.5.2 Influence of environmental variables on spatial variation in resource use determined by pellets

Firstly, looking at the explanatory variables reflecting available marine resources within the gulls' foraging range the use of marine resources by herring gulls was higher in colonies with a higher average wave fetch within their foraging range ($\chi^2_1 = 10.34$, $P < 0.001$, $R^2_{\mathrm{GLMM(m)}} = 0.63$, Figure 4.5a); with marine resources being highly correlated with the proportion of pellets containing intertidal items (Pearson's product-moment correlation: $r = 0.96$, n = 24, $P < 0.001$). There was no significant relationship between the proportion of pellets containing marine items and sea surface temperature ($P = 0.08$).

For the model looking at the explanatory variables reflecting available terrestrial resources I found that the proportion of pellets containing marine items increased the further away the colony is located from a built-up area ($\chi^2_1 = 4.33$, $P = 0.038$, $R^2_{\mathrm{GLMM(m)}} = 0.36$, Figure 4.5b). However there was a significant negative correlation between average wave fetch and nearest distance to a built-up area (Pearson's correlation: $r = -0.79$, $n = 24$, $P < 0.001$); with higher wave fetch at colonies closer to built-up areas. I found no significant relationship with the nearest distance to farmland ($P = 0.89$). There was no influence of colony size, year or breeding stage on the proportion of pellets containing marine items for the wave fetch ($P > 0.10$) or distance to built-up areas models ($P > 0.11$).

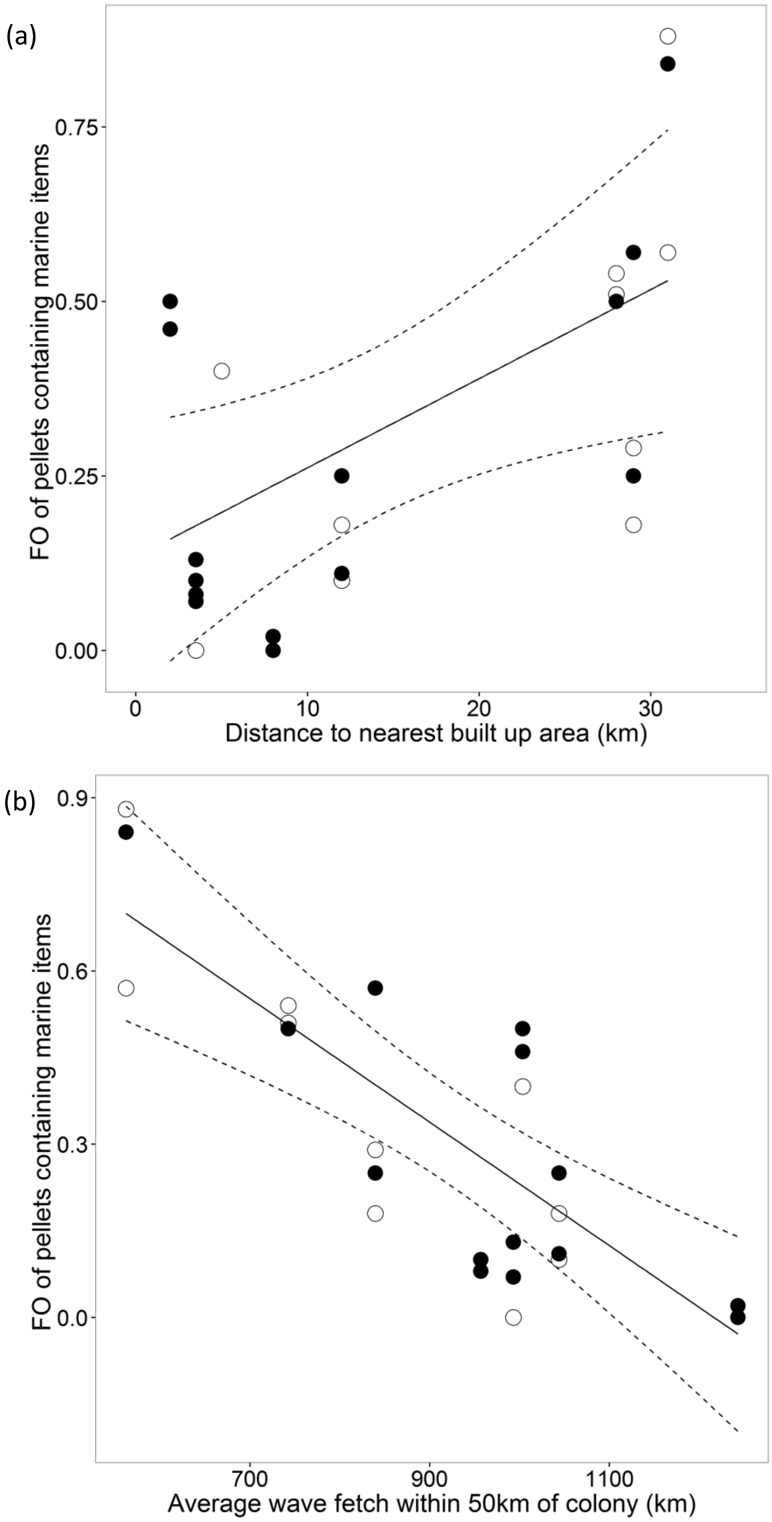


Figure 4-5. Relationship between the frequency of occurrence of marine items in pellets collected from each colony during the 2013 (open circles) and 2014 (filled circles) breeding season and (a) the average wave fetch within the breeding colony's foraging range and (b) the distance to the nearest built-up area. Solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

4.5.3 Influence of spatial variation in resource use on demographic parameters

Birds in colonies consuming a higher proportion of marine items during incubation had larger final brood sizes than birds in colonies that consumed less marine items in both years and independent of colony size (Table 4.6a, Figure 4.6a). Final brood sizes were larger in 2014 (2.00 ± 0.30 chicks) than 2013 (1.67 ± 0.18 chicks) and were larger in larger colonies (Table 4.6). The frequency of occurrence of marine items in pellets during chick rearing, however, was not related to final brood size (Table 4.6). Using average values for the proportion of pellets containing marine prey across both the 2013 and 2014 breeding season, pooled across breeding stages, I found no relationship between resource use and colony growth rate ($f = 0.35$, $F_{1,6} = 1.87$, $P = 0.22$); although not statistically significant the effect size is fairly large.

Table 4-6. Parameter estimates from the linear mixed model describing the relationship of final brood size with colony size (natural logarithm), year and the frequency of occurrence of marine (offshore and intertidal) resources in pellets collected during (a) pre- and (b) post-hatching stage, with colony as a random effect

Breeding stage	Source	Estimate	Std. Error	X^2	P	R^2
(a) Pre-hatching	Intercept	0.887	0.252			
	FO marine items (%)	0.657	0.231	5.36	**0.021**	
	Colony size	0.131	0.488	5.43	**0.020**	0.71
	Year	0.324	0.126	5.09	**0.024**	(0.71)
(b) Post-hatching	Intercept	1.009	0.324			
	FO marine items (%)	0.582	0.321	2.94	0.086	
	Colony size	0.112	0.054	3.64	0.057	0.46
	Year	0.215	0.118	2.94	0.086	(0.60)

The second order interactions with year involving FO marine items were not significant for the pre- ($P > 0.07$) and post-hatching stage ($P > 0.08$) and therefore were dropped from the models. Boldface indicates significance at the $P < 0.05$ level. R^2 is the "marginal" R^2 value ($R^2_{\mathrm{GLMM(m)}}$) which is the proportion of the variance in the dependant variable that is explained by the fixed variables. Value in brackets is the "conditional" R^2 value ($R^2_{\mathrm{GLMM}(c)}$) which is the proportion of the variance in the dependant variable that is explained by the fixed and random variables.

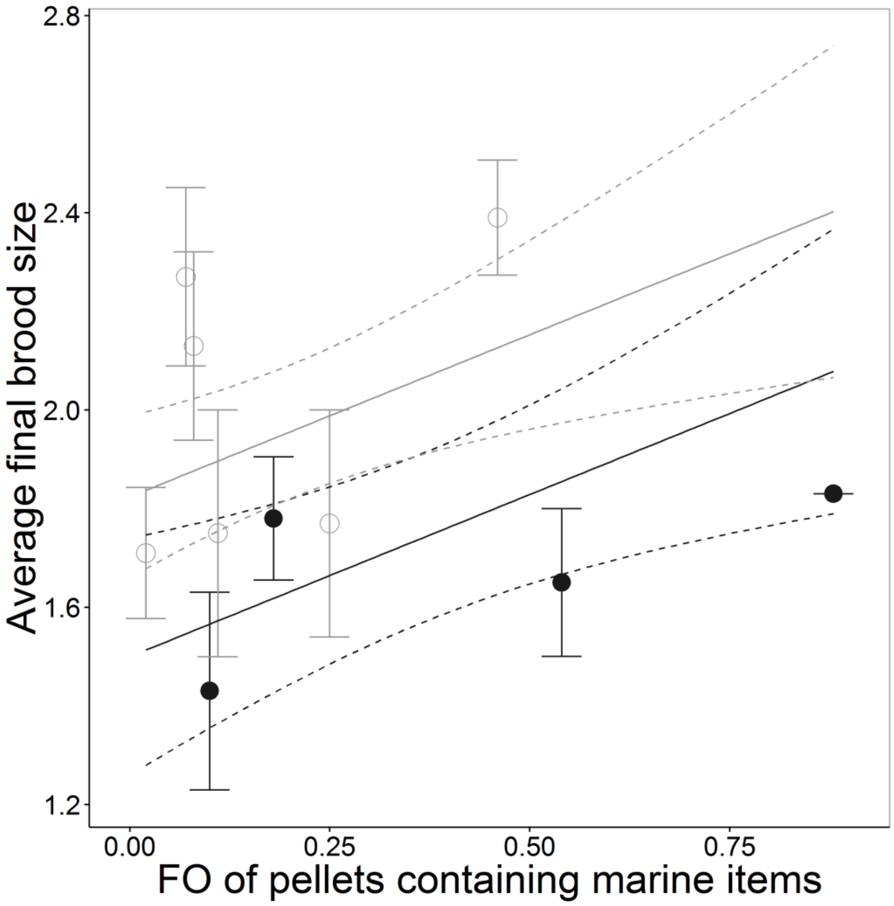


Figure 4-6. Colonies that used a higher frequency of occurrence of pellets containing marine items during the pre-laying period had larger final brood sizes in 2013 (open grey circles) and 2014 (filled black circles) (see Table 4.6 for the full statistics). Solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

4.6 Discussion

Resource use of multiple herring gull colonies was investigated to determine whether spatial variation in resource use was related to which resources were most widely available in the gulls foraging range; and whether this had consequences on the gulls' demography. My results highlight that colonies differed in the habitats they predominantly foraged in, and that these differences in resource use mainly reflect differences in foraging habitat availability in the gulls' foraging range. There was however no spatial variation in the diversity of food items they consumed. Colonies along sheltered coasts, i.e. with a low wave fetch, used more marine resources than colonies at more exposed coasts; with colonies further away from built-up areas using more marine resources than colonies nearer to built-up areas. Having a higher proportion of marine food resources in their diet had a significant impact on the gulls' demography with colonies that used more marine resources early in the breeding season having a higher seasonal breeding success. This highlights the importance of locally available natural foraging habitat which, compared to foraging predominantly on terrestrial resources, may have benefits on the gulls overall breeding success.

The two methods I used to estimate the gulls' resource use, pellets and feather stable isotope analysis gave highly comparable results indicating that pellet analyses can provide an accurate reflection of what food items parents feed to their chicks; and in particular on their use of marine resources. Therefore, despite the different biases of each method there was a good agreement between the results of pellet and stable isotope methods, which has also been observed in other studies on gulls (Ramos *et al.* 2009, 2012; Kim, Furness & Nager 2010); although not in all cases (Annett & Pierotti 1989; Steenweg, Ronconi & Leonard 2011). It also suggests that despite pellets only reflecting a snap shot of resource use this estimation is consistent with an integrated measure of resource use over a longer time period when the sampled feathers were grown. This supports the usefulness of the pellet data, for which I had data for more colonies and years, for providing an accurate estimation of the resources the gulls' consumed over the breeding season.

In this study I was primarily interested in whether the gulls were consuming marine or terrestrial resources, rather than the precise items they were foraging on. It proved not to be possible with carbon and nitrogen isotopes to distinguish between intertidal and offshore resources which would provide a more detailed view of the gulls' resource use (Bond & Jones 2009). To further try and interpret the resource use of marine generalist species additional isotopes, specifically sulphur, could be analysed to distinguish between pelagic and benthic marine resources (Ramos *et al.* 2009; Hobson *et al.* 2015). Sulphur isotopes vary across a marine to terrestrial gradient, with higher δ^{34}S ratios in marine habitats and heavier ^{34}S isotope indicating a more pelagic environment (Connolly *et al.* 2004).

The time scale over which resource use was sampled also differed between methods. In particular, during the pre-hatching period down feather samples represent a period of a few days to a few weeks prior to egg laying (Klaassen *et al.* 2004); whereas pellets represent the period during incubation after egg laying. The compatibility in estimates of use of foraging habitats from the pellet data did not differ between breeding stages, suggesting that resource use within a colony was consistent across the breeding seasons of both years. This was further confirmed by high within-colony repeatability estimates for the proportion of marine resources used. The estimates of resource use from the stable isotope data did suggest that the gulls consumed more marine sources during chick rearing than earlier in the season however this was also the case in two colonies.

Across the sampled colonies in south-west Scotland and Northern Ireland I found significant spatial variation in the herring gulls' resource use during the breeding season, and this was evident in both the pellet and stable isotope data. Spatial variation was observed in the marine, intertidal and terrestrial contribution of resources consumed by the gulls, based on pellet data. From the high within-colony repeatabilities, and that the contribution of resources from each resource type did not differ between years, it appears that the pattern of resource use within each colony were similar between the pre- and post-hatching period and over the two breeding seasons. However, the stable isotope data for a subset of the data (seven colonies in 2014) suggested that the contribution of marine resources was higher in the post-hatching than in the pre-hatching period, although only in two colonies, Oronsay and Pladda. A number of studies have found that gulls feed chicks a more marine diet during chick-rearing especially as they get larger and require high levels of protein and fat to build muscle and fuel growth (Golet *et al.* 2000; Romano *et al.* 2006; Kadin *et al.* 2012; but see Washburn *et al.* 2013). My data suggests that gulls might be limited in their capacity to expand the marine-derived resources. An increase in use of marine resources between pre- and post-hatching period was only observed in Oronsay, the colony nearest to a large intertidal area, and in Pladda, which was nearest to Nephrops trawling activity. These changes in use of marine resources might have been too small to be picked up in the pellet data. It also should be noted that it was not possible to ascertain whether the pellets collected belonged to chicks or adults. They are likely to belong to both and therefore reflect what both consumed. Studies on other seabirds have found that the foods that parents consume themselves and they provision to chicks can often differ (Spaans 1971; Nogales, Zonfrillo & Monaghan 1995; Wilson, Daunt & Wanless 2004). This might further contribute to the differences in the results on breeding stage between pellet and stable isotope data. Feathers from breeding adults from five of my colonies, however, have a similar stable signature than the chicks in those colonies (own unpublished data) although adult and chick feathers reflected the breeding seasons in different years, 2013 and 2014, respectively, suggesting it is unlikely that in my study colonies there are significant differences in adult and chick diet.

Across the target colonies I found weak among-colony differences in trophic diversity from the pellet data. However, this was a result of the diversity of resources consumed in Pladda being greater than Copeland. This is likely to be attributed to all pellets collected in Copeland predominantly being comprised of terrestrial items whilst those from Pladda contained offshore, intertidal and terrestrial items. No spatial variation in trophic diversity was also found from the stable isotope data despite the pronounced spatial variation in resource use. It therefore appears that the gulls, at the colony level, are generalists foraging on a similar range of food items, but they differ in the type of foraging habitat they mainly used. It should be noted, however, that the identification of food items from the pellets was relatively coarse, and the diversity indices were relatively low and varied little between colonies; with the coefficient of variation (CV) being nearly double for estimates from stable isotopes (CV = 30.42) than from pellets (CV = 14.77). If it would have been possible to identify food items to a lower level I might have seen more variation in trophic diversity between colonies. Ultimately, however, I was interested in the resource type the gulls were foraging on rather than which specific food items. The niche breadth estimates from the stable isotopes are arguably more accurate as they incorporate the resources the gull consumed over a longer time period over which the feathers were grown. This is reflected in the broader niche widths reflected by the higher CV values for the isotopes in comparison to that from the relatively uniform diversity index values (H).

This could also explain why I saw no correlation between the two measures. It has been suggested that trophic diversity can be unfavourable resulting in lower breeding success attributed to a species forages less on a its preferred resources (Croxall *et al.* 1999; Elmhagen *et al.* 2000; Arroyo & Garcia 2006). Conversely, greater trophic diversity may be beneficial in habitats where multiple resources are abundant and available (Whitfield *et al.* 2009). Since I did not find clear differences in trophic diversity between colonies I could not test this hypothesis with my data set. Further tests of this hypothesis would probably require data on individual niche variation, investigating trophic diversity and breeding success at the individual level (Pierotti & Annett 1991; Votier *et al.* 2010; Ceia *et al.* 2014).

The spatial variation in the contribution of marine resources to the herring gulls' diet related to the habitats most readily available within their foraging range; specifically suitable sheltered intertidal habitat, using wave fetch as a proxy, and distance to build-up area. Across the two study years and breeding stages I found no relationship between colony size and the use of marine resources by breeding gulls suggesting that density dependency and local competition did not influence what foraging habitat the gulls used. Colonies where gulls consumed a higher proportion of marine resources were those with low average wave fetch, and therefore more sheltered intertidal habitats, within the gull's foraging range, and further away from built-up areas. Rocky shores, the main shore habitat in my study region, that are more sheltered as indicated by low wave fetch values, can support a more diverse and abundant intertidal prey species community (Burrows *et al.* 2008, Burrows 2012). Therefore, colonies in sheltered coastal habitats are likely to have a higher abundance of local food availability of intertidal invertebrates to forage on than those in more exposed rocky coastlines. I also found that in colonies nearer built-up areas the proportion of marine resource was lower irrespective of the local wave fetch value. As colonies with a higher average wave fetch in their foraging range were also closer to built-up areas, the results may indicate that gulls simply exploit the nearest available resources; colonies in closer proximity to built-up area consumed more terrestrial resources, whilst colonies located on sheltered coastlines mainly exploited marine resources. It would therefore be interesting to see whether there are any active colonies that are located on exposed rocky shores away from built-up areas as they may have no alternative resources to forage on, and if such colonies exist what resources those colonies use. The amount of terrestrial resources does not necessarily only come from anthropogenic sources, although the significant effect of distance to built-up area may suggest it did. It may also come from agricultural land use, as indicated by the large amount of grain found in the pellets. Intensive agriculture in the study region is generally associated with built-up areas so that it is likely that distance to nearest built-up area is a proxy for both anthropogenic food sources and use of food from agricultural land. The one exception is Islay where the gulls breed close to a small human population but an area where barley for the local whiskey industry is grown and the resource use of that colony is characterised by one of the highest proportion of terrestrial resources. This result indicates that the gulls are foraging on the resources that are locally most available and therefore the spatial variation observed across the colonies may have arisen due to the colonies having different local foraging opportunities. This might be expected for generalist, opportunistic species such as the gulls where foraging on resources which are locally most available in space and time is beneficial (Yoda *et al.* 2012). It is likely that niche width is also potentially being influenced by local resource availability (González-Solís *et al.* 1997).

Given that there was spatial variation in the resource use between colonies I wanted to investigate whether this had any consequence on demography at the colony level. It may be that the gulls perform equally well whether they feed on marine or terrestrial resources as long as one of them is available. All colonies do forage to some extent on terrestrial resources. Terrestrial resources are often thought to be of lower quality to gulls than marine resources (Annett & Pierotti 1999; Blight *et al.* 2015b); although this resource can still be important for some populations (Pons 1992; Duhem *et al.* 2008; Weiser & Powell 2010). Therefore, perhaps those that feed more on terrestrial resources can perform as well as those foraging on potentially higher quality, more traditional resources as terrestrial resources are arguably more predictable (Burger & Gochfeld 1983; Horton *et al.* 1983; Yoda *et al.* 2012) compared to the typically more patchily distributed and temporally more variable distribution of marine resources (Hunt & Hunt 1973; Weimerskirch 2007). However, although marine, and specifically intertidal, resources may be less predictable, for example only being available at certain times due to the tides, the potentially higher quality of marine resources could compensate for this. There was an association between a colony's average final brood size and the proportion of marine resources the gulls within that colony consumed during the early breeding period; and potentially during the later chick rearing period although this was not found to be significant. That final brood size was larger in colonies where more marine resources were consumed indicates that feeding on marine, rather than terrestrial, resources is beneficial. It should also be considered that colonies with higher breeding success were those located in areas where food availability was generally higher, or that resources were closer resulting in shorter foraging trips and therefore higher nest attendance. However, at least for the second point, I found that in colonies which were largely foraging on marine resources foraging trips were generally longer although nest attendance was higher (Chapter 6).

A positive link between marine resources and breeding success is often expected, however, few other studies on gull resource use have observed this relationship (Pierotti & Annett 1991). Many seabirds are able to alter their behaviour to buffer changes in food availability, and therefore energy requirements, consequently both pre- and post-hatching stages may be equally demanding with the adults being able to obtain adequate food as long as availability is not particularly poor (Burger & Piatt 1990; Uttley *et al.* 1992); which may explain in particular why I found such a weak no-significant relationship between marine resource use and final brood size in the later, chick-rearing period. If predation or weather conditions rather than diet were more important in determining final brood size it would be expected that any influence of resources consumed during the incubation period would also be cancelled out; unless the benefits of consuming high quality resources during egg formation resulted in chicks in better condition (Williams 1994; Christians 2002; Krist 2011) being more able to survive predation/adverse weather early on in chick rearing. Alternatively, it may be that the condition of the adult is more important. If the parent birds consume a higher quantity of potentially higher quality marine items during the early breeding season then they may be in better condition to raise more chicks and have greater breeding success, although adult body condition is unlikely to be the only important factor (Chastel *et al.* 1995a; Chastel, Weimerskirch & Jouventin 1995b; Robinson *et al.* 2005). During chick rearing the resources the adults obtain are shared between themselves and the chicks, with pellets collected during this time thought to belong to both, which may result in the relationship between marine resource use and breeding success being less clear. Another possibility is that the resources the birds consumed during the non-breeding season may have important carry-over effects on the up-coming breeding season (reviewed in Harrison *et al.* 2011); as during the non-breeding season seabirds can disperse over larger areas , being less constrained by local food availability (Ainley *et al.* 2003; Ouwehand, Leopold & Camphuysen 2004; Hedd & Montevecchi 2006). Linking individual resource use to that individuals breeding success is likely to be much more informative however this is more difficult and time consuming to determine.

Given the high consistency across the two study years and the link between marine resource use and breeding success I would have expected resource use would be associated to recent colony growth; however I did not find colony growth rate to be related to the colony's resource use. This may partially be due to the small sample sizes or due to only sampling resource use over two breeding seasons; although marine resource use was consistent across the two years. In addition, the variation in resource use covers only a small time period over the annual cycle reflected in the weak relationship with final brood size, therefore it does not seem likely that resource use would impact the colonies growth rate in large way. Long-term studies on gulls have found that a decline in gull populations was most likely related to a shift in diet from marine to more terrestrial resources (Blight *et al.* 2015b), although colonies have also been observed to increase in areas where anthropogenic resources in the vicinity of the colony have also increased (Duhem *et al.* 2008). In addition, productivity has an important impact of the population growth rates of short-lived species, however, in long-lived species such as seabirds survival rates are likely to be more important to population dynamics (Saether & Bakke 2000). Therefore, in this study resource use may have had an impact on a measure of the gulls' annual productivity of chicks but not, or at least not that I can detect yet, on their survival and recruitment, and therefore the colony growth rate; although there may be a lag between any single years breeding success and its affect at the colony level (Cook *et al.* 2014) and data on a larger spatial and temporal scale may be required. This suggests that in my study region factors other than resource availability during the breeding season may limit colony growth including food availability during the non–breeding season (Robb *et al.* 2008; Harrison *et al.* 2011) or predation (Blight *et al.* 2015a); although no obvious consistent evidence of predation was observed at any of the colonies with the possible exception of Portpatrick.

In conclusion, inter-colony differences in the resource use of the gulls were associated with the availability of resources within a colony's foraging area and had consequences on demographic traits associated with annual productivity. This highlights the importance of the availability of natural, high quality, food resources within a species foraging range. It also emphasises the benefit of investigating the spatial variation in resource use of multiple colonies. Although I did not find a direct effect on colony growth rate, these results may also help in understanding the recent declines observed in herring gulls (Mitchell *et al.* 2004; Eaton *et al.* 2015). Here I looked at the colony level expressing the extent across many generalist individuals; a further step would be to elucidate how resource use affects demography of gulls might be detailed investigations at the individual level (Masello *et al.* 2013; Ceia & Ramos 2015).

