Foraging ecology and reproductive performance of sympatrically breeding larid species at a North Sea colony

Gail Sheila Robertson

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Abstract

Marine ecosystems provide essential goods and services to human populations, however anthropogenic offshore activities can adversely affect the functioning of ecosystems by reducing biodiversity. Temporal data on environmental fluctuations are required in order to implement effective ecosystem management. The health of marine ecosystems can be assessed using proximal measurements of biological data such as fishery catch statistics. However, these data are often patchily distributed and underreported. Seabirds have been shown to be useful indicators of the state of the marine environment. They are highly visible, charismatic species that are easy to count and observe in colonies and offshore foraging areas during the breeding season. In recent years the miniaturisation of electronic devices and the development of novel tracking methods have allowed a large variety of seabird species to be tracked to and from foraging areas and for environmental conditions in distant pelagic areas to be sampled.

It has been suggested that seabird foraging and breeding behaviour provide more accurate measures of environmental change than demographic parameters such as adult mortality and productivity, as many species are able to buffer the effects of low food abundance during the breeding season by increasing foraging effort. In this thesis, demographic and behavioural data of several sympatrically breeding larid species were examined over extended temporal scales and the effectiveness of these data at indicating environmental change are assessed.

Comparisons of annual fluctuations in demographic parameters were made among ecologically similar and dissimilar tern species breeding sympatrically at a North Sea colony. Species with similar foraging and breeding behaviour exhibited synchronous temporal population fluctuations, while dissimilar species showed no synchrony in population change. Similar and dissimilar species also showed differing responses to declines in predator abundance. To understand how seabird species with similar ecological requirements are able to coexist in the same area during the breeding season, foraging behaviour and reproductive parameters were examined among three morphologically similar terns (*Sterna* spp) breeding at the same colony. Species partitioned resources by both chick diet and foraging area and responded differently to increasing brood age. Sympatrically breeding Arctic (*Sterna paradisaea*) and Common Terns (*S. hirundo*) maintained comparable growth and survival rates of chicks, which suggests that species utilising different foraging strategies can be equally successful at raising chicks to

fledging. However, Common Terns were found to exploit larger prey items with higher energetic contents than Arctic Terns, which may explain why this species was able to lay larger clutches and fledge more chicks.

Temporal variation in foraging behaviour was examined further in Black-legged Kittiwakes (*Rissa tridactyla*) by comparing the foraging behaviour of individuals at the same colony during two stages of the breeding cycle (incubation and chick-rearing) and in two consecutive years (2011 and 2012). Diet, foraging areas and environmental variables associated with foraging were found to vary significantly throughout the breeding season and between years, with important consequences for marine conservation policy. Parental resource allocation in Kittiwake broods of two also varied throughout the chick development period as chick demand and environmental conditions surrounding the colony changed.

This research illustrates how long-term seabird population and foraging behaviour data can be used to examine changes in the marine environment and to address ecological questions. Variation in chick demand, environmental conditions and species interactions can explain temporal changes in the foraging behaviour of sympatrically breeding species. These results also illustrate the value of considering seabird foraging behaviour when developing effectual offshore protected areas for marine predators.

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Author's Declaration

I declare that the work in this thesis is my own, except where otherwise stated. No part of this thesis has been submitted as part of any other degree. The material included in this thesis has been produced in collaboration with co-authors as follows:

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Chapter 1

General Introduction

The marine ecosystem provides many essential goods and services including food resources, detoxification of waste products, energy production, flood defence and recreation and tourism (Peterson and Lubchenco 1997, Holmlund and Hammer 1999, Beaumont et al. 2007). As a large and increasing proportion of the world's population lives close to the coast, loss of services such as flood defence can have severe consequences (Danielsen et al. 2005, Adger et al. 2005). Economic activities such as aquaculture, offshore energy production, fisheries, shipping and coastal recreation have increased in recent decades and this increase is expected to continue in future years (Hall 2001, Jackson et al. 2001, Douvere 2008, Breton and Moe 2009). Such activities can adversely affect marine ecosystems by reducing biodiversity in coastal and offshore areas (Thrush and Dayton 2002, Sala and Knowlton 2006, Halpern et al. 2008).

Changes in marine biodiversity can be caused directly by exploitation and habitat destruction or indirectly by climate change (Dulvy et al. 2003, Worm et al. 2005, Lotze et al. 2006). Loss of marine biodiversity impedes the effectiveness of the marine ecosystem to produce food, detoxify pollutants, maintain water quality and recover from anthropogenic activities such as overfishing and changes in climate (Worm et al. 2006). The decline in marine biodiversity is increasingly impairing the quality of goods and services the ocean environment provides, with potentially devastating outcomes for human populations (Duarte 2000, Worm et al. 2006). By protecting and restoring marine ecosystems through sustainable fishery practices, pollution control and the creation of offshore marine reserves, the reliability and productivity of marine goods and services may be maintained for future generations. Careful management is necessary to implement suitable controls for anthropogenic activites in protected areas and to consistently monitor changes in ecosystem health.

A key requirement for implementing ecosystem management is to obtain temporal data on environmental fluctuations (Botsford et al. 1997). Physical data describing the ocean environment tend to be noisier and more difficult to interpret than biological data which tend to exhibit fewer annual fluctuations (Hare and Mantua 2000, Piatt et al. 2007). The status of the marine environment can be assessed using distal measurements of biological data (Boyd and Murray 2001), for example international fisheries catch statistics can be used to quantify the size of fish stocks (Deriso et al. 1985). However, catch statistics are often underreported, especially from illegal fisheries (Agnew et al. 2009) and stock biomass does not provide information on the recruitment of younger age classes into the population (Arnott and Ruxton 2002). Seabirds and other marine predators are highly sensitive to changes in prey abundance and availability, hence demographic and behavioural data are often used to examine changes in abundance and age structure of local fish populations (Cairns 1988, Einoder 2009).

Compared with fish and other marine animals, seabirds are highly visible and easy to count in breeding and foraging areas (Sydeman et al. 2006). Most species are colonial breeders and gather annually in large numbers at relatively few breeding sites allowing multiple species feeding at different trophic levels to be monitored simultaneously. Seabird populations have been identified as useful indicators of the health and status of marine ecosystems (Cairns 1988, Montevecchi 1993, Furness and Camphuysen 1997). While annual population fluctuations can provide some indication of environmental change (Morrison 1986, Temple and Wiens 1989, Barrett and Krasnov 1996), behavioural and reproductive parameters have been shown to be highly responsive to physical changes in the marine environment (Baird 1990, Montevecchi 1993, Boyd and Murray 2001, Inchausti et al. 2003, Wanless et al. 2005a). Quantifying changes in nest attendance of breeding adults, provisioning rates and the type and size of prey items delivered to chicks can provide a stronger and more immediate response to changes in prey abundance and distribution than by examining seabird population trends (Cairns 1988, Monaghan et al. 1989, Diamond and Devlin 2003, Wanless et al. 2005a). Chick provisioning data have been shown to correlate with estimates of fish stocks (Montevecchi and Myers 1995, Davoren and Montevecchi 2003, Furness 2007) and by comparing provisioning behaviour of sympatrically breeding seabirds, the distribution of fish within the water column can be deduced (Monaghan 1996). However, care must be taken when using temporal data on seabird foraging and breeding behaviour to indicate change in local environmental conditions, as responses to environmental change can vary among sympatrically breeding species (Furness and Camphuysen 1997, Piatt et al. 2007). Seabirds vary in susceptibility to changes in the environment depending on species-specific foraging and breeding strategies. Also, species which coexist in the same area and exploit limited resources vary their foraging behaviour, diet and habitat selection in order to reduce competition.

Interspecific competition has long been considered to be a major factor influencing the structure of natural communities where species compete for similar resources (Hanski

1987, Ray and Sunquist 2001, Krijger et al. 2001). The effects of interspecific competition are considered to be density-dependent (May 1973, Minot 1981, Cairns 1989), and can negatively affect distribution, productivity, growth and survival of one or both competing species (Goldberg and Barton 1992, Dyer and Rice 1999, Gurnell et al. 2004, Carrete et al. 2006). Ashmole (1963) proposed that growth of seabird populations can be restricted by density-dependent competition for food around colonies during the breeding season. This effect, often referred to as Ashmole's Halo, has been confirmed by empirical evidence showing that seabirds can deplete local food supplies (Dann and Norman 2006, Gaston et al. 2007). This can have corresponding detrimental effects on annual demographic parameters, such as breeding success (Furness and Birkhead 1984, Birt et al. 1987, Cairns 1988, 1989, Wakefield et al. 2013). Further studies have demonstrated a negative relationship between colony population size and growth rate and a positive relationship between foraging trip duration and colony size (Lewis et al. 2001a, b, Ainley et al. 2003). For communities affected by density-dependent processes, competing species can occupy different ecological niches by varying foraging behaviour, diet (type or size of prey), habitat preference or activity patterns (MacArthur 1958, Burger 1983, Ebersole 1985, Siemers and Schnitzler 2004, Garcia and Arroyo 2005). Hence by partitioning resources, species living in the same area are able to reduce interspecific competition allowing for coexistence (Lack 1971).

Competition among species and conspecifics for food and breeding areas is high in large multi-species assemblages (Pearson 1968, Burger 1981, Cairns 1992a). Large colonies are often spaced far enough apart to prevent the overlap of foraging areas used by conspecifics (Brown and Orians 1970, Furness and Birkhead 1984, Cairns 1989, Gordon and Kulig 1996, Robson et al. 2004, Wakefield et al. 2013). Interspecific competition is likely to be most apparent among closely related species which occupy similar ecological niches (May 1973, Werner and Gilliam 1984, Garcia and Arroyo 2005, Donadio and Buskirk 2006). Such species may reduce competition and allow limited resources to be shared by foraging in slightly different areas, varying dietary preferences or by exhibiting different breeding strategies (Schoener 1974, Croxall and Prince 1980, Swift and Racey 1983, Garcia and Arroyo 2005).

In this introduction, I first describe how seabird population trends in the UK have changed since 1969 and how population trends vary among species. I then describe the main foraging strategies utilised by different seabird species, examine how foraging behaviour affects vulnerability to changes in the marine environment and discuss factors influencing changes in seabird populations. This is followed by an outline of the aims of this thesis and how these have been addressed.

1.1 Changes in Seabird Populations

Seabirds are an important component of biodiversity in the UK with over seven million birds of 25 species regularly breeding (Mitchell et al. 2004). However, seabird populations worldwide are subject to increasing pressure from fisheries, pollution, human disturbance, predation and climate and oceanographic change (Aebischer et al. 1990, Carney and Sydeman 1999, Derraik 2002, Oro and Furness 2002, Frederiksen et al. 2004a, Scott et al. 2006). Since annual population surveys began in the UK in 1969, many species have shown significant spatial and temporal changes in abundance and breeding success; some have shown substantial population growth, while others have declined (Monaghan 1992, Mitchell et al. 2004, JNCC 2012). Those showing increases in population abundance since 1986 include Common Guillemots *Uria aalge* and Northern Gannets *Morus bassanus*, while Black-legged Kittiwakes (*Rissa tridactyla*; hereafter 'Kittiwakes') and particularly Roseate Terns *Sterna dougallii* have declined over the same time period. Trends in population abundance and breeding success can also vary spatially. More northerly colonies of some species have been found to exhibit greater declines in abundance and productivity than colonies further south (Monaghan et al. 1989, Mitchell et al. 2004). This has been attributed to changes in prey distribution and abundance in different regions of the UK (Furness 2002, Mitchell et al. 2004). It has been suggested that interspecific differences in susceptibility to changes in the marine environment explain variation in population changes among seabird species (Rolland et al. 2010, Somero 2010).

1.2 Seabird Foraging Strategies

Seabird species can be divided into two main groups according to their foraging strategies. Diving species (such as auks, Cormorants *Phalacrocorax carbo* and Shags *Phalacrocorax aristotelis*) forage within the water column while surface-feeding species (such as terns and gulls) forage at the sea surface (Pearson 1968). Surface-feeding and diving species differ in vulnerability to environmental change as they exhibit different diet preferences, foraging and breeding behaviour (Pearson 1968, Monaghan 1996, Furness and Tasker 2000). Small surface-feeding species such as Kittiwakes and terns (*Sterna* spp) have been identified as more vulnerable to food shortages than larger diving species as they have limited diving capabilities, restricted abilities to switch to different prey types and, in the case of terns, comparatively short foraging ranges (Furness and Ainley 1984, Furness and Tasker 2000). While diving species are able to forage throughout the water column, surface-feeders are dependent on abiotic factors affecting the availability of prey at the surface (Monaghan 1996, Schwemmer et al. 2009).

There have been significant changes in abundance, distribution, survival and breeding success of surface-feeding seabirds in the UK since the 1970s. Kittiwakes have declined by over 50% since 1986 and have shown similar declines in productivity and adult survival (Mitchell et al. 2004). Over a similar time period the number of Sandwich (*Thalasseus sandvicensis*), Arctic (*Sterna paradisaea*) and Little Terns (*S. albifrons*) breeding in Britain and Ireland have declined by ~11%, 29% and 25% respectively and have shown varying degrees of decline in productivity (Mitchell et al. 2004). Roseate Terns (*S. dougallii*) suffered a significant range contraction as well as a decline in population abundance of ~80% between 1986 and 2000. In the last 15 years there has been a slight increase in abundance and a significant increase in productivity of Roseate Terns owing to the work of conservationists at successful colonies on Rockabill, northeast Ireland and Coquet Island, northeast England; however this species still has a restricted range and breeds in only a few colonies throughout the UK (JNCC 2014). In contrast, diving species such as Common Guillemots and Razorbills *Alca torda* have shown increases in population over a similar time period. Guillemot abundance has increased by ~50% since 1986 and Razorbill abundance increased by 78% from 1986 - 2003, but has declined slightly in recent years (JNCC 2014).

Several biotic and abiotic factors have been found to influence changes in seabird abundance and productivity, such as food availability and quality (Phillips et al. 1996, Wanless et al. 2005b), weather conditions (Dunn 1975, Becker and Specht 1989, Konarzewski and Taylor 1989) and predation pressure (Oro and Furness 2002, Jones et al. 2008), and the impact of these factors on seabird populations are increasing due to recent changes in the marine environment (Montevecchi and Myers 1997, Grémillet and Boulinier 2009). However, sympatric species breeding at the same colony have been found to vary in susceptibility to environmental change depending on foraging behaviour and diet (Uttley et al. 1989, Inchausti et al. 2003, Chivers et al. 2012a). Those species with restricted diving abilities and limited diets are more severely affected by food reductions and adverse weather conditions than other species (Uttley et al. 1989, Furness and Tasker 2000).

1.3 Factors Influencing Seabird Population Change

1.3.1 Climate Change

Recent changes in climate have been attributed at least in part to increases in levels of anthropogenic greenhouse gases in the atmosphere (Crowley 2000, Solomon et al. 2009, Shindell et al. 2012). The Intergovernmental Panel on Climate Change (IPCC) has reported an average increase of 0.74°C in global surface temperature from 1906 – 2005 and that global average sea levels have risen an average rate of 1.8 mm per annum from 1961 – 2003 (IPCC 2007). The incidence of heavy rainfall has increased worldwide by 2 – 4% from 1906 – 2005 and the Northern Hemisphere is experiencing increasingly extreme weather patterns (Groisman et al. 1999, IPCC 2007, Min et al. 2011).

Various aspects of seabird breeding biology, including timing of breeding, recruitment, breeding success and adult survival, have been related to climatic conditions (La Cock 1986, Kitaysky and Golubova 2000, Druant et al. 2003, Inchausti et al. 2003). Adverse weather conditions can affect the metabolic rate of birds and negatively influence foraging conditions and chick survival (Taylor 1983, Sagar and Sagar 1989, Uttley et al. 1989, Aebischer et al. 1990, Crick 2004).

Climate change is expected to cause a further rise in sea levels, an increase in wave height and is anticipated to influence oceanographic phenomena such as the North Atlantic Oscillation (NAO) (Bacon and Carter 1991, Mitchell 2006, Christensen and Christensen 2003). Rising sea levels may reduce the extent of nesting habitat available to ground-nesting seabirds such as terns, which commonly breed in coastal areas (Mitchell 2006). Exposed colonies close to the sea are likely to be more vulnerable to sea level rises and erosion than sheltered positions on cliffs. Hence, changes in available breeding habitat may be expected to vary among regions and among species. Studies have already reported increased instances of coastal bird colonies being flooded during the breeding season due to an increase in wave height in recent years (Brinker et al. 2007, van de Pol et al. 2010); the frequency of such events is likely to increase in the future according to climate model predictions (Dale 2005, Woth et al. 2006, Beniston et al. 2007). Other direct effects of climate change on seabird demographics include increased mortality due to heat stress (Sherley et al. 2011, Oswald and Arnold 2012), winter storm intensity (Sherley et al. 2011) and increases in the frequency of toxic algal blooms (Doney et al. 2012). Increased rainfall and wind strength have been shown to adversely affect chick mortlity in some species (Dunn 1975, Demongin et al. 2010), and to detrimentally affect the foraging ability of adults during the breeding season (Dunn 1973, Dehnhard et al. 2013). Most climate models predict increases in the incidence of stormy conditions in the UK in coming years (Woth et al. 2006, Beniston et al. 2007).

The reproductive success of some UK seabird species is correlated with the NAO (Thompson and Ollason 2001, Frederiksen et al. 2004a), a periodic fluctuation in pressure gradient between the high atmospheric pressure zone over the Azores and the low pressure zone over Iceland (Hurrell et al. 2003). The NAO influences winter weather conditions in the UK and northern Europe; positive NAO indices correspond to warm and wet winter weather conditions and negative indices to cold dry conditions (Hurrell 1995, Hurrell and van Loon 1997). An increase in the frequency of positive NAO indices in Europe in recent decades has been linked to climate change (Hurrell 1995). Productivity of various seabird species breeding at colonies throughout the UK have been shown to be lower in years with positive winter NAO indices (Thompson and Ollason 2001, Frederiksen et al. 2004a) due to the effect of NAO on prey availability during the breeding season (Arnott and Ruxton 2002). While the NAO does not directly cause changes in seabird demographics, it represents variation in meteorological and oceanographic conditions such as sea surface temperature (SST), air pressure and strength and direction of ocean currents, which can influence seabird mortality and breeding success via effects on primary productivity in the ocean and the abundance and distribution of organisms at lower trophic levels, such as fish species, which seabirds rely upon during the breeding season (Dalpadado et al. 2003, Sandvik et al. 2005). Incidences of adverse weather conditions, which can negatively affect winter survival and breeding success (Schreiber 2002), are also related to changes in the NAO.

1.3.2 Food Shortage

Over the last 20 – 30 years, seabird breeding success has shown spatial and temporal variation in the North Sea (Ratcliffe 2004). Breeding success of species such as terns and Kittiwakes has declined in recent decades and these declines have been especially evident in more northerly regions (Monaghan et al. 1989, Mitchell et al 2004). Declines in breeding success have been attributed to changes in food availability, particularly the prevalence of Lesser Sandeel (*Ammodytes marinus*; hereafter ‘sandeel’) (Monaghan 1992, Wanless et al. 1998, Furness and Tasker 2000). Sandeel distribution, abundance and phenology have been linked to fishery activities and to changes in climate with potentially significant impacts for marine predators (Arnott and Ruxton 2002, Frederiksen et al. 2004a, Daunt et al. 2008).

Previous studies have described long-term distributional shifts in several species of marine fish in the North Sea in response to climate change (Genner et al. 2004, Beare et al. 2004, Perry et al. 2005). Some Clupeid species have already shown a northerly shift in distribution (Corten 2001). Winter sea surface temperature has been found to have a negative impact on sandeel recruitment (Arnott and Ruxton, 2002) and increasing sea temperatures affect distribution of fish within the water column, making foraging more difficult for surface-feeding seabirds (Dulvy et al. 2008).

The timing of the peak spring plankton bloom in the North Sea has shifted over the past 35 years and phyto- and zooplankton abundance, distribution and phenology have been altered due to changes in winter sea temperatures (Beaugrand et al. 2002, Beaugrand 2004, Edwards and Richardson 2004, Sharples et al. 2006). It has been suggested that the recent decline in sandeel numbers in the North Sea has been driven by the effect of climate change on the phenology of plankton communities (Furness 2002, Edwards and Richardson 2004, Dulvy et al. 2008), with negative impacts on seabird breeding success (Frederiksen et al. 2004a, b).

Although changes in the oceanographic environment are thought to be the main driver of sandeel declines in the North Sea, industrial sandeel fisheries can have significant local effects on prey availability for seabirds (Monaghan 1992, Frederiksen et al. 2004a). After the closure of the Firth of Forth fishery in 2000, sandeel abundance increased significantly (Greenstreet et al. 2006) with a corresponding increase in Kittiwake breeding success on the Isle of May (Daunt et al. 2008). Fishery activities have been shown to detrimentally affect seabird breeding success and adult mortality by influencing the abundance of local fish populations, which many species rely on during the breeding season (Furness and Tasker 2000, Rindorf et al. 2000), and by causing direct mortality through by-catch on fishing lines and entanglement in nets (Strann et al. 1991, Tasker et al. 2000). While the depletion of small lipid-rich fish by fisheries have led to corresponding declines in seabird abundance and breeding success in various areas including Peru, the North Sea and the Norwegian Sea (Duffy 1983, Tasker et al. 2000), the activities of fisheries have occasionally benefited local seabird populations by reducing the abundance of competing predatory fish (Tasker et al. 2000) and providing food in the form of discards and offal (Garthe et al. 1996, Ojowski et al. 2001). In a study by Frederiksen et al. (2006), productivity of four seabird species were found to be positively related to biomass of larval sandeel in the previous year, which suggests that birds rely on one-year-old fish to successfully rear chicks. As larger fish species also feed on this age cohort, reductions in large fish species by fisheries may have a positive impact on seabird breeding success at this colony. However, other studies have suggested that the presence of industrial fisheries has no observable effect on seabird breeding success (Furness 2002).