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Chapter 5

5 The potential of egg traits to monitor the coastal environment: a case study on Herring gulls

5.1 Abstract

Monitoring of the coastal environment is of particularly high priority as human pressure on coastal ecosystems has increased markedly over the last several decades. Generalist apex predators provide an attractive choice to monitor habitats. However, as many apex predators are long-lived with a low reproductive output there can be a time-lag before detecting changes in population abundance reflecting adverse environmental conditions. Instead traits which reflect conditions over short-time periods may be useful in monitoring habitats over shorter time frames. To be a useful monitoring tool, egg traits need to relate to local environmental conditions and the species demography. Here I looked at the egg traits of a conspicuous, widespread species associated with the coastal habitats of south-west Scotland and Northern Ireland – the herring gull *Larus argentatus*; a generalist which exploits a range of habitats in both the marine and terrestrial environment. As eggs are costly to produce they should reflect the females' conditions and therefore that of the local environment. Four egg traits were investigated at ten colony sites across the study area to determine their monitoring potential; egg volume, colour, maculation and shape. In all four traits I found spatial variation between colonies indicating that egg traits could be sensitive to local environmental conditions once corrected for demographic traits. Environmental variables were selected to principally act as proxies for local food availability in a range of the herring gulls' foraging habitats. Egg volume and colour were affected by the ambient temperature prior to laying, whilst maculation was related to sea surface temperature and chlorophyll a concentration; highlighting that local conditions explained part of the observed spatial variation. Only egg colour was found to relate to a short-term measure of the gulls demography, final brood size. These results therefore imply that the average egg traits of a colony can reflect information on the local environment which may ultimately impacts the gulls' demography. Egg traits, and in particular egg colour, therefore provide a useful tool for monitoring of environmental conditions specifically around the time of egg formation. Photographing eggs is a relatively simple and non-invasive way of obtaining information on the condition of the birds.

5.2 Introduction

Monitoring animal populations as a proxy of underlying environmental conditions is frequently incorporated into policies and regulations to assess the state of the environment. It can provide a cost-effective way of assessing pressures acting on an ecosystem, providing a means of collecting information on the state of the environment which cannot be measured directly due to cost, logistical or technological reasons (Carignan & Villard 2002). Animal populations have the potentially to act as monitors of their environment by reflecting what is occurring at lower trophic levels and responding to changes in environmental conditions (Gregory *et al.* 2005; Boyd *et al.* 2006; Fossi *et al.* 2012).

Traits that will be useful for monitoring need to be sensitive to changes in environmental conditions. Changes in that trait should also affect other traits such as productivity or survival ultimately impacting on demographic rates of the monitored population (Wildermuth *et al.* 2012). The majority of monitoring programmes focus on changes in population counts (Gregory, Noble & Custance 2004; Taylor *et al.* 2007; Fox *et al.* 2010, 2011) which provides valuable information on the long-term temporal variation in population abundance. However, detecting statistically significant changes at the population level can be difficult and requires long-term records which generally only detect changes in the environment long after they have occurred. In order to detect changes as they occur and help identify the underlying mechanisms it will also be valuable to collect information on traits which reflect environmental conditions over shorter-time frames (Cairns 1988; Diamond & Devlin 2003). It is likely that the environmental sensitivity of a monitoring trait, that is the extent to which it reflects what is occurring in the local environment, varies between different traits in a non-linear fashion (Cairns 1987). Whereas changes in population abundance typically respond only to severe changes in environmental conditions, behavioural and physiological changes can respond to more moderate changes in environmental conditions (Piatt & Sydeman 2007). If those alternative traits also result in changes to overall population abundance after a time-lag (Cook *et al.* 2014) they then can provide a useful early warning of adverse environmental conditions (Monaghan 1996; Wildermuth *et al.* 2012).

The sensitivity of traits to environmental conditions is likely to increase if they are related to nutritionally and energetically demanding life-history stages such as reproduction, moult and migration (Williams 1966; Lindstrom *et al.* 1993; Perrins 1996;

Wikelski & Tarlow 2003). Therefore, investigating traits during particularly demanding time periods may be informative as the individuals will less likely be able to buffer against adverse environmental conditions (Aebischer & Wanless 1992; Piatt *et al.* 2007b) and therefore environmental changes will be reflected in the traits being investigated. During reproduction provisioning dependant young is an energetically demanding period with adults birds having to increase their foraging expenditure (Ydenberg *et al.* 1994; Houston 1995). In birds monitoring provisioning rates can reflect local environmental conditions over the shorter time scale of the late breeding season (Cairns 1987; Croxall, Reid & Prince 1999; Tremblay *et al.* 2005; Hinam, Cassady & Clair 2008). However, by this time the study population may have already lost an often unknown proportion of breeders that failed to hatch chicks, potentially resulting in a biased sample. Another potential monitoring trait in birds are egg traits which reflect the early breeding season. Eggs are costly to produce (Monaghan, Bolton & Houston 1995; Monaghan & Nager 1997; Nager 2006). Egg traits can therefore reflect the body condition of the female (Christians 2002); and as female condition is largely influenced by the environment then the eggs traits are also likely to be sensitive to local environmental conditions. The sensitivity of egg trait to environmental conditions may differ between time scales; during egg formation itself, known as the rapid follicular growth period and/or the pre-laying period, where the birds may be building up body reserves for egg formation (Drent & Daan 1980; Meijer & Drent 1999).

Egg size can vary greatly among clutches (Ankney & Bisset 1976; Christians 2002). Variation in egg size can reflect the size and the age of the parent female, with larger and older females lying larger eggs, however, the majority of intraspecific variation observed in egg size is explained by environmental factors (Christians 2002). To obtain the required resources for egg formation, females depend on abundant and high quality food with low local food availability or poor food quality resulting in smaller eggs (Perrins 1996; Christians 2002; Nager 2006). Local weather conditions can also influence egg size through foraging efficiency and thermoregulation costs (Dunn 1973; Finney *et al.* 1999), specifically temperature (Nager & van Noordwijk 1992; Christians 2002; Potti 2008) and precipitation (Becker *et al.* 1985). The measurements used to determine egg volume can be used to infer information about the shape of the egg. The relationship of egg shape with the female’s condition and environmental conditions has been investigated in less detail. Although shape is generally thought to be constrained by the females’ morphology (Hendricks 1991; Encabo *et al.* 2002) egg shape may also potentially reflect environmental conditions such as nutrient availability (Ardendt 2004; Górski, Nowakowski & Bañbura 2015).

In addition to looking at the egg dimensions, eggshell colour and the extent of maculation may reflect different aspects of egg quality, and therefore female condition, not associated with egg size and therefore may provide additional information on local environmental conditions than egg size alone. Eggshell colouration is controlled by two pigments, protoporphyrin, which produces yellow, red to brown colouration, and bilieverdin which produces blue and green colours (Kennedy & Vevers 1976) which are generally deposited in the outer layers and on the surface of the eggshell (reviewed in Sparks 2011) shortly before oviposition (Poole 1965; Kilner 2006). Within the normal colour range of eggshells the level of pigmentation and patterning can be highly variable and can be related to female body condition (reviewed in Reynolds, Martin & Cassey 2009). Having potentially antioxidant properties, biliverdin may reflect the female's health and overall condition and has been interpreted as a signal to males on the females' physiological condition (Moreno & Osorno 2003; Osorno *et al.* 2004; Jagannath *et al.* 2007; Hanley, Heiber & Dearborn 2008; Soler *et al*. 2008). Protoporphyrin has also been proposed to reflect the female's condition as this pigment may be a pro-oxidant therefore has the potential to signal the female's tolerance to oxidative stress (Moreno & Osorno 2003). In addition to colouration eggshell maculation has been shown to relate to female condition and health (Martinez-de la Puente *et al.* 2007; Sanz & García-Navas 2009; Duval *et al.* 2014). Food availability before and during egg laying has been found to relate to egg colour due to the extent of biliverdin pigment present in the eggshell (Moreno *et al.* 2006a; Duval *et al.* 2013). Heavily maculated eggs have also been related to poorer female body condition (Martinez-de la Puente *et al.* 2007). Other environmental conditions through impacting directly on the physiology of the female or indirectly via effecting food availability and/or foraging efficiency may also influence egg colouration and maculation (Avilés *et al.* 2007). This suggests that egg colouration and maculation could be useful traits that can be measured in a non-disruptive way to monitor local environmental conditions.

A good monitoring trait also needs to relate to demographic parameters (Wildermuth *et al.* 2012). Egg traits, in particular egg size can, among a number of other factors, affect offspring fitness, as larger eggs contain more nutrients for the developing embryo, and egg size can be positively relate to offspring fitness with increased hatchling size, mass and conditions and fledgling success (Williams 1994; Christians 2002; Krist 2011). Fitness consequences of egg shape have been very little explored however (Barta & Szekely 1997) suggested that there is an optimal egg shape that allows for a more effective incubation of the entire clutch. Indeed egg shape can be positively associated with hatching success (Górski *et al.* 2015). There are several not mutually exclusive hypothesis explaining the variation in egg colouration, and therefore suggest a relationship between the appearance of the egg and demographic variables. Eggshell colour and maculation may promote crypsis and therefore egg survival, protect the embryo from solar radiation and/or dehydration, and add structural strength to the eggshell (reviewed in Kilner 2006).

I test here the potential of using egg traits (volume, shape, colour and maculation) of a apex predator as a monitoring tool to reflect local coastal environmental conditions as a rapid assessment of detecting environmental changes sooner than when focusing directly on species demographic parameters (Wildermuth *et al.* 2012). Monitoring of the marine coastal environment is of particularly high priority as, despite its importance, human pressure on ecosystems has increased markedly over the last several decades (Costanza *et al.* 1998; Halpern *et al.* 2008; Sutherland *et al.* 2012) and in particular the coastal environment which is influenced by pressures both on the terrestrial and marine ecosystems. Apex predators to act as monitors are particularly useful as they can reflect what is occurring at lower trophic levels and responding to changes in environmental conditions (Boyd *et al.* 2006). The herring gull *Larus argentatus* provides an attractive choice as indicator species for the coastal environment. As a largely generalist and opportunistic forager, the herring gull exploits both terrestrial and marine habitats (Götmark 1984). In addition herring gulls are relatively large and conspicuous making them easy to observe, they breed colonially so a large number of individuals can be monitored at predictable locations. For egg traits, to be a reliable monitor of environmental conditions they must be repeatable, and provide more information about between-colony variation than within-colony variation. I therefore explored the spatial variation of egg traits across ten herring gull colonies in south-west Scotland and Northern Ireland over three years. To measure egg traits efficiently in the field, and minimising disturbance to the birds, I used digital photography. Specifically, I tested whether (i) herring gull egg traits varied as a function of local environmental conditions among colonies and (ii) whether egg traits provide information on the gulls' demography. This information was then used to indicate whether egg traits would be a suitable candidate to assess environmental conditions in coastal habitats, and demographic change in this species.

5.3 Methods

5.3.1 Study area

Field work was carried out across ten herring gull colonies in 2013 to 2015, providing data from 21 colony years, not every colony was visited all years (Table 4.4). Colonies were located across a region in south western Scotland and Northern Ireland covering an approximate area of 200 by 250 km (Figure 3.1). Herring gull colonies within this area showed a wide range of population trends between the census in 1998-2002 (Seabird 2000, Mitchell *et al.* 2004) and the most recent count (Table 3.1); for methodology of counts see Demographic variables below. In order to potentially sample colonies exposed to a large range of local environmental conditions I selected study colonies representing the whole range of population trends (Table 3.1). In each colony I collected data on egg measurements and seek to relate variation in egg traits to environmental variables that might explain that variation and to demographic variable in order to determine the relationship between egg traits and colony success.

5.3.2 Egg Measurements

Colonies were visited once during the incubation period (between 6th May and 2nd June 2013, 5th May and 3rd June 2014 and 15th - 27th May 2015) when clutches were complete. They were typically mixed-species colonies and herring gull nests were identified by direct observations of who attended the nest. At the larger colonies (Copeland, Lady Isle, Oronsay, Portpatrick, Round and Green Island and Pladda) nests within one or more accessible sub-sections of the colony, where it was possible to do nest observations, were selected. At the smaller colonies clutches were selected from all accessible known herring gull nests. Clutches in the selected nests were photographed in situ. Colony visits were kept short to minimise the disturbance to the breeding birds. Due to variation in the size of the colonies, the proportion of nests that were accessible and the time window available for the photographs to be taken, the number of sampled nests varied between colonies and years (Table 5.1).

Table 5-1. Summary of number of herring gull clutches (number of eggs in brackets) photographed during the 2013, 2014 and 2015 breeding seasons and the number of feather samples collected in 2014 from the ten study colonies across south-west Scotland and Northern Ireland

Colony	Number of clutches				Stable Isotope Analysis	
	2013	2014	2015	Total	Feather samples[2]	Egg Clutches[3]
Copeland[1]	19 (56)	48 (141)	-	67	22	33
Islay	23 (57)	9 (24)	10 (24)	41	11	9
Jura	6 (18)	16 (42)	-	22	-	-
Lady Isle	-	24 (72)	23 (68)	47	28	24
Isle of Muck	-	8 (24)	-	8	-	-
Oronsay	58 (154)	31 (75)	20 (60)	109	33	31
Pladda	23 (64)	15 (38)	13 (35)	51	24	15
Portpatrick	20 (44)	28 (59)	-	48	12	28
Strangford	29 (76)	39 (106)	-	68	16	39
Total	178 (469)	218 (581)	66 (190)	462	146	179

[1]Lighthouse Island in 2013, Lighthouse Island and Big Copeland in 2014. [2]Number of down feather samples taken from chick broods [3]Number of clutches from 2014 that down feathers were collected from chicks for stable isotope analysis. - indicates sites where egg photographs were not taken or no feather samples were taken in that year. Number of eggs in parenthesis.

At the nest site, all eggs from the same clutch were laid together horizontally in the holes of a custom-made egg holder and photographs were taken with Canon EOS 500D digital cameras. Cameras were set in manual exposure mode with spot metering enabled, the ISO set at 200 and the aperture at F8.0. The egg holder was covered with graph paper and a test QPcard+201 colour checker panel (www.qpcard.com) with scale bar situated at the top of the holder (Supplementary Figure 1). Two identically set-up cameras with holder were used in 2013 by two different observers whereas all photos in 2014 and 2015 were taken with the same camera that also had been used the previous year. Photographs were taken with the egg holder filling the image frame. The central autofocus point was used on the centre of the middle egg to ensure the grid background and eggs were in focus. The shutter speed was adjusted to be equal, or faster than 1/the focal length. The egg holder was shaded so that the photo was taken in diffuse light rather than direct sunlight to avoid any glare and prevent the images from being over-exposed. Photographs were not taken in the rain as this could affect the colour of the eggs and the colour checker panels. Images were recorded and stored in RAW format to prevent loss of information (Stevens *et al.* 2007) and used for all subsequent analyses. I measured egg size, shape and colour using ImageJ (http://imagej.nih.gov/ij/) with RAW-files being uploaded into ImageJ through the plug in "DCRAW" (http://ij-plugins.sourceforge.net/plugins/dcraw). Maculation was measured using *NaturePatternMatch* (Stoddard, Kilner & Town 2014).

Egg size: Maximal length l and width w of eggs were measured from the digital photographs using the *Egg Measurement Tool* plugin developed by Troscianko (2014) in ImageJ with the scale bar and grid square on the egg holder serving as a reference scale. I then calculated the egg volume V (in cm^3) as $V = klw^2$ (Hoyt 1976) where k is a species-specific shape constant here taken as 0.000476 (Harris 1964). To validate whether size measurements from photographs were accurate I measured a sample of 32 eggs, comprised of gull, chicken and fake clay eggs, directly using a calliper to the nearest 0.05 mm and from digital photographs in ImageJ as above. These eggs covered the natural range of herring gull eggs; length: 43.9 – 79.8mm, width: 35.4 – 54.2mm. Although egg measurements from both methods were highly correlated (length: $y = 0.78 \pm 0.017x + 8.51$, $R^2 = 0.99$; width: $= 0.68 \pm 0.023x + 11.34$, $R^2 = 0.97$; y = photographic measurement and x = direct measurement), the values of the slopes were less than one indicating that the larger the egg the more the photography measurement underestimated the calliper measurement; possibly because the scale bar and the maximum width and length of the egg were not at the same depth of the photo. i therefore used the regression equations for length and width of our sample eggs to correct the photographic measurements. To validate the correction i directly and photographically measured length and width of a further twelve chicken eggs within the size range of eggs used to calculate the correction equations. I corrected the photographic length and width measurements using our equations and compared those corrected values with the direct measurements using the calliper; giving a $R^2 = 0.96$ and an estimate of the slope = 1.034±0.006 for the egg volume. For the twelve test eggs the difference between the corrected photographically determined length and width and the direct calliper measurements were 1.4% (mean length = 5.77 cm versus 5.68 cm) and 0.9% (mean width = 4.42 versus 4.38 cm), respectively. I measured the size of a total of 1240 eggs from 462 clutches. One very small egg (from a clutch of two from Oronsay in 2013) had a volume of $20.23cm^3$, more than 7 standard deviations below the mean, and was not considered in any of the subsequent analyses.

Egg shape: To measure egg shape I used again the *Egg Measurement Tool* plugin in ImageJ (Troscianko 2014) and marked twelve points along the contour of the egg in the digital image. The software then calculated a shape index that indicates how much the egg deviates from an ellipse. A perfect ellipse has a deviation score of 0: with the higher the shape index the pointier the egg (Supplementary Figure S.2). For egg shape a sample size of 1239 eggs from 462 clutches were included in further analyses.

Eggshell colour: In ImageJ I used the *Pixel Inspector Tool* to obtain the red, green and blue colour values (R, G, B) from individual pixels. In order to check for the effect of light on the recorded RGB values (normalisation), I took RGB values from 3 pixels at the centre of each of the seven grey squares within the colour checker chart (P03 black to P09 grey, Supplementary Figure S.1) of known RGB values. For each photograph I regressed the known RGB values of reference squares on the extracted RGB values for that reference square using a second order polynomial forced through the origin, as this fitted the data better than a linear regression. This regression was calculated for each colour (RGB) and image separately and yielded an image-specific correction equation for each colour channel. The correction equation was applied to the mean RGB values that I extracted from six pixels from the central section of each egg, avoiding maculation and areas of glare, shade and dirt. To check that the readings from the two cameras were similar I extracted colours for the same nine gulls eggs that were photographed with both cameras, both egg holders and each egg in different positions on the egg holder. Repeatabilities *r* of the corrected RGB values across cameras, egg holders and positions on the egg holder, calculated using the 'rptR' package in R (Nakagawa & Schielzeth 2010, R Development Core Team 2014) were high (R: *r* = 0.93, G: *r* = 0.94, B: *r* = 0.90). Six clutches had to be removed from the dataset due to the images being oversaturated in either the green or blue channel, therefore for the colour analyses I had a sample size of 1223 eggs from 456 clutches.

I checked the reliability of the RGB values by looking at the equalisation of RGB values in the grey squares P03 to P09 of the QPcard; the grey squares are designed as R = G = B. The absolute difference between corrected R, G and B values from the same grey square were: R–G = 10.6 ± 6.2 (SD) (4.2% of a maximum difference of 255), G–B = 10.4 ± 6.0 (4.1%), and R–B = 21.0 ± 11.4 (8.2%). I then checked whether the corrected R, G and B values matched the expected R, G and B values of the colour panel P15 on the QPcard, chosen due to it being similar in colour to a typical herring gull egg and these differences were relatively small for R (1.7%, n = 12), G (2.2%, n = 12) and B (9.2%, n = 12).

For a sample of nine gull eggs I also measured egg colour using a reflectance spectrophotometer and compared with the RGB values measured from photographs of these same eggs. I used a S2000 (Ocean Optics, Dunedin, FL, USA) with a deuterium bulb (UV light) and a tungsten halogen bulb (visible light) as light sources. All reflectance measurements were calculated relative to a Spectralon reflectance standard (WS-1-SL, Ocean Optics). Reflectance spectra were measured from 5 different points on the eggshell, avoiding maculation, in the same equatorial area where colour from the images were also measured. I averaged the 5 measurements for each egg into one spectrum (300-700 nm). The colour of herring gull eggs ranges from a blueish-green to brown colour, with the pigments biliverdin and protoporphyrin, respectively, being responsible for these colours (Kennedy & Vevers 1976). I therefore extracted a blue-green chroma at 450-550nm and a brown chroma at 605-700nm relative to the entire avian visible spectrum (300-700nm) from the averaged spectra. Blue-green and brown chroma approximates the concentrations of biliverdin and protoporphyrin, respectively (Hanley & Doucet 2012). There was a strong negative correlation between an egg's blue-green and brown chroma (R^2 = 0.80, n = 9). As the individual colour values are not informative on their own, only in relation to the other channels (Bergman & Beehner 2008). I decided to use the G/B ratio for further analysis due to the high correlation with the blue-green and brown chroma from the spectrophotometer. I found that the G/B ratio was negatively correlated with blue-green chroma (r = -0.72, n = 9, $p = 0.029$) and positively correlated with brown chroma (r = 0.90, n = 9, $p < 0.001$). Therefore, an egg with a high G/B ratio is more brown-coloured whereas an egg with a low G/B ratio is more pale green-blueish coloured (see Supplementary Figure S.3). As egg colour may fade over time due to exposure to sunlight (Moreno, Lobato & Morales 2011b), I looked at the correlation between colour and date, assuming eggs photographed at a later date were exposed for a longer period. I found no evidence that G/B was related to the date the eggs were photographed (2013: $F_{1,175}$ =-0.03, $p = 0.98$; 2014: $F_{1,216} = 0.04$, $p = 0.97$; 2015: $F_{1,61} = 0.74$, $p = 0.46$).

Eggshell maculation: Images of each individual gull egg were cut out from the background using the ImageJ *Egg Measurement Tool* plugin (Troscianko 2014) and uploaded into the *NaturePatternMatch* software (Stoddard *et al.* 2014). To quantify eggshell maculation individual gull eggs were compared to an image of an un-maculated reference egg (pure white unmarked goose egg). To ensure that only the egg, not the black background, was compared I first run the Region-of-interest Selection in the *NaturePatternMatch* software. The *NaturePatternMatch* software uses Scale-Invariant Feature Transform (SIFT) to identify egg pattern features from the images and compares them between eggs by calculating a similarity score of each individual gull egg relative to the reference egg. Higher similarity scores indicate eggs that are more similar to the unmaculated reference egg, therefore are less maculated (see Supplementary Figure S4). Sixty eggs were not uploaded to *NaturePatternMatch* due to the eggs being dirty or were starting to pip which would have biased the number of identified SIFTS. A further 374 eggs did not return any data back from *NaturePatternMatch*, assumedly their image being too dark to be distinguished from the black background or insufficient focus for the software to pick out features, which left 806 eggs from 307 clutches for the analyses.

5.3.3 Environmental correlates of egg traits

I collected information on environmental factors which could potentially affect egg formation. Egg formation can be influenced over a relatively long period of time and I distinguished between the pre-laying period when females build up resources for egg formation and the laying period when eggs are formed during rapid follicular growth. The period of rapid follicular growth takes approximately two weeks in large gulls (Brown 1967; Parsons 1976). In all years and across all study colonies laying peaked in early May therefore the last two weeks of April (17th – 30th) immediately preceding this period were taken as the laying period. The pre-laying period covered the preceding six-week period (Parsons 1976; Houston, Jones & Sibly 1983); in our case 1st March – 16th April.

Weather conditions can influence egg traits (Becker *et al.* 1985; Christians 2002; Avilés *et al.* 2007). As the weather conditions varied over the relatively large study region I included local weather variables into the analyses. Daily total precipitation and minimum ambient temperatures were obtained from the Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations Data (Met Office 2012) and averaged separately across the pre-laying and laying period. Weather data were downloaded from the nearest weather station that recorded the relevant weather variables; on average 16.9±11.5 (SD) km from the colony.

Environmental variables reflecting the state of the foraging conditions in the local coastal environment are likely to influence the gulls' body condition. The female's condition preceding egg formation can influence egg traits (Hiom *et al.* 1991; Nager, Monaghan & Houston 2000) and colour (Moreno *et al.* 2006b); as can the quantity and quality of local food resources prior and during egg laying (Hiom *et al.* 1991; Bolton, Houston & Monaghan 1992). Laridae are generalist apex predators exploiting a wide range of resources from marine, intertidal and terrestrial habitats (Cramp & Simmons), although the different food types can influence reproductive output differentially (Pierotti & Annett 1990). In particular, the type of resources females consumed prior to and during egg formation can influence egg traits (Bolton *et al.* 1992; Pons 1992; Steigerwald *et al.* 2015). I therefore included environmental variables which potentially reflect the different resources the gulls may utilise measured at the scale of foraging range of colonies; herring gulls forage up to 50 km from their colony (Spaans 1971; Götmark 1984). As a proxy for marine productivity I used sea surface temperature (SST) and chlorophyll concentration. SST (as 11µ night-time) and chlorophyll concentration (mg/m^3) composites were extracted from Aqua MODIS at 4 km resolution (http://oceancolor.gsfc.nasa.gov/cgi/l3), separately for the pre-laying and laying period in each year and averaged over the foraging range around each study colony.