1.3.3 Predation

Local declines in sandeel abundance can increase predation risk of seabird chicks by increasing the likelihood of chick neglect by parents (Wanless et al. 2005a, b) and by reducing availability of predators' primary food supply (Hamer et al. 1991, Votier et al. 2004). In Shetland, Great Skuas (*Stercorarius skua*) mainly feed on sandeels but a decline in sandeel abundance in the late 1970s increased reliance on fishery discards and seabirds as alternative food sources (Hamer et al. 1991).

Ground-nesting seabirds such as terns are particularly vulnerable to predation from mammalian predators (Clode and MacDonald 2002, Sanders and Maloney 2002), but also lose eggs and chicks to aerial predators (Shealer and Burger 1992, Becker 1995, Yorio and Quintana 1997). The effect of predation on breeding population abundance and productivity may be expected to vary among sympatrically breeding terns, as species show consistent interspecific differences in nesting behaviour and predator defence strategies (Burger and Gochfeld 1988a, Yorio and Quintana 1997, Jones et al. 2008). Black-headed Gulls (*Chroicocephalus ridibundus*), Common (*Sterna hirundo*) and Arctic Terns have been shown to behave more aggressively towards predators than Sandwich Terns (Fuchs 1977), which respond to the threat of predation by forming denser colonies and becoming less likely to flush from nests (Cullen 1960, Fuchs 1977). Sandwich Terns commonly associate with other species to benefit from predator defence strategies (Fuchs 1977).

1.4 Aims

The main aim of this thesis is to investigate intra- and interspecific variation in foraging behaviour and demographic parameters in a multi-species seabird community, examine how variation in foraging behaviour affects reproductive parameters, and to consider the implications of these findings for seabird conservation. The utility of seabirds as indicators of change in the marine ecosystems is then evaluated. These aims are addressed by examining long-term data sets of tern species and their predators breeding on Coquet Island, northeast England and by examining changes in foraging behaviour and reproductive parameters of three tern species and Black-legged Kittiwakes breeding at the same colony during the breeding season in 2011 and 2012. It has been previously shown that seabird foraging behaviour can vary temporally as well as among sympatrically breeding species (Duffy 1986, Weimerskirch et al. 1993, Mori and Boyd 2004, Chivers et al. 2013). However, many previous studies have examined foraging behaviour in only two sympatric seabirds and have limited their investigations to a single stage of the breeding season (Duffy 1986, Lewis et al. 2002, Lance and Thompson 2005, Weimerskirch et al. 2007). This project aims to expand on previous research by examining foraging behaviour over longer temporal periods and in several sympatrically breeding species, as well as examining how foraging ecology influences vulnerability of seabirds to environmental change. I make recommendations for the extent and location of MPAs to represent foraging areas of seabird species breeding on Coquet Island.

The history of research and conservation on Coquet Island is explored in Chapter 2 and details are given of the limitations affecting field work at this site. Chapter 3 examines inter-annual variation in demographic parameters of four sympatric tern species breeding on Coquet Island from 1975 – 2013 and investigates the extent to which changes in predator abundance influence temporal fluctuations in breeding population abundance and productivity. The next four chapters are based on observational and tracking data collected on Coquet Island during field work from May – July 2011 and 2012. Chapter 4 examines resource partitioning in three sympatric tern species breeding on Coquet by comparing diet and habitat use throughout the chick-rearing period. This work extends previous studies by examining mechanisms used to partition resources in several morphologically similar sympatric species, and employs a more accurate tracking method than has been previously used to identify tern at-sea foraging areas. Chapter 5 examines how interspecific variation in foraging behaviour influences chick growth, survival and fledging success in two sympatrically breeding tern species and improves upon previous studies by quantifying changes in several reproductive parameters. Chapter 6 compares the size and location of foraging areas used by Kittiwakes breeding on Coquet Island in different years and breeding stages and highlights the value of such studies for identifying useful MPAs for seabirds. Chapter 7 investigates intra-brood parental resource allocation in broods of two Kittiwake chicks on Coquet Island and examines how parental investment varies with increasing brood age. Chapter 8 discusses the use of seabirds as biological indicators, summarises the findings of the data chapters and considers the implications of this work for marine conservation.

Chapter 2

Methods

As we used several different methods when collecting data, detailed descriptions of methods are available in respective data chapters. Data were collected from several seabird species (Arctic *Sterna paradisaea*, Common *S.hirundo* and Roseate Terns *S.dougallii* and Black-legged Kittiwakes *Rissa tridactyla*) breeding at the same study site, Coquet Island, Northumberland, England (55° 20' N, 1° 32' W) from May – July 2011 and 2012. Long-term data on breeding population abundance and productivity for four tern species (Arctic, Common, Roseate and Sandwich Terns *Thalasseus sandvicensis*) and two large gull species (Lesser Black-backed Gulls *Larus fuscus* and Herring Gulls *L. argentatus*) were available on Coquet from 1975 and 1991 respectively (data were downloaded from www.jncc.defra.gov.uk/page-4460 and were available from RSPB unpubl. data.). This chapter describes the history and ecology of the study site and the limitations affecting research on Coquet Island.

2.1 Study Site

Coquet Island is a small (5 ha) low-lying island approximately 1 – 2 miles off the coast of Northumberland, northeast England, 30 kilometres south of the Farne Islands (55º 20' N, 1º 32' W; Figure 2. 1). The island has multiple habitats for breeding seabirds including sandy and pebble beaches at the south end, low-lying areas in the centre and small cliffs <7 m in height on the eastern side (Figure 2. 2). Terns breed in specially maintained plots close to the lighthouse at the southwestern edge of the island, while Kittiwakes breed on the small cliffs on the east side of the island (Figure 2. 1). Coquet is a Site of Special Scientific Interest (SSSI) and a Special Protected Area (SPA) under European Law for aggregations of breeding seabirds and has been managed as a reserve for four nationally and internationally important tern species by the Royal Society for the Protection of Birds (RSPB) since 1970. The island currently supports approximately 1000 pairs of Sandwich Terns, 70 – 80 pairs of Roseate Terns, 1200 pairs of Common Terns and 1100 pairs of Arctic Terns (RSPB unpubl. data. 2013). Coquet Island also supports significant numbers of breeding Northern Fulmars *Fulmaris glacialis* (70 pairs), Puffins *Fratercula arctica*

(15,000 pairs), Common Eiders *Somateria mollissima* (300 pairs) and Black-headed Gulls *Chroicocephalus ridibundus* (3000 pairs). Kittiwakes started visiting Coquet in significant numbers in 1990 and a breeding colony was established in 1991 (Coulson and Coulson 2008). Since then the colony expanded each year to 215 pairs in 2012.

Arctic, Common and Roseate Terns have similar body sizes (average body weights of Common Tern = 110 – 140 g, Arctic Tern = 90 – 120 g, Roseate Tern = 105 – 135 g; Cramp 1985, Malling Olsen and Larsson 1995) and bill lengths (Arctic Terns = 3.0 – 3.4 cm, Common Terns = 3.4 – 4.1 cm, Roseate Terns = 3.7 – 4.0 cm; Dunn 1975, Lemmetyinen 1976, Ramos et al. 1998), while Sandwich Terns are considerably larger (average body weight = 210 – 260 g, bill length = 5.0 – 5.4 cm; Dunn 1973, Cramp 1985, Malling Olsen and Larsson 1995). Arctic, Common and Roseate Terns occupy similar ecological niches and exhibit similarities in diet and foraging range. Sandwich Terns, being larger, are able to forage further from the colony and carry larger prey items than smaller tern species. They also have broader diets than other terns and winter in more extensive areas from the Mediterranean to the coast of South Africa (Pearson 1968, Cabot and Nisbet 2013). Tern colonies were distributed homogenously across Coquet Island in the early 1970s, but after 1976 colonies became concentrated in southwestern areas following an increase in the extent of large gull territories (Booth and Morrison 2010). Between 1998 and 2000, the number of breeding pairs of Herring and Lesser Black-backed Gulls increased on Coquet from 11 to 49 (345%) and 20 to 184 (820%) respectively due to disturbance at nearby colonies, such as the Isle of May (Booth and Morrison 2010, JNCC 2012). The RSPB implemented a program of lethal large gull disturbance and population control on Coquet under licence from Natural England annually from 2000 to present, with the aim of limiting gull predation on tern species and reducing competition for nest sites (Thomas 1972, Quintana and Yorio 1998, Morrison and Allcorn 2006). Eggs and nests were destroyed and adult birds disturbed throughout the year using various scaring methods (Morrison and Allcorn 2006, Booth and Morrison 2010). In the years following the introduction of the control program, large gull numbers declined to pre-1998 levels (Morrison and Allcorn 2006, Booth and Morrison 2010). The number of large gulls breeding on the island is currently stable at ~20 – 30 breeding pairs.

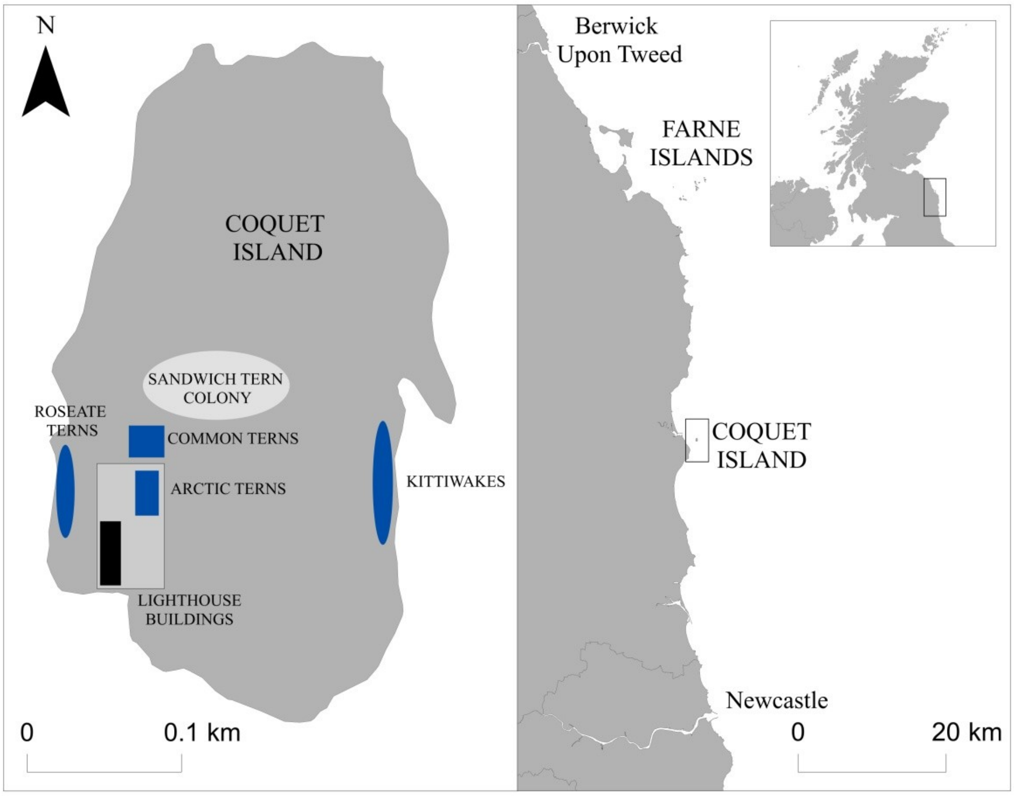

Figure 2. 1 Location of the study site, Coquet Island (55º 20' N, 1º 32' W), Northumberland, northeast England. The first panel details the locations of study plots (blue shaded areas) for Arctic, Common and Roseate Terns and Black-legged Kittiwakes. Location of the Sandwich Tern colony and lighthouse buildings with courtyard are also shown

Figure 2. 2 Aerial view of Coquet Island from the southwest showing locations of the lighthouse buildings, the sandy beach and low-lying central plateau. Photograph courtesy of Paul Morrison

Figure 2. 3 Photographs showing artificial terrace constructed for Roseate Terns on Coquet Island and Roseate Tern eggs in nest box provided by Coquet wardens. Photographs courtesy of Paul Morrison

Coquet Island was home to lighthouse keepers and their families in the 1800s, during which time disturbance from humans and livestock prevented terns from breeding. In 1882 all tern species had disappeared from the island. It is thought that Common Eiders were the only species to breed on the island during this period (Marples and Marples 1934). Terns returned to breed on Coquet after the farming activities of the lighthouse keepers ceased in the 1950s (Langham 1968).

The island is currently leased annually to the RSPB by the Duke of Northumberland. The RSPB liaise with other nature conservation and maritime bodies including the Natural History Society of Northumbria, Trinity House, Northumberland Estates and Northumberland Wildlife Trust to form the Coquet Management Committee, which oversees conservation management and makes decisions regarding the extent of research permitted on the island each year. Coquet is wardened from April – October, is subject to careful conservation management developed by the Coquet Management Committee and has a strict no landing policy.

2.2 Conservation Management for Tern Species on Coquet

The reserve is managed primarily for tern species and vegetation is controlled to maintain suitable breeding habitat for terns. Terns tend to settle in study plots approximately 10 x 10 m in dimension, which are maintained regularly by cutting grass and controlling vegetation in the months leading up to the breeding season. As part of the Coquet Island reserve management plan, conventional herbicides are sprayed at least one month prior to the return of terns to breeding sites in April. Spraying efforts are focused on nettle beds to reduce vegetation growth. Herbicides do not persist in the environment for more than one month and hence have no effect on tern eggs or chicks (Robinson et al. 2001a).

Coquet is the only major breeding site for Roseate Terns in the UK, although two colonies in Ireland also support large breeding populations (Rockabill; 53° 35’ N, 6° 00’ W and Lady’s Island Lake; 52° 12’ N, 6° 23’ W). Numbers of Roseate Terns have fluctuated in the British Isles and throughout Europe since the 1980s due to trapping of adults and juveniles at wintering grounds in Ghana, disturbance at breeding sites by humans and predators and habitat loss (Avery et al. 1995, Mitchell et al. 2004). A European wide action plan was developed for this species to prevent disturbance at breeding colonies through legal protection, to increase available breeding habitat through reserve management and to prevent trapping at wintering grounds through local education (Avery et al. 1995). Wardens on Coquet Island implemented conservation measures to protect and aid the recovery of Roseate Terns in 2000, which included constructing terraces to provide breeding habitat, providing nest boxes to protect eggs and chicks from predation and implementing a large gull control program on the island (Morrison and Gurney 2007, Booth and Morrison 2010).

After discussions with wardens at the Rockabill colony, northeast Ireland, wooden nest boxes 45 x 30 x 15 cm in dimension were constructed and deployed on an artificial shingle terrace on Coquet in 2000 (Morrison and Gurney 2007; Figure 2. 3). Natural Roseate Tern nesting sites occur under beach debris, under boulders or in unused seabird burrows (Cabot and Nisbet 2013), hence providing nest boxes was deemed appropriate for improving the breeding success of this species (Morrison and Gurney 2007). Nest boxes provide shelter for eggs and chicks from predators and from adverse weather conditions. Twelve nest boxes had been provided for Roseate Terns before 2000, but were not enough to accommodate all breeding pairs on Coquet. Since 2000 the number of nest boxes provided has exceeded the number of Roseate Tern breeding pairs. A three tier artificial terrace composed of brick, sand and shingle was constructed before the breeding season commenced in 2000 on a low cliff close to traditional Roseate Tern breeding sites on the southwest side of the island (Figure 2. 1). The terrace was ~25 m long and each tier consisted of a low dry stone wall topped with flagstones covered in shingle taken from a beach on the island’s east side (Figure 2. 3). The length of the terrace was extended in 2001 to allow more nest boxes to be provided. Since 2003, all Roseate Tern pairs breeding on Coquet have used nest boxes as nest sites or as shelters for chicks.

2.3 Limitations to Research on Coquet Island

Due to the sensitive nature of the site, research activities are regulated on Coquet Island by the Coquet Island Advisory Committee to prevent investigators from having significant adverse impacts on breeding success of terns and other seabirds. While permission to conduct research for this study on terns and Kittiwakes was granted by the Committee, limitations were put in place to prevent unnecessary and potentially damaging disturbance. The handling of tern and Kittiwake chicks on a regular basis was not permitted due to the disturbance this would cause to their respective colonies hence chick growth rate had to be calculated during the linear growth phase from two measurements of weight. I was not permitted to carry out observations or chick measurements of Roseate Terns due to the importance of the Coquet Island colony for the survival of this species in the UK, and observations quantifying diet and provisioning rate of Roseate Terns were carried out by the Reserve Warden (Wesley Davies). As the Kittiwake colony was situated on the east side of the island, attempts to reach the colony without disturbing terns were impossible. From May – July 2011 intensive research was conducted on Arctic and Common Terns and unnecessary disturbance to tern colonies was limited during this period. Hence, regular checks of Kittiwake nests could not be made in 2011 to reduce disturbance to breeding terns, and data on productivity and fledging success of Kittiwake study nests in 2011 were not recorded.

Chapter 3

Population synchrony within a multi-species seabird community: changes in abundance of sympatric species following implementation of large gull control

3.1 Abstract

Species breeding sympatrically in the same area are subject to changes in their shared environment. Ecologically similar sympatric species with the same general foraging and breeding behaviour may be expected to exhibit synchronous temporal fluctuations in demographic parameters, while populations of dissimilar species may be expected to fluctuate asynchronously. Previous studies examining synchrony in populations have mainly focused on single species and those which include data from more than one species have compared fluctuations in only one demographic parameter. We tested for synchrony in long-term inter-annual fluctuations of breeding population abundance and productivity among four sympatric tern species breeding on Coquet Island, northeast England. We also examined how changes in the numbers of potential predators (large gull species) affected ecologically similar and dissimilar tern species. The demographic parameters of ecologically similar species (Arctic *Sterna paradisaea,* Common *S. hirundo* and Roseate Terns *S. dougallii*) fluctuated in synchrony over time while those of a species with different foraging and breeding behaviour (Sandwich Terns *Thalasseus sandvicensis*) did not. The population abundance of Roseate Terns was negatively correlated with that of large gulls breeding on the island from 1975 – 2013, while that of Common Terns was positively correlated with large gull abundance and no significant correlations were found between large gull and Arctic and Sandwich Tern populations. The implementation of a large gull control program on Coquet Island in 2000 was strongly correlated with an increase in Roseate Tern breeding abundance and weakly correlated with an increase in Arctic Tern breeding abundance, but was not related to changes in breeding abundance or productivity of other tern species. Examining synchrony in multi-species assemblages improves our understanding of how whole communities react to long-term changes in the

environment and suggests that changes in predator abundance may differentially affect populations of sympatric seabird species.

3.2 Introduction

Spatial synchrony in population fluctuations has been documented in a range of different taxa (Pollard 1991, Ranta et al. 1995a, b, Paradis et al. 2000, Peltonen et al. 2002), but less information is available regarding extent of temporal synchrony among populations of different species (but see Ranta et al. 1995b, Raimondo et al. 2004a, b, Lahoz-Monfort et al. 2011). The majority of studies examining temporal fluctuations in demographic parameters have focused on analysing single parameters for single species (Lebreton et al. 1992, Williams et al. 2003). Synchrony between sympatrically breeding populations of different species has received less attention than that of separate populations of a single species (Raimondo et al. 2004b), and of the limited number of studies examining synchrony in more than one species variation in only a single demographic parameter, such as population abundance, has been analysed (Swanson and Johnson 1999, Raimondo et al. 2004a, b). Examining synchrony in larger species assemblages and incorporating several demographic parameters increases our understanding of the mechanisms responsible for influencing changes in population trends of whole communities (Loison et al. 2002, Lahoz-Monfort et al. 2013).

Seabird species within a community may be expected to react in similar ways to changes in the common environment and to exhibit synchronous temporal variations in population demographics. However, several sympatrically breeding seabird species have been shown to vary in diet and in preferred foraging and nesting habitat, and are therefore differentially affected by environmental conditions (Pearson 1968, Croxall and Prince 1980, Ballance et al. 1997). Ecologically similar seabirds with similar foraging and breeding behaviour might be expected to respond in the same way to changes in the environment, compared with ecologically dissimilar species (Hopkins and Wiley 1972, Bryant and Jones 1999, Trathan et al. 2007, Sandvik and Erikstad 2008). Hence, demographic parameters of species with similar ecological requirements in the breeding and non-breeding seasons are more likely to fluctuate in synchrony than those of species with less similar requirements (Raimondo et al. 2004a, Loreau and Mazancourt 2008, Lahoz-Monfort et al. 2011, 2013).

It is unclear which specific mechanisms cause synchrony or asynchrony in population dynamics among sympatrically breeding species. Hypotheses have suggested that shared stochastic events such as changes in weather conditions and in the presence of generalist predators may influence population fluctuations among species (Ranta et al. 1995a, b, Hawkins and Holyoak 1998, Bjørnstad et al. 1999, Raimondo et al. 2004b). Studies have shown that the presence of predators can differentially affect sympatric species with similar ecological requirements (Lawler 1989, Raimondo et al. 2004b), resulting in synchronous or asynchronous temporal fluctuations in population demographics (Ims and Steen 1990, Korpimäki and Krebs 1996).

Seabird breeding population abundance and productivity have been shown to be closely correlated with food availability, weather conditions and predation pressure in breeding and wintering areas (Crawford and Dyer 1995, Phillips et al. 1999, Ramos et al. 2002, Gaston 2003, Schroeder et al. 2009). While various studies have examined how changes in food availability and oceanographic conditions drive temporal variation in demographic parameters among sympatric species (Crawford and Dyer 1995, Frederiksen et al. 2004a), few have examined how changes in predator abundance influence population fluctuations in multi-species communities (but see Paine et al. 1990, Yorio and Quintana 1997). Colony-based predation can have significant deleterious effects on seabird populations (Oro 1996, Yorio and Quintana 1997, Jones et al. 2008), but sympatrically breeding seabird species with broadly similar ecological requirements have been shown to vary in their vulnerability to predation (Yorio and Quintana 1997, Jones et al. 2008). Hence, the presence of generalist predators may have varying impacts on seabird species of differing conservation concern breeding within multi-species assemblages.

Ground-nesting seabirds such as terns (*Sterna* spp) are vulnerable to predation from mammalian predators (Clode and MacDonald 2002, Sanders and Maloney 2002), but also lose eggs and chicks to aerial predators (Shealer and Burger 1992, Becker 1995, Yorio and Quintana 1997). Large gulls are opportunistic generalist predators and various studies have suggested that gulls can negatively affect tern abundance and breeding success through direct predation of eggs and chicks as well as through competition for nest sites (Courtney and Blokpoel 1983, Côté and Sutherland 1997, Yorio and Quintana 1997, Quintana and Yorio 1998, Vidal et al. 1998, Whittam and Leonard 1999, Schneider 2001). However, many of these studies provide only correlational evidence, and cannot definitively determine whether large gulls directly influence tern populations. Another study failed to show a corresponding decline in sympatric seabird populations (including terns) after the growth of Yellow-legged Gull *Larus michahellis* colonies in the Mediterranean (Oro and Martínez-Abraín 2007), although evidence suggests that Yellow-legged Gulls can negatively affect survival, foraging success and availability of nesting habitat for some species. It has been shown that a few specialised individual gulls can be responsible for the majority of depredation incidents of vulnerable species at seabird colonies, and that the removal of these individuals can significantly improve population demographics of prey species (Sanz-Aguilar et al. 2009).

The effect of predation on breeding population abundance and productivity may be expected to vary among sympatrically breeding terns, as species show consistent interspecific differences in nesting behaviour and predator defence strategies (Burger and Gochfeld 1988a, Yorio and Quintana 1997, Jones et al. 2008). Due to perceived negative effects of the presence of large gulls on tern abundance and breeding success, gull control programs have been implemented in some UK tern colonies, including Rockabill and Coquet Island, which support internationally important numbers of endangered Roseate Terns (*Sterna dougalli*) (Wanless et al. 1996, Mavor et al. 2002, Morrison and Allcorn 2006). Studies at some colonies have suggested that culling gulls can enhance productivity in tern species (Magella and Brousseau 2001), however the extent to which these induced changes in gull numbers were associated with changes in tern numbers on Coquet Island has not previously been evaluated.

In this study, we examine inter-annual variation in two demographic parameters of four tern and two large gull species breeding sympatrically on Coquet Island, northeast England. We test for synchrony in long-term fluctuations of breeding population abundance and productivity among the four tern species and compare the effect of declining large gull abundance on ecologically similar and dissimilar tern species. We examine how tern breeding population abundance and productivity change after the implementation of a large gull control on Coquet Island in 2000. We expect 1) demographic parameters of ecologically similar species to fluctuate in synchrony, 2) demographic parameters of sympatric tern species to change after the commencement of large gull control and 3) changes in large gull populations to differentially affect tern species depending on specific foraging and predator defence behaviours. Our study will determine how changes in abundance and productivity of species within a multi-species seabird community correlate with changes in predator abundance after the implementation of a large gull control program.

3.3 Methods

3.3.1 Demographic Data Collection

Demographic parameters of four tern species (Arctic, Common, Sandwich and Roseate) have been collected annually by reserve staff on Coquet Island since 1975. Number of breeding pairs on the island (breeding population abundance) was recorded for each species by carrying out one to two whole island nest censuses. Censuses were carried out between mid-incubation and early chick-rearing for each species. On occasions when two censuses were carried out, that which produced the largest total nest count was used as the final annual breeding population abundance. Breeding population abundance was therefore defined as the total number of pairs which attempted to breed on the island per annum. Overall productivity (number of fledged chicks per nest) was estimated from a subset of 30 – 50 Arctic and Common Tern nests from study sites located in the centre of their respective colonies, and from colony wide counts of Roseate and Sandwich Tern fledglings (Pearson 1968, Nisbet and Drury 1972). Arctic and Common Tern study sites were selected from areas with dense tern breeding populations and lower vegetation length than peripheral areas, allowing chick survival to be easily monitored throughout the breeding season. Approximately 1 – 4 m² was enclosed around groups of two to three nests within study sites using plastic netting ~0.3 – 0.5 m high to prevent chicks from moving away from nests after hatching (Pearson 1968, McKearnan and Cuthbert 1989, Ramos et al. 1998). Counts were made of the number of eggs and chicks in each study nest every 2 – 7 days allowing survival to fledging to be estimated for each chick and for annual productivity to be calculated for each species. Roseate Terns nests were checked every 7 days to record the number of chicks in each nest from first observed laying date until the last chick fledged. The number of Sandwich Tern fledgings was estimated using close colony observations and photographs, and this estimate was compared with the number of Sandwich nests recorded during whole colony counts. The total number of chicks fledged per nest could then be calculated for Sandwich and Roseate Terns. Methodologies used to estimate productivity were applied consistently from 1991 – 2013. Sandwich Tern fledgling counts could not be carried out in some years due to the position of the colony. In some years, the colony could not be safely approached later in the season when fledglings were present due to the risk of large chicks being scared into the sea.

Herring (*Larus argentatus*) and Lesser Black-backed Gulls (*L. fuscus*) are the only species of large gull which breed regularly on Coquet Island and the only significant predator of resident tern species. The annual breeding abundance of Herring and Lesser Black-backed Gulls was quantified by carrying out a whole island census of nests during mid incubation (within two weeks of first nest being found). As nests belonging to each gull species could not be conclusively differentiated, the breeding population abundances of both species were combined for analyses.

3.3.2 Data Analyses

Data on the breeding population abundance and productivity of four tern species and the breeding population abundance of two large gull species on Coquet Island from 1975 – 2013 were downloaded from www.jncc.defra.gov.uk/page-4460 and were available from Coquet reserve wardens (RSPB unpubl. data. 2013). Breeding population abundance and productivity were collected annually for all four tern species from 1975 and 1991 respectively, and breeding abundance of both large gull species was recorded from 1975. The year on which productivity data collection began varied among tern species (from between 1983 – 1991). Consecutive annual productivity data for all four species were available from 1991, hence inter-annual changes in productivity were compared among species from 1991 – 2013.

A continuous time series of breeding abundance data spanning 39 years was available for four tern species and two large gull species breeding on Coquet Island. Large gull breeding abundance data were missing for one year (2003) hence this year was removed from analyses comparing tern and gull populations. Due to difficulties in measuring productivity of Sandwich Terns on Coquet in some years (owing to annual variation in the position and density of the colony), productivity data for this species were severely fragmented and were therefore excluded from analyses. Productivity data for Arctic, Common and Roseate Terns were available for 23 consecutive years with no missing values. Twenty-five years of tern and large gull breeding abundance data were available before large gull control measures were implemented in 2000 after which a further 13 years of abundance data were available (excluding 2003).

Data on population size are likely to exhibit temporal auto-correlation, and long-term trends may obscure short-term fluctuations (Buonaccorsi et al. 2001), such as those which may be linked to variation in gull numbers. Long-term trends were therefore removed from time series by subtracting actual data values from a cubic smoothing spline (fitted using R version 2.13.1), where the number of knots in the spline was equal to the number of decades in the time series (rounded) + 1 (Chatfield 1989, Sokal and Rohlf 1981, Kerlin et al. 2007). A smoothing spline can be fitted to a series of noisy data points to represent a general trend in the data. A cubic smoothing spline is constructed from a series of third-degree polynomials and is commonly used in analyses (fitted using the 'smooth.spline' function in R version 3.1.2). Various types of smoothing spline were constructed using different numbers of knots and degrees of freedom before a final cubic spline was chosen. This appeared to represent general overall trends in time series for each species. The number of knots included in a spline can vary the degree of smoothing. Making the number of knots used in splines equal to the number of decades in the time series + 1 resulted in a spline which best represented trends in breeding abundance and/or productivity for each species. This method of choosing a smoothing spline has also been used in previous studies (Kerlin et al. 2007). Therefore, this justification was used each time a smoothing spline was constructed. The resulting values were then standardised by dividing each by the standard deviation of the detrended time series. This was repeated for each tern species. Detrended and standardised time series for each species pair combination were plotted against each other and a Pearson's product-moment correlation coefficient calculated after testing data for normality using Shapiro-Wilks tests. A Bonferroni correction was then applied to resultant *p*-values to account for multiple comparisons on the data, using the 'corr.test' function from the package 'psych' (Revelle 2014) in R version 3.1.2. This analysis was repeated for Arctic, Common and Roseate Tern annual productivity data.

Cross-correlation functions (carried out using the 'ccf' function in R version 3.1.2) were used to examine correlations between large gull and tern populations at different time lags using detrended and standardised data. Large gull and tern breeding abundance data were detrended and standardised using smoothing splines as described above for previous analyses. Cross-correlation functions were used to determine whether breeding abundance of large gulls and those of four sympatric tern species were correlated from 1975 – 2013 (Chatfield 1989, Pollard 1991, Ranta et al. 1995a, b). As disturbance and predation by large gulls in one year may influence the number of terns returning to breed on the island in subsequent years, we examined correlations between large gull abundance at lag 0 and tern abundance at lags 1 – 3 (juvenile terns which fledged on Coquet usually returned to breed within 2 – 3 years (Nisbet et al. 1984, Cabot and Nisbet 2013)). Species with cross-correlation coefficients which were not included within 95% confidence intervals were regarded as significantly correlated. Cross-correlations between large gull and tern productivity could not be examined as productivity of large gulls was not recorded on Coquet Island.

Due to temporal autocorrelation within breeding population abundance and productivity data, bootstrapping procedures were used to determine whether the breeding abundance of Arctic, Common, Sandwich and Roseate Terns and the productivity of Arctic, Common and Roseate Terns were significantly greater during years when a large gull control program was implemented on Coquet. One data point was randomly sampled from years before control was implemented and another from years when control was carried out. The difference between the two points was calculated and the procedure repeated 10,000 times to generate 95% confidence intervals taken from the resulting distribution. If confidence intervals overlapped 0, the difference in breeding abundance or productivity before and after control was not regarded to be significant. Analyses were carried out in R version 3.1.2 (R Development Core Team 2014). Means are presented ± SE throughout.

3.4 Results

3.4.1 Temporal Fluctuations in Breeding Population Abundance of Tern Species

Arctic, Common and Roseate Terns showed similar overall trends in breeding population abundance from 1975 – 2013. All three species showed reduced breeding abundance in the mid 1980s followed by an increase after 2000 (Figure 3. 1). Sandwich Terns did not show any clear trend in breeding abundance over time due to large inter-annual population fluctuations, but the number of breeding pairs on Coquet appeared to decline after 2000 (Figure 3. 1). The apparent lack of trend in Sandwich Tern abundance is unlikely to be a reflection of poorer quality data available for this species, as the annual number of breeding pairs on the island was recorded using similar methods for each tern species (namely, counting number of active nests). Large gull breeding abundance was relatively stable on Coquet Island from 1980 to the mid 1990s, after which numbers increased before declining again after 2000.

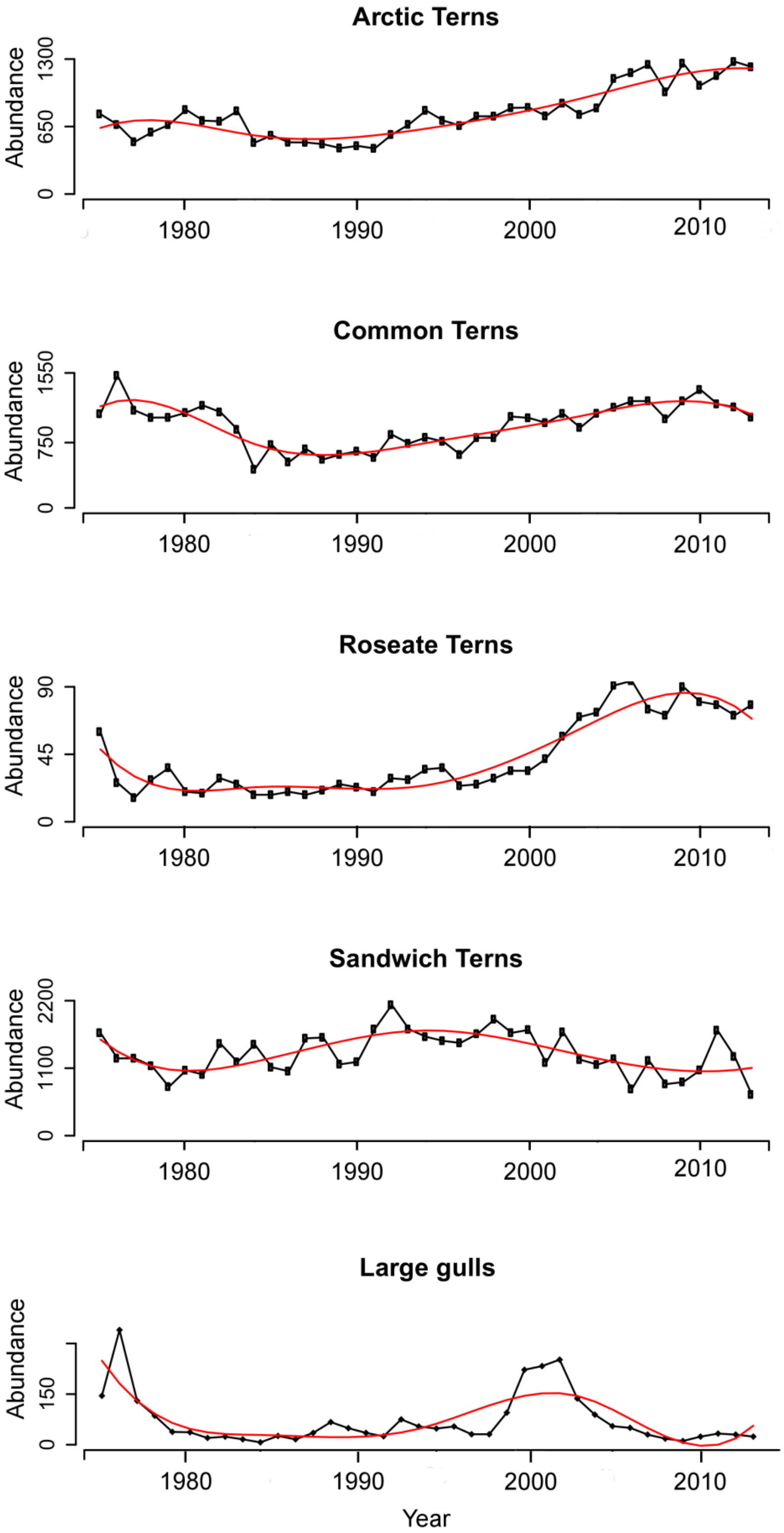

Figure 3. 1 Time series showing Arctic Tern, Common Tern, Sandwich Tern, Roseate Tern and large gull (Herring and Lesser Black-backed) breeding population abundance (number of breeding pairs) on Coquet Island from 1975 – 2013. Cubic smoothing splines were fitted to the data to illustrate general population trends for each species and are displayed here as red lines. Residual values between splines and data points were compared between tern species to examine interspecific synchrony in breeding abundance. One year (2003) of large gull breeding population abundance is missing

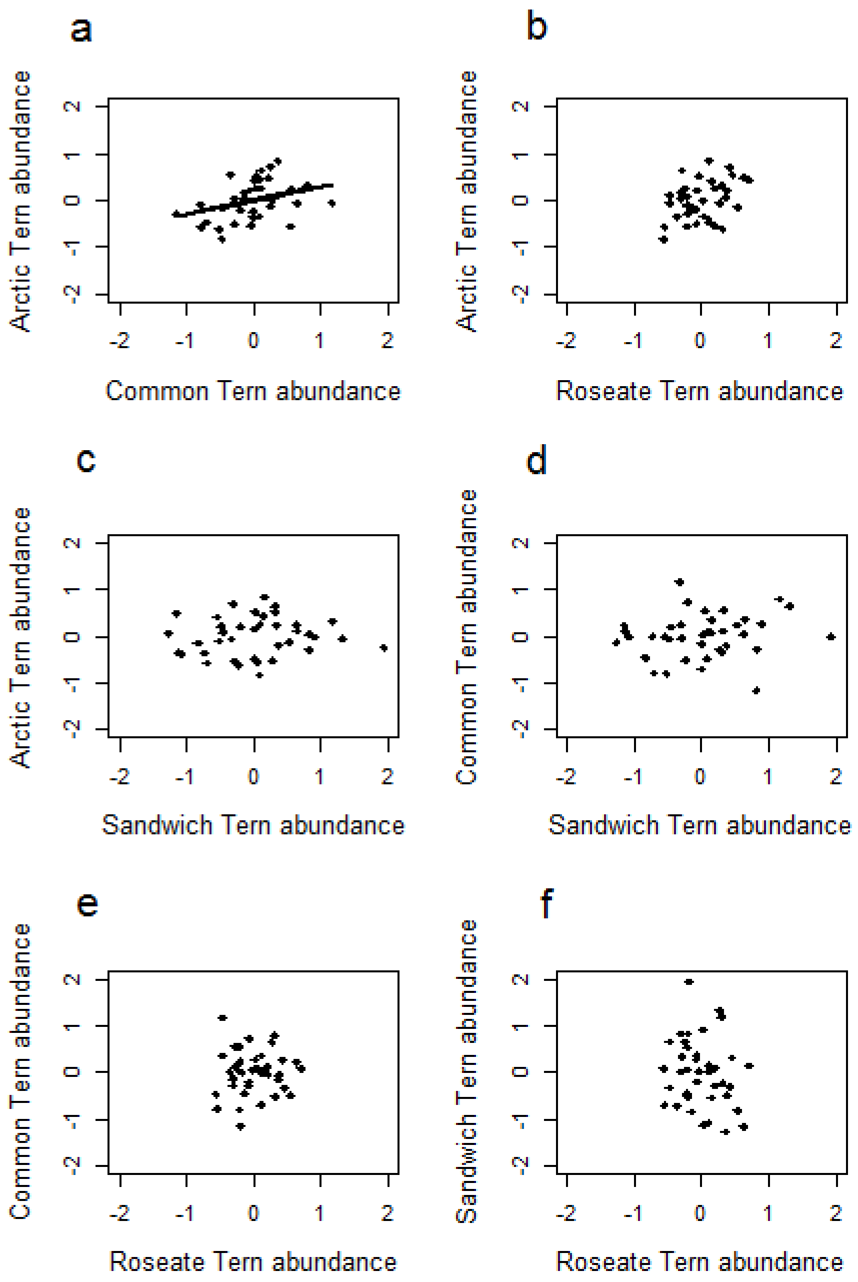

Figure 3. 2 Correlations in detrended and standardised breeding population abundance for each tern species pair breeding on Coquet Island from 1975 – 2013 (**a**: Arctic and Common Terns; **b**: Arctic and Roseate Terns; **c**: Arctic and Sandwich Terns; **d**: Common and Sandwich Terns; **e**: Common and Roseate Terns; **f**: Sandwich and Roseate Terns). The straight line represents median quantile regression line (fitted using the 'rq' function from the package 'quantreg' in R version 3.1.2 (Koenker 2009)). Almost significant Pearson's product-moment correlations with Bonferroni corrections were found for Arctic and Common Terns ($p = 0.07$)

We calculated Pearson's product-moment correlation coefficients from detrended standardised breeding abundance data for each combination of tern species. Significant positive coefficients were found for Arctic and Common Terns ($p = 0.01$, $r = 0.39$, $n = 39$) and Arctic and Roseate Terns ($p = 0.02$, $r = 0.36$), while no significant correlations were found for Common and Roseate Terns (*p* = 0.83, *r* = 0.03), Common and Sandwich Terns (*p* = 0.29, *r* = 0.17), Arctic and Sandwich Terns (*p* = 0.61, *r* = 0.08), and Sandwich and Roseate Terns (*p* = 0.23, *r* = -0.20). However, after applying the Bonferroni correction to these comparisons, only an almost significant correclation between Arctic and Common Terns was apparent (Table 3. 1). Figure 3. 2 illustrates correlations between standardised detrended breeding population abundance for each combination of tern species pair. A Pearson's product-moment correlation test with a Boferroni correction was almost significant for Arctic and Common Terns (Figure 3. 2 a), although no significant correlations were found for other tern species pairs.

Table 3. 1 Results of Pearson's product-moment correlations with Bonferroni corrections calculated from detrended and standardised breeding population abundance (number of breeding pairs) data for each combination of tern species pair. The almost significant correlation between Arctic and Common Terns is highlighted in bold

	Arctic	**Common**	**Roseate**
Arctic	-		
Common	***r* = 0.39, *p* = 0.07**	-	
Roseate	*r* = 0.36 , *p* = 0.13	*r* = 0.03, *p*>0.99	-
Sandwich	*r* = 0.08, *p*>0.99	*r* = 0.17, *p*>0.99	*r* = 0.20, *p*>0.99

Inter-annual fluctuations in productivity appeared to be similar for Arctic, Common and Roseate Terns (Figure 3. 3). All three species were found to exhibit similar temporal fluctuations in productivity (Table 3. 2 Results of Pearson's product-moment correlations with Bonferroni corrections calculated from detrended and standardised productivity (number of fledged chicks per nest) data for each combination of tern species pair. , Figure 3. 4). This suggests that inter-annual fluctuations in the productivity of these three tern species were significantly similar. Productivity of Sandwich Terns was not recorded consistently on Coquet hence no comparisons could be made with productivities of other tern species.