Terrestrial food sources for herring gulls are in particular offered by landfill sites and built-up areas (Pons 1992; Belant *et al.* 1993). I therefore included the extent of built-up area and number of landfill sites within each colony's foraging range as a proxy for the availability of terrestrial food sources. I obtained the number of landfill sites for Scotland from SEPA (2015) and for Northern Ireland from NIEA (Eugene Kelly, pers. comm.). The amount of built-up area within the colonies' foraging ranges was obtained from Landsat 2000 in ArcMap 10.1 (Fuller *et al.* 2002).

The abundance of marine invertebrate prey in intertidal areas, another important food source of the herring gull (Götmark 1984; Kubetzki & Garthe 2003) can be predicted for rocky shores, the main shore habitat within the study region, from wave fetch (Burrows, Harvey & Robb 2008). The average wave fetch (km) of the shoreline within each colony's foraging range was calculated in ArcMap 10.1 based on wave fetch data obtained from SAMS (Burrows 2009).

To identify what resources were used during egg formation I used stable isotope analyses of carbon and nitrogen of down feathers from hatchlings. Down feathers are grown by the offspring while developing in the egg using the resources the female laid down in the egg, therefore reflect the resources used by the adult females before and during egg formation (Klaassen et al. 2004; Kim, Furness & Nager 2010). Down feather samples were collected from chicks which were less than a week old at colony visits during 2014 (Table 5.1) and analysed for nitrogen and carbon isotopes. Where more than one chick was sampled from the same brood feathers material was homogenised to provide one sample per brood. The nitrogen isotope ratios ($^{14}N/^{15}N$) reflect trophic level whilst the carbon isotope ratio ($^{12}C/^{13}C$) varies along a gradient from marine, coastal to terrestrial habitats (Hobson *et al.* 1994; Hobson & Wassenaar 1999). Prior to analysis, herring gull down samples were washed in liquid detergent (Ecover^{TM}) diluted with deionised water (approximate 1:99 dilution), and then in a 2:1 mixture of chloroform: methanol to remove impurities from the feather surface. Dried samples were then cut, homogenized and weighed (mass between 0.7-0.8mg) into tin capsules before being combusted and analysed by continuous-flow isotope ratio mass spectrometry (Costech Elemental Analyser, Milan Italy, linked to a Thermo Finnigan Delta Plus XP Mass Spectrometer, Bremen Germany) at NERC Life Sciences Mass Spectrometry Facility, East Kilbride. The stable isotope ratios are expressed as $\delta^{13}C$ and $\delta^{15}N$ in parts per thousand (‰) relative to the international references PeeDee belemnite marine fossil limestone for carbon and atmospheric N_2 for nitrogen. Measurement accuracy was ±0.09 ‰ for $\delta^{13}C$ and ±0.12 ‰ for $\delta^{15}N$ based on the standard deviation of the repeated analyses of an internal standard (tryptophan).

5.3.4 Demographic variables

I want to determine whether any spatial differences in the four egg traits were associated with the short- and long-term success of the colony (Table 4.4). For the short-term success I used the number of chicks of at least three weeks old, and therefore assumed to be likely to fledged (Bolton 1991) determined from nest watches. For the long-term success of the colony I calculated colony growth (GR) between the last seabird census in 1998-2002 (Mitchell *et al.* 2004) and the most recent available counts of each study colony (Table 3.1). Recent counts for colonies were obtained from land owners/managers following the methodologies for gulls described in Walsh *et al.* (1995) that count the number of apparently occupied nests (AON). GR was calculated as described in Nager & O'Hanlon (in press):

$$GR = (N_t - N_{t-1})/\text{Maximum } [N_t, N_{t-1}]$$

where N_t is the last seabird census and N_{t-1} is the most recent available count, and Maximum $[N_t, N_{t-1}]$ is the highest count of either census.

5.4 Statistical analyses

All statistical analyses were performed in R, Version 2.12.0 (R Development Core Team 2014). For each egg trait the average value of all eggs within a clutch was used as the unit of analysis. I first tested the repeatability of egg traits among colonies and years. I found no evidence that the expected values of egg traits varied over time across the colonies using a linear mixed-effects model (LMM) in R's *rptR* package (Nakagawa & Schielzeth 2010) with random intercept and slopes (results not shown). To determine the repeatability of egg traits I therefore used Consistency Repeatability (*Rc*) (Biro & Stamps 2015) with year as the fixed effect and colony as a random effect in a LMM model.

To investigate the spatio-temporal variation in egg traits across the study region I carried out a two-way analysis of variance (ANOVA) with each egg trait as the response variable in turn and year, colony and the interaction between the two as explanatory variables. To calculate the effect size of the spatial variation in each egg trait for each monitoring year I calculated f_2 values using the power calculations for general linear models in R's *pwr* package (Champely 2012). To further explore the spatio-temporal variation in egg traits between colonies in relation to local environmental conditions I used analysed the effects of local environmental conditions, clutch size, year and colony size on egg traits using mixed effect multivariate models in R's *lme4* package (Bates *et al*. 2014). I used a separate model for each egg. Clutch size was included as eggs from smaller clutches may differ from those from larger clutches; however this was non-significant in all cases therefore was not included in the final analysis presented in the Results. Our study colonies varied considerably in size (Table 4.4) and as colony size can influence egg traits (Coulson *et al.* 1982) by individuals in larger colonies experiencing higher levels of competition that depletes food resources in close proximity of the colony (e.g. Furness & Birkhead 1984; Birt *et al.* 1987; Lewis *et al.* 2001) I also included colony size in our statistical model. For local environmental conditions I used weather variables and proxies for potential resource availability. As I am only interested in the effects of local environmental conditions on within-year variation rather than on the between-year differences in egg traits where I only had three years, environmental variables were standardised to remove between year differences. Variables were standardised by taking its difference from that year's mean and divided by the standard deviation. Due to the potential multi-collinearality of the explanatory variables pairwise correlations and variance inflation factor (VIF) values were checked and only variables that were significant in univariate models and with a VIF < 3 were included in the multivariate analysis (Zuur, Ieno & Elphick 2010). As the environmental variables were highly correlated between the pre-laying and laying period values were averaged across the two periods to reflect the entire two month period of egg formation and laying. The number of landfill sites and the amount of built-up area within the colony's foraging range were correlated with colony size and therefore had to be removed from the model. Year was included in the model as in particular I was interested in interactions with the environmental variables in order to test whether the response of egg traits to the environment differed between years. Colony was included as a random effect to account for the non-independence of clutches from the same colony.

For 2014, the stable isotope ratios of δ^{13}C and δ^{15}N of down feathers were determined to analyse the influence of resource use of the female during egg formation on egg traits. I carried out a principal component analysis using *prcomp* in R's *stats* package (R Core Team 2014) to determine the combined contribution of δ^{13}C and δ^{15}N. The first principal component (PC1) explained 91.7% of the variation in isotopic ratios, with an eigenvalue of 4.86 (factor loadings: δ^{13}C: 0.94, δ^{15}N: 0.35). Each egg trait in turn was included as the response variables in a mixed effect multivariate model with the isotope-PC1, reflecting the gull's resource use during egg formation, included as an explanatory variable and colony as a random effect. Models were compared to an intercept only model.

To determine whether egg traits were related to the gulls' demography linear mixed effect multivariate models were carried out using R's *lme4* package (Bates *et al.* 2014) with demographic variables (final brood size and GR) as response variable, colony as a random effect, and egg trait, year and current colony count as the explanatory variables; separate models were made for each egg trait. Current colony count was included to check for density-dependent processes interacting with the association between egg traits and demographic variables. Final brood size was included as the response variable as a measure of short-term colony success; final brood size was not available for 2015 and therefore data for 14 colony years from 2013 and 2014 were included in the model. Colony GR was used as the response variable for long-term colony success and this analysis is based on nine colonies averaged egg trait across years as the explanatory variable in turn.

Diagnostic plots were checked to ensure all model assumptions were met. The maculation scores, averaged per clutch, had to be ln-transformed. All relationships were visually inspected for linearity and the plot between isotope PC1 and egg volume suggested a non-linear relationship where I then also tested the fit of a second order polynomial function. I performed model simplification starting with the most complex model including second-order interactions where appropriate. The minimal adequate model was then determined by carrying out Likelihood Ratio tests, that follows a χ^2 distribution, to establish whether the exclusion of a term resulted in a significantly poorer fit of the model (Crawley 2007). R^2 values for the linear mixed effect multivariate models were calculated in the R package *MuMIn* (Barton 2012). Main effects that are part of significant interaction terms were not tested as they could not be removed from the model in isolation. Significance threshold was set at two-tailed $p < 0.05$. The effect size (f) of traits were calculated using the adjusted R^2 values from the linear models, with $f = \sqrt{(R^2 / (1-R^2))}$.

5.5 Results

The variability differs between egg traits with an average egg volume of 71.285 ± 7.408 cm^3 (± SD), n = 1239, coefficient of variation (CV) = 10.4%; average egg shape index of 0.000458 ± 0.000171, n = 1239, CV = 37.3%; average G/B ratio of 1.130 ± 0.038, n = 1223, CV = 3.4%; and average maculation score of 0.954 ± 0.027, n = 806, CV = 2.8%.

The within-colony repeatabilities *Rc* of egg traits across the three breeding seasons were relatively low; it was highest for egg volume (*Rc* = 0.220, lower and upper 95% confidence intervals (CI): 0.060 – 0.398 and was significantly different from zero: $P < 0.001$). The within-colony repeatabilities for maculation (*Rc* = 0.111, CI: 0.002 – 0.231), egg colour (*Rc* = 0.039, CI: 0.000 – 0.100) and egg shape (*Rc* = 0.008, CI: 0.000 – 0.044), however, were all not different from zero: $P > 0.99$. Using data pooled across the three years, I found no inter-relationship between any of the four egg traits (all Pearson's product-moment correlations $P > 0.15$).

5.5.1 Spatial and temporal variation

Egg colour, maculation and volume varied between colonies, with the between-colony differences varying between years (Table 5.2a, b, d). In all years there was a significant spatial variation in egg volume, however the differences between colonies were most pronounced in 2014 and least pronounced in 2013 (one-way ANOVAs, 2013: $f = 0.30$, $F_{6,171} = 2.67$, $P = 0.016$; 2014: $f = 0.69$, $F_{8,209} = 12.17$, $P < 0.001$; 2015: $f = 0.59$, $F_{3,62} = 7.31$, $P < 0.001$). Egg colour and maculation differed significantly between colonies in 2014 and 2015 but not in 2013 (one-way ANOVAs, Colour - 2013: $f = 0.20$, $F_{6,168} = 1.12$, $P = 0.35$; 2014: $f = 0.30$, $F_{8,209} = 2.46$, $P < 0.014$; 2015: $f = 0.37$, $F_{3,59} = 2.80$, $P = 0.048$; Maculation - 2013: $f = 0.33$, $F_{6,98} = 1.74$, $P = 0.12$; 2014: $f = 0.48$, $F_{8,134} = 3.90$, $P < 0.001$; 2015: $f = 0.51$, $F_{3,57} = 4.89$, $P = 0.004$). Egg shape consistently differed between colonies across all years (Table 4.3c, $f = 0.20$), but did not differ between years. Colony, however, explained only a very small part of the observed variance in egg shape (Table 5.2c) and between-colony differences were driven by Portpatrick having, on average, rounder eggs than Copeland and all other colonies having intermediate egg shapes. Due to the small amount of variation explained by colony, egg shape was not included in further analysis. Egg volume was explained more by variation between colonies than between years whereas for colour and maculation more of the variation was explained by year than between colonies (Table 5.2).

Table 5-1. Results of ANOVAs with (a) Egg colour, (b) Egg maculation, (c) Egg shape and (d) Egg volume. I used within-clutch averaged values of egg traits as individual response variables and year, colony and the interaction between year and colony as explanatory variables.

Variable	Variable	*df*	Residual *df*	Sum sq.	Mean sq.	*F*	*P*	Variation Explained[1]
(a) Colour (G/B)	Year	2		0.038	0.0192	23.73	**<0.001**	9.06
	Colony	8		0.018	0.0022	2.73	**0.006**	4.17
	Year* Colony	9	436	0.015	0.0017	2.03	**0.034**	3.50
(b) Maculation (similarity score)	Year	2		0.054	0.0271	51.83	**<0.001**	21.72
	Colony	8		0.030	0.0038	7.24	**<0.001**	12.13
	Year* Colony	9	289	0.014	0.0016	2.96	**0.002**	5.56
(c) Shape (index score)	Colony	8	453	0.270	0.0337	2.19	**0.027**	3.72
(d) Volume (cm^3)	Year	2		1660	830.2	24.35	**<0.001**	7.81
	Colony	8		3498	437.2	12.83	**<0.001**	16.45
	Year* Colony	9	442	1040	115.5	3.39	**<0.001**	4.89

df = degrees of freedom. [1] Percent of variation in egg trait explained by year, colony and the interaction between the two; adds up to the unadjusted R^2 value from the linear model.

5.5.2 Environmental variables associated with between-colony variation in egg traits

The factors associated with the between-colony variation in egg traits are presented in Table 5.3. Only egg volume was related to colony size with smaller eggs in larger colonies (Figure 5.1). I found no relationship between colony size and egg colour ($P = 0.34$) or maculation ($P = 0.33$). Both egg colour and volume were associated with the local minimum ambient temperature before and during egg laying (Table 5.3a, b). Less brown eggs and larger eggs were associated with colonies which experienced higher than average ambient temperatures during the eight weeks before and during egg formation (Figure 5.2a, b). As expected from the previous results all three egg traits differed between years, however there was no evidence that environmental factors influenced egg traits differently in the three years (all interactions with year $P > 0.05$). Of the variables of interest which might reflect local environmental conditions potentially reflecting food availability, I found that higher chlorophyll a concentration and SST in the period leading up to egg laying were associated with more maculated eggs (Table 5.3c, Figure 5.3a, b). Precipitation ($P > 0.05$) and wave fetch ($P > 0.41$) did not explain any egg trait variation between colonies.

Table 5-2. Parameter estimates from general linear mixed models (colony as random effect) describing the influence of environmental parameters, standardised by year, on (a) Egg Colour, (b) Egg Volume and (c) Egg Maculation (egg traits averaged per clutch). Model selection based on Likelihood Ratio tests.

Response variable	Explanatory variable	Estimate	Std. Error	X^2	P	R^2
(a) Colour	Intercept	1.128	0.003			
(GB ratio)	Minimum temp. (°C)	-0.005	0.002	8.97	**0.003**	0.05
	Year	-0.005	0.002	9.64	**0.002**	(0.09)
	Intercept	73.134	2.437			
(b) Volume (cm^3)	Colony Size (AON)	-1.676	0.462	5.833	**0.016**	
	Minimum temp. (°C)	0.870	0.384	4.530	**0.033**	0.19
	Year	3.609	0.423	63.34	**<0.001**	(0.23)
	Intercept	0.057	0.003			
(c) Maculation	Sea surface temp. (°C) [1]	-0.005	0.002	5.40	**0.020**	
(similarity score)	Chlorophyll a conc. (mg/m^3) [2]	-0.008	0.003	6.67	**0.009**	0.22
	Year	0.011	0.002	22.57	**<0.001**	(0.33)

[1] Average SST within 50km of the breeding colony. [2] Average Chlorophyll a concentration within 50km of the breeding colony. Weather variables (minimum temperature and precipitation) were standardised by year. AON – Apparently occupied nests. R^2 is the "marginal" R^2 value ($R^2_{\mathrm{GLMM(m)}}$) which is the proportion of the variance in the dependant variable that is explained by the fixed variables. Value in brackets is the "conditional" R^2 value ($R^2_{\mathrm{GLMM}(c)}$) which is the proportion of the variance in the dependant variable that is explained by the fixed and random variables.

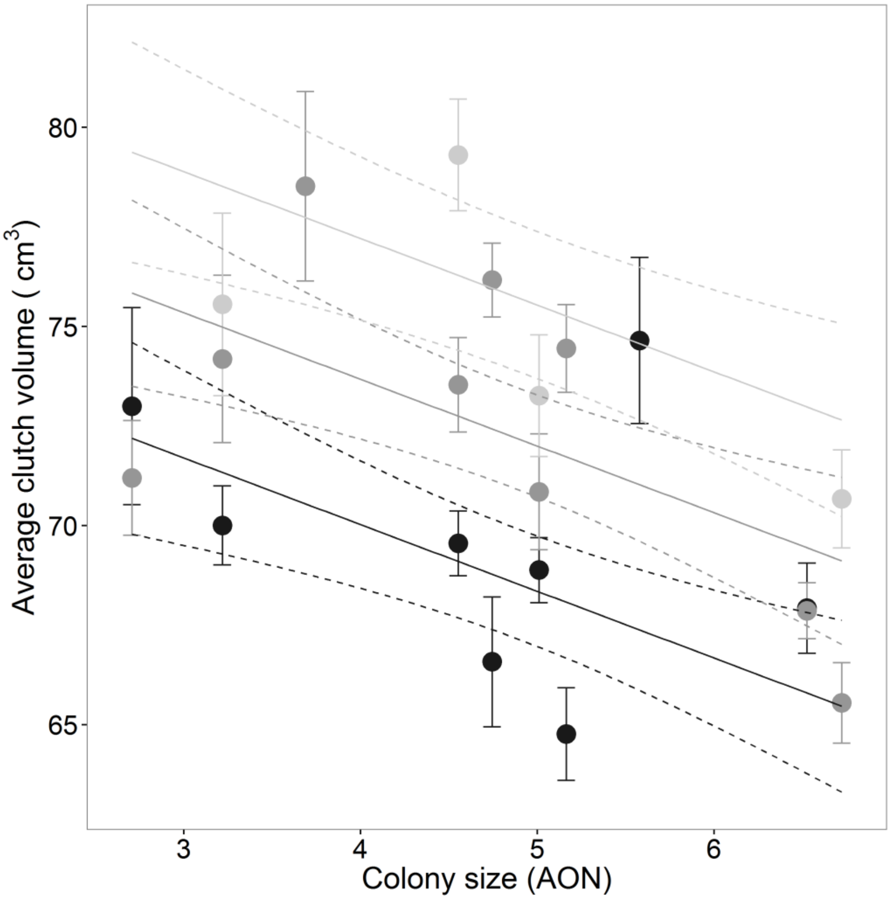

Figure 5-1. Mean ± 1 SE clutch volume (clutch averages) against colony size (log-transformed) for 21 colony years; 2013 (black circles), 2014 (dark grey circles) and 2015 (light grey circles). The solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

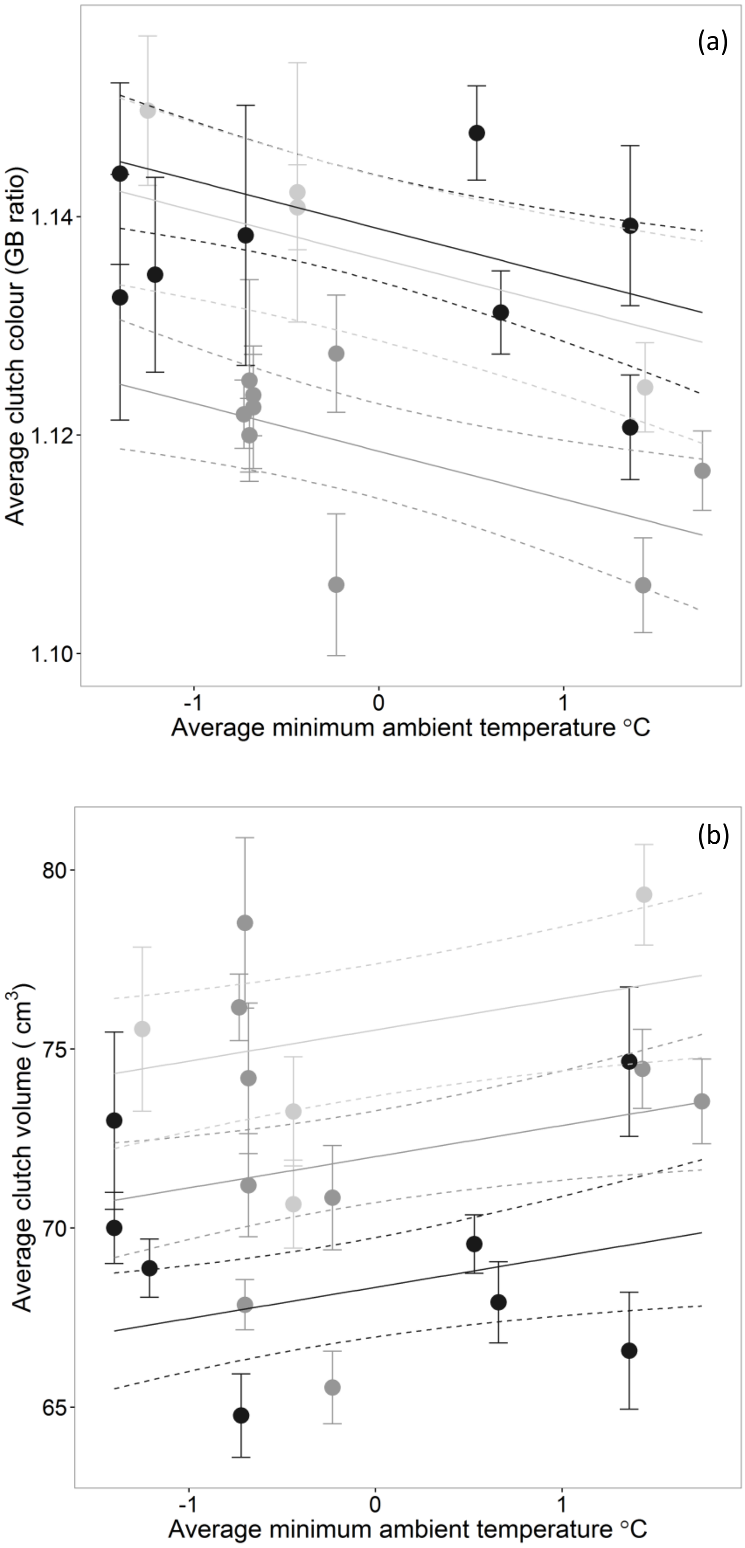

Figure 5-2. Mean ± 1 SE (a) clutch volume and (b) clutch colour (higher GB scores relate to browner eggs) against average minimum ambient temperature (standardised) for 21 colony years; 2013 (black circles), 2014 (dark grey circles) and 2015 (light grey circles). The solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

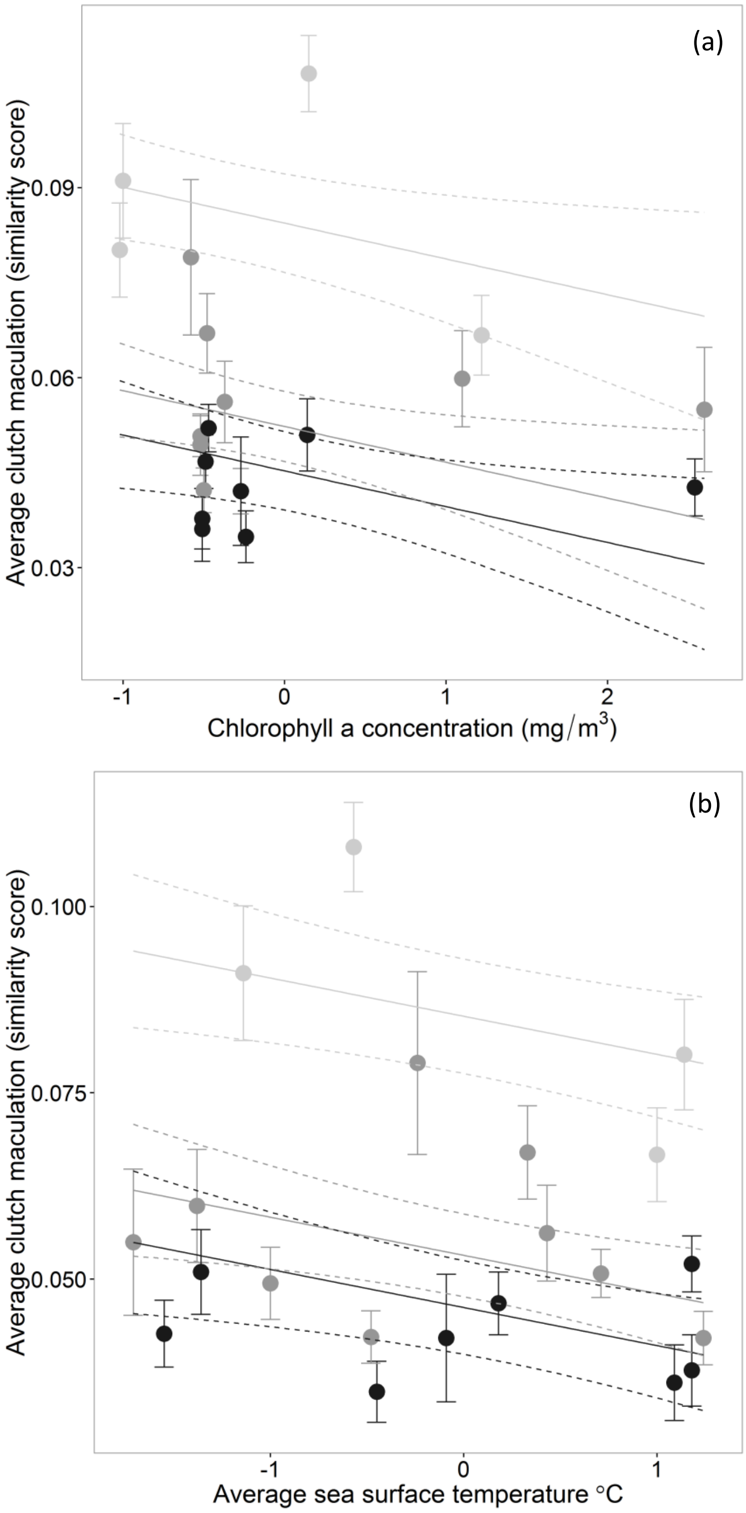

Figure 5-3. Mean ± 1 SE clutch maculation (clutch averages) against standardised (a) sea surface temperature (b) chlorophyll a concentration for 2013 (black circles), 2014 (dark grey circles) and 2015 (light grey circles). Higher maculation similarity scores relate to less maculated eggs. The solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

5.5.3 Resource use and between-colony variation in egg traits

Egg maculation and volume were significantly related to the PC1 of the stable isotope ratios of chicks' down feathers (Figure 5.4). Females laying more maculated eggs consumed a diet with a higher isotope PC1 value (χ^2_1 = 7.88, P = 0.005, R^2 = 0.10; Figure 5.4a). Egg volume was non-linearly related to isotope PC1 (χ^2_2 = 8.03, P = 0.02, R^2 = 0.25); with larger egg volumes at colonies characterised by low and high isotope PC1 values (Figure 5.4b). No relationship was found between egg colour and isotope PC1 of down feathers (P > 0.46).