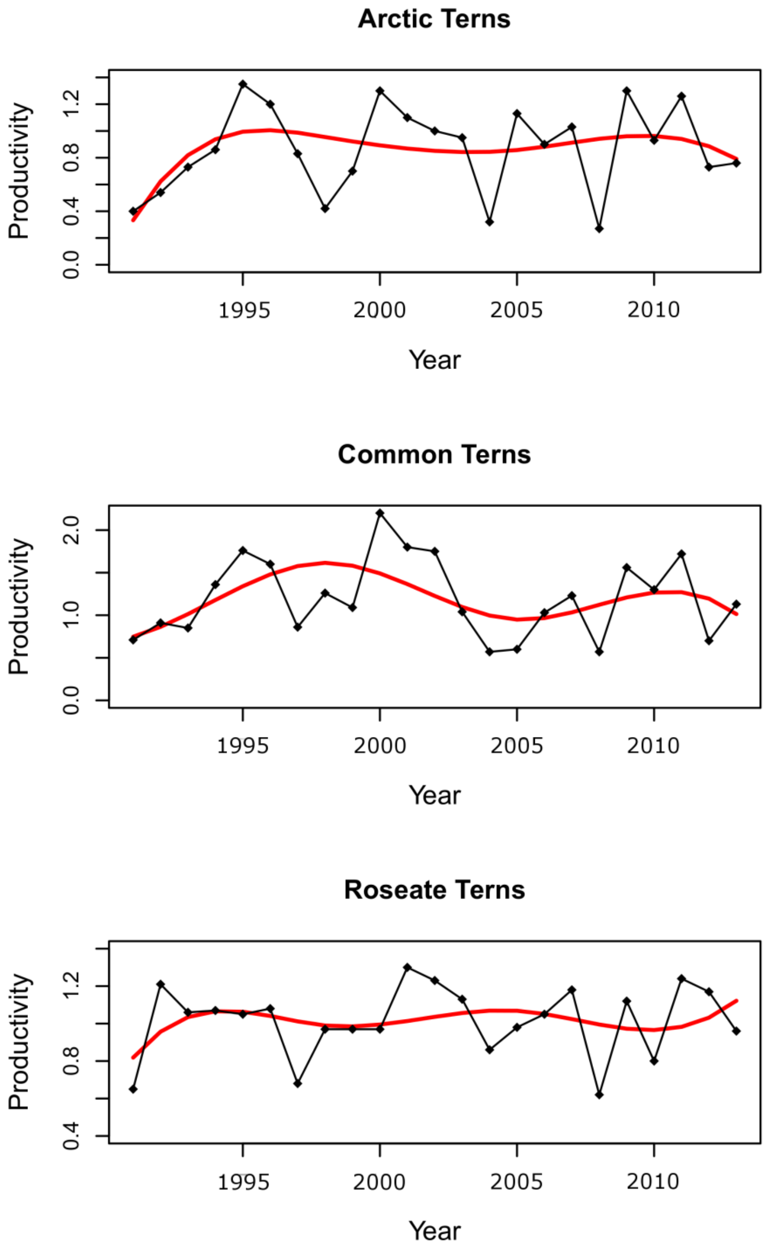

Figure 3. 3 Time series showing productivity (number of fledged chicks per nest) of Arctic, Common and Roseate Tern populations breeding on Coquet Island from 1991 – 2013

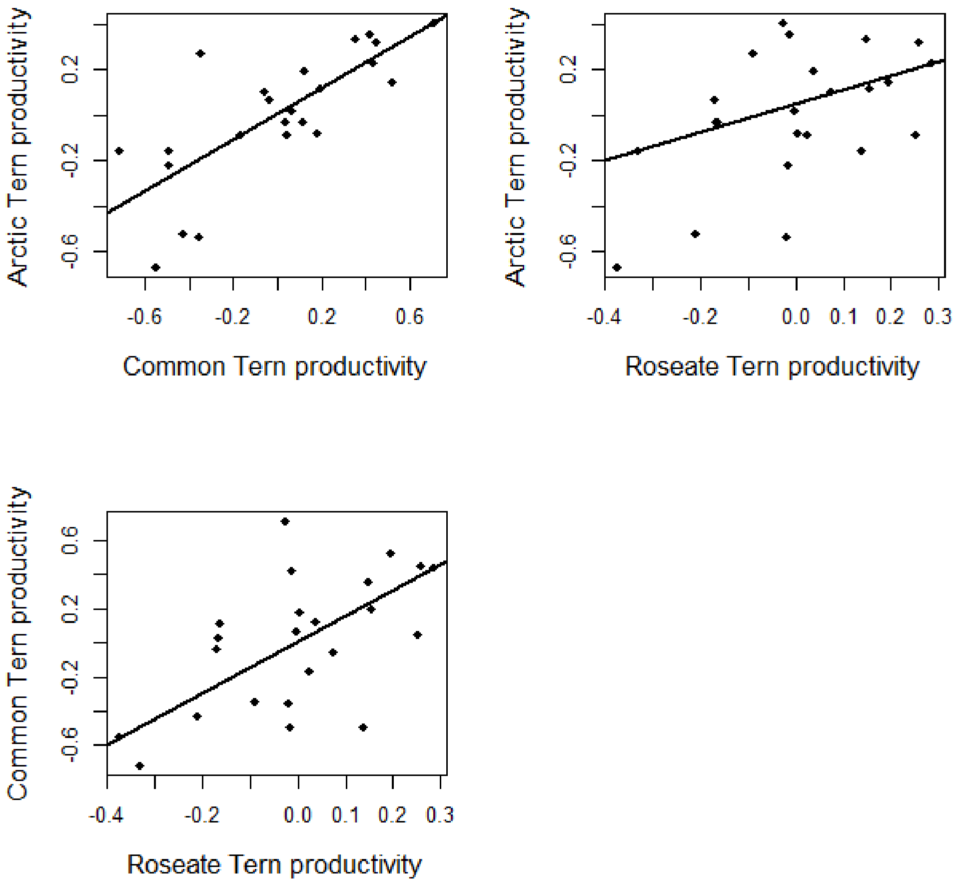

Figure 3. 4 Correlations between tern species pairs using detrended and standardised productivity time series for Arctic, Common and Roseate Terns breeding on Coquet Island from 1991 – 2013. Straight lines represent median quantile regression lines (fitted using the ‘rq’ function from the package ‘quantreg’ in R version 3.1.2 (Koenker 2009)). Significant Pearson’s product-moment correlations with Bonferroni corrections were found for all three species pairs

Table 3. 2 Results of Pearson's product-moment correlations with Bonferroni corrections calculated from detrended and standardised productivity (number of fledged chicks per nest) data for each combination of tern species pair. Significant correlations are highlighted in bold

	Arctic	**Common**
Arctic	-	
Common	**$r = 0.76, p<0.001$**	-
Roseate	**$r = 0.53, p = 0.03$**	**$r = 0.59, p = 0.01$**

3.4.2 Changes in Large Gull Abundance and Tern Demographic Parameters

Figure 3. 1 appears to show that Arctic, Common and Roseate Tern breeding abundance increased following a decline in large gull breeding abundance in 2000 after the commencement of a large gull control program. To examine this effect further, large gull abundance data from 1975 – 2013 (excluding 2003) were compared with the breeding population abundance of each tern species over the same time period.

Cross-correlation coefficients were calculated to compare breeding abundance of large gulls with those of the four tern species breeding on Coquet for 3 positive time lags (years) from 1975 – 2013 (Figure 3. 5). Figure 3. 5d shows that the breeding abundance of large gulls and that of Roseate Terns were significantly negatively correlated during concurrent (lag 0 (r_t)) years (r_{t0} = -0.40). There was a significant positive correlation between abundance of large gulls and Common Terns at lag 0 (r_0 = 0.51; Figure 3. 5b). Conversely, no significant correlations were found between large gull and Sandwich Tern breeding population abundance or between large gull and Arctic Tern breeding population abundance at any time lag (Figure 3. 5a and c). It may be that significant correlations between tern species and large gulls were influenced by four years of particularly high large gull abundance (1976, 1999, 2000, 2001). To test this, 95% confidence intervals of detrended standardised abundance data, excluding years of high gull abundance, were calculated for Common and Roseate Terns. Detrended and standardised tern data for 1976, 1999, 2000 and 2001 were included within the confidence intervals for Roseate Tern data, however 1976 was not included within conficence intervals for Common Tern data. Hence, the significant correlation between Common Tern and large gull abundance may have been influenced by large gull abundance in 1976.

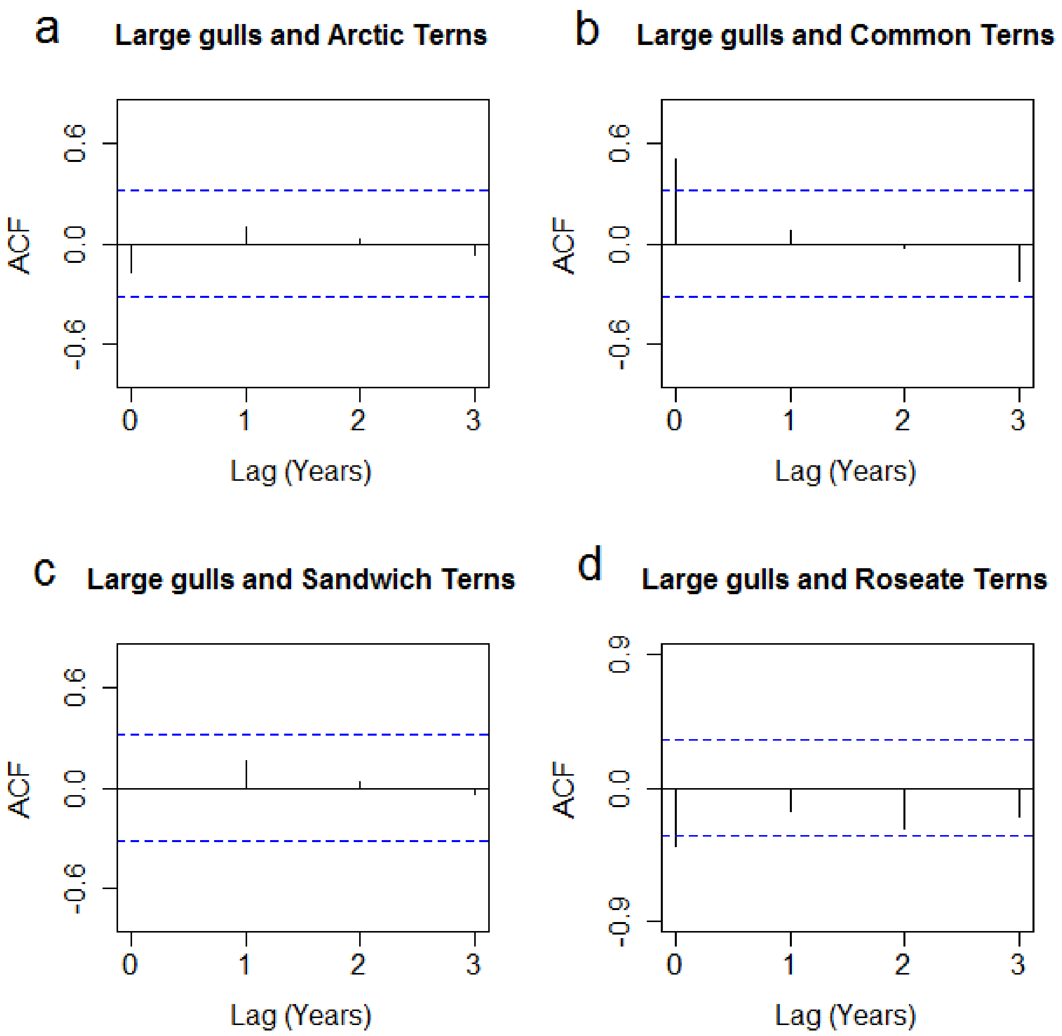

Figure 3. 5 Cross-correlation functions calculated for large gull and tern detrended and standardised breeding population abundance (number of breeding pairs) from 1975 – 2013 (excluding 2003) for **a)** large gull and Arctic Terns, **b)** large gull and Common Terns, **c)** large gulls and Sandwich Terns and **d)** large gulls and Roseate Terns. A significant negative correlation (where the correlation coefficient lay outside the lower 2.5% confidence interval) were found at lag 0 for Roseate Terns (r_{t0} = -0.40). There was a significant positive correlation between large gull and Common Tern abundance at lag 0 (r_{t0} = 0.51). There were no significant correlations between large gull and Sandwich Tern and large gull and Arctic Tern breeding population abundances at any time lag

For each tern species breeding on Coquet, we examined the difference between breeding population abundance before and after large gull control was implemented in 2000 using a bootstrapping procedure. Only Roseate Terns showed a significant increase in breeding population abundance (26.48 ± 1.83 and 71.71 ± 4.62 breeding pairs before and during control years respectively; bootstrapping 95% confidence intervals = 5 – 74, iterations = 10,000). Although Common Terns showed an increase in abundance after 2000 (850.32 ± 51.17 and 1122.14 ± 31.83 breeding pairs), this difference was not significant (95% confidence intervals = -365 – 745). Sandwich Terns showed a slight decrease in breeding population after 2000 (1423.8 ± 64.15 and 1192.29 ± 91.53 breeding pairs), but there was no significant change in abundance (95% confidence intervals = -1066 – 661). Arctic Terns showed an almost significant increase in breeding population abundance over the same time period (633.68 ± 25.91 and 1036.14 ± 51.81 breeding pairs; 95% confidence intervals = -5 – 795). However, when this analysis was repeated comparing magnitude and direction of interannual changes before and after the introduction of gull control, no significant difference was found for any tern species (95% confidence intervals, Arctic: -75.34 – 126.63; Common: -110.79 – 112.23; Roseate: -3.51 – 11.61; Sandwich: -364.91 – 171.11).

Arctic, Common and Roseate Terns exhibited slight increases in productivity in years when large gull control was carried out (Arctic = 0.78 ± 0.11 and 0.93 ± 0.09 fledged chicks per nest; Common = 1.16 ± 0.12 and 1.28 ± 0.14; Roseate = 0.97 ± 0.06 and 1.04 ± 0.05 before ($n = 9$) and during ($n = 14$) control years respectively). However, no species showed a significant change in productivity after the implementation of large gull control (Arctic 95% bootstrapping confidence intervals = -0.88 – 0.88; Common = -1.06 – 1.29; Roseate = -0.44 – 0.59, iterations = 10,000).

3.5 Discussion

Our results suggest that temporal fluctuations in breeding population abundances of Arctic and Common Terns on Coquet Island may be synchronous, but there were no significant correlations in inter-annual population fluctuations among other tern species. Temporal variations in Sandwich Tern population breeding abundance were not synchronous with those of other tern species breeding on Coquet Island. Arctic and Common Terns, Arctic and Roseate Terns, and Common and Roseate Terns showed significantly similar temporal fluctuations in productivity, which did not vary with changes in gull numbers. Inter-annual comparisons with Sandwich Tern productivity could not be made as productivity data for Sandwich Terns were not consistently recorded on Coquet.

Previous studies have shown that sympatrically breeding seabird species can exhibit similar fluctuations in population demographics in response to general changes in the marine environment (Lahoz-Monfort et al. 2011, 2013). Declining food availability and adverse weather conditions have been shown to reduce foraging ability and breeding success in whole seabird communities (LaCock 1986, Barrett and Krasnov 1996, Frederiksen et al. 2004a, Monticelli et al. 2007, Daunt et al. 2008, Loreau and Mazancourt 2008, Cabot and Nisbet 2013, Lahoz-Monfort et al. 2013). Organisms which coexist in the same habitat over time tend to be affected in similar ways by changes in their environment, hence, in the absence of complete niche differentiation, demographic parameters of coexisting species should fluctuate together (Loreau and Mazancourt 2008). While diet and foraging behaviour of Arctic and Common Terns breeding at various colonies including Coquet Island have been shown to vary (Uttley et al. 1989, Rock et al. 2007, Robertson et al. 2014a), there are some general similarities in prey preferences and nesting behaviour among these species which may influence changes in demographic parameters (Hopkins and Wiley 1972, Cabot and Nisbet 2013).

Various studies have illustrated the importance of sandeel availability to seabird breeding success in the North Sea (Safina et al. 1988, Monaghan et al. 1989, Monaghan 1992, Furness and Tasker 1997, Wanless et al. 1998, Furness and Tasker 2000). Terns have been identified as being especially vulnerable to reductions in sandeel abundance, due to their relatively short foraging ranges, restricted dietary preferences and limited diving ability (Furness and Tasker 2000). However, it has been suggested that Sandwich Terns are less at risk from food shortages than Arctic, Common and Roseate Terns due to their longer foraging ranges, wider diets and ability to exploit prey deeper in the water column (Furness and Tasker 2000, Perrow et al. 2011, Cabot and Nisbet 2013). Increased storminess and poor weather conditions have been shown to have a detrimental effect on seabird population breeding abundance and productivity (Steel et al. 2005, Mitchell 2006, Frederiksen et al. 2008a). Tern populations are vulnerable to poor weather as they nest in areas with little natural cover and adult foraging success can be significantly reduced in periods of high winds (LeCroy and LeCroy 1974, Taylor 1983, Snow and Perrins 1998, Ramos et al. 2002).

Sympatric populations of Arctic, Common and Roseate Terns can vary significantly in diet, foraging areas and breeding habitat (Duffy 1986, Burger and Gochfeld 1988a, Safina et al. 1990), which may explain the lack of synchrony in breeding population abundance between Common and Roseate Terns and Arctic and Roseate Terns. Roseate Terns construct nests close to cover, in burrows and rock revices and utilise nest boxes, while Arctic and Common Terns tend to have more variable nesting habitats (Burger and Gochfeld 1988b, Cabot and Nisbet 2013). However, productivity was synchronous between Arctic, Common and Roseate Terns over time, perhaps due to certain general similarities in chick provisioning behaviour, such as reliance on sandeel and restricted foraging range and foraging behaviour (Cabot and Nisbet 2013). Productivity is likely to be influenced by local conditions during the breeding season which could affect the ability of parents of all three species to deliver food to chicks, whereas the number of pairs that return annually to nest on the island may be affected by various factors such as conditions in wintering grounds and on migration, and availability of suitable nesting habitat. As tern species vary in wintering habitat and migration strategies (Cabot and Nisbet 2013), as well as in preference for nesting areas, interspecific synchrony in breeding population abundance is less likely than synchrony in productivity. This may explain why there was evidence of synchrony in breeding populations abundance in only in one species pair (Arctic and Common Terns), while three species pairs exhibited synchrony in productivity (Arctic and Common Terns, Arctic and Roseate Terns and Common and Roseate Terns).

Sympatrically breeding Arctic and Common Terns exhibit some overlap in diet and in breeding behaviour (Rock et al. 2007, Cabot and Nisbet 2013). Although there are differences in the foraging and breeding behaviour of Arctic and Roseate Terns, both species tend to have more restricted diets and to forage in deeper waters than Common Terns (Cabot and Nisbet 2013, Robertson et al. 2014a). While synchrony in breeding population abundance and productivity was evident among Arctic, Common populations on Coquet, dissimilarities between these species and Sandwich Tern breeding population abundance suggest that Sandwich Terns responded differently to changes in the shared environment. This confirms our initial expectations that ecologically similar species will exhibit more similar temporal fluctuations in demographic parameters than species which are ecologically dissimilar.

Sandwich Terns are reported to have the most erratic trends in population, distribution and productivity of any seabird species breeding in Britain and Ireland (Mitchell et al. 2004, JNCC 2012, Cabot and Nisbet 2013). Their dramatic inter-annual population fluctuations are thought to be the result of variation in the number of adults attempting to breed in a given year and from movements of individuals between colonies (Mitchell et al. 2004). Sandwich Tern populations on Coquet also exhibit stochastic temporal fluctuations in breeding abundance which may explain why this species' abundance did not synchronise with those of other tern species breeding on the island. Sandwich Terns are ecologically and morphologically dissimilar to Arctic, Common and Roseate Terns (Snow and Perrins 1998) and exhibit very different foraging, migratory and nesting behaviour (Cabot and Nisbet 2013). Being larger, Sandwich Terns are able to forage more successfully during periods of adverse foraging conditions, such as in high winds, than smaller tern species and have less restrictive energy budgets (Dunn 1975, Taylor 1983, Furness and Tasker 2000).

Tern species vary in their vulnerability to predation and in predator defence strategies. Arctic, Common and Roseate Terns nest in comparatively low densities and rely on aggression or camouflage for predator defence (Langham 1974, Snow and Perrins 1998, Cabot and Nisbet 2013). Sandwich Terns, however, exhibit very different predator response behaviour and form dense colonies and become less likely to flush from nests than other more aggressive species when under threat of predation (Cullen 1960, Langham 1974, Fuchs 1977, Veen 1977, Cabot and Nisbet 2013).

Tern breeding abundance and productivity can be detrimentally affected by the presence of predators at the breeding colony (Hunter and Morris 1976, Nisbet and Welton 1984, Yorio and Quintana 1997, O'Connell and Beck 2003). Coquet Island has no natural or invasive mammalian predators, but does support limited numbers of Herring and Lesser Black-backed Gulls. Breeding population abundance of both species was relatively low prior to 1998 when populations started in increase, perhaps due to disturbance at nearby colonies (Booth and Morrison 2010). Since 2000, both species of large gulls have been controlled through nest and egg destruction and consistent adult disturbance, resulting in a gradual decline in large gull abundance to pre-1998 levels (Morrison and Allcorn 2006, Booth and Morrison 2010). We therefore examined the extent to which this was associated with changes in tern numbers.

Our results do suggest that changes in the abundance of generalist predators can differentially affect population demographics of sympatrically breeding seabird species. The breeding population abundance of Roseate Terns was found to increase significantly following corresponding declines in large gull abundance, while the breeding population abundance of Common Terns was found to be positively correlated with that of large gulls. Arctic and Sandwich Tern populations did not respond to changes in large gull abundance. This may be due to reduced vulnerability of Sandwich Terns to predation (Veen 1977), or due to differences in diet and foraging behaviour of these species (Shealer 1998a, Cabot and Nisbet 2013). Arctic and Common Terns have effective predator defense strategies and are highly aggressive during the breeding season (Cabot and Nisbet 2013). These species tend to have wider diets than Roseate Terns and often forage in similar areas (Safina et al. 1990, Robertson et al. 2014a). Roseate Terns may be more vulnerable to predation and disturbance from gulls than other tern species as they arrive at breeding sites comparably late in the breeding season, are less aggressive than Arctic and Common Terns on Coquet, and lack nest defense strategies as effective as those of other tern species (Cabot and Nisbet 2013). Roseate Terns naturally nest under boulders and in rocky crevices and are easily disturbed by the activities of predators, hence the provisioning of nest boxes and predator control is most likely to benefit this species (Morrison and Gurney 2007). It is unclear why Common Tern populations were positively affected by increases in large gull abundance. Common Terns are highly aggressive during chick-rearing (Whittam and Leonard 2000), making this species less at risk from disturbance and predation. Perhaps Common Terns benefited from gulls making nesting habitat available by disturbing and predating Roseate Terns.

To attribute interspecific variation in temporal fluctuations in breeding population abundance only to predator abundance requires an examination of a control site close to Coquet Island where gull control measures have not be implemented. The Farne Islands ~40 km north of Coquet might be expected to be useful as a control site as they support breeding populations of Arctic, Common and Sandwich Terns, but some evidence suggests that methods have been previously carried out on the Farne Islands to disturb and displace large gulls (Booth and Morrison 2010, Wesley Davies pers. comm.).

Breeding population abundance of Roseate Terns increased significantly during years in which large gull control was implemented and Arctic Terns showed an almost significant increase in abundance over the same time period. There was no change in Sandwich or Common Tern abundance during this period and productivity of tern species did not change significantly after 1999. Common Tern breeding population abundance was positively correlated with large gull abundance, which may explain why Common Tern breeding abundance did not increase significantly in years after large gull control commenced. However, Roseate Tern breeding population abundance was negatively correlated with changes in large gull abundance from 1975 – 2013, which may explain why this species increased significantly after the implementation of gull control. However, when this analysis was repeated comparing magnitude and direction of interannual changes before and after the introduction of gull control, no significant difference was found for any tern species. This suggests that interannual fluctuations in tern abundance on Coquet may have been unaffected by the introduction of large gull control.

Previous studies have shown that large gulls can detrimentally affect tern populations through direct predation, disturbance and competition for nest sites (Sadoul et al. 1996, Vidal et al. 1998, Whittam and Leonard 1999, Magella and Brousseau 2001). As tern breeding population abundance is determined by the number of birds which settle at the colony towards the beginning of the breeding season and as there was no change in productivity of tern species in years after large gull control was introduced, disturbance and nest site competition are more likely to be the mechanisms by which large gull abundance influenced the number of terns breeding on Coquet than predation of eggs and chicks (Booth and Morrison 2010). Herring Gulls typically roost at breeding sites throughout the year and pairs may start occupying nest sites as early as December, although nest-building does not usually begin in earnest until early spring (Harris 1963, Brown 1966). Lesser Black-backed Gulls return to breeding territories from February to March and eggs are usually laid in April to May (Harris 1963, Brown 1966). Terns usually do not return from wintering grounds until April – June, with Sandwich Terns arriving as early as March, Arctic and Common Terns in early April and Roseate Terns from late April – May (Cabot and Nisbet 2013). Roseate Terns may be more likely to be affected by reductions in availability of nest sites due to disturbance from large gulls, as they arrive from wintering grounds later than other tern species when competition for space is greatest.

Multi-species seabird assemblages can include species of varying conservation concern. Coquet Island supports breeding populations of four tern species including internationally important numbers of breeding Roseate Terns, and is one of only three regular breeding sites for this species in Britain and Ireland (Mitchell et al. 2004, JNCC 2012). Roseate Terns suffered a range restriction as well as a decline in breeding abundance of ~80% between 1986 and 2000 (Mitchell et al. 2004), but in the last 15 years populations in Britain and Ireland have increased in abundance and productivity owing to the cessation of trapping in wintering sites and to the artificial improvement of breeding habitats at colonies including Coquet (Mitchell et al. 2004, Morrison and Gurney 2007, Mavor et al. 2008, Booth and Morrison 2010). The Roseate Tern population on Coquet Island could have increased for reasons other than predator control, such as the introduction of nest boxes in the 1990s, an increase in the number of nest boxes provided in 2000 and general improvement of breeding habitat on the island (Morrison and Gurney 2007, Booth and Morrison 2010). Hence, the significant cross-correlation between the abundance of large gulls and Roseate Terns from 1975 – 2013 does not provide conclusive evidence that anthropogenic declines in large gull abundance influence tern populations. However, our results suggest that the control program on Coquet Island may at least partly influence changes in endangered Roseate Tern populations, but long-term tern demographic data from a nearby colony where no large gull control had been implemented is necessary to confirm or refute the results of this study.

Measuring synchrony in demographic parameters at a multi-species seabird assemblage improves our understanding of how whole communities react to long-term variations in the marine environment. Such studies are invaluable when considering the effect of climate change and other long-term environmental changes on communities of apex predators (Inchausti et al. 2003, Piatt et al. 2007, Gaston et al. 2009). Our results confirm our initial expectations that the demographic parameters of ecologically similar species fluctuate in synchrony over time and that the effects of changes in predator abundance on demographic parameters differ among species. Tern species which exhibited similarities in inter-annual fluctuations of demographic parameters did not respond in similar ways to changes in predator abundance. Arctic and Sandwich Terns were unaffected by changes in gull abundance, Common Tern populations were positively correlated with those of large gulls, while Roseate Tern populations were negatively correlated with changes in gull abundance on the island. This suggests that predator abundance may be partly responsible for the interspecific variation in temporal fluctuations of population demographics observed on Coquet Island. While gull control in other UK colonies have had mixed results, our study suggests that the Coquet Island gull control program may positively influence breeding populations of threatened seabird species, such as the Roseate Tern, although further evidence is required.

Chapter 4

Resource partitioning in three congeneric sympatrically breeding seabirds; foraging areas and prey utilisation

4.1 Abstract

Morphologically similar sympatric species reduce competition by partitioning resources, for example by occupying different dietary niches or foraging in different areas. In this study, we examine the foraging behaviour of Arctic (*Sterna paradisaea*), Common (*S. hirundo*) and Roseate Terns (*S. dougallii*) breeding on Coquet Island, northeast England using colony-based observations and coincident at-sea visual tracking of foraging birds to quantify interspecific overlap in prey selection and foraging areas. Although visual tracking methods have been used in previous studies, our study is the first example of this method being used to quantify multi-species overlap in foraging areas and the first time Roseate Tern foraging locations have been conclusively identified using a visual tracking method. Percentage overlap in foraging areas varied among species with Arctic and Common Terns sharing a higher percentage of their foraging range with each other (62.63%) than either species did with Roseate Terns (Common = 40.50% and Arctic = 0%). Arctic and Common Terns utilised similar foraging areas and partitioned resources by diet while Roseate Terns differed from other species in both diet and foraging area. Arctic and Common Terns varied provisioning rate, prey length and foraging areas with increasing brood age, while Roseate Terns fed similar prey and foraged consistently inshore. Whilst there were some similarities in areas utilised by these species, there were sufficient differences in behaviour to minimize interspecific competition. Our study further demonstrates the successful use of a visual tracking method to show how morphologically similar sympatric seabird species partition resources by diet, foraging area and response to increasing brood age.

4.2 Introduction

Interspecific competition occurs in closely related morphologically similar species with similar resource requirements and limited foraging ranges. Various studies examining how seabirds reduce interspecific competition through resource partitioning have been carried out (Duffy 1986, González-Solís et al. 1997, Mori and Boyd 2004, Lance and Thompson 2005) however most of these have compared only two species. While studies on two species provide useful data on resource partitioning, studies on larger seabird assemblages can determine the extent to which variation in foraging strategies, such as diet and foraging area, reduce interspecific competition in a highly competitive environment. By examining diet and foraging habitat utilisation among several species, the extent of each species' ecological niche may be determined and the methods by which resources are partitioned can be examined more accurately than by comparing foraging behaviour in only two species. The local abundance of different fish species and age classes surrounding the colony may also be determined using multi-species comparisons of diet and foraging behaviour. Few studies have compared foraging behaviour in more than two seabird species (but see Pearson 1968, Surman and Wooller 2003, Linnebjerg et al. 2013) and many of these used only colony-based data. For those that also compared species' foraging areas, locations of feeding birds were recorded indirectly using boat transects which cannot determine the origin and breeding status of observed birds or the extent of potential competition (Tasker et al. 1984, Daunt et al. 2002, Surman and Wooller 2003). Although the more established bird-borne device tracking method has allowed interspecific comparisons of foraging areas (Phalan et al. 2007, Young et al. 2010), foraging locations have to be inferred from track characteristics (e.g. sinuosity). In this study, the visual tracking method allowed us to use observed, rather than inferred, foraging location data, by visually confirming the locations of dive sites (Perrow et al. 2011). There is a need to compare foraging behaviour of multiple seabird species using a direct estimation of foraging locations, to link foraging areas to a specific breeding colony and develop a comprehensive understanding of how species partition resources.

Terns (*Sterna* spp) are small seabirds which feed mainly by snatching food from the sea surface or by plunge diving up to one metre in depth (Shealer 2001). Most tern species have relatively short foraging ranges of ≤10 km (Cabot and Nisbet 2013), while larger seabird species such as Gannets have been shown to have mean foraging ranges of ~200 km (Hamer et al. 2000, Hamer et al. 2001). This makes terns more vulnerable to local food shortages than species with greater foraging ranges (Furness and Ainley 1984, Furness and Tasker 2000). Terns are useful species for studying resource partitioning as they are morphologically similar with limited foraging ranges and diving ability. Most species carry prey individually in their bills allowing dietary observations to be made (Burness et al. 1994).

Morphologically similar tern species foraging in a limited area around the breeding colony may be expected to reduce interspecific competition by varying diet or foraging areas. Sympatrically breeding tern species exhibit considerable dietary overlap by feeding chicks high percentages of the same prey types and sizes (Hopkins and Wiley 1972, Safina et al. 1990, Surman and Wooller 2003), for example three tern species breeding at the same colony were found to share 78 – 87% of prey species (Surman and Wooller 2003). However, studies have also shown that some sympatrically breeding tern species exhibit different prey preferences (Safina 1990a, b, Safina et al. 1990, Rock et al. 2007). Arctic Terns (*Sterna paradisaea*) tend to deliver a higher percentage of small prey items (0 – 4 cm) than Common (*S. hirundo*) and Roseate Terns (*S. dougallii*) (Uttley et al. 1989, Safina et al. 1990, Cabot and Nisbet 2013) and when nesting in the same colony as Arctic or Roseate Terns, Common Terns deliver a greater diversity of prey to chicks (Safina et al. 1990, Robinson et al. 2001b). Tern species can also partition resources by varying the location of foraging areas around the breeding colony. Previous studies in the tropics and North America found that Roseate Terns have more restricted foraging areas than other tern species and tend to forage in shallow inshore waters, associate with predatory fish (Randall and Randall 1980, Safina 1990b, Safina et al. 1990, Shealer 1996) and rely on relatively few prey species during the breeding season (Nisbet 1981, Safina et al. 1990). Due to the small number of Roseate Tern colonies, little is known about foraging interactions between Roseate Terns and other tern species in the North Sea.

The way in which species partition resources has been shown to vary throughout the year, depending on spatial overlap and prey availability (Cherel et al. 2008, Linnebjerg et al. 2013). As chick energy demands change during the breeding season (Drent and Daan 1980), the mechanisms by which species partition resources (provisioning rate, prey size and foraging area) may vary temporally (Williams and Rothery 1990, Bertram et al. 1996). If species utilise different mechanisms to partition resources, we may predict that responses to increasing brood age will also vary interspecifically.

We combine colony-based data on parental provisioning behaviour with coincident at-sea tracking data for Arctic, Common and Roseate Terns breeding on Coquet Island, northeast England, to examine resource partitioning in a multi-species seabird assemblage in the North Sea. We 1) compare the type and size of prey items delivered to chicks by different tern species, 2) compare the location of foraging areas used by each species and 3) examine how resource partitioning changes throughout the breeding season, with the expectation that morphologically similar sympatric species use provisioning rate, diet or foraging area to partition resources and that response to increasing brood age varies interspecifically. We expect species to use at least one mechanism to partition resources; species exhibiting an overlap in foraging areas should differ in diet and species with similar diets should forage in different areas. We discuss the implications of our results for understanding interspecific competition in a multi-species seabird assemblage.

4.3 Methods

4.3.1 Colony-based Data Collection

The study took place on Coquet Island, Northumberland, northeast England (55º 20' N, 1º 32' W) during the 2011 breeding season. Arctic, Common and Roseate Terns were studied during chick-rearing from 2 June – 9 July 2011. Prey delivered to chicks was recorded for a sample of 10 Arctic and Common Tern nests and 12 Roseate Tern nests. Each Arctic and Common Tern study nest was checked daily to obtain accurate hatching dates. Precise Roseate Tern hatching dates are not known as nests were checked every seven days to limit disturbance to the colony. As in other studies using tern diet observations (Pearson 1968, Ramos et al. 1998), 1 – 4 m^2 was enclosed around each Arctic and Common study nest using plastic netting ~0.3 – 0.5 m high. This facilitated feeding observations by preventing the precocial chicks from moving away from the nest site when adults delivered food. Roseate Tern nests were not enclosed to reduce disturbance since this is one of few UK breeding sites for this endangered species.

Provisioning watches took place from a hide positioned ≤12 m from study nests from 2 June – 9 July. Common Tern study nests started hatching ~5 days before Arctic Tern nests although there was considerable overlap in hatching dates (Table 4. 1). Mean age of chicks on the first day of provisioning observations differed only slightly among species (Table 4. 1). By comparing foraging behaviour when chicks were approximately the same age, interspecific variation in diet and foraging areas could be examined while avoiding bias caused by variation in chick age.

Table 4. 1 Hatching dates, data collection start dates, mean chick ages ± SE when data collection began and percentage chick survival for Arctic, Common and Roseate Terns breeding on Coquet Island in 2011. Data were collected from 10 Arctic and Common Terns nests and 12 Roseate Tern nests

	Arctic Tern	**Common Tern**	**Roseate Tern**
Hatch dates:			
Min	June 1	May 26	June 14
Median	June 5	May 30	June 21
Max	June 11	June 6	June 29
Date provisioning watches started	June 9	June 2	June 15
Chick age (days after hatching) on first day of provisioning watches	5.8 ± 0.3	4.2 ± 0.2	~1.1 ± 0.1
Date tracking started	June 7	June 7	June 20
Chick age (days after hatching) on first day of tracking	3.9 ± 0.3	8.7 ± 0.1	~6.1 ± 0.03
Chicks survived to fledging (%)	65.00	62.96	83.33

Three-hour watches included every time period from 0400 – 2100 h for each tidal state. Each Arctic Tern nest was observed for approximately 63 hours (21 watches per nest), Common Tern nests for 69 hours (23 watches per nest) and Roseate Terns for 78 hours (26 watches per nest). Species and size categories of prey items delivered to chicks were recorded and grouped into four categories: Lesser Sandeel (*Ammodytes marinus*; hereafter ‘sandeel’), sprat (*Sprattus sprattus*), juvenile fish (larvae not identifiable at species level) and miscellaneous (including crustaceans, cephalopods and demersal fish). Prey size was measured in tern bill lengths as in previous studies (Safina et al. 1990, Shealer 1998b, Rock et al. 2007). Type and size categories were agreed on by observers before watches started and were validated by examining discarded fish. Bill lengths of Arctic (3.0 – 3.4 cm), Common (3.4 – 4.1 cm) and Roseate Terns (3.7 – 4.0 cm) differ only slightly and there is considerable overlap between species (Lemmetyinen 1976, Ramos et al. 1998)). Prey length (cm) was calculated by multiplying prey size category by median bill length. Roseate Tern watches were carried out by WD while GSR observed Arctic and Common Terns. Prey size recording methods were standardised for different observers by agreeing on prey size categories of items carried by the same selected individuals. Separate observations were only carried out by different observers after prey size category estimations made during simultaneous test watches were found to be comparable.

4.3.2 At-sea Data Collection

While GPS devices have been used to track various seabird species (Burger and Shaffer 2008, Wakefield et al. 2009), terns are considered too small to carry such devices (Perrow et al. 2011). We used a visual tracking method which successfully identified foraging areas of tern species in a previous study carried out in Norfolk and North Wales, UK (Perrow et al. 2011). Although this method has been used previously, our study is unique in its use of visual tracking to identify foraging areas utilised by Roseate Terns, an endangered UK seabird species for which foraging behaviour data are scarce, and in quantifying overlap in foraging areas utilised by multiple species. Due to weight restrictions, GPS devices cannot be safely used to track tern species meaning that detailed data on at-sea foraging behaviour is difficult to collect. Studies examining interspecific differences in species' foraging areas are limited and at-sea foraging behaviour of some tern species has not been studied in detail. Visual tracking allows detailed information on foraging areas utilised by small seabird species to be examined and for ecological questions regarding area partitioning to be addressed.

Individual terns were tracked to and from foraging sites by observers on board a rigid inflatable boat (RIB) using tracks obtained from the onboard GPS as proxies for foraging tracks. The starting position around the colony was varied so as to track an adequate representation of the breeding population. We took care to observe any changes in behaviour, such as evasive flight, which might indicate an adverse reaction to the presence of the vessel, and if so, increased the distance of the RIB from the bird. Observers recorded few instances of birds visibly reacting to the RIB and most appeared to ignore the vessel, consistent with Perrow et al. (2011). Birds were tracked for the duration of foraging trips although trips were aborted if birds were lost or it was no longer possible to follow them due to deteriorating sea conditions (a total of 67 of 122 tracks were aborted for all three species). Locations of foraging attempts (where birds dived or surface-dipped) were recorded as was the duration of each track. Incomplete tracks were those where individuals were lost before returning to the colony and comprised 27/49 (55.10%), 24/42 (57.14%) and 16/31 (51.61%) of Arctic, Common and Roseate Tern tracks respectively. Tracked birds dived throughout the trip allowing dive locations to be recorded even if tracking was later aborted. The cumulative probability of losing visual contact with a bird by chance increases with time, and if birds are likely to travel further with time, this may have resulted in maximum foraging distance being underestimated. However, we found no significant difference in maximum foraging distances (km) calculated from complete and incomplete tracks recorded from 7 June – 1 July (mean ± SE = 3.17 ± 0.26 km (n = 75) and 3.49 ± 0.36 km (n = 40) respectively; t-test: $t_{78.79} = -0.72$, $p = 0.47$, $n = 115$). Arctic and Common Terns were tracked from 7 June – 1 July and Roseate Terns from 20 June – 1 July. Twenty-six Arctic, 19 Common and 31 Roseate Terns were tracked in total, generating 111, 77 and 206 dive locations for Arctic, Common and Roseate Terns respectively. Hence, 4.27 dive locations per track were recorded for Arctic Terns, 4.05 dive locations per track for Common Terns and 6.65 for Roseate Terns.

4.3.3 Data Analyses

To avoid temporal bias, tracking and provisioning data from 20 June – 1 July were used for species comparisons and data collected before 20 June and after 1 July used to examine changes in foraging behaviour with increasing brood age. Provisioning rate was defined as number of deliveries made to each chick per hour. The percentage of sandeel (most commonly fed prey item) delivered to chicks in each nest, and variation in the mean length of prey items (cm) per nest were compared among species using Kruskal-Wallis tests.

Foraging trip parameters (maximum foraging distance, total distance travelled, trip duration and mean bearing on departing the colony) were compared among species using a circular ANOVA and Kruskal-Wallis tests. The circular ANOVA (from packages CircStats and circular (Jammalamadaka and SenGupta 2001) in R version 3.1.2) compared mean bearings calculated from the first five bearings in each track (Patrick et al. 2013), accounting for the bounded nature of data between 0° and 359°. Tracks where the start or end time had not been recorded were excluded from analysis.

Kernel density plots were generated using dive locations from complete and incomplete tracks, to compare species- and stage-specific foraging areas for all three species and for those tracked during early and late chick-rearing. Dive locations were not observed during every track: 111 Arctic, 77 Common and 206 Roseate Tern dive locations were used in kernel density estimations from 26 Arctic, 18 Common and 31 Roseate Tern tracks. We examined species-specific differences in foraging ranges (95% contour) and core foraging areas (25% contour) from fixed kernel density estimation in a European Albers equal-area conic projection (ArcGIS 10.1) using a grid size of 100 m^2 calculated in R with adehabitatHR and maptools packages (Calenge 2006). Contours of 25% and 95% were selected as it was expected that these contours would be most appropriate for examining foraging areas at large and small spatial scales. The *ad hoc* method was used to calculate the smoothing parameter (h), where $h = \sigma n^{(-1/6)}$, $\sigma = 0.5 \times \left(sd(x) + sd(y)\right)$ and n = number of locations, which resulted in a smoothing parameter that retained sufficient detail in distribution patterns to allow identification of high density areas without excessive smoothing. Percentage overlap in species' foraging ranges and core foraging areas was calculated by dividing the area of overlap by the combined area utilised by both species and multiplying by 100. This quantifies the degree of similarity between foraging areas used by Arctic, Common and Roseate Terns. The percentage of foraging areas used by one tern species which coincided with that of another tern species was also calculated.

Brood age (in days after hatching) was separated into seven five day categories from 0 – 35 days. For each category, mean provisioning rate and prey length were calculated for each species and plotted against brood age. Relationships between provisioning rate and brood age and prey length and brood age were examined using generalized linear mixed models (GLMMs) with normal error distributions and logit link functions fitted using the lme4 package in R (Bates et al. 2014). We included species, brood age, brood size for each nest at each brood age (in days) and a 2-way interaction between species and brood age as fixed effects, and nest ID as a random factor. We fitted fully parameterized models using maximum likelihood (ML), and removed terms by sequential deletion while testing for significant changes in model variance using Likelihood Ratio Tests (LRTs) (Crawley 2007). We then refitted the minimum adequate model using restricted maximum likelihood (REML) to estimate effect sizes. REML takes into account the loss of degrees of freedom caused by estimating parameters, and is therefore more appropriate when estimating effect sizes than ML. Provisioning rate and prey length were log-transformed to reduce heteroscedasticity.