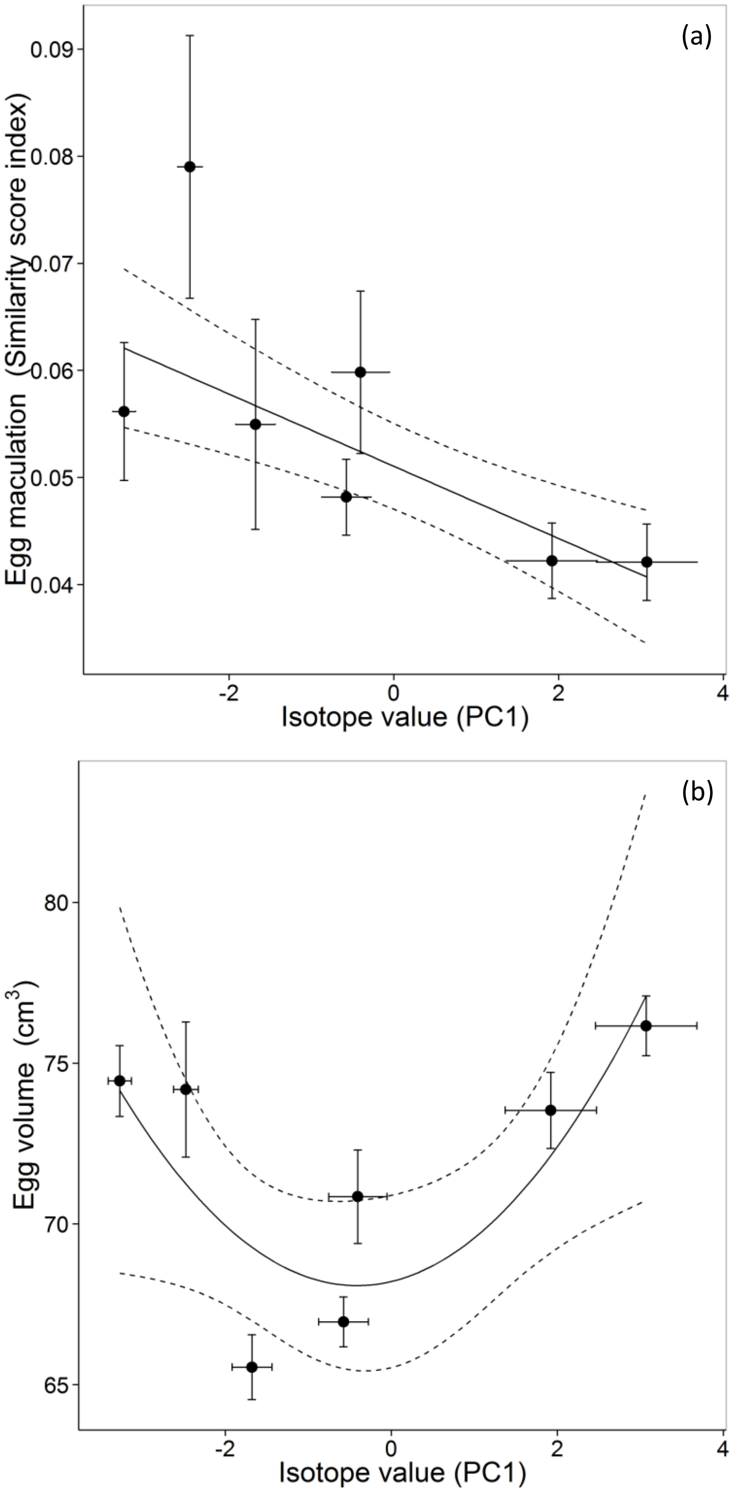

Figure 5-4. Mean ± 1 SE (a) clutch maculation (higher similarity scores relate to less maculated eggs) and (b) clutch volume against stable isotope values (PC1 eigenvalues). Low isotopic scores reflect terrestrial resources at a low trophic level. High isotopic scores reflect marine resources at a high trophic level. The solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

5.5.4 Relationship of egg traits with demographic parameters

I found that egg colour explained variation in a short-term colony success, dependent on year (Figure 5.5). For 2014 a positive relationship was observed with lower final brood sizes in colonies with browner eggs ($\chi^2_1 = 4.10$, $P = 0.04$, $R^2 = 0.72$) but the relationship in 2013 was non-significant ($\chi^2_1 = 2.70$, $P = 0.10$). I found no relationship between final brood size and egg volume ($\chi^2_3 = 0.81$, $P = 0.37$) or egg maculation ($\chi^2_3 = 0.17$, $P = 0.68$).

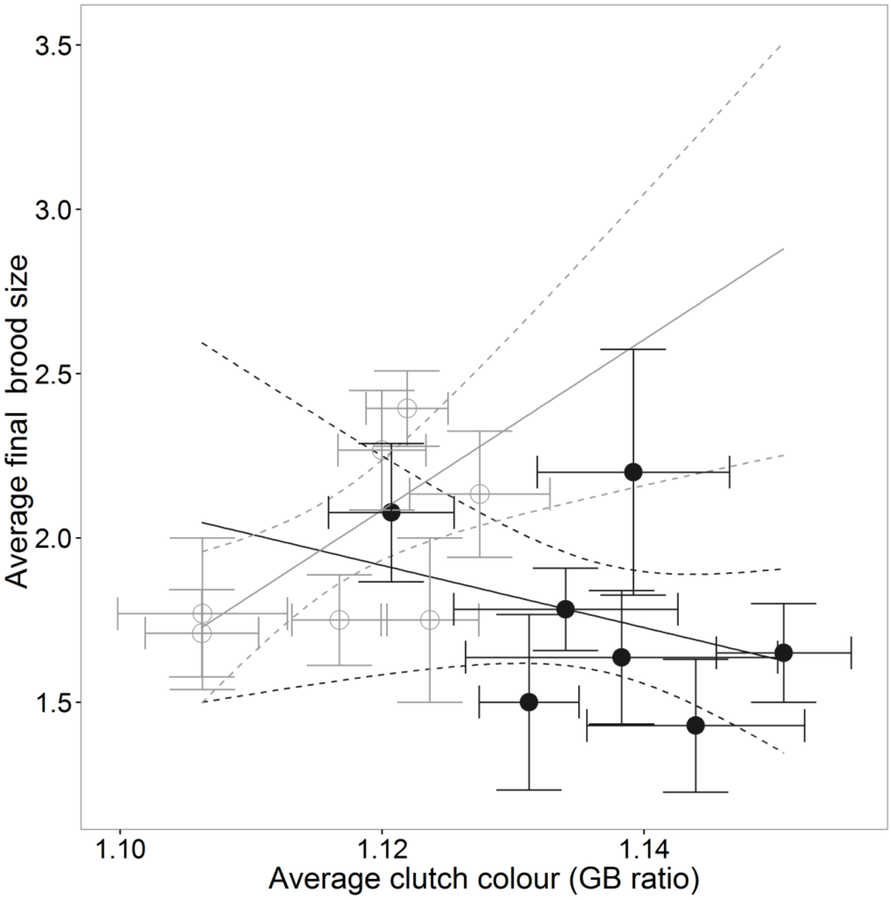

Figure 5-5. Interaction plot showing the mean egg colour (higher GB scores relate to browner eggs) against mean final chick brood size for 2013 (black filled circles) and 2014 (open grey circles). Solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

There was no significant relationship between the mean egg traits per colony across the study years and colony GR (colour: $f = 0.26$, $F_{1,7} = 0.54$, $P = 0.49$; maculation: $f = 0.19$, $F_{1,7} = 0.26$, $P = 0.63$; egg volume: $f = 0.44$, $F_{1,7} = 2.52$, $P = 0.16$). Although the relationship between egg volume and colony GR was not statistically significant there was a weak pattern with larger eggs found in colonies which were increasing in the decade preceding this study (Figure 5.6).

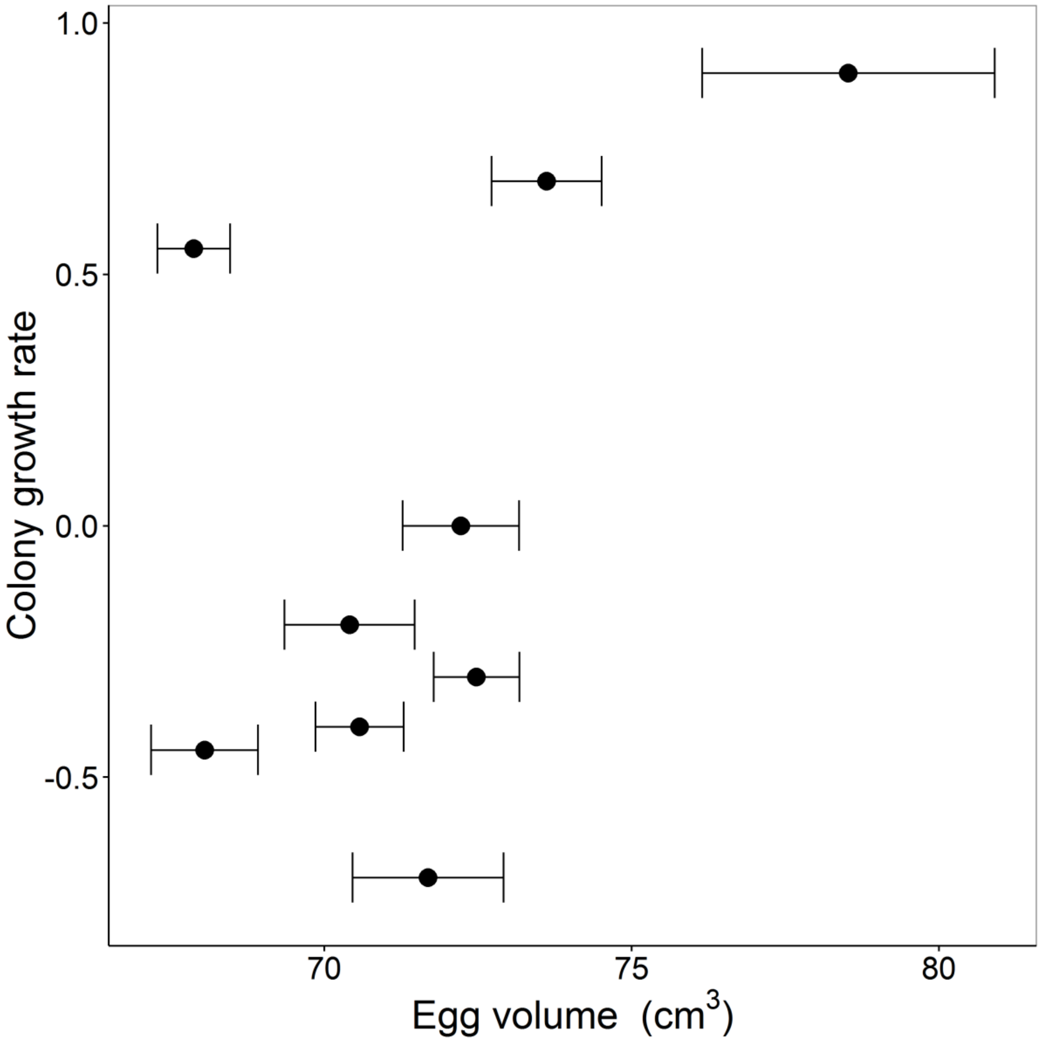

Figure 5-6. Mean ± 1 SE clutch volume (clutch averages), and across the two years for each colony, against colony growth rate, calculated between Seabird 2000 and the most recent count.

5.6 Discussion

I found spatio-temporal variation in all four traits associated with the herring gull's eggs across 21 colony years. The within-colony repeatability of the four egg traits over time varied across the four egg traits with egg volume being the most repeatable trait. Egg colour and egg maculation were repeatable to a lesser extent, with egg shape showing too little variability between sites to be useful. In addition, for egg volume more variation was explained by differences between colonies rather than between year, as was the case for colour and maculation. Looking at variables potentially reflecting local foraging opportunities I found that average sea surface temperature and chlorophyll a concentration during the early season were related to egg maculation and that the resources the gulls consumed during egg formation was related to spatial variation in egg volume and maculation. This demonstrates that egg traits are sensitive to local environmental conditions at the breeding site. Moreover, I found that egg colour, depending on year, did relate to a short-term measure of gull demography, final chick brood size. This suggests that the measurement of a combination of egg traits that can be collected in the field rapidly can provide a potentially useful monitoring tool of the coastal environment during the early breeding season.

Of the environmental variables that I was not directly interested in average minimum ambient temperature during the pre-laying period was related to egg colour and volume, with less brown and larger eggs in colonies which experienced warmer conditions during this period. Colony size was also related to egg volume, with larger eggs in smaller colonies. Potentially this reflects the results suggest that eggs of an intermediate colour reflect better local conditions resulting in highest final chick brood size. None of the egg traits related to overall colony growth rate however this might be expected given the egg traits within colonies did not differ consistently across years, although there is suggestion that larger eggs are found in colonies which are increasing.

5.6.1 Spatial and temporal variation

In order to be a reliable monitor of local environmental conditions the egg traits must be repeatable and the variation in egg traits must provide more information about between-colony than within colony variation across years. Across the three years I monitored herring gull eggs there were differences in the amount of variance each trait explained. Egg shape in particular had a very low repeatability explaining only a small proportion of the between-colony variation and therefore is unlikely to be useful as a monitor of the local environment at least of herring gulls; and so was excluded from further analysis. Between-year variation in egg shape had been found in few cases (Ardendt 2004; Górski *et al.* 2015), and here I found subtle but consistent differences in egg shape between colonies. This is an interesting finding although due to the little variation I could not identify any environmental correlates of that pattern or demographic consequences.

Of the three herring gull egg traits with reasonable repeatability all demonstrated spatial variation across the study region, indicating these traits are sensitive to local environmental conditions. However, I did find differences in the extent of spatial variation observed across the three sampling years. As with repeatability, effect sizes of spatial variation in egg traits, reflecting small to medium effects, were highest in 2015 and lowest in 2013; with effect sizes for egg volume being higher than colour and maculation in all years. As egg traits were related to the temperature in the early season, this between-year variation in egg traits may be attributed to differences in the spatial pattern of weather conditions across the three years, but with three years I do not have a sufficient sample size to formally test this possibility. During the pre-laying and laying period, birds in 2013 experienced cooler and wetter conditions than in 2014 and 2015 (Met Office 2015), possibly explaining the smaller eggs laid in 2013 than in 2014 and 2015 and final brood size being lower in 2013 than 2014. If so, then this suggests that there may be less variation in egg traits between colonies under harsh conditions as all gulls in all colonies are experiencing unfavourable conditions whilst in more favourable conditions the differences between colonies may be more noticeable.

Across the three study years egg volume was the most repeatable trait suggesting that it will be the most useful long-term monitor the local environment. The variation in egg volume explained by colony was also greater than by year whereas the variation in egg colour and maculation was explained more by year than colony. This may be due to colour and maculation being more sensitive to local weather and sea conditions that varied across the three years in a similar manner for all study colonies, whereas egg volume may be more sensitive to changes in local environmental conditions that are consistent between years. If different egg traits reflect different aspects of the environment then a combination of traits may be useful as a monitoring tool.

5.6.2 Environmental variables driving between-colony variation in egg traits

Our analysis demonstrated that there is spatial variation in herring gull egg traits across colonies suggesting egg traits are sensitive to, and therefore reflect, local environmental conditions. Identifying which environmental conditions are driving the observed spatial variation in egg traits across the colonies is less straightforward. Moreover among the potential factors affecting egg traits there are factors like weather conditions and colony size that I am not directly interested in to monitor the local ecosystem, but could mask those effects and therefore need to be accounted for.

I found that minimum ambient temperature averaged across the period before and during laying influenced egg colour and volume. Favourable weather conditions resulted, on average, in less brown and larger eggs. A number of studies have found that egg size increased with increasing ambient temperatures during egg laying, although largely in terrestrial systems (e.g. Magrath 1992; Christians 2002; Hargitai *et al.* 2005; Potti 2008), but one other study also found this for a seabird (Crossin *et al.* 2010). During low temperatures females may need to expend more energy in thermoregulation (Nager & van Noordwijk 1992; Stevenson & Bryant 2000). Most studies on egg size and temperature has been carried out on insectivorous passerine species where ambient temperature also affects their foraging efficiency on invertebrate prey (Bryant 1973; Nager & Zandt 1994; Hargitai *et al.* 2005). An indirect effect of temperature on food availability may also be relevant for herring gulls as they feed on marine invertebrates and terrestrial invertebrates such as earthworms (Pienkowski 1983; Götmark 1984; Coulson & Coulson 2008).

I know less how egg colour is related to environmental conditions. Reed warblers *Acrocephalus scirpaceus* laid blue-greener eggs in years with lower spring temperatures indicating that female condition maybe directly or indirectly affected by the weather, which is then reflected by egg colour (Avilés *et al.* 2007). The colour measured on the eggshell can approximate pigment concentration (Moreno *et al.* 2006b; Martinez-de la Puente *et al.* 2007; López-Rull, Miksik & Gil 2008; Walters & Getty 2010 but see Duval *et al.* 2013; Butler & Waite 2015; Wegmann, Vallat-Michel & Richner 2015), and bluer / greener eggs may reflect higher biliverdin concentrations. Higher biliverdin to protoporphyrin deposition, possibly indicated by more intensively blue-green egg colouration, relates to females in good body condition during egg formation (Moreno & Osorno 2003; Osorno *et al.* 2004; Siefferman, Navara & Hill 2006; Krist & Grim 2007;

Morales, Velando & Moreno 2008; Soler *et al.* 2008 but see Cassey *et al.* 2008; Hargitai, Herényi & Torok 2008; Dehnhard *et al.* 2015). The majority of these studies are on species with white maculated or blue-green eggs. For herring gulls I found less brown eggs, possibly indicating higher biliverdin to protoporphyrin deposition, at higher ambient temperatures. From the positive relationship of egg volume and ambient temperature this suggests that less brown eggs reflect more favourable local conditions consistent with the interpretation of a higher deposition of biliverdin to protoporphyrin in the eggshell reflecting females in better condition. However,Hanley & Doucet (2009) found no relationship between female condition and eggshell colouration. In experimental studies with the Japanese quail *Coturnix coturnix japonica*, which like the herring gull has typically brown egg, females in good condition still laid eggs with increased deposition of biliverdin compared to protoporphyrin (Duval *et al.* 2013); therefore likely resulting in less brown / more blue-green eggs, supporting our interpretation, although in open ground nesting species like Japanese quails and herring gulls the need for egg crypsis (Baerneds *et al.* 1982) may constrain the observed changes in visible egg colour (Duval *et al.* 2013). Our results on egg colour therefore indicate that more favourable weather conditions and therefore better female conditions results in less brown, and larger, eggs in agreement to Duval *et al.* (2013). However the herring gull's need for cryptic eggs as an open, ground nesting species crypsis may mean that egg colour does not reliably reflect actual levels of biliverdn and protoporphyrin within the eggshell and pigment concentrations may be better indicators of environmental conditions than visible colouration.

Colony size is another variable that might influence egg traits but is not of direct interest with respect of monitoring the local environmental conditions at the time of study. I found that smaller eggs were laid at larger colonies. A negative correlation between egg size and colony size had been shown between years for an expanding population of herring gulls (Coulson *et al.* 1982) where there might be other confounding factors that changed between years that affected both colony and egg size. Here I showed the same negative correlation between colony and egg size across colonies of different sizes within the same year. Birds may experience greater resource depletion around larger colonies due to greater competition for resources in close vicinity of the colony and may have to forage further afield (Ashmole 1963; Lewis *et al.* 2001; Wakefield *et al.* 2013). These potentially poorer foraging conditions around larger colonies can result in female gulls being unable to invest as much in their eggs (Houston *et al.* 1983; Kilpi, Hillstrom & Lindstrom 1996; Nager *et* *al.* 2000). I found no relationship between colony size and egg colour and maculation, further suggesting that these traits maybe more sensitive to alternative aspects of the environment such as weather conditions.

In our data colony size was positively correlated with the amount of built-up area and number of landfill sites within the foraging range of the colony (see also spatial variation in population trends). Therefore the effect of colony size on egg volume may not only reflect competition but may also reflect the importance of anthropogenic, terrestrial resources for the gulls during egg formation. In the yellow-legged gull *Larus michahellis* average egg volume decreased, as well as average body mass of females, after a decrease in the availability of local anthropogenic, terrestrial resources (Steigerwald *et al.* 2015). Our data cannot distinguish between these two alternative explanations for the relationship between egg volume and colony size.

After taking into account colony size and weather variables, of the environmental variables associated with local foraging conditions, sea surface temperature and chlorophyll a concentration before and during the laying period were the only variables found to explain any of the observed variation in egg traits, and only for egg maculation. For many seabird species foraging from the sea surface, like the herring gull when feeding at sea, higher SST generally results in poorer foraging conditions, due to a reduction in surface water productivity and movement of fish to deeper waters, resulting in less energy intake and therefore lowered egg production (Mills *et al.* 2008; Tomita *et al.* 2009). However, I used SST relatively early in the season when SST is increasing. Marine productivity is largely controlled by the timing of the thermal stratification of marine water and the spring bloom which can vary annually (Townsend *et al.* 1994). During the study period, average SST during March and April 2013 was lower than in the same period in 2014 and 2015. Warmer early season SST in 2014 and 2015 may have led to faster development of the gulls' intertidal prey species (Hiscock *et al.* 2004) and/or resulted in higher productivity earlier in the season due to more favourable timing of the spring algal bloom (Sharples *et al.* 2006) which could have contributed to larger eggs and less brown eggs, both thought to be associated with better female condition, in 2014 and 2015 than in 2013. This suggests that more maculated eggs indicate more favourable foraging conditions in the marine environment in the early breeding season in March and April, although the exact mechanisms underlying this relationship is not known and much variation was left unexplained.

5.6.3 Effect of female resource use on between-colony variation in egg traits

I also investigated how different resources that the gulls were consuming during egg formation influenced egg traits. Larger and more maculated eggs were associated with colonies were the females consumed predominantly marine resources at a relatively high trophic level. Gulls consuming a more marine diet at a high trophic level are expected to be in better condition and invest more heavily into eggs (Annett & Pierotti 1999; Hebert *et al.* 2002). Marine diets at high tropic levels have a higher protein content that can increase egg production capacity in gulls (Bolton *et al.* 1992). More maculated eggs showing a greater marine signal is also consistent with our finding that maculation scores were lower at higher SST and chlorophyll a concentrations, which presumably reflected better foraging conditions in the marine habitat. Therefore favourable local marine foraging conditions in the early season are likely to be reflected in low maculation scores and less maculated eggs signal adverse marine conditions in March and April.

Unexpectedly, colonies where females consumed a predominantly terrestrial diet at a low trophic level were also associated with larger eggs. Terrestrial resources at a low trophic level are arguably be of lower quality to the gulls than marine resources (Pons 1992; Belant *et al.* 1993; Duhem *et al.* 2008; Weiser & Powell 2010; Hobson *et al.* 2015). However, anthropogenic terrestrial resources are likely to be more predictable than food resources in the open sea which are typically patchily distributed (Weimerskirch 2007) or in intertidal habitats which are constrained by the tides (Hunt & Hunt 1973); athough its high and predictable abundance can make up for the low quality, at least in terms of egg size (Steigerwald *et al.* 2015). Larger eggs are not necessarily better eggs (Nager et al. 2000) and this might be reflected by the higher maculation score of eggs laid in colonies predominantly feeding on terrestrial resources and an absence of a relationship with egg colour that could have indicated high egg quality (e.g. Morales, Sanz & Moreno 2006).