Differences in size and location of core foraging areas during early (before 20 June when chicks were <18 days old) and late chick-rearing (from 20 June when chicks were ≥18 days old) were compared for Arctic and Common Terns. Sample sizes of Roseate Tern tracks were too small to allow foraging areas at different chick-rearing stages to be examined. Kernel density estimations were generated for each species and breeding stage using the *ad hoc* method to estimate h (value varies depending on number of dive locations) and a grid size of 100 m^2. Overlap in foraging ranges and core foraging areas between stages was quantified for both species illustrating the degree of similarity in foraging areas as brood age increased. Analyses were carried out in R version 3.1.2 (R Development Core Team 2014) and ArcGIS version10.1 (ESRI, USA). Means are presented ± SE throughout.

4.4 Results

4.4.1 Chick Provisioning

There were significant differences in the proportion of sandeel (Kruskal-Wallis test: $\chi^2_2 = 25.67$, $p<0.001$, $n = 31$) and mean prey length (Kruskal-Wallis test: $\chi^2_2 = 19.71$, $p<0.001$, $n = 31$) delivered to chicks of different tern species. Arctic Tern chicks received the highest percentage of juvenile fish (Table 4. 2) and were fed smaller prey items than chicks of other tern species. Roseate Tern chicks were fed a higher percentage of sandeel than Arctic or Common Tern chicks and were fed significantly larger prey items than Arctic Terns ($\chi^2_1 = 15.66$, $p<0.001$, $n = 22$; Table 4. 2). Provisioning rates were significantly higher for Arctic Terns than for Common or Roseate Terns ($\chi^2_1 = 22.41$, $p<0.001$, $n = 31$; Table 4. 2).

Table 4. 2 Percentage of prey types fed to chicks and lower quartiles, medians and upper quartiles of prey lengths (cm) and provisioning rates (deliveries per chick h^{-1}) for each species

	Arctic Tern	**Common Tern**	**Roseate Tern**	**Number of deliveries**
Sandeel (%)	49.57	69.44	86.24	1675
Sprat (%)	2.87	26.23	13.76	241
Juvenile fish (%)	34.07	1.86	0	516
Miscellaneous (%)	13.49	2.47	0	210
Number of observations	1497	338	821	
Prey length (cm)	1.60, 1.60, 3.20	3.75, 5.63, 5.63	3.85, 5.78, 5.78	
Provisioning rate (deliveries per chick h^{-1})	3.00, 3.58, 4.90	0.88, 1.31, 1.57	1.09, 1.32, 1.72	

4.4.2 Foraging Areas

Maximum foraging distance, total distance travelled and trip duration were calculated from complete tracks while mean bearing on leaving the colony was calculated using both complete and incomplete tracks (25 and 76 tracks respectively). This prevents maximum foraging range, total distance travelled and trip duration from being underestimated, as incomplete trips are likely to be shorter than complete trips. As mean bearing on leaving the colony is unlikely to be affected by whether or not an individual was followed for the complete duration of a foraging trip, both complete and incomplete tracks were included in its calculation. Figure 4. 1 illustrates complete and incomplete foraging tracks and dive locations for Arctic, Common and Roseate Terns from 20 June – 1 July. Arctic Terns foraged north of the colony (Figure 4. 1a) and Common Terns further south (Figure 4. 1b). Arctic and Common Terns core foraging areas, estimated using kernel density plots of dive locations, were centred close to the colony (Figure 4. 2 a, b) while that of Roseate Terns was situated slightly further away and closer to shore (Figure 4. 2c). There were no significant differences in mean maximum foraging distance, total foraging distance or trip duration of complete tracks among tern species (Table 4. 3). However, there were significant differences in mean bearing on departing the colony with Roseate Terns leaving to forage almost exclusively to the northwest (Figure 4. 1). There was less variation in departure direction among Roseate Terns than among Arctic and Common Terns and Roseate Terns left the colony in a significantly different direction to other species (Table 4. 3).

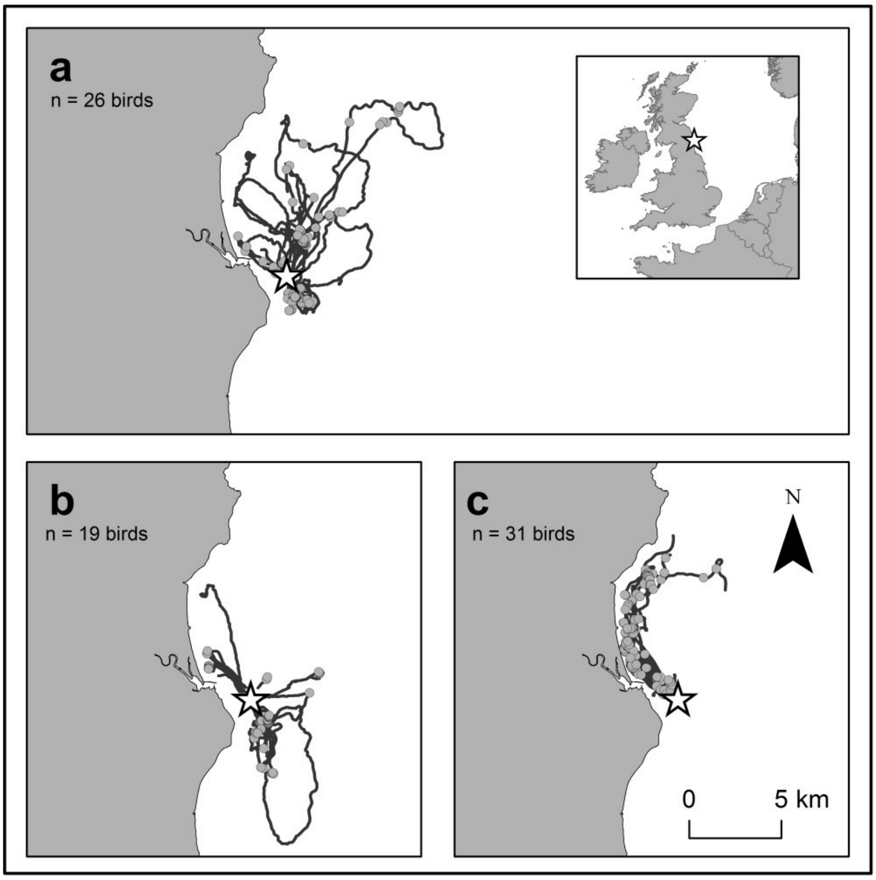

Figure 4. 1 Complete and incomplete foraging tracks and dive locations for **a)** Arctic Terns (Number of track locations = 19,467; Number of dive locations = 111), **b)** Common Terns (Number of track locations = 11,136; Number of dive locations = 77) and **c)** Roseate Terns (Number of track locations = 18,001; Number of dive locations = 206) from 20 June – 1 July 2011. Tracks are represented by solid lines and dive locations by shaded dots. Coquet Island is represented by a star

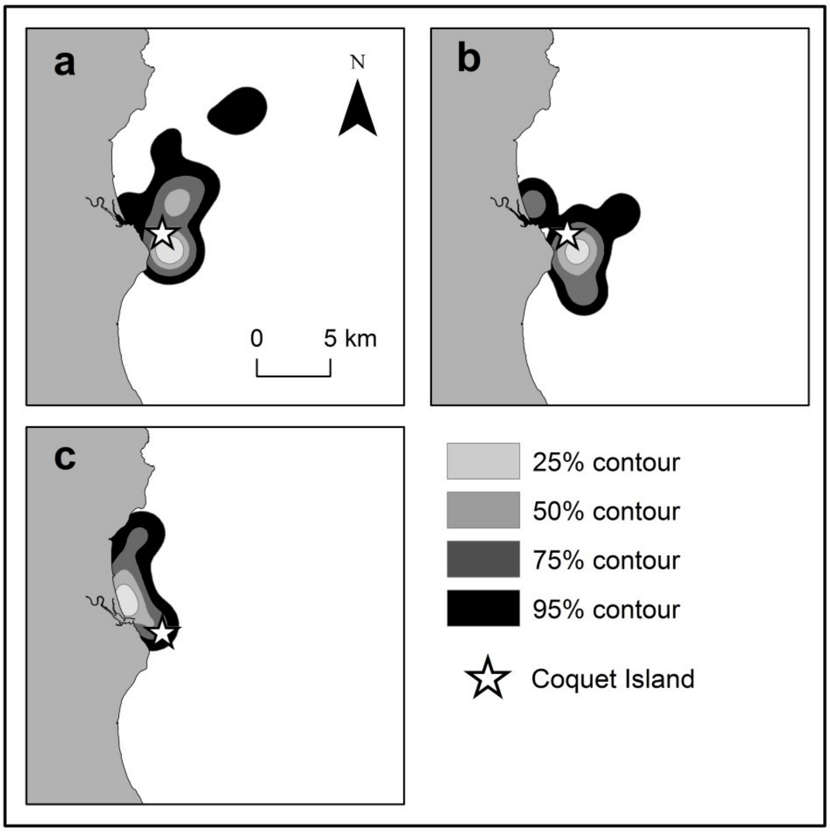

Figure 4. 2 Kernel utilisation distribution of 394 dive locations (Arctic = 111; Common = 77; Roseate = 206) using tracks from **a)** 26 Arctic Terns, **b)** 18 Common Terns and **c)** 31 Roseate Terns

Table 4. 3 Foraging trip characteristics of three tern species. Sample size (*n*) describes whether complete tracks or both complete and incomplete tracks were used to calculate values. Mean max foraging distance, total distance travelled and mean trip duration were calculated using complete tracks only while mean bearing on leaving the colony (degrees where 0° = North) was calculated using both complete and incomplete tracks. Lower quartiles, medians, upper quartiles are given where non-parametric tests were used to examine differences among species and mean values ± SE are given where parametric tests were used. Significant differences are indicated in bold

	Mean max foraging distance (km)	**Total distance travelled (km)**	**Mean bearing on leaving colony (degrees where 0° = North)**	**Mean trip duration (min)**
Arctic	1.17, 1.76, 3.39 ($n = 13$)	1.41, 2.35, 4.73 ($n = 13$)	**239.55 ± 20.93 ($n = 25$)**	3.20, 9.88, 15.72 ($n = 13$)
Common	3.35, 3.60, 3.93 ($n = 7$)	4.95, 6.08, 6.72 ($n = 7$)	**267.24 ± 24.04 ($n = 19$)**	9.28, 10.23, 11.07 ($n = 7$)
Roseate	1.22, 1.62, 3.30 ($n = 15$)	1.93, 2.77, 6.23 ($n = 15$)	**101.41 ± 1.70 ($n = 31$)**	3.03, 5.75, 9.38 ($n = 13$)
	Kruskal-Wallis: $\chi^2_2 = 4.45$, $n = 35$, $p = 0.11$	Kruskal-Wallis: $\chi^2_2 = 2.11$, $n = 35$, $p = 0.35$	**Circular ANOVA: $F_{2,74} = 7.34$, $n = 75$, $p = 0.001$**	Kruskal-Wallis: $\chi^2_2 = 1.99$, $n = 35$, $p = 0.37$

There were differences in the extent of species' foraging ranges with Arctic Terns covering a larger area than those of Common and Roseate Terns (Table 4. 4). Common and Roseate Tern core foraging areas were only slightly smaller than that of Arctic Terns and while species shared less than 41% of core foraging areas, high percentages of Common and Roseate Tern foraging ranges and Common Tern core foraging areas were found within that of Arctic Terns (Table 4. 4).

Table 4. 4 Foraging range (95% contour) and core foraging area (25% contour) sizes (km^2) for three tern species and percentage of species' foraging areas located within those of Arctic Terns

	Arctic Tern	**Common Tern**	**Roseate Tern**
Foraging range (km^2)	54.10	42.42	36.57
Core foraging area (km^2)	2.91	2.20	2.83
Foraging range shared with Arctic Terns (%)	-	62.63	40.50
Core foraging area shared with Arctic Terns (%)	-	94.24	0

4.4.3 Effect of Brood Age and Size on Foraging Behaviour

Relationships between provisioning rate, prey length and brood age were examined for each species using diet observations from 2 June – 9 July. While Arctic and Common Tern provisioning observations were available for broods from 0 – 35 days old, Roseate Tern observations were only available for broods aged 0 – 25 days. Arctic Tern mean provisioning rate increased with brood age while provisioning rates of Common and Roseate Terns did not change (Species x Brood age interaction: $\chi^2_2 = 23.13$, $p<0.001$, $n = 594$; Figure 4. 3a). In addition, provisioning rate decreased with brood size for all species ($\chi^2_2 = 32.84$, $p<0.001$); chicks from smaller broods had higher provisioning rates than chicks from larger broods (Table S. 1).

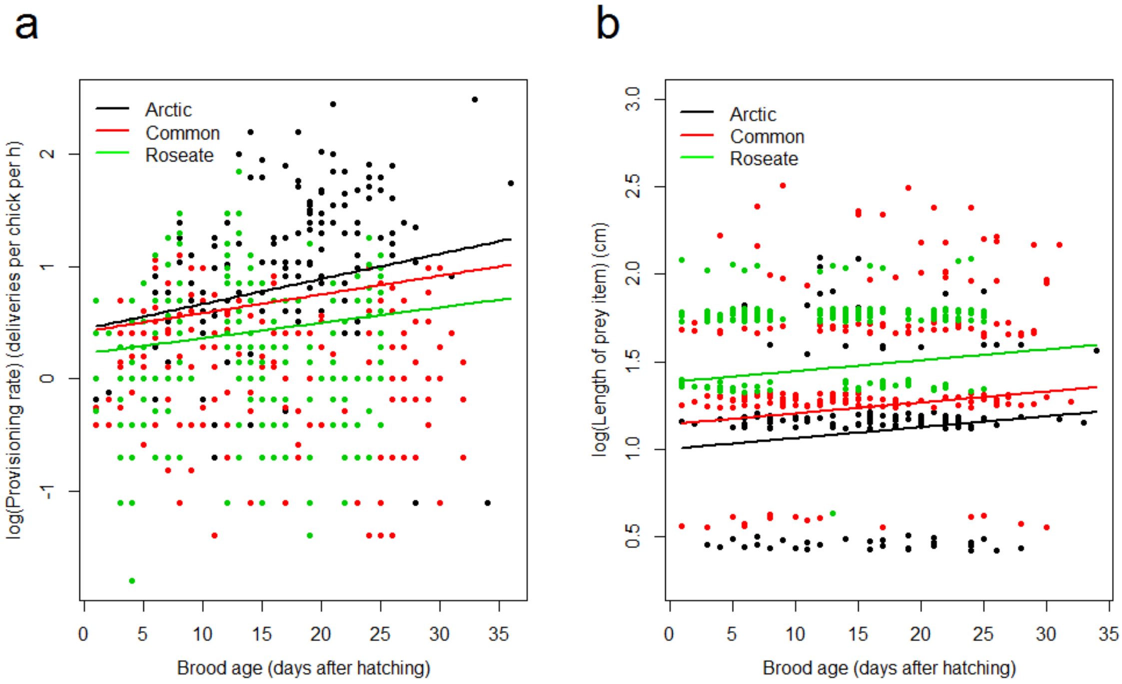

Figure 4. 3 **a)** Relationship between log-transformed provisioning rate (deliveries per chick h^{-1}) and brood age (days after hatching) for each tern species (black = Arctic, red= Common and green = Roseate). Straight lines were made using coefficients extracted from GLMMs and illustrate the significant interaction between Species and Brood age. **b)** Relationship between log-transformed prey length (cm) and brood age (days after hatching) for each tern species (black = Arctic, red= Common and green = Roseate). Straight lines were made using coefficients extracted GLMMs and show similar rates of increase in length of prey delivered to chicks with increasing brood age among species

There was a significant effect of brood age on prey length ($\chi^2_1 = 10.80$, $p<0.001$, $n = 511$), suggesting that in general, species delivered larger prey items with increasing brood age (Table S. 2). With respect to prey length, there was no significant interaction between species and brood age ($\chi^2_2 = 4.36$, $p = 0.11$). Brood size had no effect on prey length ($\chi^2_1 = 0.03$, $p = 0.87$) and Common and Roseate Terns continued to feed chicks significantly larger prey items than Arctic Terns as brood age increased ($\chi^2_2 = 64.56$, $p<0.001$; Figure 4. 3b). A LMM with nest as a random factor was used to examine whether larger prey types, such as sprat, were fed to chicks more often as brood age increased. Prey length was used as the response variable, with prey type and brood age included as explanatory variables. There was a significant interaction between prey type and brood age ($\chi^2_3 = 104.71$, $p< 0.001$), which suggests that terns delivered different prey types to chicks over time. The number of sprats fed to chicks increased with brood age (Estimate ± se = 0.19 ± 0.02, *t*-value = 7.88, *p*-value<0.001), while there was no significant change in the number of sandeel fed to chicks with increasing brood age (Estimate ± se = -0.02 ± 0.01, *t*-value = 1.17, *p*-value = 0.24). This might explain the increase in prey length we observed, as there was a tendency for adults to deliver larger prey types to chicks over time.

Arctic and Common Tern core foraging areas shifted closer to the colony during late chick-rearing, reflecting the increased provisioning rate of Arctic Terns described above (Figure 4. 3a, Figure 4. 4). Late chick-rearing foraging areas were smaller than those of early chick-rearing in both species and while a high percentage of late chick-rearing foraging ranges were found within those of early chick-rearing, no overlap in core foraging areas between stages was evident in either species (Table 4. 5). However, core foraging areas of both species overlapped by 40% during late chick-rearing (Figure 4. 4). Although Arctic and Common Terns shared similar foraging areas during late chick-rearing, they partitioned resources by varying both prey length and frequency of delivery.

Table 4. 5 Foraging range (95% contour) and core foraging area (25% contour) sizes (km^2) during early (<18 days old) and late chick-rearing (>18 days old) and percentage overlap between breeding stages. The 'Overlap' column refers to the percentage area which overlaps between areas used during early and late chick-rearing and the column 'Within early chick-rearing' refers to the percentage of late chick-rearing area found within that used during early chick-rearing by each species

	Arctic				**Common**			
	Early chick-rearing (km^2)	Late chick-rearing (km^2)	Overlap (%)	Within early chick-rearing (%)	Early chick-rearing (km^2)	Late chick-rearing (km^2)	Overlap (%)	Within early chick-rearing (%)
Foraging range	92.02	45.92	26.74	80.31	108.22	51.56	19.12	59.21
Core foraging area	5.44	3.27	0	0	6.16	3.04	0	0

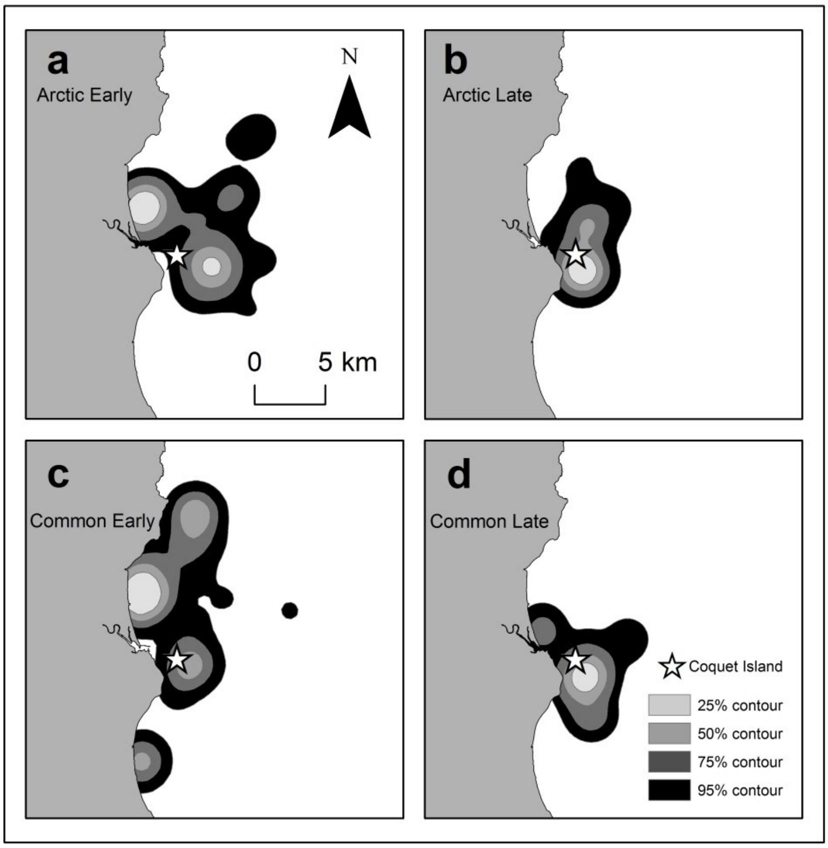

Figure 4. 4 Kernel utilisation distribution of 470 dive locations during early (<18 days old) and late (>18 days old) chick-rearing for **a)** Arctic Terns early chick-rearing = 202 locations; 11 tracks, **b)** Arctic Terns late chick-rearing = 95 locations; 11 tracks, **c)** Common Terns early chick-rearing = 96 locations; 18 tracks, **d)** Common Terns late chick-rearing = 77 locations; 7 tracks

4.5 Discussion

Resource competition should favor adaptations that reduce niche overlap (Gause 1934), which may explain species-specific differences in seabird foraging areas and feeding behaviour (Rome and Ellis 2004, Lance and Thompson 2005). There are several explanations for how competition facilitates resource partitioning among species. One species may outcompete and directly exclude another from foraging areas or species may use habitats which suit preferred feeding methods. Even if competition is not currently affecting species interactions, previous competition could have produced interspecific variation in ability to exploit different habitats (Trivelpiece et al. 1987, Wood et al. 2000). Studies have suggested that other seabirds exclude Roseate Terns from feeding flocks and that Roseate Terns forage more efficiently in flocks containing only conspecifics (Duffy 1986, Shealer and Burger 1993). Our results show that Roseate Terns utilise separate foraging areas from other tern species, but it is unclear whether this is caused by a preference for specific foraging conditions or from tern species excluding Roseate Terns from other areas.

Our findings provide direct evidence of resource partitioning by both foraging area and diet composition within a multi-species seabird assemblage. As in previous studies, Common and Roseate Terns fed chicks large energy-rich prey items less regularly while Arctic Terns fed a higher proportion of small juvenile fish at a higher rate (Safina et al. 1990, Robinson et al. 2001b, Rock et al. 2007).

Roseate Terns fed chicks a high proportion of sandeel and large prey items throughout the chick-rearing period. This species is a dietary specialist over most of its range and relies on few fish species during the breeding season, especially sandeel (Randall and Randall 1980, Nisbet 1981, Safina et al. 1990). This specialisation may be a consequence of competition with other species (Duffy 1986, Shealer and Burger 1993) or a preference for specific foraging conditions (Safina 1990a, Shealer 1996). While relatively small, the breeding population of Roseate Terns on Coquet Island is currently stable suggesting there is sufficient food available close to the colony.

Arctic Terns have a limited diving ability and forage more regularly by surface-dipping than Common and Roseate Terns which mainly plunge dive (Shealer 2001, Cabot and Nisbet 2013). Fish larvae and juvenile fish are more likely to congregate near the surface than adult fish, but are smaller than prey usually selected by terns (Rindorf et al. 2000, Cabot and Nisbet 2013). Arctic Terns may have preferentially selected small juvenile fish as they were readily available and easy to catch and transport (Hopkins and Wiley 1972), and delivered them regularly to compensate for their lower energy content. Common and Roseate Terns selected larger fish, which may have been in range of their deeper diving capabilities and are easier for these larger-billed tern species to carry (Nisbet 1981, Snow and Perrins 1998, Shealer 2001). Shealer (1996) suggested the limited diet of Roseate Terns was a consequence of foraging habitat specialisation. Roseate Tern foraging areas are associated with various biotic and abiotic habitats, including presence of predatory fish (Shealer 1996) and shallow water (Safina 1990a), which affect the availability of sandeel in surface waters. The region in which Roseate Terns were observed foraging around Coquet Island was restricted to depths of <30 m (JNCC pers. comm.).

Interspecific variation in time spent in specific habitats has been linked to dietary differences, suggesting that dietary segregation is associated with spatial partitioning (Waugh et al. 1999). In our study, Arctic and Common Terns foraged over a wider area than Roseate Terns, Arctic Terns concentrating further north of the colony and Common

Terns further south. There was considerable variation in the mean bearing in which Arctic and Common Terns left the colony, while Roseate Terns departed consistently to the northwest. Roseate Tern departure direction could have been influenced by the location and orientation of the colony and the foraging areas utilised by Roseate Terns may have been influenced by proximity to the colony. Although the starting position of the RIB around the island was varied to ensure an adequate representation of the breeding population was tracked and that variation in departure direction could be assessed, it was not practical to implement a formal randomisation procedure. Hence, as Roseate Terns were found breeding on only one area of the island and therefore were rarely observed leaving the island in other locations, departure direction may have been biased for this species. All three tern species nested mainly in the southwestern side of the island, so minimising distance between foraging locations and nest sites is unlikely to have been an important factor.

Arctic and Common Tern core foraging areas showed some overlap while neither species overlapped with Roseate Tern core foraging areas. However, a large percentage of Common and Roseate Tern foraging ranges were found within that of Arctic Terns. Individual variation in foraging area, departure direction and prey selection was greater in Arctic and Common Terns than in Roseate Terns, which foraged mainly on sandeel in a restricted area. Lack of individual variation can have significant effects on species' vulnerability to environmental change (Lomnicki 1978, Safina et al. 1990, Bolnick et al. 2003) and may have important consequences for Roseate Tern conservation. It is possible that individuals' dive locations are spatially related to those of conspecifics and other species, as conspecifics often forage together in flocks (Gochfeld and Burger 1982, Cabot and Nisbet 2013); some species also actively exclude others from foraging in the same area (Duffy 1986).

Extent of foraging areas may explain the greater diversity of prey types and sizes delivered by Arctic and Common Terns and the limited diet of Roseate Tern chicks. This could have been examined by comparing individual sites used by each tern species in greater detail. For Arctic and Roseate Terns, dietary segregation coincided with spatial partitioning of foraging areas. However, Arctic and Common Terns delivered different prey items while sharing a high percentage of foraging areas. We show that dietary segregation occurs when foraging areas are spatially partitioned and also when species forage in similar areas. Similarities in diving ability may explain why Common and Roseate Terns, which dive to depths of up to 0.8 m and 1.2 m respectively, partitioned foraging habitats more completely than Arctic and Common Terns, which differ significantly in diving ability (Arctic Terns rarely penetrate more than 0.5 m below the surface; Cabot and Nisbet 2013). Although our analysis is limited to a single year, visual tracking data from 2009 and 2010 indicate little inter-annual variation in distributions of all three species around Coquet Island (JNCC pers. comm.). Data from 2009 are presented in an unpublished report by the JNCC (see Wilson et al. 2009) and are comparable to results presented in this study. Colony-based data from 2009 and 2010 for Arctic, Common and Roseate Terns were unavailable, hence our analysis could not be wholly repeated for 2009 and 2010 data.

Species also partition resources by differentially varying foraging behaviour in response to increasing brood age (Safina et al. 1990). Chicks require more energy as they approach fledging age (Ricklefs and White 1981) and studies have shown that seabirds increase prey size with brood age, rather than provisioning rate (Wiggins and Morris 1987, Smith 1993). This strategy is more efficient as it requires fewer foraging trips to deliver a given amount of energy. However, there may be costs to delivering larger prey items such as transport, vulnerability to kleptoparasitism and difficulty in capture (Barrett and Krasnov 1996, Ratcliffe et al. 1997, Dies and Dies 2005). Safina et al. (1990) found that Common Terns fed larger prey items to chicks as the breeding season progressed while Roseate Terns did not.

Arctic Terns in our study responded to increasing chick energy demands by providing more frequent prey deliveries, and while this species also increased the length of prey items with increasing brood age, they consistently delivered smaller prey items than Common and Roseate Terns. Common Terns delivered larger prey items as brood age increased while maintaining the same provisioning rate as in a previous study (Safina 1990a). The tendency for all three tern species to increase the proportion of larger prey types, such as sprat, delivered to chicks with increasing brood age may partly explain this result. Both Arctic and Common Tern chicks were of similar ages when provisioning observations began, hence changes in provisioning rate and prey length were unlikely to have been caused by seasonal effects. Roseate Tern observations started ~11 – 16 days after those of Arctic and Common Terns. Roseate Tern provisioning rates did not change significantly as brood age increased and large prey items were delivered consistently to chicks throughout the chick-rearing period. The length of prey items delivered by Roseate Terns did increase with increasing brood age, contrary to results of a previous study (Safina 1990a). While we did not observe a significant change in provisioning rate with increasing brood age in Roseate Terns, this may have been influenced by the more limited brood age range available for Roseate Terns (0 – 25 days old) compared with Arctic and

Common Terns (0 – 35 days old). However, we suspect that the trend for Roseate Terns to deliver large fish is unlikely to have changed within the last 10 days of chick-rearing.

Interspecific variation in foraging behaviour with increasing brood age could be explained by changes in foraging areas. Arctic and Common Tern foraging ranges and core foraging areas shifted closer to Coquet Island during late chick-rearing. This may have allowed Arctic Terns to increase their provisioning rates, but no corresponding increase was evident in Common Terns; instead this species fed larger prey with increasing brood age. By foraging closer to the colony, Common Terns may have been able to reduce travelling time and increase time spent selecting larger prey items for chicks. Areas used by Arctic and Common Terns during early and late chick-rearing showed some overlap. While species' core foraging areas were slightly different during early chick-rearing those of both species were located close to the colony during late chick-rearing. Although Arctic and Common Terns used the same small foraging area during late chick-rearing, each delivered different prey items. Studies have suggested that partitioning of foraging areas explains interspecific variation in seabird diets (Shealer 1996, Waugh et al. 1999). Our results show that dietary segregation can occur independently of foraging area partitioning and may be due to differences in foraging methods.

Visual tracking increases the likelihood of recording foraging locations of birds of known breeding status and origin. However, a limitation of this method is that it cannot definitively determine whether tracked birds were breeders or non-breeders. Our study shows that three morphologically similar tern species partition resources using different mechanisms. Arctic and Common Terns showed variation in diet, provisioning rate and response to increasing brood age but shared similar foraging areas, while Roseate Terns differed from other tern species in both diet and foraging area and showed no change in foraging behaviour with increasing brood age. Arctic and Common Terns generally exhibit more similarities in foraging behaviour and nesting habitat than either species does with Roseate Terns (Cabot and Nisbet 2013), so it seems unusual that these two similar species breed together at the same time, while Roseate Terns begin breeding approximately two weeks later. Perhaps the interspecific variation in diet, provisioning rate and response to increasing brood age observed in this study explains how Arctic and Common Terns are able to avoid competition and breed synchronously in the same area. It is unclear why Roseate Terns arrive at their breeding grounds later than Arctic and Common Terns, but it is unlikely that Arctic and Common Terns breed earlier to avoid competition with Roseate Terns as Common Terns have been shown to exclude Roseate Terns from foraging flocks (Duffy 1986, Shealer and Burger 1993), and sympatrically breeding Roseate Terns have very different diets and utilise different foraging habitats (Safina 1990a, b, Safina et al. 1990). We show how studies on multi-species assemblages can effectively compare mechanisms used to partition resources among species breeding sympatrically in a competitive environment, and illustrate the extent to which overlap in diet and foraging areas can vary among morphologically similar species.

We provide strong evidence of three sympatric seabird species partitioning resources by diet, foraging area and response to increasing brood age. Our findings complement those of previous studies comparing diet and foraging area partitioning in two seabird species. We show that dietary segregation does not always reflect differential forging area utilisation, but that birds foraging in the same area select different prey items.

4.6 Supplementary Material

Table S. 1 Output from minimum adequate model fitted using restricted maximum likelihood (REML) from a GLMM with a normal error distribution and logit link function examining which variables are most significant in explaining variation in log(provisioning rate; deliveries per chick h^{-1}). Random factor = Nest. *n* = 594

	Estimate	**SE**	***t*-value**
Intercept	1.08	0.18	5.92
Species:			
Arctic	0	-	-
Common	-0.15	0.17	0.91
Roseate	-0.47	0.17	2.71
Brood size	-0.32	0.06	5.76
Brood age	0.02	0.01	3.41
Species x Brood age:			
Arctic	0	-	-
Common	-0.04	0.01	4.77
Roseate	-0.02	0.01	2.13

Table S. 2 Output from minimum adequate model fitted using restricted maximum likelihood (REML) from a GLMM with a normal error distribution and logit link function examining which variables are most significant in explaining variation in log(prey length; cm). Random factor = Nest. *n* = 511

	Estimate	**SE**	***t*-value**
Intercept	1.00	0.05	20.10
Species:			
Arctic	0	-	-
Common	0.38	0.05	7.82
Roseate	0.62	0.05	13.24
Brood age	0.07	0.01	3.11

Chapter 5

Influence of diet on reproductive success of two morphologically similar sympatrically breeding seabird species

5.1 Abstract

Sympatrically breeding seabird species exhibit different foraging behaviour and diet preferences, which can influence their vulnerability to changes in the marine environment. While previous studies have compared chick diets among a variety of sympatric seabird species, few studies have examined how interspecific variation in chick provisioning strategies can affect reproductive parameters. Here, we compare provisioning rates and diets of nestling Arctic (*Sterna paradisaea*) and Common Terns (*S. hirundo*), two morphologically similar species, breeding on Coquet Island, northeast England and examine how interspecific variation in chick and brood provisioning behaviour relates to reproductive parameters of each species. Arctic Terns delivered higher percentages of smaller sandeel (*Ammodytes marinus*) and juvenile fish to their chicks than did Common Terns, which delivered comparatively high percentages of larger sprat (*Sprattus sprattus*). Arctic Terns had smaller clutch sizes than Common Terns and made more prey deliveries to each chick per hour, delivering a similar amount of energy per chick per hour as Common Terns despite feeding smaller prey items. Although chick growth rate during the linear growth phase, chick survival and fledging success were not significantly different between the two species, Common Terns fledged more chicks than Arctic Terns in total due to their larger clutch sizes. Our study shows that sympatric species may differ in how they provision broods to reduce interspecific competition. In consequence, variation in foraging strategies and in the distribution of prey types and sizes in the environment may differentially affect the reproductive parameters of closely related species breeding at the same colony.

5.2 Introduction

Reproductive parameters of closely related, sympatrically breeding seabird species compared over similar time periods have been found to differ significantly (Waugh et al. 2000, Lynnes et al. 2004, Jenouvrier et al. 2005). This may be explained by species-specific foraging strategies and variation in vulnerability to changes in the environment surrounding the breeding colony. Morphologically similar sympatric species have been shown to utilise different foraging areas and to deliver different proportions of prey types and sizes to chicks (Safina et al. 1990, González-Solis et al. 1997, Lance and Thompson 2005, Rock et al. 2007, Robertson et al. 2014a), which differentially affects species' vulnerability to environmental change (Uttley et al. 1989, Furness and Tasker 2000).

The marine environment is highly changeable and subject to considerable temporal fluctuations in temperature and productivity. Changes in sea surface temperature (SST), phytoplankton abundance and weather conditions can affect availability of prey to marine organisms by influencing prey abundance and distribution in the water column (Cairns 1988, Guinet et al. 1998, Arnott and Ruxton 2002, Diamond and Devlin 2003, Forcada et al. 2005, Frederiksen et al. 2004a, 2006, 2011). During the breeding season, seabirds are restricted to foraging in a limited area surrounding a central colony, making availability of prey species and foraging conditions around the colony important predictors of reproductive success (Orians and Pearson 1979, Baird 1990, Murphy et al. 1991, Gaston et al. 2005, Burke and Montevecchi 2009).

Some seabird species have been identified as being especially vulnerable to food shortages during the breeding season due to certain aspects of their foraging behaviour, such as their diving capability, foraging range and ability to exploit different prey species (Furness and Ainley 1984, Furness and Camphuysen 1997, Furness and Tasker 2000, Diamond and Devlin 2003). Surface-feeding seabirds such as Black-legged Kittiwakes (*Rissa tridactyla*) and terns (*Sterna* spp) have shorter foraging ranges, more restricted diving capabilities and limited abilities to switch prey compared with other seabirds and are therefore vulnerable to environmental conditions which affect abundance of preferred prey species (Furness and Tasker 2000). Reproductive success of Kittiwakes and terns is more likely to decline in years of adverse foraging conditions and low food availability than that of larger less sensitive species.

Terns are small seabirds with limited time and energy budgets during the breeding season (Pearson 1968, Cabot and Nisbet 2013). They mainly feed by snatching food from the surface of the sea or by plunge diving to depths of up to one metre (Shealer 2001), and as such are dependent on biotic and abiotic processes making prey available at the water surface (Schwemmer et al. 2009). Interspecific variation in foraging behaviour influences tern species' vulnerability to environmental change; smaller tern species with more specialist diets and restricted diving capabilities are at increased risk of food shortages than larger generalist species (Furness and Tasker 2000, Perrow et al. 2011). Arctic Terns (*Sterna paradisaea*) have been identified as the most sensitive UK seabird species to reductions in food abundance due to their specialist diets and foraging behaviour (Furness and Tasker 2000). Arctic Terns have an extremely limited diving ability (<0.5m; Cabot and Nisbet 2013) and forage more regularly by surface-dipping than other tern species which mainly plunge dive (Shealer 2001, Cabot and Nisbet 2013). They also have restricted diets and tend to feed chicks on small sandeels (0 – 4 cm) (Uttley et al. 1989, Furness and Tasker 2000, Cabot and Nisbet 2013). Hence, Arctic Tern reproductive success is more likely to be adversely affected during periods of low availability of sandeel of the right size close to the sea surface than that of other sympatric tern species (Uttley et al. 1989).

Arctic and Common Terns are closely related species often found breeding together in close proximity. Despite some overlap in body weight and near overlap in bill length between these species (see Chapter 2; Dunn 1975, Lemmetyinen 1976, Cramp 1985, Malling Olsen and Larsson 1995, Ramos et al. 1998, Snow and Perrins 1998), interspecific differences in foraging behaviour and reproductive parameters have been observed both when Arctic and Common Terns breed separately at single-species colonies, and when species breed together at the same colony (Pearson 1968, Dunn 1975, Uttley et al. 1989, Cabot and Nisbet 2013). Pearson (1968) compared the diets and foraging areas utilised by Arctic and Common Terns breeding on the Farne Islands, Northumberland and showed that the two species fed on broadly similar prey species and shared similar foraging areas. There were slight differences in diet however; Common Terns fed on a higher proportion of clupeid species, while Arctic Tern diet comprised a higher proportion of sandeel. In contrast, comparisons between Arctic and Common Terns breeding at different colonies show that diet, foraging behaviour and reproductive success can vary significantly between populations breeding in different areas (Morris et al. 1976, Uttley et al. 1989, Cabot and Nisber 2013). Terns are thought to adjust their diet to whatever prey items are available in different areas and at different times (Cramp 1985, Cabot and Nisbet 2013). Hence, variation in local food supply may influence the diet, foraging behaviour, and ultimately the reproductive success of populations breeding in different areas.

While previous studies have shown that interspecific variation in chick provisioning behaviour, foraging habitat preference and behavioural response to changes in offshore conditions can occur in sympatrically breeding seabirds (Taylor 1983, Safina et al. 1990, Croxall et al. 1997, Sapoznikow and Quintana 2003, Surman and Wooller 2003, Schwemmer et al. 2009, Robertson et al. 2014a), few studies have examined whether interspecific variation in foraging behaviour explains differences in reproductive success of closely related species (but see Uttley et al. 1989, Inchausti et al. 2003, Chivers et al. 2012a). We compared the characteristics of prey items fed to chicks in two morphologically similar tern species, Arctic and Common Terns, over a single breeding season at a North Sea colony and examined whether variation in diet and provisioning rates differentially affected reproductive parameters of each species. We 1) compare the type, size and energy content of prey items delivered to chicks and broods by different tern species and 2) examine the relationship between prey delivery and chick growth rate, survival to fledging and overall breeding success. We discuss the implications of our results for predicting responses of sympatrically breeding species to changes in the marine environment.

5.3 Methods

5.3.1 Nest Observations

The study took place from May – July 2011 on Coquet Island, Northumberland, England (55º 20' N, 1º 32' W) during the chick-rearing periods for Arctic and Common Terns. Coquet Island is managed for terns by the Royal Society for the Protection of Birds (RSPB) and vegetation control is carried out in the southwestern part of the island to maintain suitable breeding habitat for tern species. Study plots were selected from this area as it had dense tern breeding populations, lower vegetation length than peripheral areas and allowed for the simultaneous observation of many nests. Study plots were easily accessible without disturbing large numbers of breeding terns and the short vegetation length allowed the survival of chicks to be routinely recorded. Plots were situated near the centre of tern colonies, and as the position of nests within seabird colonies has been found to affect fledging success and survival (Tenaza 1971, Aebischer and Coulson 1990), nests in study plots may have had higher productivities than peripheral nests. Productivity of peripheral nests could not be recorded due to the length of surrounding vegetation and proximity to rare Roseate Terns (*Sterna dougallii*) breeding on the west side of the island. As study nests for both species were situated near the centre of respective study plots, comparing productivities of Arctic and Common Terns using central study nests is unlikely to have resulted in significant bias.

Fifty study nests were selected from respective study plots for each species, 10 of which were used for regular nest observations. Approximately 1 – 4 m^2 was enclosed around each of the 10 nests using plastic netting ~0.3 – 0.5 m high (Pearson 1968, McKearnan and Cuthbert 1989, Ramos et al. 1998), to facilitate feeding observations and prevent precocial chicks from moving away from the nest and becoming difficult to observe when adults delivered food. The remaining nests in the group of 50 were enclosed in groups of two or three and were used to estimate clutch size (number of eggs per nest after completion of the clutch) and fledging success (number of fledged chicks / number of chicks hatched) for each species. The 50 nests were not enclosed individually to reduce disturbance to the colony when fitting plastic netting around nests. Chicks from each nest were ringed using uniquely numbered metal rings (supplied by the British Trust for Ornithology (BTO)) 3 – 4 days after hatching allowing individual chick mortality and fledging success to be calculated for each nest. Clutches were considered to be complete when on three consecutive days no additional egg had been laid. A similar method was used by Brinkhof et al. (1993) in a study examining variation in the timing of reproduction on fledging success in Coots. As Coquet Island does not have any mammalian predators and as large gulls are controlled, egg predation is rare. No incidence of egg predation was observed for study nests on Coquet Island, and once the final clutch size was recorded, no eggs were recorded to have been removed from study plots. Counts were made of the number of eggs and chicks in each of the 50 study nests every 2 – 3 days allowing hatching date, age and survival to be estimated for each chick.

Chicks in each of the 10 individually enclosed nests were ringed and marked shortly after hatching using temporary leg flags of unique colour combinations. Each chick also had small amounts of water-soluble nontoxic Tippex® applied to the crown to allow individuals to be recognised from a hide on occasions when leg flags were obscured by vegetation. Chick weight was only recorded on two occasions during the linear growth phase to limit disturbance to the nearby Roseate Tern colony (Coquet Island is one of only a few breeding colonies for this species in the UK; Mitchell et al. 2004, Cabot and Nisbet 2013).