5.6.4 Influence of between-colony variation in egg traits on the gulls' demography

In order for the egg traits to be useful in acting as an early warning system of population declines they need to relate information on the gulls' demography (Diamond & Devlin 2003; Parsons *et al.* 2008). I expected that within a year, spatial variation in egg traits would be related to the colony’s productivity. Due to logistical reasons I was unable to determine reliable productivity measures at each of the colonies. Instead I took the brood size towards the end of the breeding season when the chicks were at least three weeks old and therefore likely to survive (Bolton 1991) as a measure of productivity which is relatively straightforward to determine and therefore useful if developing a monitoring tool. Final brood size will reflect the level of offspring mortality with smaller final brood sizes in years with higher offspring mortality, although will over-estimate productivity because it ignores all total nest failures. I found that egg colour related to final brood size, dependent on year, indicating the potential in egg traits to monitor effects of the environment on the gulls’ demography. In 2014, the more favourable year, browner eggs were associated with colonies which had on average a higher final brood size; however there was no significant relationship between final brood size and egg colour in 2013. That a relationship between egg trait and breeding success was only found in the more favourable year may reflect differences in the main causes of breeding failure between years (Robert *et al.* 2015) and therefore breeding failure in 2013 may have been unrelated to the environmental conditions that affected egg colour. On average final brood sizes tended to be higher in 2014 when eggs were also less brown, which had been identified to reflect favourable local environmental conditions. However, the observed relationship between egg colour and final brood size in 2014 was not what I expected. Comparing across the two years it may be that eggs of intermediate brownness were associated with the largest final brood sizes with a decline in final brood size with eggs that were browner than observed in 2014. However, the relationship between final brood size and colour was not significant in 2013 and unfortunately there was little overlap in the colour values between the two years which makes it more difficult to explain why the observed relationships are different between years. One possibility is that there may be a trade-off for females in depositing biliverdin, resulting in bluer-green eggs, and maintaining a more typical brown colouration for crypsis (Duval *et al.* 2013, 2015), then intermediate egg colour values may reflect females in good condition. Surprisingly, neither egg volume nor maculation were sensitive to the environmental conditions when the eggs were formed or found to relate to final brood size. It may be that environmental effects during the early part of the breeding season have relatively little impact on the productivity of the colony compared to factors determining foraging conditions later in the season. Moreover, carry-over effects from environmental conditions experienced during the previous non-breeding season may influence the birds’ condition and their ability and efficiency to forage when they return to the breeding colony (Sorensen *et al.* 2009; Kouwenberg *et al.* 2013; Marra *et al*. 2015).

Egg traits were not related to colony growth between the Seabird 2000 census and the most recent count during 2012/2013 maybe with the exception of a weak relationship between egg volume and colony growth rate, which had a relatively large effect size, although this was not statistically significant. However, given the variable repeatabilities in the extent of spatial variation in egg traits between years this is not surprising. This appears to be attributed to the egg traits responding to inter-annual differences environmental conditions, specifically weather variables and changes in sea surface temperatures between years and highlights the importance of multi-year monitoring.

In conclusion the analysis of herring gull eggs demonstrates that spatial variation occurs in egg traits across south-west Scotland and Northern Ireland which to varying extents relates to local conditions; however only in egg colour does this relate to spatial variation also observed an aspect of the gulls' demography, final brood size. Although it is difficult to identify the drivers of the spatial variation in egg traits local ambient temperature, colony size, marine productivity and the types of resources the females were consuming during egg formation may be contributing factors. Of the four egg traits investigated egg volume was the most sensitive to local conditions and potentially may be weakly associated with colony growth rates; it also the easiest trait to interpret as more information is known about this trait with larger eggs thought to reflect more favourable conditions. However, egg maculation maybe more informative as provides information on local marine conditions which was less clear with egg volume. In addition egg colour was the only trait which related to the colonies productivity; at least in one year. It could therefore be beneficial to investigate multiple egg traits to attain more information about the local environment.

Egg traits are relatively easy and rapid to monitor in herring gulls and other open nesting species, especially using digital photography which reduces the time required in the colony and therefore disturbance to the breeding birds. Although egg maculation was informative on the environmental conditions, it is more difficult to obtain data on as a considerable proportion of eggs did not yield a result using *NaturePatternMatch* but alternative methods (Wegmann *et al.* 2015) may give useful information on a larger proportion of the eggs and would be alternatives worth exploring in the future. Extracting information on egg traits in seabirds has the potential to be a useful technique to monitor the state of the marine environment, at least during the early breeding season which is not covered by monitoring the productivity of seabird colonies. This may provide a new monitoring tool increasing the temporal coverage of the marine ecosystem and at the same time may also serve as an early warning system of adverse conditions impacting a seabird community.

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Supplementary Information

Figure S-1. Egg holder to photograph herring gull eggs in the field with the graph paper background and QPcard+201 colour checker panel and scale.

Figure S-2. Contrasting egg shapes with (a) low egg shape deviation scores describing oval eggs and (b) high deviation scores describing pointy eggs.

Figure S-3. Contrasting egg colour with (a) bluer, less brown egg reflecting a low GB ratio and (b) brown egg reflecting a high GB value.

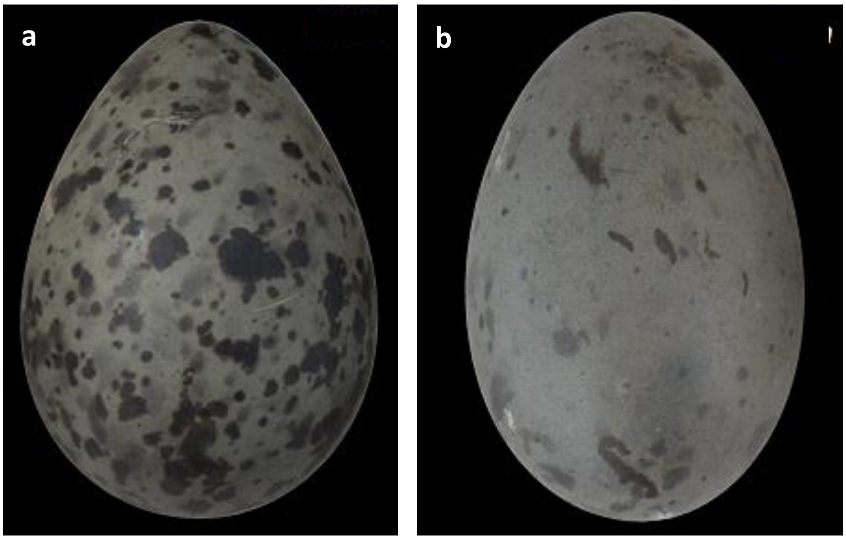

Figure S-4. Contrasting egg maculation with (a) highly maculated egg reflecting a low similarity score and (b) less maculated egg reflecting a high similarity score.

Chapter 6

6 Spatial variation in the foraging behaviour of the herring gull

6.1 Abstract

Population trends are frequently used and invaluable in determining changes in animal populations. However, especially in long-lived species, it can be difficult to determine significant changes in the population level without many years of data. Instead, alternative species traits need to be investigated that can identify changes occurring in an animal's environment over shorter time periods and that ultimately impact on population level are required. The behaviour of animals has recently been suggested as a means of looking for changes in the environment – for example foraging or breeding behaviours. In long-lived seabirds observing foraging behaviour is relatively easy and are directly influenced by local food availability especially in the breeding season when the birds are constrained to the breeding colony. I investigated spatial variation in several foraging behaviours (nest attendance, provisioning rate and trip duration) of a widespread coastal seabird across south-western Scotland and Northern Ireland, the herring gull *Larus argentatus*. Spatial variation was found in the foraging behaviours of herring gulls during the chick-rearing period; which were to some extent related to local environmental conditions. The proportion of time nests were left unattended related to the amount of built-up area within the foraging range of the colony and nearest distance to farmland, the latter depending on year. Provisioning rate and trip duration were both related to standardised SST; whilst provisioning rate was also related to average wave fetch within the gulls' foraging range. Of the three foraging behaviours trip duration was found to be associated with a measure of the gulls' demography, final brood size. I also found a large effect size for the association between nest attendance and colony GR, although the relationship was not statistically significant. These results highlight that during the chick-rearing period foraging behaviour is sensitive to proxies of local resource availability, likely to be driven by environmental conditions; with trip duration and nest attendance having the potential to be used in monitoring of the coastal marine environment.

6.2 Introduction

A wide variety of traits can be investigated to provide information on how a species is responding to its local environment; and which can then be used to determine the state of that species or its habitat. These traits can be associated with an animal's demography, such as population abundance, survival and productivity which will reflect conditions over long time periods of a breeding season to years (Cairns 1987a; Diamond & Devlin 2003). Traits can be associated with an animal's physiology such as body condition and stress which reflects the condition of the bird and its environment over shorter time periods of hours, days to weeks (Cairns 1987a; Le Maho 1993; Montevecchi 1993; Shultz & Kitaysky 2008; Legagneux *et al.* 2013). Other traits that can potentially reflect environmental conditions over these smaller time frames are traits associated with an animal's behaviour (Monaghan 1996; Wildermuth *et al.* 2012). Traits which reflect environmental conditions over shorter time frames have the advantage of detecting responses of species to change of environmental conditions at time scales that are more useful to inform conservation, management and policy decisions.

Behaviour has been used in conservation to determine the impact of fragmented habitats, exploitation and disturbance of species, disease and re-introductions of species as well as in population monitoring (reviewed in Caro 1999). In particular individual differences in behaviour can be important in determining how susceptible individuals are to changes in their environment; with variability in mobility, mating systems and foraging all potentially impacting on how they respond to a changing environment (Berger 1996; Ulfstrand 1996). Specifically, behaviours relating to movement, foraging and breeding have the ability to influence survival and reproduction and therefore impact on population trends; these behaviours can therefore reveal pressures acting on a population or the resources/habitats they rely on (Berger-Tal *et al.* 2011). In return behaviours can then be used to monitor changes occurring within the environment whether due to natural or anthropogenic causes (Berger-Tal *et al.* 2011). Use of behaviour can therefore act as an early warning system of changes in the environment that eventually could lead to population declines, especially if the behaviour can act as a proxy to demographic parameters, for example with behavioural indices as indicators of population trends (Wildermuth *et al.* 2012; New *et al.* 2014). Investigating animal behaviour has therefore been identified as an important aspect of monitoring, however it is not always incorporated into conservation/management decisions (Caro 2007). It should also be noted that variation in the correlation between behavioural traits and measures of an animal's demography may be influenced by factors such as weather conditions that might mask a species responses to changes in environmental conditions of interest (Wildermuth *et al.* 2012).

Foraging behaviours are particularly effective in reflecting local environmental conditions over relatively short time periods of hours, days to weeks, particularly food availability (Croll *et al.* 1998; Wilson *et al.* 2002; Austin *et al.* 2006; Lewis *et al.* 2008; Wildermuth *et al.* 2012). A better understanding of causes of variation in foraging behaviours can therefore provide important insights into the status of the environment (Guilford *et al.* 2008; Wildermuth *et al.* 2012), as well as potential drivers of population abundance. Behaviours associated with a species' foraging strategies can be impacted upon by numerous factors, specifically by the availability, quality and distribution of food (Pyke 1984; Quintana 2008) as well as environmental conditions such as weather (Finney *et al.* 1999; Bustnes *et al.* 2010, 2013).

The marine environment is one which is currently experiencing increasing pressures, especially in coastal habitats (Costanza *et al.* 1998; Halpern *et al.* 2008). However, monitoring environmental change in marine habitats is challenging due to its inaccessibility, therefore the response of species, largely apex predators, are frequently investigated to infer changes within this ecosystem (Boyd *et al.* 2006). Of these apex predators seabirds have a number of advantages, especially in terms of observing their behaviour, as they are relatively conspicuous, particularly during the breeding season when they are constrained to return to land to breed, and being largely colonial many individuals can be observed at once (Furness & Greenwood 1993; Rice & Rochet 2005; Piatt *et al.* 2007b; Durant *et al.* 2009).

During the breeding season once the chicks have hatched behaviours of adults related to foraging can be readily observed including foraging trip duration, provisioning rates and nest attendance (Uttley *et al.* 1992; Wanless & Harris 1992; Kitaysky *et al.* 2000; Chivers *et al.* 2012). These foraging behaviour traits can provide useful indices of the status of food resources and provide an indication on the abundance and spatial and temporal distribution of their prey (Monaghan 1996).

In general where environmental conditions result in poorer foraging conditions, resulting in lower food availability, birds spend more time foraging, have reduced provisioning rates, and attend the nest less, often resulting in lower productivity due to higher chick starvation, predation and exposure risk (Hamer *et al.* 1992; Uttley *et al.* 1992; Harding *et al.* 2007; Chivers *et al.* 2012). If changeover times at the nest are short, resulting in few instances with both parents attending the nest simultaneously, it indicates that the adults are required to spend as much time foraging as possible (Quintana 2008). If poor conditions necessitate even longer times spent on foraging trips, nests may be unattended for increasing proportions of time. A high nest attendance by at least one parent is important as it impacts on the adult's ability to protect their young from unfavourable weather conditions and predation (Hamer *et al*. 1991). The predation risk of unattended nests can be further exacerbated by poor foraging conditions when eggs and chicks provide an attractive alternative food availability for potentially nest predating seabird species (Uttley *et al.* 1989; Bukacińska *et al.* 1996; Regehr & Montevecchi 1997). In years where local environmental conditions result in adults spending more time foraging away from the nest and bringing in less food for the chicks, breeding success is often reduced (Schreiber & Kissling 2005; Chivers *et al.* 2012).

In this study I aim to investigate foraging behaviours (nest attendance, provisioning rate and trip duration) from multiple colonies of a generalist gull species, the herring gull *Larus argentatus* (Hunt & Hunt 1973; Götmark 1984). I therefore hypothesised that (i) where local foraging conditions are favourable nest attendance and provisioning rates will be high and trip durations will be relatively short; conversely where local environmental conditions are poor it is expected that nest attendance and provisioning rates will be low and trip durations will be longer. I then test (ii) whether any observed variation in foraging behaviours impacts on the gulls' demography; hypothesising that greater breeding success and increasing colony size will be observed in colonies where foraging behaviours indicate more favourable local environmental conditions. I tested these predictions by comparing foraging behaviours in seven contrasting colonies over two years. The results will indicate which foraging behaviours are sensitive to local environmental conditions and whether they are related to aspects of the gulls' demography; and therefore whether foraging behaviours can act as useful monitoring traits for management and conservation of coastal marine habitats.

6.3 Methods

6.3.1 Study area

I studied the foraging behaviour from seven herring gull colonies over south-west Scotland and Northern Ireland during 2013 and 2014 (Table 6.1, Figure 3.1). The study region covered an approximate area of 200 by 250 km. Colonies were selected where numbers of herring gull breeding pairs had experienced contrasting population trends between the late 1960s and 2000 (see Chapter 2). Herring gull nest observations were carried out in each colony over two breeding seasons to record foraging behaviour and breeding success.

6.3.2 Nest observation watches

Colonies were visited on multiple occasions throughout the chick rearing period between 01/06/2013-16/07/2013 and 03/06/2014-04/07/2014 at 10-14 day intervals (Table 6.1). On average each colony was visited on six separate dates across each breeding season (range 2-14) with multiple watches completed on each visit. A watch was defined as a three hour observations period from specific vantage points allowing up to 24 focus nests to be observed simultaneously whilst not causing disturbance to the birds, using an observation hide where necessary. Focus nests had to have unobstructed view from the vantage point had been identified as herring gull nests from observing the attending adults. Watches from the same vantage point were repeated on different colony visits and hence I had multiple observations of the same nests.

Table 6-1. Number of herring gull observational watches and total number of nests observed per colony

Colony	2013		2014		Total	
	Nests[1]	Obs. Hours[2]	Nests	Obs. hours	Nests	Obs. hours
Copeland[3]	11	171	36	447	47	618
Islay	17	387	8	263	25	650
Lady Isle	-	-	19	117	19	117
Oronsay	18	486	34	312	52	798
Pladda	40	588	33	255	73	843
Portpatrick	15	345	66	849	81	1194
Strangford[4]	25	240	41	381	66	621
Total	126	2217	237	2624	363	4841

[1] Total numbers of nests observed for each colony. [2] Total observation hours from all nests and watches. [3] All observational watches were completed on Lighthouse Island. [4] Observational watches at Strangford were undertaken on two different sites (Round Island and Green Island in 2013, Green Island in 2014) that are within 7km of each other.

Watches were carried out in daylight hours between 06:00 and 20:00; categorised into morning (06:00-10:00), mid-day (11:00-14:00) and evening (14:00-20:00) at low and high tide (± three hours of lowest and highest level, respectively; watches outside of this time frame were classified as slack tide) randomly distributed throughout the day. All watches were carried out in weather conditions with no or light rain and when the sea state/wind conditions were below a Beaufort scale of five. There was no difference in the mean date in which watches were carried out across colonies and years (two-way ANOVA including interaction between colony and year: all $P > 0.33$). During each watch the number of chicks present at each nest (brood size) was recorded. As all colonies showed a similar timing of breeding, and therefore hatching dates (Chapter 5), chicks observed later in the season were also older chicks. As a proxy for chick age through the breeding season Julian day was included in the analysis. All colonies hatched around the same time (Chapter 5) and the differences in dates watches took place were larger than variation in hatching date within individual colonies, so that Julian date gives a good approximation of chick age although it may also reflect changes in environmental conditions through the season. The number of chicks and Julian day may affect the parent's behaviour; for example provisioning rates may be higher at nests with more and larger chicks (Emms & Verbeek 1991), whilst nest attendance may be higher, and trip durations shorter, when the chicks are young (Coulson & Johnson 1984; Ojowski *et al.* 2001). Observation watches were carried out by eight observers; four in 2013 and five in 2014; including one observer in both years.

To determine whether observation watches at each colony over the two years were equally distributed across time of day (morning, mid-day or evening) and tidal state (low, slack, high) I carried out Pearson's χ^2 tests of independence in R, Version 3.2.1 (R Development Core Team 2015) with the number of watches carried out during each time or tide category for each colony across the two years. There were no significant differences in the number of observation watches carried out at different times of day ($\chi^2_{12} = 15.36$, $P = 0.22$) or at different tidal states ($\chi^2_{12} = 18.38$, $P = 0.11$) across colonies.

During observation watches, nests were scanned every five minutes and recorded whether zero, one or two adults were attending the territory. Birds were recorded as attending a territory if they were present on the nest; were present in close proximity of the nest and positively interacted with the chicks or other attending adult if present; or were present in close proximity to a nest which was known to be part of the territory from observing the birds from that territory on previous watches. Nest non-attendance was defined as the proportion of observation time per nest and watch where no adult was present on the territory. Provisioning of chicks was recorded when it occurred. When chicks were provisioned on more than one occasion within the same watch a new provisioning event was only recorded if that adult had left the territory and undertaken another foraging trip (minimum time away: 20 minutes – see below), or if the chicks were fed by the other returning adult. This definition treats all parents' attempts of feeding chicks from the preceding foraging trip as one provisioning event. For each nest the provisioning rate was calculated as the number of provisioning events per three hour watch. Foraging trip duration was defined as the time from when a bird left the territory to the time it returned to the territory's vicinity; derived from the nest attendance information. In a few cases the individuals of the pair could be identified due to one being ringed or where one of the pair was a sub-adult. However, as most adults within a pair were not marked foraging trip duration of these birds could not be distinguished as individuals and therefore trip duration could only be estimated when both birds were on the territory and one bird left and returned whilst the partner remained at the nest. For the analysis only trips of twenty minutes or more in length were included as short periods away from the colony less than twenty minutes are unlikely to be foraging trips (Bukacinski, Bukacinska & Spaans 1998).

To determine whether there was any variation in the quantification of behaviours between different observers carrying out watches in the same colony and at the same date I carried out linear mixed-effects models in the R package *lme4* (Bates *et al.* 2014) with nest non-attendance and provisioning rate as the response variable, respectively. This was not repeated for trip duration as this was calculated from the nest non-attendance values. Observer, number of chicks, year and Julian day were also included as fixed effect to take into account potential confounding effects of brood size and different external circumstances, respectively, and colony as a random effect. There was a significant difference in nest non-attendance between observers ($\chi^2_1 = 96.72$, $P < 0.001$); driven by one observer recording significantly higher nest non-attendance than five of the seven other observers ($P < 0.01$). Provisioning rate also differed between observers ($\chi^2_1 = 22.05$, $P = 0.003$); again this was only due to the same observer recording significantly lower provisioning rates than one of the seven other observers ($P < 0.001$). Therefore watches from that one observer were not included in further analysis; resulting in six less watches included for 2014, three from Copeland and three from Strangford. There were no differences in nest non-attendance ($\chi^2_1 = 8.85$, $P = 0.18$) and provisioning rate ($\chi^2_1 = 5.67$, $P = 0.46$) between the remaining observers included into the analyses.

6.3.3 Environmental correlates of foraging behaviours

Data on environmental variables which could potentially affect the foraging behaviour of herring gulls during the chick rearing period (start of June to mid-July) were obtained for the 2013 and 2014 breeding seasons. As herring gulls are generalist foragers (Hunt & Hunt 1973; Kubetzki & Garthe 2003) these environmental variables need to represent the range of marine and terrestrial resources that the gulls are utilising. To correspond to the foraging range of herring gulls, environmental variables were extracted for an area of 50 km around each study colony (Spaans 1971; Götmark 1984). To represent the marine offshore foraging habitat, I obtained data on sea surface temperature (SST - 11µ night-time) and chlorophyll a concentration (mg/m^3) over the chick rearing period from http://oceancolor.gsfc.nasa.gov/cgi/l3 as a proxy for marine productivity. Chlorophyll a concentration is a proxy for primary productivity at the base of the marine food web, with higher chlorophyll a concentrations reflecting higher primary productivity, whilst SST influences marine processes associated with thermoclines and upwelling which will influence the distribution and abundance of the gulls' potential marine prey species (Huot *et al.* 2007). Herring gulls also forage extensively in the marine intertidal area (Hunt & Hunt 1973; Kubetzki & Garthe 2003), and the abundance of invertebrate prey in the intertidal area of rocky shores, the main shore habitat in my study region, can be predicted from wave fetch (Burrows *et al.* 2008; Burrows 2009). Wave fetch is the length of water over which a given wind has blown, therefore higher wave fetch reflects a more exposed coastline; wave fetch data were obtained from Burrows (2009). In terrestrial habitats gulls are known to utilise resources associated with farmland (agriculture and improved grassland), landfill sites and in built-up areas (e.g. Pons 1992; Belant *et al.*

1993). Therefore I used the extent of and distance to the nearest farmland and built-up area and the number of landfill sites within each colony's foraging range as a proxy for the potential availability of anthropogenic food. Data on farmland and built-up areas were obtained from (Fuller *et al.* 2002); whilst information on number of landfill sites for each foraging range was obtained for Scotland from SEPA (2015) and for Northern Ireland from NIEA (Eugene Kelly, pers. comm.). More detailed description of the environmental variables can be found in the Chapter 2.

6.3.4 Demographic variables

To determine whether any spatial differences in foraging behaviours were associated with demographic traits, behaviour traits, averaged over all observed nests from each colony and year, were related to measures of success of that colony. First, I used final brood size, as a measure of current breeding success; defined as the number of chicks of at least three weeks old, and therefore likely to successfully fledge (Bolton 1991). Final brood size was estimated from a sample of nests known to have hatched eggs as determined from observation watches (mean of 16±9 nests, range 4-33, n = 7 colonies). If colonies consistently differ in in how favourable the environment is for successful breeding then good breeding success in the long-term could translate into positive colony growth rate (GR). GR was calculated between the last seabird census, between 1998-2002, Seabird 2000 (Mitchell *et al.* 2004) and the most recent available count; using a formula as explained in Nager & O'Hanlon (in press): GR = $(N_t - N_{t-1})/\text{Maximum}\ [N_t, N_{t-1}]$.

6.4 Statistical analyses

All statistical analyses were performed in R, Version 3.2.1 (R Development Core Team 2015). Diagnostic plots were checked to ensure all model assumptions were met. To ensure the residuals of the nest non-attendance and trip duration models met the normality assumption of the general linear mixed effect multivariate models both were natural *logarithm* transformed; however this was not required for the demography models. The unit of analysis was therefore the number the nests; with multiple values for each nest due to being observed on multiple watches. For nest non-attendance 0.01 was added to all values before being natural *logarithm* transformed due to the presence of zero values. Starting with the most complex model, including only biologically relevant two-way interactions, I performed model simplification to identify the minimal adequate model by carrying out Likelihood Ratio tests, that follows a χ^2 distribution, to establish whether the exclusion of a term resulted in a significantly poorer fit of the model (Crawley 2007). Main effects that were part of significant interaction terms were not tested as they could not be removed from the model in isolation. Interaction terms are only shown when statistically significant. R^2 values for the linear mixed effect multivariate models were calculated in the R package *MuMIn* (Barton 2012). This calculates the "marginal" R^2 value ($R^2_{GLMM(m)}$) which is the proportion of the variance in the dependent variable that is explained by the fixed variables and the "conditional" R^2 value ($R^2_{GLMM(c)}$) which is the proportion of the variance in the dependent variable that is explained by the fixed and random variables (Johnson 2014). Significance thresholds were set at two-tailed $P < 0.05$. Mean ± standard deviation values are reported.

Factors like time of day or tidal state can affect the gull's foraging behaviour (Burger 1976). However, none of the three behaviours were related to the time of day (mixed effect multivariate models with colony and year as random effects; provisioning rate: $\chi^2_1 = 0.04$, $P = 0.98$; nest non-attendance: $\chi^2_1 = 0.79$, $P = 0.67$; trip duration: $\chi^2_1 = 0.77$, $P = 0.68$) or tidal state (provisioning rate: $\chi^2_1 = 1.76$, $P = 0.42$; nest non-attendance: $\chi^2_1 = 0.80$, $P = 0.67$; trip duration: $\chi^2_1 = 4.12$, $P = 0.13$). Therefore, I did not have to account for these factors in any further analysis of the gulls' behaviour.

I determined the repeatability of the foraging behaviours per colony between the two study years. The expected values of behavioural traits did not vary over the two breeding seasons across the colonies (analysis not shown), therefore I calculated consistency repeatabilities, *Rc*, (Nakagawa & Schielzeth 2010; Biro & Stamps 2015) using linear mixed-effects models (LMM) in R's *lme4* package (Bates *et al.* 2014); with year as the fixed effect and colony as a random effect. The three behavioural traits are expected to be related as if foraging conditions are good nest non-attendance and provisioning rate are expected to be high and trip duration short; whilst if local conditions are poor then nest non-attendance and provisioning rate are expected to be low and trip duration long. I investigated the pairwise relationships between foraging behaviours using LMMs with one foraging behaviour as the dependent variable, another foraging behaviour and year as a fixed effects. To account for multiple observations of the same nests on repeated watches I used watch as a random effect and nested it within colony as another random effect. To investigate the spatial and temporal variation in foraging behaviours I carried out several LMMs using the *lme4* package (Bates *et al.* 2014), one for each foraging behaviour as the response variable, and location and year as fixed effects and watch as a random effect.

To determine whether local environmental variables representing resources that the gulls use influenced the three foraging behaviours I carried out three separate LMMs; one LMM with each behaviour as the response variable. Environmental variables (extent and distance to the nearest built-up area and farmland, number of landfill sites, chlorophyll a concentration, sea surface temperature and wave fetch) and year were included as explanatory variables; whilst watch nested within colony were included as random effects to account for multiple observation watches of the same nests and watches from the same colony in the two years. Julian day (1 – 1st January) when the watch took place and brood size at that observation were also included as fixed effects to account for any potential confounding effects of season, age and number of chicks on the three foraging behaviours. As I was only interested in the effects of local environmental conditions on within-year variation rather than on the between-year differences in behaviours, chlorophyll a concentration and sea surface temperature were standardised to remove between year differences. Variables were standardised by taking its difference from that year's mean and divided by the standard deviation. Due to the potential multi-collinearality of the explanatory variables, pairwise correlations and variance inflation factor (VIF) values were checked and only variables with a VIF < 3 were included in the multivariate analysis (Zuur *et al.* 2010). Due to a strong correlation between the number of landfill sites and the amount of farmland and built-up area within the gulls' foraging range I could only include amount of built-up area as a proxy of these terrestrial resources in the analysis (Spearman $r > 0.78$, $P < 0.001$). There was also a significant negative correlation between distance to the nearest built-up area and to the nearest farmland (Spearman $r > 0.29$, $P < 0.001$) so I only included distance to nearest farmland in further models, but it meant the models could capture the influence of two important anthropogenic characteristics. Finally, a positive correlation between standardised chlorophyll a concentration and sea surface temperature (Spearman $r > 0.70$, $P < 0.001$) meant I could only include standardised sea surface temperature, which had the lower VIF value, of these two proxies for marine conditions. Therefore, environmental variables that could be included into the final LMMs were distance to nearest farmland and extent of built-up area as proxies for terrestrial resources, and wave fetch and standardised SST as proxies of marine resources.

To determine whether the foraging behaviours per colony were related to the demographic characteristics of that colony LMMs were carried out using R's *lme4* package (Bates *et al.* 2014) with demographic trait as response variable, foraging behaviour (separate models for each behaviour) and year as fixed effects, and colony as a random effect. Foraging behaviours were averaged per colony and year therefore as demographic characteristics I had data on average final brood size for 13 colony years; the unit of analysis. To investigate the relationship between the foraging behaviours and colony GR separate linear models were carried out with each foraging behaviour as an explanatory variable in turn and colony GR as the response variable. Data on colony GR and behaviours were available for seven colonies. For the linear models the effect size (*f*) of the foraging behaviours on colony GR were also calculated; using the adjusted R^2 values from the linear models, with $f = \sqrt{(R^2 / (1-R^2))}$.

6.5 Results

Average nest non-attendance and provisioning rate were calculated for on average 28 ± 16 (± SD) nests and 12 ± 4 observation watches per colony across seven colonies and two breeding seasons (Table 6.1). From these observation watches I identified 552 complete foraging trips, 229 from six colonies in 2013 (mean trip duration = 53 ± 30 minutes) and 323 from seven colonies in 2014 (48 ± 29 minutes).

Among the three foraging behaviours only nest non-attendance and trip duration were correlated (LMM with year as a fixed effect and watch nested within colony as random effects; $\chi^2_1 = 22.54$, $P < 0.001$, $R^2_{\mathrm{GLMM(m)}} = 0.04$); with longer trips carried out where nest were left unattended for less often There was no relationship between provisioning rate and adult non-attendance ($\chi^2_1 = 0.04$, $P = 0.835$) or trip duration ($\chi^2_1 = 0.25$, $P = 0.617$).

6.5.1 Spatial and temporal variation

All three behaviours differed between colonies (Figure 6.1) but only nest non-attendance also differed between years. Nest non-attendance differed between colonies and years (colony: $\chi^2_1 = 176.75$, $P < 0.001$; year: $\chi^2_1 = 11.33$, $P < 0.001$; $R^2_{\mathrm{GLMM(m)}} = 0.14$). The spatial variation in nest non-attendance (Figure 1a) was attributed to Islay having nests unattended for longer than Pladda and Copeland; and Pladda having nests unattended for longer than all colonies except Islay and Lady Isle; whilst Copeland had significantly lower nest non-attendance than Pladda and Oronsay. Nests were left unattended for a lower proportion of time in 2013 (0.08 ± 0.17) than in 2014 (0.12 ± 0.20). Provisioning rate also varied between colonies ($\chi^2_1 = 95.59$, $P < 0.001$, $R^2_{\mathrm{GLMM(m)}} = 0.08$) attributed to Lady Isle and Portpatrick having higher provisioning rates than the remaining colonies (Figure 1b). Trip duration varied between colonies ($\chi^2_1 = 19.24$, $P < 0.004$, $R^2_{\mathrm{GLMM(m)}} = 0.04$), however no differences were found between individual colonies from the post-hoc multiple comparisons (Figure 1c).

The within-colony repeatabilities (*Rc*) of foraging behaviours across the two breeding seasons were relatively low. *Rc* for nest non-attendance (*Rc* = 0.099, 95% confidence intervals (CI): 0.018 – 0.208) and provisioning rate (*Rc* = 0.074, CI: 0.014 – 0.166) were low but both significantly different from 0 ($P < 0.001$). The within-colony repeatability for trip duration, however, was not different from zero (*Rc* = 0.04 CI: 0.0 – 0.121, $P > 0.99$).

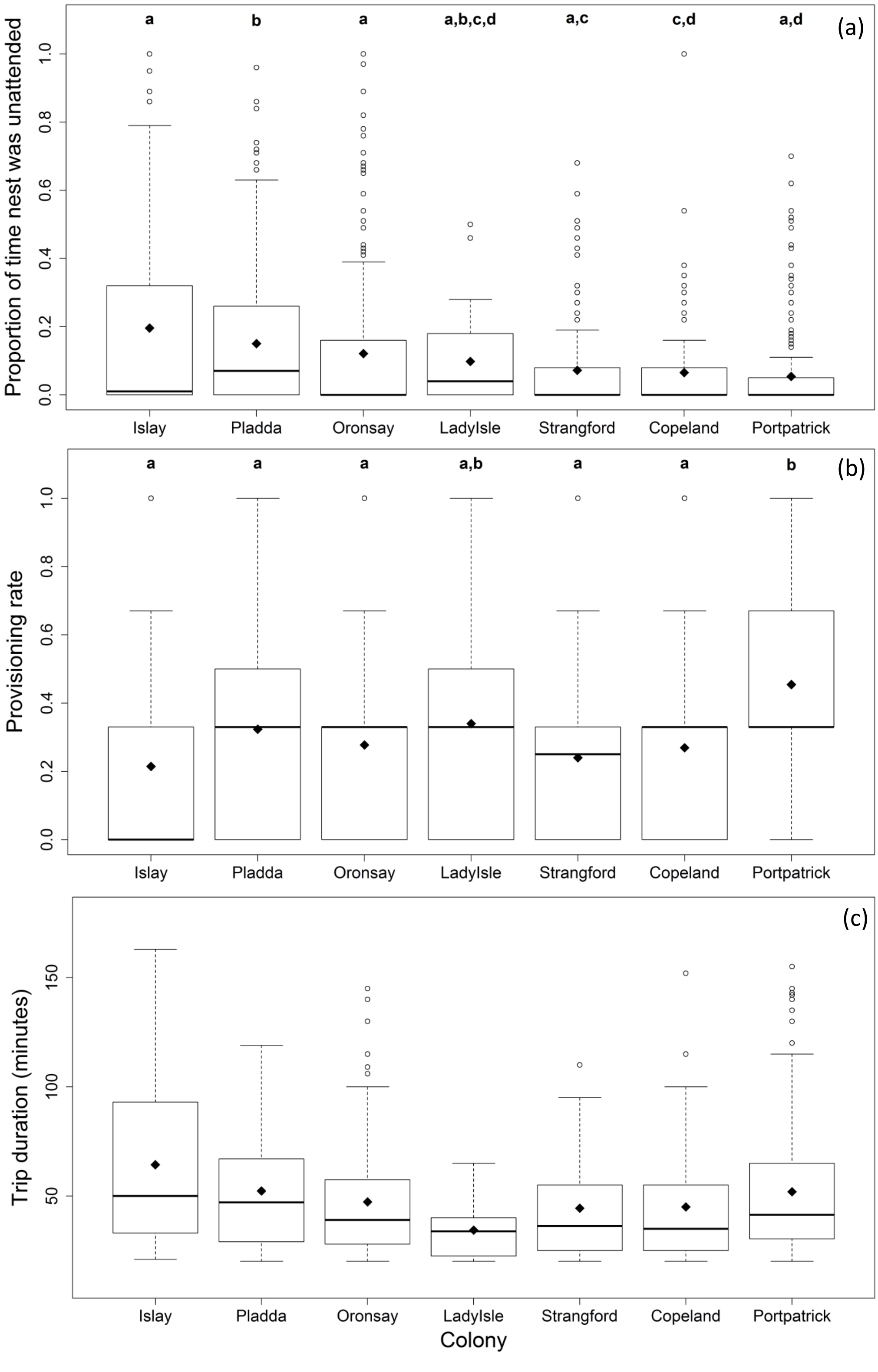

Figure 6-1. Between-colony differences in the three foraging behaviours (a) nest non-attendance, (b) provisioning rate and (c) trip duration across the two study years. Boxplots show median (horizontal line), inter-quartile ranges (box), and minimum and maximum values (whiskers). Diamonds show the mean values. Colonies are ordered based on the highest to lowest mean nest non-attendance. Means with different letters above the boxes are significantly different (Tukey's HSD post-hoc multiple comparisons with Bonferroni correction, *P* < 0.002).

6.5.2 Environmental variables associated with between-colony variation in foraging behaviours

The environmental variables significantly associated with the between-colony variation in foraging behaviours are presented in Table 6.2. Brood size, Julian day (as a proxy for brood age) and year all accounted for some of the variation observed in foraging behaviours. For nest non-attendance I found that the proportion of time adults left the nest site unattended increased with Julian day (Table 6.2a), however provisioning rate and trip duration were not associated with Julian day ($P > 0.08$). I also found that provisioning rates were higher in nests containing more chicks (Table 6.2b); however, no relationship of brood size was found with nest non-attendance or trip duration ($P > 0.28$).

Of the environmental variables that serve as proxies for availability of resources, I found that the amount of built-up area in the foraging range of the colony, and the distance to farmland dependent on year, were associated with nest non-attendance (Table 6.2a). In colonies with high amounts of built-up area in the foraging range nests were left unattended for a lower proportion of time (Figure 6.2a). The location of colonies in relation to farmland had a different influence on nest non-attendance in the two breeding seasons (Figure 6.3b) with nests in colonies closer to farmland being left unattended for a lower proportion of time in 2013 than in 2014. Variation in provisioning rates between colonies was associated with the average wave fetch and standardised SST (Table 6.2b). Provisioning rates increased with increasing average wave fetch (Figure 6.3) and SST (Figure 6.4a) in the colony's foraging range. I also found that SST was related to trip duration (Table 6.2c); with shorter foraging trips associated with higher SST (Figure 6.4b).

Table 6-2. Parameter estimates from general linear mixed models of the relationship between foraging behaviours, (a) nest non-attendance, (b) provisioning rate and (c) trip duration as the response variables in turn against environmental variables as well as year, Julian day and brood size as fixed effects. Observational watch nested within colony was included as random effects.

Response variable	**Explanatory variable**	**Estimate**	**SE**	X^2	P	R^2
(a) Nest non-attendance	Intercept	-11.707	1.145			
	Year	0.635	0.152	-	**-**	
	Dist. to farmland (km)	0.354	0.086	-	**-**	
	Built-up area (km^2)	-0.344	0.056	33.60	<**0.001**	
	Day	0.047	0.007	42.08	<**0.001**	0.20
	Farmland * Year	-0.343	0.111	8.10	**0.005**	(0.35)
(b) Provisioning rate	Intercept	0.181	0.026			
	Wave fetch	0.062	0.012	24.24	<**0.001**	
	Standardised SST	0.029	0.012	6.09	**0.014**	
	Brood size	0.085	0.010	75.07	<**0.001**	0.09
	Year	-0.051	0.024	4.45	**0.035**	(0.21)
(c) Trip duration	Intercept	3.819	0.028			0.02
	Standardised SST	-0.066	0.028	5.69	**0.017**	(0.13)

R^2 is the "marginal" R^2 value ($R^2_{\mathrm{GLMM(m)}}$) which is the proportion of the variance in the dependent variable that is explained by the fixed variables. Value in brackets is the "conditional" R^2 value ($R^2_{\mathrm{GLMM}(c)}$) which is the proportion of the variance in the dependent variable that is explained by the fixed and random variables.

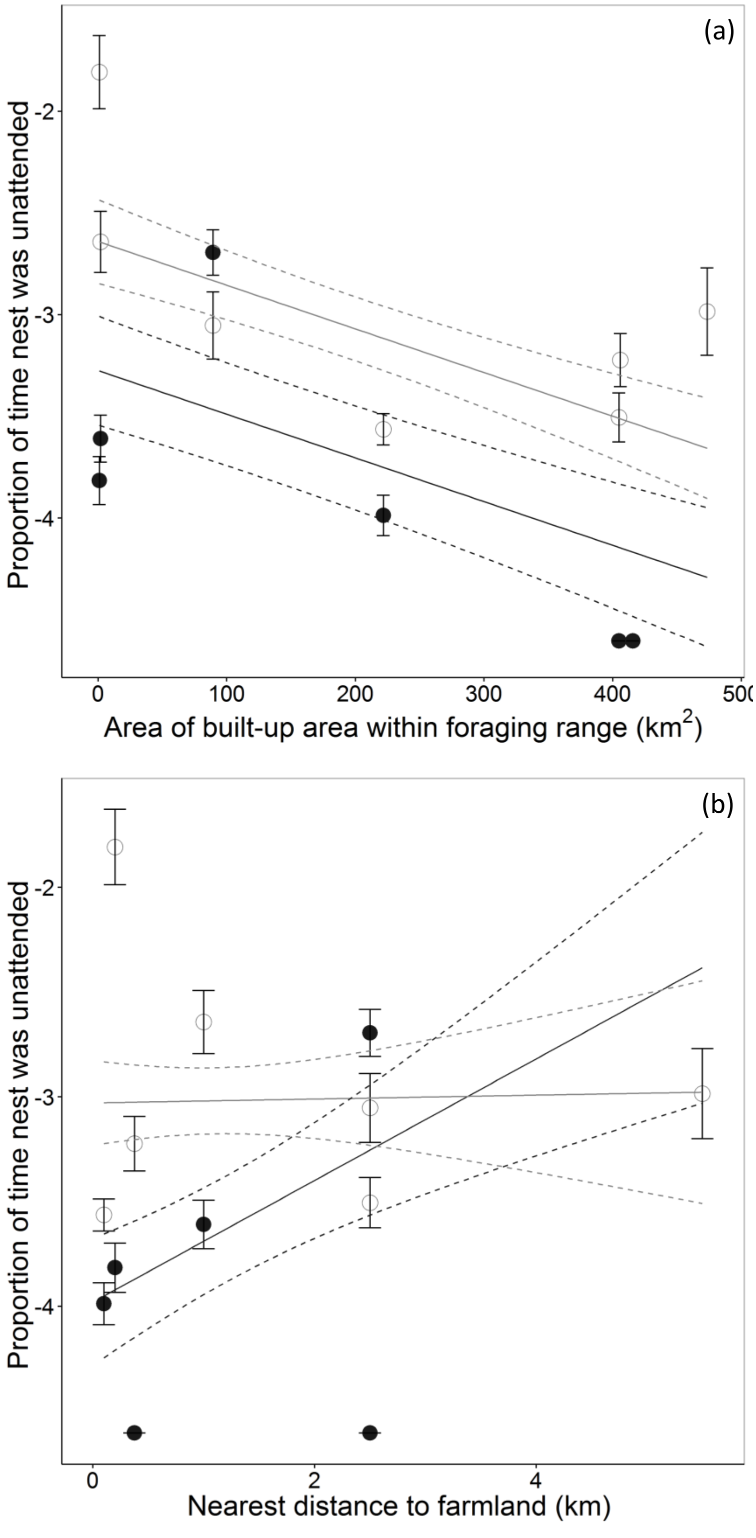

Figure 6-2. Mean ± 1 SE of the proportion of time the nest was left unattended (natural logarithm transformed) against (a) amount of built-up area within 50km of the colony (km^2) and (b) nearest distance to farmland (km). Black filled circles and black lines: 2013, grey open circles and grey lines: 2014. The solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

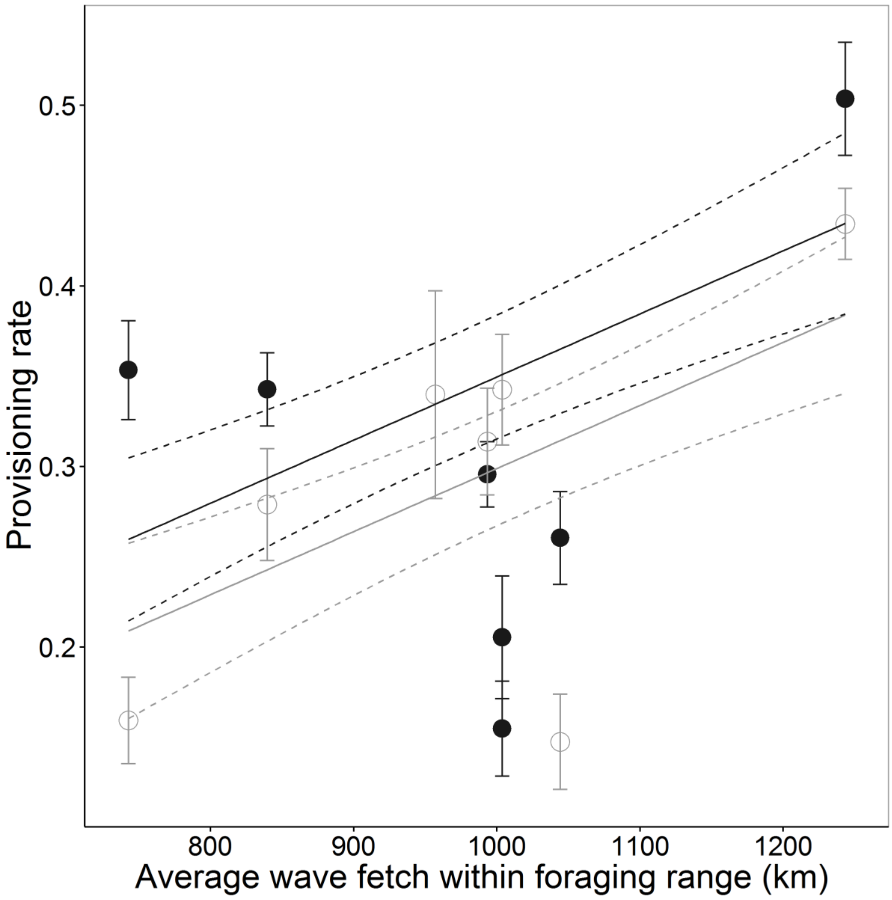

Figure 6-3. Mean ± 1 SE of average provisioning rate against average wave fetch within 50km of the colony (km). Black filled circles and black lines: 2013, grey open circles and grey lines: 2014. The solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

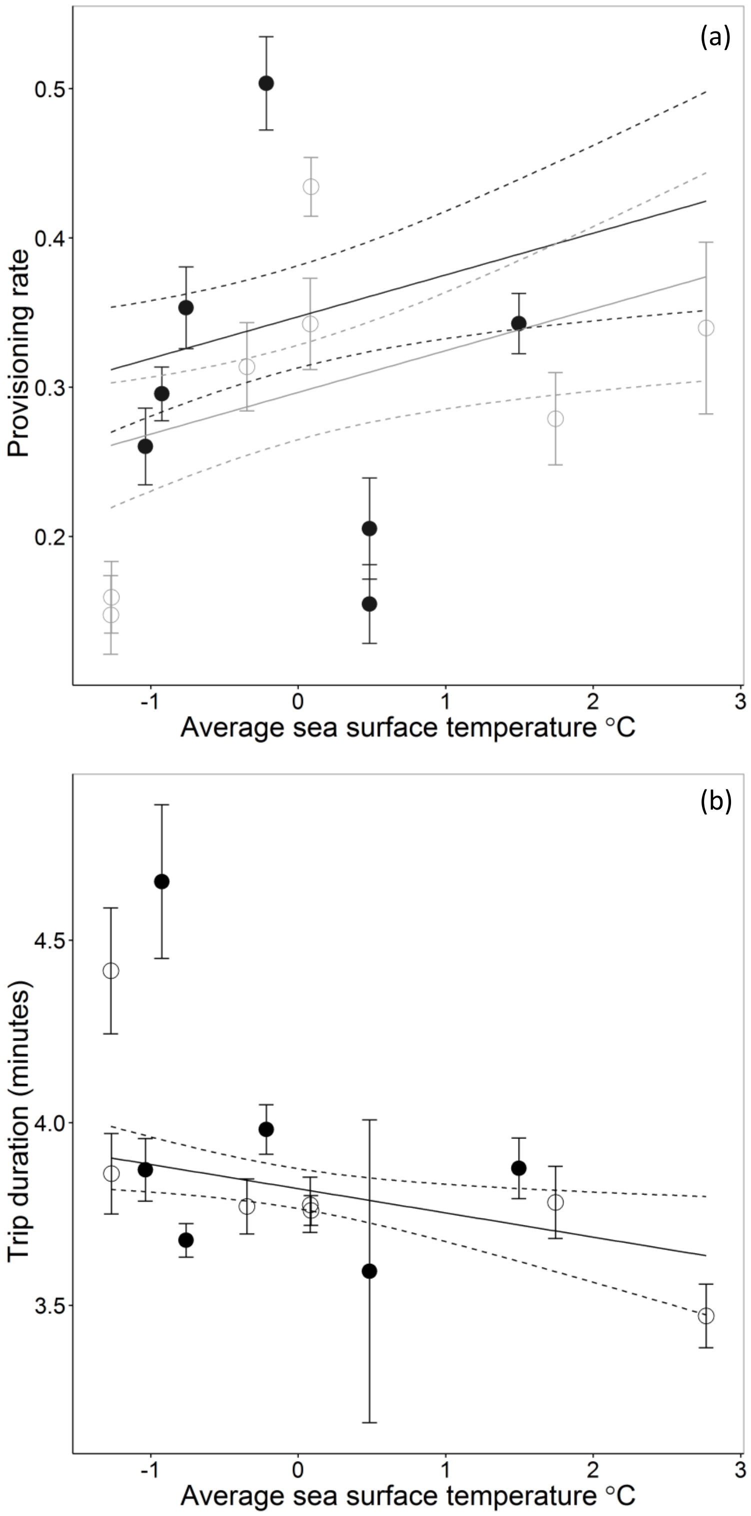

Figure 6-4. Mean standardised annual sea surface temperature (SST °C) within 50km of the colony against mean ± 1 SE (a) provisioning rate and (b) trip duration (natural logarithm transformed). Black filled circles and black lines: 2013, grey open circles and grey lines: 2014. The solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model. As only the model for provisioning rate included year, separate lines for 2013 and 2014 are shown in (a) but not in (b).

6.5.3 Demographic variables

I found that trip duration was significantly related to final chick brood size. Final brood size was larger in 2014 than in 2013, with, in both years, shorter trip durations recorded in colonies with larger final brood sizes (LMM, year: $\chi^2_1 = 4.60$, $P = 0.032$; trip duration: $\chi^2_1 = 5.50$, $P = 0.019$; $R^2_{\mathrm{GLMM(m)}} = 0.44$; Figure 6.5). Final brood size was not related to nest non-attendance ($P = 0.569$, $R^2_{\mathrm{GLMM(m)}} = 0.09$) and provisioning rate ($P = 0.512$, $R^2_{\mathrm{GLMM(m)}} = 0.05$).

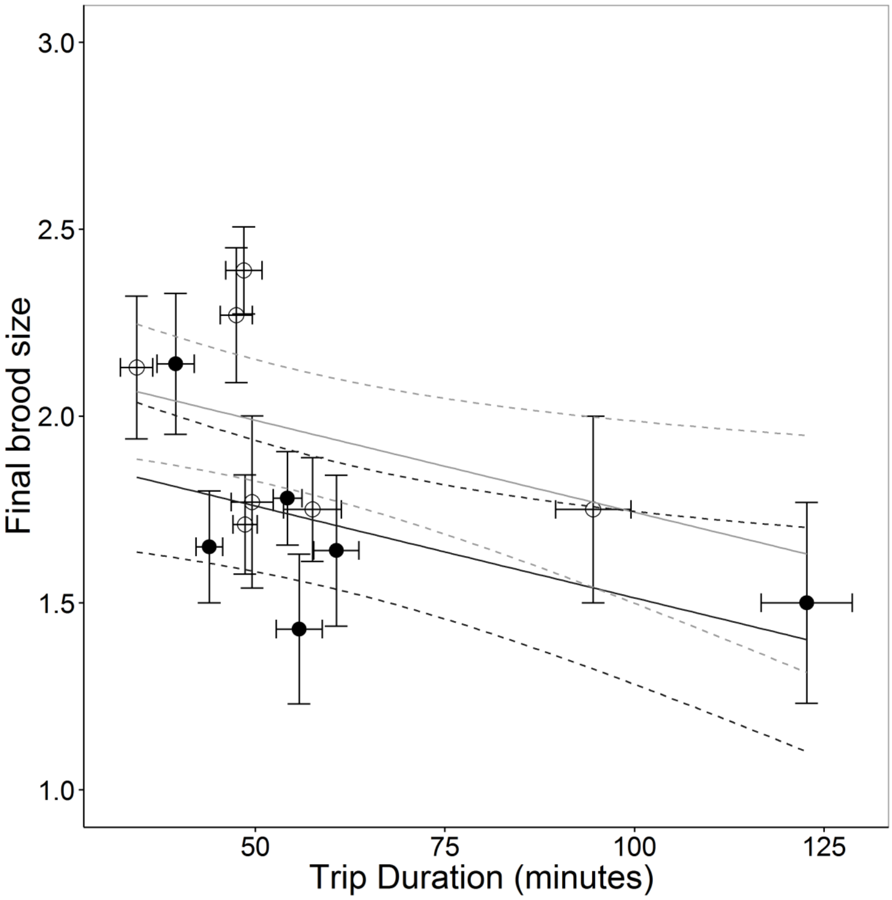

Figure 6-5. Mean ± 1 SE of trip duration against mean ± 1 SE final brood size. Filled black circles and black lines: 2013, open grey circles and grey lines: 2014. The solid line indicates the trend line with 95% confidence intervals (dashed lines) predicted from a Mixed Effect Model.

I found no statistically significant relationship between foraging behaviours per colony across the two years and colony GR (nest non-attendance: $f = 0.81$, $t_{1,5} = 2.23$, $P = 0.08$; provisioning rate: $f < 0.01$, $t_{1,5} = 0.78$, $P = 0.47$; trip duration: $f < 0.01$, $F_{1,5} = 0.74$, $P = 0.49$). Although not statistically significant, the large effect size of nest non-attendance suggests that colonies which have increased since Seabird 2000 were those that left nests less often unattended in 2013 and 2014 (Figure 6.6).

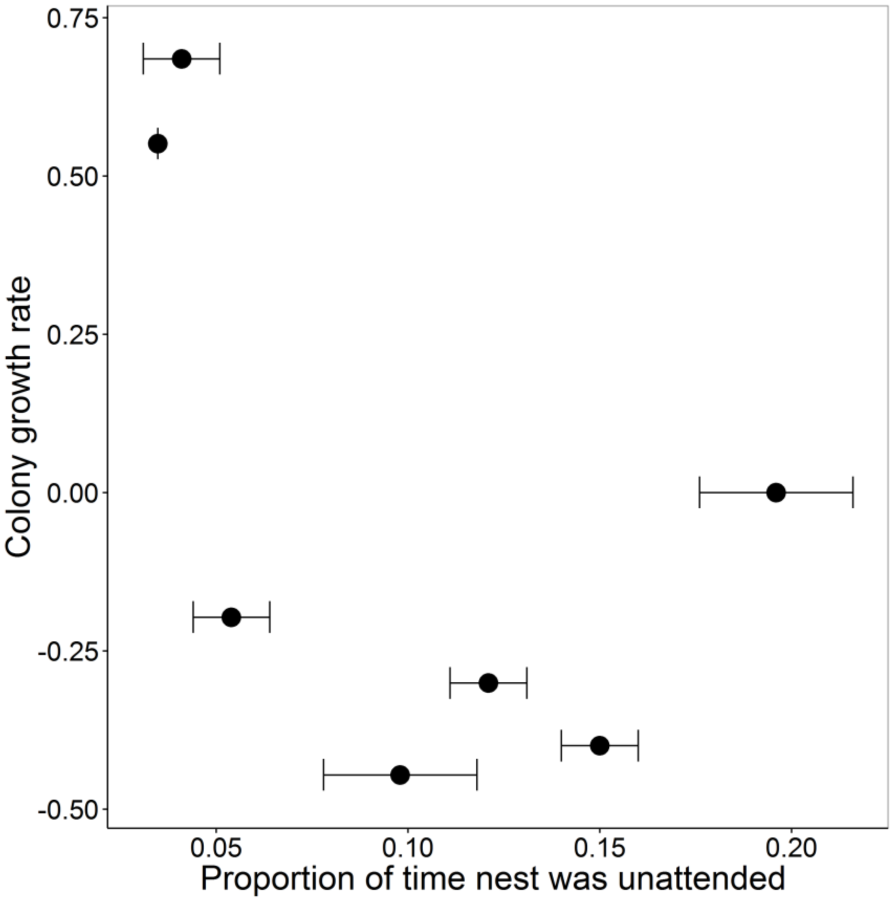

Figure 6-6. Mean ± 1 SE of the proportion of time the nest was left unattended against mean the colony growth rate. There is a strong effect ($f = 0.81$) that colonies where nests where less often left unattended had a higher colony growth rate over the preceding decade, although this was not statistically significant ($P = 0.08$).

6.6 Discussion

Foraging behaviours from seven herring gull colonies over two breeding season were compared to determine which behaviours were sensitive to local environmental conditions and whether they related to the gulls' demography; and therefore whether these foraging behaviours could be useful in monitoring coastal marine habitats. I identified spatial variation in foraging behaviours and that between-colony differences were associated with local environmental conditions related to local resource availability. There was spatial variation in all three foraging behaviours across 13 colony years; with temporal variation across years also observed for nest non-attendance. Variation in provisioning rate and trip duration was explained by variables representing marine resource availabilities with shorter trip durations and higher provisioning rates with increasing SST. In contrast variation in the proportion of time nests were left unattended was related to proxies of terrestrial resources: nests were left unattended less often with increasing amount of built-up area within the vicinity of the colony and, dependent on year, decreasing distance to the nearest farmland. This demonstrates that the gulls are sensitive to local environmental conditions during the chick rearing period and that their foraging behaviours are influenced by environmental conditions thought to be associated with local resource availability. The possible demographic consequences of variation in trip behaviours were also investigated. Trip duration was found to be related to a short-term measure of the gulls' demographic success, final brood size, indicating that local environmental conditions can impact the gulls' breeding success through their foraging behaviour. These results demonstrate that foraging behaviours are influenced by environmental conditions, specifically associated with local resource availability, in close proximity to the colony; which in turn influences the gulls' overall breeding success.

Observational watches were carried out across different times of day and tidal states to take into account the gulls' behaviour potentially varying with these (Burger 1976). Timing of observation watches did not differ between colonies nor was there evidence to suggest that gulls preferentially foraged at certain times of day or tidal states. Foraging has been found to be unrelated to time of day in another study on gulls (Yoon *et al.* 2014) although this may depend on the resources the gulls are exploiting (Sibly & McCleery 1983a). For example peak foraging in some populations were associated with the timing of trawler/fishing activities (Mañosa, Oro & Ruiz 2004; Bécares *et al.* 2015). Tidal state has been found to be important in other gull studies where individuals predominantly forage on intertidal resources (Burger 1976; Yoon *et al.* 2014); although gulls can forage in intertidal areas over all tidal states (Yorio, Bertellotti & Quintana 1995). In this study the gull colonies were found to differ in the resources they predominantly foraged on (Chapter 4) which may explain why no relationship with tidal state and the three foraging behaviours were observed.

One potential variable that was not included in this analysis but does have potential to affect the gulls' foraging behaviour is colony size. Local prey depletion and increased competition from conspecifics in larger colonies can specifically increase foraging trip durations, as individuals have to forage further from the colony (Lewis *et al.* 2001; Davoren & Montevecchi 2003b; Ballance *et al.* 2009). Birds from large colonies foraging close to the colony may have to switch to an alternative poorer quality resource (Forero *et al.* 2002). Both can result in lower breeding success (Davoren & Montevecchi 2003b; Ballance *et al.* 2009). However, within this dataset colony size could not be included in the analysis as it was positively correlated to the three environmental variables reflecting terrestrial resources: amount of built-up area and farmland, and number of landfill sites within the foraging range of the colony. This suggests that of the selected colonies, the largest ones are located nearer built-up areas; whilst the smaller colonies are more remote; however, this was not observed in the larger sample size of herring gull colonies included in Chapter 2 and therefore is due to the location of colonies selected for this project.

It was expected that where local foraging conditions were favourable nest attendance and provisioning rates would be high and trip durations short; and therefore the three foraging behaviours would be related to one another. Within this dataset I, however, found the opposite pattern that longer trip duration was associated with nests left unattended less frequently. Provisioning rate was not associated with trip duration and nest attendance. It could be that in colonies where nest non-attendance was low, local foraging conditions were good so only one adult has to forage at a time, however the resources they are consuming were located further away, or took longer to obtain, resulting in longer foraging trips. For example, if they were foraging on marine resources foraging trips may be longer, either due to the distance to suitable habitat and/or due to the foraging effort to find and capture prey; however, if these marine resources are of higher quality then the synchrony of the foraging adults is not affected and the nest is not left unattended. That provisioning rates were not related to trip duration and nest attendance may be attributed to the watches not being long enough; as only few trips were observed within a three hour period, so that a small decrease in numbers of provisioning events may not have been detected.

It should be considered that biases in observations could have occurred when measurements of behavioural traits were recorded. Trip duration could be under-estimated as, due to the three hour length of the observation watches, it will not include very long trips where one parent is on a long trip and its partner leaves before the other returned. It is also possible that trips may have been missed if adults returned without the observer noticing; however as in general nests were not often left unattended it is likely that only a few such trips could have been missed and therefore that will only be a slight under-estimate, although it could be bigger in colonies where nests were left unattended more often. Provisioning trips could also have been missed, especially in colonies where there was a potential for birds to hide between vegetation and rocks. However, in all colonies nests were selected which could be observed well from a vantage point to reduce this error. One thing that could not be quantified was the quality and size of provisions to chicks. The low variability in provisioning rates across colonies and years may be attributed to the gulls increasing the size and quality of meals rather than the number of provisions when local conditions are good (Oro *et al.* 1996; Burke & Montevecchi 2009).

Spatial variation in herring gull foraging behaviour was observed across multiple colonies, however this was weak for trip duration with no significant variation revealed by the post hoc tests. There was also no significant within-colony repeatability in trip duration across the breeding seasons suggesting that the relative ranking of colonies with respect to trip duration differed between years. The repeatabilities for nest non-attendance and provisioning rate were also low. The overall nest attendance was lower during 2013 than 2014. As described in Chapter 5, the 2013 early breeding period was cooler and wetter than during 2014, as well as final brood size being lower in 2013 than 2014, suggesting conditions during 2013 were harsher for breeding gulls than in 2014. This may also therefore explain why nest attendance was also lower in 2013; as if local foraging conditions were poorer the gulls would need to increase their foraging effort to maintain an appropriate level of provisioning in both years (Smout *et al.* 2013). For example through both parents foraging more often simultaneously, resulting in nest being left unattended for longer (Wanless *et al.* 2005; Ashbrook *et al.* 2008). It would also be expected that there would be a difference in trip duration between the two years; as under less favourable conditions adults may have to either travel further or spend longer to collect a meal. However, this was not observed. It may be that the gulls within an each individual colony responded differently to less favourable conditions. Alternatively, only certain colonies may have been affected by poorer local conditions, therefore on average there was no significant difference. Unfortunately this could not be tested with an interaction between colony and year.

As was expected brood size impacted provisioning rate, although not nest attendance or trip duration, with higher provisioning rates in nests which contained more chicks, probably due to the higher energy demand of larger broods (e.g. Weimerskirch, Chastel & Ackermann 1995; Ratcliffe & Furness 1999). For nest non-attendance I found that through the season, as the chicks got older and larger, the proportion of time adults left the nest site unattended increased; likely to be due to these large chicks needing less protection from adverse weather and/or predation. However, it could also be that the chicks’ energy demand increases through the season requiring greater effort by the parents, or that local food availability changed. Unfortunately my data cannot distinguish between these possibilities.

The spatial variation observed in how long nests were left unattended was related to two environmental proxies of terrestrial food resources; amount of nearest distance to farmland and built-up area in the foraging range. The relationship between nest attendance and farmland was different between the two breeding seasons; with colonies closer to farmland being left unattended less during the arguably poorer breeding season of 2013. Farmland may be particular important in early chick rearing when soft items such as earthworms are important for small gull chicks (Coulson & Coulson 2008). Farmland sites, particularly grassland, are highly predictable in both time and space (Pons 1994); and it is known that herring gulls forage on farmland, specifically pastures, for grain and invertebrates, particularly earthworms (Sibly & McCleery 1983b; Pons 1994; Schwemmer, Garthe & Mundry 2008). Therefore, when foraging conditions in other habitats are poor, as it might have been in 2013, close proximity to farmland might be beneficial to the gulls; whilst, in better years the distance to these sites may be less important. Moreover, foraging for earthworms may be more efficient in years with higher precipitation, as it was the case in 2013, due to the earthworms' greater availability (Sibly & McCleery 1983a; Pons 1992).

Colonies with a greater amount of built-up area in their foraging range left their nests unattended less often. Terrestrial resources, such as built-up areas and farmland, are thought to be more predictable and constantly available than intertidal and marine resources (Burger & Gochfeld 1983; Horton *et al.* 1983). Although, foraging on marine resources associated with discards can also be predictable to some extent, however it may not always be available, for instance on the weekend (Tyson *et al.* 2015); whilst resources associated with landfill may also be limited at the weekend. This suggests that having access to potentially highly predictable and reliably available terrestrial resources, related to anthropogenic activities, results in favourable foraging conditions where at least one adult can attend the nest and therefore nest were less often left unattended. It could be that where resources are predictable foraging trips, and therefore nest attendance, is easier to synchronise between parent birds. Alternatively, these resources may require less foraging effort, in terms of searching and capturing prey, allowing adults to spend more time at the nest. Sibly & McCleery (1983) found that herring gulls foraging on anthropogenic terrestrial resources, explicitly landfill sites, had higher energetic returns and therefore this resource would be more profitable to visit. However, despite being energetically more profitable anthropogenic resources can be nutritionally less valuable than marine resources (Pierotti & Annett 1991). My results from looking at the resource use of herring gulls in Chapter 4 suggests that in this region colonies which predominantly consume marine resources have higher breeding success than those consuming more terrestrial items. Therefore, there may be an issue of food quantity versus quality, with terrestrial anthropogenic foods potentially being of lower quality but the gulls can consume a large amount of it. Another consideration is that this could be related to colony size, as the amount of built-up area within the foraging range of the colony was positively related to colony size. It therefore cannot be ruled out that in larger colonies nest were left unattended less. It could be that in larger colonies risk of cannibalism is higher due to higher competition for local food resources, due to lower resource availability (Hunt 1972; Hayward *et al.* 2014); therefore the adults attend their nests more to prevent predation. At smaller colonies there may be less risk from conspecifics predating on chicks as competition for local resources is reduced.

Interestingly, provisioning rate and trip duration were not dependent on proxies of terrestrial resources but were found to relate to proxies of marine resources. For provisioning rate, colonies in more sheltered coastlines, associated with lower wave fetch, had lower provisioning rates. If colonies in areas of lower wave fetch have greater intertidal foraging opportunities and therefore greater potential intertidal prey availability; it might be expected that these colonies would have higher provisioning rates. However, if intertidal prey is of higher nutritional value, in comparison to alternative resources, then in colonies where the gulls are predominantly foraging in this habitat they may not need to provision as frequently if what they bring back is of higher quality (Pierotti & Annett 1991). In areas of high wave fetch, where intertidal foraging conditions are thought to be poorer, provisioning rates may be higher because the gulls are instead foraging on arguably lower quality terrestrial resources; therefore they need to make more frequent trips to provide enough food for the chicks. In Figure 3 the two data points which have the highest provisioning rates are Portpatrick. From the analysis on resource use (Chapter 4), the gulls from Portpatrick almost exclusively consumed terrestrial items. This therefore suggests that the adults in Portpatrick have to seek alternative, less preferred food resources and compensate for potentially poorer quality items by increasing their provisioning rates in order to increase the quantity of nutrients brought back to the chicks. In addition, the data point with the lowest provisioning rate was Islay in 2014. This colony was the most consistently observed colony during the project, due to being also part of a separate study, especially when the gulls had small chicks therefore this may have resulted in a lower provisioning rate than the other colonies which were not observed so frequently at the early stage. These points highlight a limitation of having a relatively small sample size of colony years when there are multiple potential influencing factors; as if these three points were excluded there could be a negative relationship between the remaining points of provisioning rate against wave fetch; which would suggest higher foraging rates where the colony is located near potentially more favourable intertidal habitats.

Provisioning rate and trip duration were both found to relate to standardised SST; which was positively correlated with the other environmental proxy for marine food resources, chlorophyll a concentration. Colonies located in areas of higher SST were associated with higher provisioning rates and also shorter foraging trips. Generally it would be expected that lower SST reflect better foraging conditions for the gulls, as higher SST may result in reduced marine food availability (Frederiksen *et al.* 2004, 2007) and/or small fish prey to move to deeper waters (Mills *et al.* 2008; Tomita *et al.* 2009). Due to the positive correlation observed with chlorophyll a concentration it could be expected that higher SST reflects a more favourable, productive marine habitat. However, it is generally accepted that the relationship between SST and chlorophyll a concentration is negative as higher chlorophyll and lower SST are associated with higher marine productivity. Instead, it is thought that around the coastline and sea-lochs of the study region nutrient input from agricultural runoff may be responsible for the higher chlorophyll a concentration, as the satellite data cannot distinguish between chlorophyll from phytoplankton and nutrient runoff (Smith, Tilman & Nekola 1998; Nielsen *et al.* 2002). Within the study region the Clyde Sea is known to have high nutrient levels due to runoff from local agriculture as well as domestic and industrial waste (Grantham & Tett 1993). A decline in benthic marine life has been associated with higher contaminants and runoff from farmland (Hiscock *et al.* 2004); whilst, rocky shore diversity is lower near built-up areas and intensive agriculture, likely due to the greater nutrient input from waste water and agricultural runoff (Burrows *et al.* 2008). However, higher nutrient levels can benefit the abundance of some marine invertebrate species, such as starfish (Brodie *et al.* 2005; Chiu *et al.* 2008), which the gulls can forage on. High nutrient levels associated with runoff from local agriculture and waste may also therefore result in higher SST. Within my dataset there is a positive correlation between standardised SST and the amount of built-up area within the foraging range of a colony (Spearman $r = 0.62$, $P = 0.02$, n =13). This suggests that the relationship with

SST could be more associated with the location of the colony in relation to terrestrial resources than with marine productivity. Therefore, the shorter foraging trips in colonies associated with higher SST might relate to the potentially higher abundance of marine intertidal prey, meaning they could provision chicks more frequently. Alternatively, colonies with higher local SST are those closer to terrestrial resources which are more predictable, therefore foraging trips to those terrestrial resources were shorter; but because of the resources' lower quality, the adults were required to make more foraging trips. In colonies with lower average SST in the vicinity of the colony, and potentially away from terrestrial resources, the gulls are likely to be foraging in the intertidal area which due to the prey being less predictable foraging effort is higher, or the gulls have to travel further to obtain resources, resulting in longer foraging trip durations. Due to the correlations between multiple environmental variables it is difficult to ascertain exactly the relationships between these variables and the gulls' foraging behaviours, and it could be a combination of explanations. In order to distinguish between the different interpretation of the observed patterns between behaviour and the environment it would be useful to consider what resources the gulls' actually utilised. Using the proportion of pellets containing marine resources from Chapter 4, with colony years and the unit of analysis, might not allow this due to lacking statistical power. This could be determined by having information for individual birds where behaviour and resource utilisation is tracked simultaneous.

It would be expected that foraging behaviours which reflect favourable local foraging conditions, lower nest non-attendance, higher provisioning rate and shorter trip durations (Bukacinski *et al.* 1998), would result in higher breeding success. Variation in trip duration was indeed found to be related with final brood size; with colonies where foraging trips were shorter being those with higher overall breeding success. Higher productivity when trip durations are shorter has been observed in other studies on gulls (Bukacinski *et al.* 1998; Chivers *et al.* 2012). This may be explained by gulls shorter foraging trips being able to maintain provisioning rates and nest attendance, which resulted in higher chick survival.

I found no relationship between provisioning rate and breeding success which would be expected given that within this study provisioning rate appears to be buffered by the gulls increasing their foraging effort. By altering their behaviour in this way seabirds can buffer against poor conditions and therefore maintain their breeding output (Hamer *et al.* 1992; Uttley *et al.* 1992), but this could come at the expense of prey quality and/or nest attendance. It would therefore have been expected that nest non-attendance would be related to breeding success given the spatial variation in this trait and that it differed across the two years. Nest attendance's sensitivity to local environmental conditions indicates that at least this behaviour could be useful in monitoring the environment.

If colonies breed successfully in successive years, and variation in breeding success are an important factor in determining how fast a colony can grow then I would also expect that similar behaviours that correlated with annual breeding success correlate with colony GR. However, although trip duration was found to relate to breeding success it was not reflected in the relationship with colony GR; which might be expected given the low repeatability between years. This could be due to the small sample size of colonies, or due to trip duration only being monitored over two years which may not be representative of conditions during the longer term which will have influenced the colony GR since Seabird 2000. In addition, although the chick rearing stage is arguably more sensitive to local food availability than the pre-laying or incubation period (Gill, Hatch & Lanctot 2002), it still only covers a short time period of the gull's annual cycle. Finally, although trip duration was related to breeding success, it not also being related to colony GR could suggest that the observed spatial variation in colony GR between colonies is not driven by breeding success but that other demographic variables, such as survival, are important; further highlighting that the relationship between breeding success and population growth are currently poorly understood (Camphuysen & Gronert 2012). There was however, a strong positive effect of nest attendance on colony GR although not statistically significant; with higher nest attendance associated with increasing colonies. In addition, nest attendance was the foraging behaviour with the highest repeatability, therefore may be the most promising trait to relate to colony GR, a longer-term measure of the gulls' demography.

In conclusion, these results suggest that gulls buffer against adverse environmental conditions by increasing their foraging effort through leaving the nest unattended or increasing the length of their foraging trips. The relationships of the behaviours with local environmental conditions reflecting resource availability suggest that where gulls have access to predictable terrestrial resource, which they can visit during short foraging trips, to maintain provisioning rate without having to sacrifice nest attendance time. However, they may do this at the expense of reduced resource quality and future work should also consider what resources are brought back to the colony. In contrast, in colonies which rely more on marine resources, gulls need to increase their foraging effort to maintain provisioning rates by carrying out longer foraging trips and leaving nests unattended for longer periods. This highlights that provisioning rates may not be useful in monitoring local environmental conditions as the gulls alter their nest attendance and trip durations to maintain provisioning; therefore the latter two behaviours are more likely to be useful in monitoring. In this study, trip duration has the most potential to reflect local conditions due as this trait was found to be sensitive to local conditions as well as being related to a measure of the gulls overall breeding success. As nest attendance is generally related to trip duration, this trait should also be considered when recording behaviours, especially given its potential to be related to colony GR.

7 Final Discussion

This thesis explored a range of herring gull *Larus argentatus* traits that could serve as alternative monitoring traits to the commonly used trends in abundance. The main aims of this thesis were to (i) determine whether spatial variation existed in the population trends of several coastal seabird species widespread across south-west Scotland; (ii) in an appropriate coastal seabird species determine whether, across multiple colonies, spatial variation also occurred in alternative traits to colony GR; (iii) establish whether the observed traits were sensitive to variation in local environmental conditions; and (iv) whether spatial variation in seabird traits had consequences on the gulls' demography. I investigated several traits of a widespread, generalist, coastal seabird the herring gull, across the region of interest, south-west Scotland and Northern Ireland, which might relate to the gulls' demography for their sensitivity to local environmental conditions. In this final discussion I summarise my main findings and consider the limitations; as well as setting my findings in a wider context and highlighting any future directions.

Spatial variation in colony GR of several widespread coastal seabirds (aim i)

Looking at the colony growth rate (GR) of seven widespread coastal seabird species within my study region of south-west Scotland Northern Ireland calculated between the first and last national seabird census, a time period over thirty years, spatial variation was observed in four gull species herring gull, lesser black-backed gull *L. fuscus*, great black-backed gull *L. marinus* and common gull *L. canus*, but not for the European shag *Phalacrocorax aristotelis*, Arctic tern *Sterna paradiseae* and common tern *S. hirundo*. For the four gull species, colony size at the end of the census period was significantly and positively related to colony GR; with the colonies which have increased the most are now the largest colonies. The environmental variables available for these analyses were most suitable for the gulls, the four species that did show spatial variation. They covered proxies of potential food availability in the marine, intertidal and terrestrial habitats that all four species are known to utilise, albeit to differing extents: wave fetch, amount of built-up area, number of landfill sites, SST and chlorophyll a concentration. However, relationships were only found for herring and lesser black-backed gulls with wave fetch, and between herring gull colony GR and the amount of built up area within the gulls' foraging area. More favourable colony GR were observed in herring and lesser black-backed colonies located in more sheltered coastlines, potentially due to higher availability and predictability of intertidal resources at these locations. Herring gull colonies also had more favourable colony GR in locations with greater proportions of built-up area in their foraging range suggesting a positive effect of anthropogenic food available in built-up areas.

In addition to the selected environmental variables there could have been several other variables included such as information of discards and fishery landings as a proxy for local marine fish availability which would have been particularly relevant for the shag and terns, and for fisheries activities which would be relevant to the large gulls. However, it was not possible to obtain these datasets at the resolution required to compare individual colonies. Instead I used sea surface temperature (SST) and chlorophyll a concentration as a proxy for local marine productivity.

The results of this preliminary analysis highlighted that in order to investigate the coastal environment the herring gull was the species that would most likely be appropriate given that spatial variation that was found to exist in colony GR across my study region and that this variation could be explained to some extent by differences in local environmental conditions. Among the coastal seabirds breeding in my study region, the herring gull is the most widespread species and therefore was selected to investigate spatial variation in alternative monitoring traits in more detail. It also allowed multiple, relatively accessible, colonies to be studied that had contrasting colony GR over the national census periods.

Spatial variation in herring gull traits – alternatives to colony GR (aim ii)

Traits associated with several aspects of the herring gull's breeding biology, and therefore could be related to their demography, were selected to determine whether they sensitive to variation in local environmental conditions over the breeding season. These were associated with the herring gulls' eggs, resource use and foraging behaviour. Spatial variation was found in all three of these traits, although the amount of explained variation varied between traits, indicating that throughout the breeding season colonies could have experienced different environmental conditions; as well as being influenced by colony size.

The resources the gulls consumed during the breeding season were expected to reflect the resources most available within the foraging range on the colony. Looking at the resource use of the gulls, there was spatial variation in the extent of marine and terrestrial resources they were consuming at the colony level. This was found with methods that were used to estimate resource use, pellets and stable isotope analysis of feathers. Each of the methods have their own associated biases therefore the fact that they gave similar results indicates that the estimated resource use of the gulls reflect what they are actually consuming during the breeding season.

Four traits associated with eggs were investigated: eggshell colour, eggshell maculation, egg shape and egg volume. Egg traits were expected to be sensitive to variation in local environmental conditions early in the breeding season. Data of these egg traits were extracted from digital photographs, which were taken in the field over three breeding seasons. Spatial variation was observed in all these traits, however, colony explained the largest amount of variation for egg volume; with less variation explained for colour and maculation. Although there was weak spatial variation in egg shape, this coupled with a low repeatability across the three years suggested that egg shape was not a useful trait in reflecting local environmental conditions during the early part of the breeding season.

Spatial variation was also observed in all three of the herring gull's foraging behaviours that were investigated: nest attendance, provisioning rate and trip duration, although this was very weak for trip duration. Nest non-attendance and provisioning rate indicated that during chick rearing (the later part of the breeding season) the gulls' foraging behaviour is being influenced differently between colonies by external factors, and therefore are sensitive to changes in local environmental conditions.

Environmental factors driving observed spatial variation in herring gull traits (aim iii)

To try and determine what factors were driving the observed spatial variation in herring gull traits information of environmental variables were obtained which reflected local terrestrial (built-up area, farmland and landfill sites) and marine resources (wave fetch, SST and Chlorophyll a concentration). Although I found that environmental variables explained some of the observed spatial variation in traits, in all cases there was a considerable amount of variation left unexplained. There could have been a number of unmeasured environmental variables that influenced the monitoring traits such as data on fishery discards and landings and more detailed information on local marine invertebrate availability and farmland use.

The resource use of herring gulls across the multiple colonies was found to be linked to average wave fetch and the nearest distance to built-up areas. Interestingly, colonies which were located in areas on lower wave fetch, a proxy for higher availability of intertidal prey, consumed a higher proportion of marine resources; whilst colonies nearer to built-up areas consumed less marine resources. This suggests that at the colony level the gulls are foraging on the resources most available within the vicinity of the colony.

Spatial variation in eggs traits was associated with local weather conditions in addition to local environmental conditions reflecting resource availability. The impact of weather on a species is not necessarily of direct interest when monitoring the species to provide information on the local environment, as it does not reveal anything about the state on the environment. However, it is still important when looking at egg traits as it is known that the weather does influences traits associated with bird eggs (Christians 2002) and therefore need to be accounted for when wanting to detect effects of local environment on egg traits. Egg colour and volume were found to be associated with ambient air temperature during the pre-laying period. Egg maculation was the only egg trait that was found to be sensitive to local environmental conditions relating to proxies of productivity in the marine environment, SST and chlorophyll a concentration. Therefore egg maculation has potential to be useful in monitoring marine coastal habitats. Egg colour and size were also sensitive to local environmental conditions, but in this study it is thought that any relationships were masked by the influence of ambient air temperature. Investigating the direct influence of the gulls' preferred resource (marine prey) on egg traits revealed that the proportion of marine resources used influenced egg maculation and egg volume; therefore monitoring egg traits can also potentially indicate whether the local foraging conditions in the marine habitat allow the gulls to consuming their favourable resources.

Finally, of the herring gull's foraging behaviours, nest attendance was associated with two proxies of local terrestrial resource availability, amount of built-up area and distance to the nearest farmland; with nests left unattended for longer in colonies further away from farmland and colonies with less built-up areas in their foraging range. Provisioning rate and trip duration were related to a proxy of the marine environment, standardised SST; with higher provisioning rates and shorter trip durations in colonies with higher average SST, although here the proxy with marine resource availability might be confounded with availability of terrestrial resources and it is not clear exactly what environmental variable influences provisioning rates and trip durations. Provisioning rates were also higher in areas of high wave fetch. The exact mechanisms underpinning the observed relationships between herring gull traits and SST are difficult to ascertain.

The correlation between environmental variables is problematic as it makes it more difficult to decipher what is driving the relationship between environmental variables and spatial variation in monitoring traits. In most cases correlations were between variables that were proxies of the same resource type; so between chlorophyll a concentration and SST, and between the amounts of the three terrestrial habitats: built-up area, farmland and number of landfill sites. The relationship between built-up area and number of landfill sites is to be expected and therefore using built-up area is likely to provide a good reflection on the gulls' use of anthropogenic resources which is not solely landfill but also scavenging within built-up areas, for example around waste bins and where people eat outdoors along seaside promenades and schools for example. The positive relationship between built-up and farmland is more difficult to explain, but may be attributed to more intensively farmed areas being nearer built-up areas.

Demographic consequences of spatial variation in herring gull traits (aim iv)

Despite the spatial variation in herring gull traits, and their sensitivity to local environmental conditions, only weak associations with the gull's demography were observed. Across the study colonies for which it could be determined, there was also spatial variation in final brood size, a proxy for the gulls' annual breeding success, with high repeatability of final brood size between the 2013 and 2014 breeding seasons. This demonstrates that the gulls' breeding success is being influence by local conditions, however determining what is driving this variation is challenging, and is likely to be a combination of factors. The significant positive relationship between resource use and breeding success indicates that the resources the gulls' are foraging on during the breeding season are important. The relationship between egg colour and breeding success was not as straight forward but indicates that in the year which was arguably more favourable, at least in terms of local weather conditions, egg colour was associated with final brood size; although the mechanism behind this relationship was not identified. Of the three foraging behaviours only trip duration was found to be associated with final brood size; with, in both years, higher breeding success in colonies where foraging trips were shorter. This indicates that trip duration can provide an indication of local environmental conditions during the chick rearing period important for gulls, although at the moment we do not yet know exactly what these are.

None of the investigated herring gull traits were found to be significantly related to colony GR; however, there were fairly large effect sizes for the proportion of marine resources consumed and colony GR and also the proportion of time the nest was left unattended and colony GR, indicating a weak potential relationship between these traits. That the relationships between herring gull traits and colony GR were statistically non-significant is most likely due to the small sample sizes, the traits being averaged at the colony level, and only looking at these traits for a maximum of three years. The colony GR cover a maximum time period of 14 years, between Seabird 2000 (1998-2002) and the most recent counts; carried out in 2011 or 2012. In addition, this study only focused on the breeding season; however colony GR will also be influenced by conditions during the non-breeding season affecting survival and carry over effects which influence the following year's breeding success (Harrison *et al.* 2011; O'Connor *et al.* 2014).

Table 7.1 provides a summary of the herring gull traits investigated in relation to which environmental variables they were sensitive too and whether they were associated with the gulls’ demography. These table highlights that several environmental variables are important to the gulls; demonstrating their use, and potential reliance, on multiple resources from both the marine and terrestrial environment. In particular, average wave fetch and amount of built-up area within the gulls’ foraging range appear to be important; specifically being in close vicinity to areas of low wave fetch, with higher diversity/abundance on intertidal invertebrates or having a high amount, or being in close vicinity, of built-up area to exploit terrestrial/anthropogenic resources. In addition, sea surface temperature is also important; however the mechanisms behind this relationship are less understood. Of the traits investigated, focusing directly on what resources the gulls are consuming may be the most effective as it is sensitive to environmental conditions and relates to the gull’s demography. It is also a trait that can reflect both the early (pre-egg laying/incubation) and later (chick rearing) stages of the breeding season. However, egg colour and volume as well as trip duration and nest attendance also have potential. Focusing on the proportion of marine resources consumed by the gulls which does look to be the strongest trait, the results suggest that the gulls forage on the resources which most available within the vicinity of the colony; which in the selected colonies is either intertidal or built-up areas. With those colonies which predominantly forage on marine resources benefiting, resulting in a higher breeding success.

Table 7-1. Summary table of herring gull traits

Herring gull trait	Spatial variation in trait	Environmental variables sensitive to	Related to breeding success	Related to colony GR
Colony GR	Yes	Wave fetch Built-up area	-	-
Egg colour	Yes	Ambient temperature	In 2014 colonies with browner eggs had lower breeding success	No
Egg maculation	Yes	SST Chlorophyll a concentration	No	No
Egg shape	Yes	NA	-	-
Egg volume	Yes	Ambient temperature	No	Large effect size – with larger eggs in colonies with more favourable GR
Proportion of pellets containing marine resources	Yes	Wave fetch Built-up area	Colonies consuming a higher proportion of marine resources had higher breeding success	Large effect size-with more favourable GR in colonies consuming more marine resources
Nest attendance	Yes	Farmland Built-up area	No	Large effect size – higher nest attendance in colonies with more favourable GR
Provisioning rate	Yes	Wave fetch STT	No	-
Trip duration	Yes	STT	Shorter trip durations related to higher breeding success	-

This project highlights the benefits of studying multiple colonies of a species, over at least two years, in order to obtain information on what environmental conditions might influence a species with, for some of the herring gull traits, data from 21 colony-years being obtained. Although these colonies may still not be representative of the whole of the species’ range, or that within the UK and Ireland, it is arguably more representative and informative than solely investigating traits from one colony over many years. However, single colony studies also have many benefits especially in terms of being able to study a species’ long-term over multiple years, and in keeping variables not directly of interest consistent; for instance breeding habitat and to some extent levels of predation and disturbance. The study colonies are likely to have slight differences in predation and disturbance levels; however from the observation watches evidence of predation and disturbance were relatively low across all colonies. This is potentially related to all the colonies, with the exception of Portpatrick, being located on islands in relatively remote locations. In addition although this is a relatively good sample size for studies on seabird traits, this sample size still had limitations due to so many multiple potential influencing variables impacting on these colonies and potentially driving the observed spatial variation in colony GR. This might be a disadvantage of selecting a generalist species rather than a specialist, where fewer potential drivers might need to be considered. However, specialist species generally only reveal a narrow view of their local environment whilst generalists can provide a broader assessment of the environment (Montevecchi 1993).

Comparing between multiple colonies over at least two breeding seasons was also informative as the weather conditions during the breeding season of 2013 and 2014 differed; with 2013 being wetter and colder, and the response of some of the herring gull traits differed between the two years. This means that the herring gull traits could be investigated over two different years to determine relationships with environment and demography rather than relying on one year. It is more difficult to ascertain whether foraging conditions were different between the two years, however due to the high repeatability in colony resource use over the two years it could that, even if the availability of resources varied between years, they were still feeding in the same habitats to a similar extent in both years.

Another highlight this project demonstrates is that using two methods to estimate resource/diet use of a species can help validate these methods and increase the confidence of what the estimated resource use of the species was. This has been demonstrated in other studies with gulls (Ramos *et al.* 2009). However, this is very useful as especially in using MixSIAR to estimate resource use based on stable isotopes it is often implied that this method is less useful for generalist species such as gulls due to the vast range of potential food items and the associated range of isotope values they can consume. Although this may not have been such an issue in this study as I was predominantly interested in marine versus terrestrial resources. Splitting the resource categories further when using the stable isotopes would not have been possible given the isotope values of the selected food items could not even distinguish between offshore and intertidal resources, and terrestrial (i.e. invertebrates and grain) and anthropogenic (cooked meats, bread etc..) resources. Analysing additional isotopes may help further to distinguish between resource categories; for example, sulphur can be analyses to distinguish between pelagic and benthic marine resources (Ramos *et al.* 2009; Hobson *et al.* 2015). Identifying whether birds are foraging in offshore versus intertidal habitats, or terrestrial (i.e. farmland) versus anthropogenic (i.e. landfill) habitats is also likely to be more attainable using data from GPS tracking, but this will not allow determining what they ate.

This study also highlights the potential of photography to document information on egg traits; with the validations I undertook indicating that this is a reliable technique of obtaining information on eggs in field conditions with different light conditions. As long as multiple cameras are calibrated, settings are standardised and there is a scale bar and reference colour charts in the image, taking digital images of eggs in the field, at least for a species with relatively accessible nests such as the herring gull, is quick and straightforward. From the resulting images a wide range of information can be obtained as was demonstrated in this study. It also provides images which can be archived for future use; for example, if or when advances in technology/software may be able to more accurately extract data, particularly associated with maculation. Photographing eggs compared to taking egg measurements in the field means less time is spent in the colony disturbing the breeding birds. However, both methods can bias results as only accessible nests can be sampled. In seabirds, gull nests are particularly accessible, however other species may also be monitored by this method; for example cavity and burrow nesting species as well as other open nesting species such as terns. Extracting information on egg traits from digital photographs also means that the same protocols can be carried out by others in the field at different locations in different years. This technique can also be used to photograph museum specimens; which is currently being undertaken to look at the variation in gull egg traits over a larger temporal and spatial scale.

Observing the behaviour of a species is another non-invasive way to determine how a species is responding to its environment, especially where several different behaviours which may tell different things can be recorded during the same watch. For example, additional behaviours that could have been recorded include territorial interactions. On the other hand recording too many behaviours should be avoided to ensure the observer does not miss any of the behaviours, especially when observing multiple nests at the same time. Observation watches are, however, time consuming, and differences between observer and the visibility of nest sites may lead to biases.

Further limitations of this study

Collecting data on several herring gull traits from multiple colonies was logistically challenging, especially as colonies in both south-west Scotland and Northern Ireland were required to be monitored over the same breeding season. This therefore required multiple observers. For the data collected on egg traits, this is not an issue as the camera settings were standardised, and shown not to be different between cameras, egg trays or lighting conditions. In addition the same field protocol was followed by all four people who took photographs over the three years. Collecting of pellets was also straightforward, as only whole pellets from herring gull territories were collected; and all dissections were predominantly carried out by one person. The only area where observer differences might be of concern is from undertaking the observation watches. This was accounted for in the analysis of the foraging behaviours in Chapter 6. However, it should be noted that differences in detectability of provisioning and nest attendance between colonies associated with nest location and vegetation growth may have led to between-colony differences, although the nests observation were carried out on nests that were chosen so that they could be viewed well.

Monitoring multiple nests also meant that it was difficult to get a good indication of breeding success, especially in the more densely occupied colonies. This is why my measure of breeding success was final brood size as this is relatively straightforward to determine especially form carrying out nest observations. The observed relationships between egg traits and final brood size may have therefore been stronger if actual breeding success was obtained. Therefore, if there is an indication that traits are associated with final brood size, using this measure of breeding success may be a more effective measure that can be obtained more easily in monitoring programs than actual overall productivity.

There are a number of additional traits associated with the herring gull that could have been monitored. However, the traits I did choose were those which were thought to be most easily monitored logistically and thought to be repeatable. Monitoring diet is arguably the most effective way of monitoring a species as the breeding success and population growths of most species is directly related to food availability. For species such as gulls, which regurgitate the indigestible remains of what they have consumed, collecting pellets is a relatively non-invasive and cost-effective way of obtaining details on their diet and resources use, which in this study, and others, has been validated against other methods of estimating resource use, in this case stable isotope analysis. Therefore although other methods of estimating diet and resource use exist the two methods I used here are thought to provide a reliable and effective estimation of the gulls' broad resource utilisation. Stable isotope analysis is a useful technique and collecting feathers from chicks is more straightforward than catching adults. In addition, it is known that these feathers reflect the local environment during the breeding season; it cannot be as confidently determined where the feathers from adults are grown and therefore might not necessarily reflect conditions around the breeding colony. In future monitoring pellets could be used as the sole method, as collecting feather still causes more disturbance and stress to the birds than entering the colony to collect pellets. In addition, it is time consuming to prepare stable isotope analysis samples and is costly to run the analysis especially if sulphur as well as carbon and nitrogen are required.

Of the other traits that were considered looking at stress and measuring the corticosterone of adult breeders and chicks can provide useful details about how local food availability affects the physiology of individuals (Kitaysky *et al.* 1999, 2001, 2010; Benowitz-Fredericks *et al.* 2008). However this is an invasive technique as it requires the birds to be caught and blood to be extracted. In addition, to obtain baseline levels blood needs to be sampled quickly; although alternative methods such as using fake eggs containing blood-sucking bugs to obtain blood (Becker *et al.* 2005) or obtaining corticosterone values from feathers (Bortolotti *et al.* 2009) are less invasive but are still expensive and require access to specialised laboratories. Taking measurements of chicks and/or adults can also provide information on a birds' conditions but again requires capturing the birds, which is particularly challenging if wanting to sample adults. In addition, capturing adult and taking blood are not ideal for large scale monitoring programmes as they are not less cost-effective and require more skilled/qualified people than for example taking photographs of eggs and collecting pellets.

There are also other traits such as time of first laying and hatching however, again this is logistically challenging when multiple colonies are being monitored by few observers. In addition, it is time consuming to repeatedly visit a colony to ensure these dates are accurate; potentially also causing repeated disturbance to the colony.

Another point to consider is that due to the logistics of monitoring multiple colonies during the same breeding season, it was not possible to attribute breeding success to the individual nests where eggs were photographed or foraging behaviours were recorded; or to match the resource use of individuals to their breeding success. Therefore, all traits were considered at the colony level. In terms of monitoring, looking at traits averaged across colonies like I did here is likely to be simpler and more cost effective. In addition, monitoring species responses is arguably more relevant at this level as you want to know how the population as a whole responds to changes in the environment, not just individuals. However, it does mean that any relationships between environmental variables and demography are likely to be underestimated; as individuals may respond differently to environmental conditions based on their age, size and body condition, experience as well as on their past experiences and genetic quality (Bolnick *et al.* 2003); which may also dilute the influence of environmental conditions. If a large enough and representative sample of individuals are monitored then averaging their responses to get a colony response is a useful monitoring tool of how the population responds to the state of their environment. However, it is potentially useful to look at individual responses when trying to establish the relationship between the trait under investigation and demography and what environmental conditions drive the variation in the trait to give a clearer indication of the relationship.

Within this study only traits reflecting the breeding season were considered. Traits which provide information on the non-breeding season may also affect the breeding success of the gulls, though carryover effects, as well as colony GR. Two techniques which can, and will in future, be investigated are stable isotope analysis of feathers which were grown during the non-breeding period and information from tracking data obtained from deploying GPS loggers on adult herring gulls year round. Investigating resource use during the non-breeding season may determine whether this part of the gulls annual cycle influences breeding success and/or colony GR to a greater extent than resource use during the breeding season. Tracking data in particular could provide information on where the gulls are foraging when they are not constrained by the breeding colony.

A final comment is that within this project I only considered the herring gull; therefore it is not known whether the responses of these gulls will be the same as other seabirds. Although the large gulls in the UK have slightly varying foraging preferences (Kubetzki & Garthe 2003) the responses of the lesser and great black-backed gulls may be similar to the herring gull. In chapter 2 both the herring and lesser black-backed gull colony GR was found to be related to wave fetch, however the great black-backed gull was not found to be related to any of the same environmental variables suggesting that different environmental variables may be more important. In the coastal environment, shags and terns are likely to respond differently as they forage exclusively in the marine environment. However, if unfavourable marine conditions are responsible for the herring gulls foraging more on terrestrial resources then I would expect that these conditions would impact on shags and terns as they have less opportunity to swap to alternative resources. In order to determine whether different species do respond similarly or differently to the herring gull then the traits of these species could also be investigated at the same locations this study was carried out.

Herring gulls as indicators of the coastal marine environment

This study demonstrates that several of the selected herring gull traits are sensitive to local environment around the colony during the breeding season; however establishing what factors are driving these differences was more difficult. It was also hard to establish whether the variation is driven by variables directly associated with the state of the coastal environment, or instead are influenced by other variables such as the weather. In terms of resource use and availability it was also difficult to determine whether the gulls were using resource that were most readily available to them, whatever the state of the coastal environment. However, the results from this project do suggest that the gulls benefit from consuming marine resources, and they may only be able to do this if the local coastal habitat is in a good state. Therefore, where they do not feed on marine resources it could indicate that these coastal areas are in a less favourable state, and this can negatively impact on their breeding success.

Combining the findings of this project with future planned analysis of tracking data, collected from several of my study colonies and over the same time period as this study, may help further establish the use of the herring gull as a monitor, as well as helping to address some of the limitation discussed above. For example, looking in more detail at potential differences between the sexes and in body condition from a small sample of adults measured during the 2014 breeding season. Traits reflecting the non-breeding season to consider carry-over effects can also be investigated; again from a sub-sample of breeding adults from four of the focal Scottish colonies. Resource use during the non-breeding season can be established from stable isotope analysis of feathers grown during this period; whilst non-breeding movements can be obtained from GPS tracking.

Nevertheless, even if the herring gull is not thought to be an effective monitor of the coastal environment, these findings reveal some potential indications about the spatial variation in colony GR for this species, a red-listed bird of conservation concern in the UK (Eaton *et al.* 2015), where currently the causes of decline for this species are not fully understood. The results of this study indicate that the availability of intertidal and terrestrial resources within the foraging range of the herring gulls' breeding colony is important. Consuming marine rather than terrestrial resources was found to benefit the gulls' breeding success; whilst the resources the gulls' forage is also thought to influence the gulls' foraging behaviour which may then have consequences on the gulls' demography. Having predictable and abundant terrestrial resources within the foraging range may be beneficial in terms of higher nest attendance and shorter foraging trips but this is at the expense of resource quality. This could suggest that declining populations are those in areas of unfavourable intertidal habitats which do not have alternative terrestrial resources to exploit.

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