Chicks were weighed to the nearest 0.25 g using 50 g and 300 g pesola scales 2 – 3 days after hatching and for a second time close to fledging or on the day of death (at 8 – 24 days). Chick weight has been shown to increase linearly with age (in days) before reaching asymptotic weightat 19 and 15 days old for Common and Arctic Tern chicks respectively (LeCroy and LeCroy 1974, Klaassen et al. 1989, Klaassen et al. 1994). As adverse weather conditions restricted access to the study plots when chicks of both species approached asymptotic weight, 19 chicks (17 Arctic and 2 Common) from a total of 42 could not be weighed until 1 – 8 days after the end of the linear growth phase. However, chick weight does not increase significantly after reaching asymptote (LeCroy and LeCroy 1974, Klaassen et al. 1989), hence weights recorded after the end of the linear growth phase were assumed to be similar had they been recorded earlier. Hence, for chicks measured after they reached asymptote, the second weight measurement was still used to calculate growth rate. Fewer second weight measurements were taken for Arctic Terns than for Common Terns as the number of days when chicks grew at a linear rate was more restricted (Arctic = 2 – 15 days, Common = 2 – 19 days; LeCroy and LeCroy 1974, Klaassen et al. 1989, Klaassen et al. 1994). Chick growth rate (g day^{-1}) was calculated using the following equation (Coulson and Porter 1985, Nisbet et al. 1995):

$$Chick\ growth\ rate = \frac{(W2 - W1)}{(D2 - D1)}$$

Where: $W1$ = Weight (g) at first measurement (2 < chick age < 3 days old)

$W2$ = Weight (g) at second measurement (8 < chick age < 24 days old)

$D1$ = Date of first measurement

$D2$ = Date of second measurement

Chicks which died before the age at which they could be initially weighed and marked were excluded from analyses. Chick growth rate was calculated for a total of 42 chicks (19 Arctic and 23 Common Tern chicks), from which a total of 30 survived to fledging and the remainder died from starvation (n = 12). An equal number of chicks from both species (n = 6) died before fledging. Growth rate was compared between those chicks which survived to fledging and those which did not using Mann Whitney *U* tests. This test was also used to compare growth rates of chicks which were measured twice during the linear growth phase and those which were measured late.

Clutch size and fledging success recorded from 50 study nests per species (100 nests in total) were compared between Arctic and Common Terns using generalised linear models (GLMs) with quasipoisson error distributions (to account for overdispersion) and log link functions, or with Gaussian error distributions and identity link functions where appropriate. Fledging success calculated from 10 individually enclosed nests was similar to that calculated using the remaining 40 nests for both species (Arctic: 10 nests = 0.65 ±

0.48, 40 nests = 0.58 ± 0.33; Common: 10 nests = 0.63 ± 0.22, 40 nests = 0.60 ± 0.27), although the larger samples gave greater accuracies.

Nest observations for each species took place from a hide positioned <12 m from study nests (maximum distance at which prey could be conclusively identified) from 2 June – 9 July 2011. Only observations which took place during the linear growth phase were used for analyses in this study. Common Tern study nests started hatching ~5 days before Arctic Tern nests although there was considerable overlap in hatching dates (see Table 4. 1). Mean age of chicks on the first day of nest observations differed only slightly between species (Table 4. 1). To avoid biases related to chick age, interspecific comparisons in diet and rates of prey delivery were made for chicks of approximately the same age.

Three-hour watches were carried out for every time period from 0400 – 2100 h and tidal state (low, high, rising, falling). For each nest, time of arrival and departure of adults, type and size of prey items fed to chicks and identity and hatching order of fed chicks (first, second or last-hatched) was recorded. Prey types were grouped into four categories: Lesser Sandeel (*Ammodytes marinus*; hereafter 'sandeel'), sprat (*Sprattus sprattus*), juvenile fish (larvae not identifiable at species level) and miscellaneous (including crustaceans, cephalopods and small demersal fish). Prey size was measured in tern bill lengths as in previous studies (Safina et al. 1990, Shealer 1998b, Rock et al. 2007). Bill lengths of Arctic and Common Terns differ only slightly (Dunn 1975, Lemmetyinen 1976), hence estimates of prey size categories were comparable between species (Robertson et al. 2014a). Type and size categories were validated for both species before observations began by examining discarded fish of known categories. Prey length (cm) was calculated by multiplying prey size category (<0.5, 0.5, 1, 1.5, 2, >2 bill lengths) by species' median bill length and the mean prey length of items delivered to each chick during the linear growth phrase was calculated. Nest observations for both species were carried out by the same observer.

5.3.2 Data Analyses

Chick provisioning rate was defined as number of deliveries made to each chick per hour and was calculated for chicks in 10 study nests of each species during the linear growth phase. Brood provisioning rate was defined as the number of deliveries made to each brood per hour and was also calculated during the linear growth phase. The percentage of each prey type and the mean length of prey items (cm) delivered to chicks during the linear growth phase were also calculated. The total amount of energy delivered to each chick and brood per hour during the linear growth phase was calculated using energy equations relating prey length to energy content (kJ) of sandeel and sprat (Hislop et al. 1991). As the species identity of prey items recorded as 'juvenile fish' was unknown, the mean energy content of sandeel and sprat was used for this prey type. This method is unlikely to have grossly under- or overestimated the energy content of juvenile fish as very small sandeel and sprat have similar energy contents (Hislop et al. 1991). Little could be inferred about the identity and energy content of miscellaneous species but because these only comprised 1.89% of total number of prey items delivered, miscellaneous species were discounted from energy calculations.

Interspecific differences in proportions of different prey type categories fed to chicks were examined using linear mixed models (LMMs). LMMs used normal error distributions, identity link functions and nest ID as a random factor unless otherwise stated. Differences in the mean length of prey items delivered to Arctic and Common Tern chicks and to chicks of different hatching order were also examined using an LMM. Variables expected to explain a significant amount of variation in chick provisioning rate such as tern species, hatching order, brood size, energy delivery rate per chick, proportion of sandeel and juvenile fish fed to chicks and the following 2-way interactions: species x energy delivery rate per chick; species x proportion of sandeel; species x proportion of juvenile fish fed to chicks were examined using an LMM. Chick provisioning rate was log-transformed to reduce heteroscedasticity in the residuals of the minimum adequate model. As 70% of Common Tern broods in this study contained three chicks while no Arctic Terns had brood sizes greater than two, hatching order was categorised as 'first-hatched', 'second-hatched' and 'last-hatched' for each species allowing interspecific comparisons of prey delivered to chicks of different hatching order to be made. Second-hatched Arctic Tern chicks were classified as 'last-hatched', while the 'second-hatched' category referred to second-hatched chicks in Common Tern broods. Separating hatching order in this way allowed comparisons to be made between first- and last-hatched chicks of different species. Differences in brood provisioning rate and energy delivery rate per brood were examined between species using Mann Whitney *U* tests. Variation in energy delivery rate per chick between species and chicks of different hatching order was examined using LMMs. Only uncorrelated fixed effects were included in each model (identified using Pearson's product moment correlation coefficient where $r \geq 0.7$ was taken to be a significant correlation (the use of 0.7 as a significant correlation was justified in a previous study (Dormann et al. 2012)) We also tested for correlation among fixed effects before fitting the model using generalised variance inflation factors adjusted for the number of degrees of freedom (GVIF^(1/2*df) using package 'car' in R version 3.1.2 (Fox and Weisberg 2011). A GVIF > 2 was regarded to be correlated with another variable included in the model (Wheeler 2007).

Variables likely to explain a significant amount of variation in chick growth rate during the linear growth phase were examined using an LMM. The model initially included species, chick provisioning rate, energy delivery rate per chick, brood size, whether or not chicks survived to fledging, hatching order, proportion of sandeel and juvenile fish delivered to each chick and 2-way interactions: species x energy delivery rate per chick and species x chick provisioning rate. The inclusion of a 2-way interaction between species and hatching order prevented the model from converging and was therefore not included. The GVIF for these variables was not greater than two, which suggests this was not caused by multicollinearity among variables included within the initial model.

Throughout the chick-rearing period, individually enclosed nests of both tern species were checked daily from a hide using binoculars and date of death or fledging was recorded for each chick (a chick was considered to have fledged when it was able to fly out of the nest enclosure). Larger enclosures for each species were checked every 2 – 3 days to record the number of chicks which had fledged or died. Variation in probability of chick survival in the 10 individually enclosed nests was examined using a generalised linear mixed model (GLMM) with a binomial error distribution, complementary log-log link function (to control for unequal size of groups within the response variable (Piegorsh 1992, Petersen and Hardy 1996): chicks survived = 30, chicks did not survive = 12)) and with nest ID as a random factor. Species, chick provisioning rate and energy delivery rate per chick during the linear growth phase as well as hatching order were included in the initial model, as was a 2-way interaction between species and chick provisioning rate. Chick growth rate was not included as a previous model showed that growth rate was related to energy delivery rate per chick and the two variables were also found to show some correlation (Pearson's product-moment correlation: $t_{40} = 3.73$, $p<0.001$, $r = 0.51$).

For each LMM and GLMM, we first fitted a fully parameterised model using maximum likelihood (ML) and removed terms by sequential deletion while testing for significant changes in model variance using likelihood ratio tests (LRTs) (Crawley 2007). We then refitted the minimum adequate model using restricted maximum likelihood (REML) to estimate effect sizes. Models were tested for goodness-of-fit using residual plots, receiver operating characteristic (ROC) curves and associated area under the curve

(AUC) using the 'ROCR' package in R (Sing et al. 2005). LMMs were fitted using the 'nlme' R package (Pinheiro et al. 2014) and GLMMs using the 'lme4' R package (Bates et al. 2013). Analyses were carried out in R version 3.1.2 (R Core Development team 2014). Means are presented ± SE throughout.

5.4 Results

5.4.1 Comparing Chick Diet and Provisioning Rates

There was a significant difference in the percentage of sandeel delivered to chicks of different species with Arctic Terns delivering a higher percentage than Common Terns during the linear growth phase (69.91 ± 0.02% and 63.05 ± 0.01% respectively; LMM: $\chi^2_1 = 5.59$, $p = 0.02$, $n = 42$). Whilst the percentage of juvenile fish delivered to chicks by Arctic Terns was greater than that delivered by Common Terns (23.74 ± 1.71% and 16.98 ± 1.06% respectively) this difference was only marginally significant (LMM: $\chi^2_1 = 4.29$, $p = 0.04$). Figure 5. 1 shows that Common Terns delivered a higher percentage of different prey types than Arctic Terns and fed chicks a significantly greater percentage of sprat (LMM: $\chi^2_1 = 30.49$, $p<0.001$).

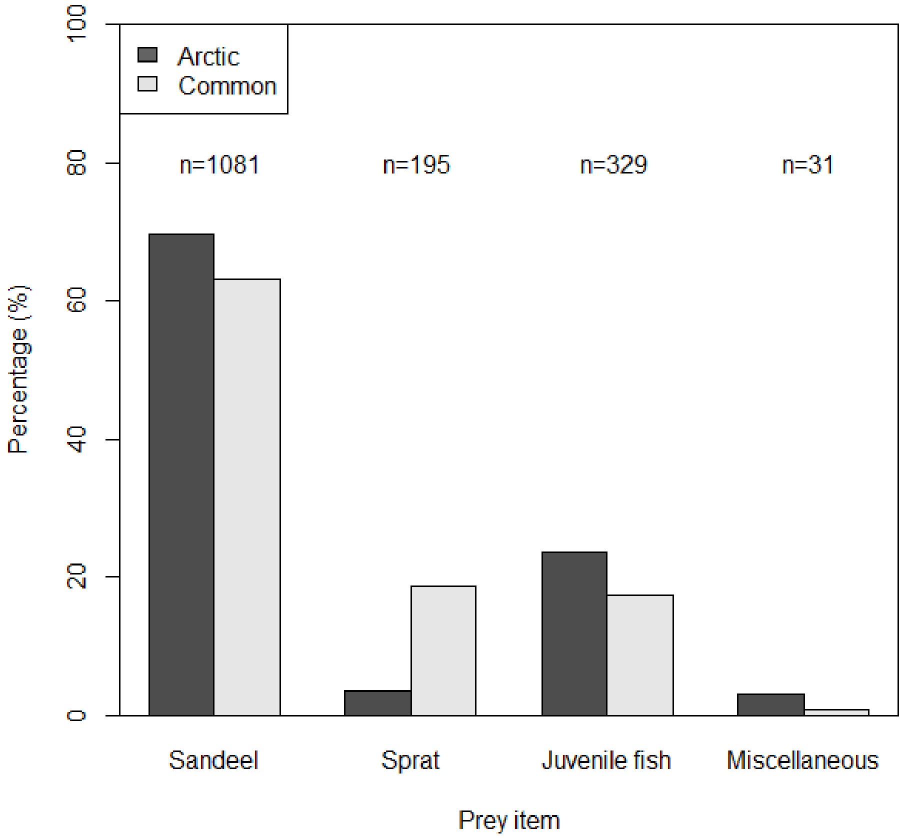

Figure 5. 1 Percentage (%) of prey types delivered to Arctic and Common Tern chicks during the linear growth phase calculated from the total number of prey items delivered to chicks of each species (Arctic: sandeel = 511, sprat = 26, juvenile fish = 173, misc = 23; Common: sandeel = 570, sprat = 169, juvenile fish = 156, misc = 8)

Mean length of prey items was found to differ significantly between species with Arctic Terns delivering smaller items than Common Terns (3.06 ± 0.05 cm and 3.68 ± 0.06 cm respectively; LMM: $\chi^2_1 = 16.26$, $p<0.001$, $n = 42$), but there was no significant effect of hatching order on mean length of prey items delivered to individual chicks ($\chi^2_1 = 4.66$, $p = 0.10$). As Arctic Terns fed a higher percentage of prey types, such as juvenile fish, which tend to be smaller than species delivered more often by Common Terns, interspecific differences in prey length may have been confounded with prey type.

Mean prey length (correlated with energy delivery rate per chick and proportion of juvenile fish fed to chicks) was excluded from an initial model examining variation in chick provisioning rate. There were significant differences in chick provisioning rates (deliveries per chick h^{-1}) between the two tern species, with Arctic Terns delivering food to chicks at a higher rate than Common Terns (LMM: $\chi^2_1 = 19.62$, $p<0.001$, $n = 42$; Table 5. 1, Table 5. 2). Last-hatched chicks in broods of both species were fed significantly less frequently than older chicks ($\chi^2_1 = 10.19$, $p = 0.01$; Table 5. 2). Brood provisioning rate (deliveries per brood h^{-1}) was only slightly higher for Arctic Terns than for Common Terns

(Table 5. 1), and a Mann Whitney *U* test showed there to be no significant difference between species ($W = 67$, $p = 0.22$, $n = 20$). Energy delivery rate per brood (kJ per brood h^{-1}), however, was found to be significantly higher for Common Tern broods than for Arctic Tern broods ($W = 20$, $p = 0.02$, $n = 20$; Table 5. 1). Despite interspecific differences in provisioning rates and in prey type and size fed to chicks, there was no significant difference in the total amount of energy delivered to Arctic and Common Tern chicks per hour (LMM: $\chi^2_1 = 3.47$, $p = 0.06$, $n = 42$; Table 5. 1) or to chicks of different hatching order (LMM: $\chi^2_1 = 3.80$, $p = 0.12$).

Table 5. 1 Mean ± SE clutch size, provisioning rates, energy delivery rates and number of chicks fledged per pair for Arctic and Common Terns breeding on Coquet Island in 2011

	Arctic Terns	**Common Terns**
Mean clutch size per pair	2.38 ± 0.06 ($n = 50$)	2.84 ± 0.05 ($n = 50$)
Mean brood size per pair when nest observations began	2.18 ± 0.07 ($n = 50$)	2.84 ± 0.04 ($n = 50$)
Mean provisioning rate per chick (deliveries per chick h^{-1})	2.02 ± 0.10 ($n = 19$)	1.12 ± 0.05 ($n = 23$)
Mean energy delivery rate per chick (kJ per chick h^{-1})	1.35 ± 0.07 ($n = 19$)	1.98 ± 0.19 ($n = 23$)
Mean provisioning rate per brood (deliveries per brood h^{-1})	3.26 ± 0.22 ($n = 10$)	3.06 ± 0.31 ($n = 10$)
Mean energy delivery rate per brood (kJ per brood h^{-1})	2.55 ± 0.19 ($n = 10$)	4.44 ± 0.53 ($n = 10$)
Number of chicks survived to fledging per pair	1.24 ± 0.07 ($n = 50$)	1.90 ± 0.11 ($n = 50$)

Table 5. 2 Output from minimum adequate model fitted using restricted maximum likelihood (REML) from a LMM with a normal error distribution and identity link function examining which variables are most significant in explaining variation in log(chick provisioning rate; deliveries per chick h^{-1}). Random factor = Nest ID (n = 20). Random Intercept standard deviation = 0.16 and Residual standard deviation = 0.24. n = 42

	Estimate ± SE	**DF**	***t*-value**	***p*-value**
Intercept	0.80 ± 0.09	20	9.39	<0.001
Species:				
Arctic	0	-	-	-
Common	-0.61 ± 0.11	18	5.55	<0.001
Hatching order:				
First-hatched	0	-	-	-
Second-hatched	-0.06 ± 0.11	20	0.55	0.59
Last-hatched	-0.29 ± 0.09	20	3.38	0.003

5.4.2 Comparing Reproductive Parameters

Mean clutch size, calculated from 50 study nests for each tern species, was found to be significantly larger in Common than in Arctic Terns (GLM: χ^2_1 = 2.03, p<0.001, n = 100; Table 5. 1). Brood size was also found to be significantly greater in Common Terns (χ^2_1 = 4.35, p<0.001, n = 100; Table 5. 1). Conversely, fledging success, was not significantly different between the two species (GLM: χ^2_1 = 0.09, p = 0.66, n = 100). However, Common Terns succeeded in raising significantly more chicks to fledging overall than Arctic Terns (GLM: χ^2_1 = 7.18, p<0.001, n = 100; Table 5. 1). There was no significant difference in the growth rates (g day^{-1}) of chicks which were measured during the linear growth phase and those which were measured after 19 or 15 days old (W = 219, p = 0.84, n = 42). First-hatched chicks of both species had comparable mean growth rates (g day^{-1}) (Arctic = 6.28 ± 0.35, Common = 6.23 ± 0.22; $t_{15.28}$ = 0.08, p = 0.93, n = 19), as did last-hatched chicks (Arctic = 3.69 ± 0.57, Common = 3.34 ± 0.50; $t_{11.25}$ = 0.26, p = 80, n = 15). Second-hatched Common Tern chicks had significantly higher growth rates than last-hatched Arctic Tern chicks (5.93 ± 0.26 and 3.69 ± 0.57 respectively; $t_{11.41} = -2.34$, $p = 0.04$, $n = 17$), and this effect was marginally significant. However, it is important to note that last-hatched Arctic Terns chicks were from broods of two, and were compared with second-hatched Common Tern chicks from broods of three. Hence growth rates of chicks of different hatching order may not be directly comparable between species.

Mean prey length was excluded from an LMM examining variation in chick growth rate as this variable was correlated with energy delivery rate per chick (kJ per chick h^{-1}). There was a significant difference in the growth rates of chicks which survived to fledging and those which did not ($W = 8$, $p<0.001$, $n = 42$). Therefore, survival to fledging was included as a 2-level factor (did survive to fledging and did not survive to fledging) in the LMM examining variation in chick growth rate. The model showed that both brood size and chick survival to fledging explained significant amounts of variation in chick growth rate ($\chi^2_1 = 3.88$, $p = 0.04$, $n = 42$ and $\chi^2_1 =13.2$, $p<0.001$ respectively) and that chicks which died before fledging and chicks from larger broods had lower growth rates than chicks which survived to fledging and chicks from smaller broods in both species (Table 5. 3). Chick provisioning rate did not significantly affect chick growth rate ($\chi^2_1 = 0.27$, $p = 0.27$) and hatching order had an almost significant effect on chick growth rate ($\chi^2_1 = 4.86$, $p = 0.08$; Table 5. 3). The inclusion of chicks which survived to fledging in the model explained a significant amount of variation in chick growth rate. Excluding chicks which did not survive to fledging would have significantly reduced the number of data points in the model ($n = 13$), hence chicks which survived and chicks which did not survive to fledging were both included in the initial model.

Table 5. 3 Output from minimum adequate model fitted using restricted maximum likelihood (REML) from a LMM with a normal error distribution and identity link function examining which variables are most significant in explaining variation in chick growth rate (g day^{-1}). Random factor = Nest ID (*n* = 20). Random Intercept standard deviation = 0.13 and Residual standard deviation = 1.12. *n* = 42

	Estimate ± SE	**DF**	***t*-value**	***p*-value**
Intercept	3.69 ± 1.24	18	2.98	0.003
Species:				
Arctic	0	-	-	-
Common	2.27 ± 1.08	18	2.11	0.03
Survival:				
Did not survive	0	-	-	-
Survived	2.24 ± 0.63	18	3.56	<0.001
Energy delivery rate per chick	1.72 ± 0.66	16	2.59	0.01
Brood size	-0.99 ± 0.42	16	2.34	0.02
Hatching order:				
First-hatched	0	-	-	-
Second-hatched	-0.02 ± 0.54	16	0.03	0.97
Last-hatched	-1.09 ± 0.54	16	2.00	0.04
Species x Energy delivery rate				
Arctic	0	-	-	-
Common	-1.34 ± 0.67	16	1.97	0.04

The LRT suggested that there was an almost significant interaction between species and energy delivery rate per chick with respect to chick growth rate ($\chi^2_1 = 3.15$, $p = 0.07$), hence this interaction was retained in the minimum adequate model (Table 5. 3). The significance of this interaction term in the minimum adequate model indicates that the impact on chick growth rate of energy delivery rate was greater for Arctic Terns than for Common Terns. The growth rates of Arctic Tern chicks increased faster with energy delivery rate than growth rates of Common Tern chicks. Common Tern chick growth rates increased more slowly with increasing energy delivery rate as illustrated in Figure 5. 2. Figure 5. 2 shows that the significance of this interaction may be influenced by two outliers. These data points correspond to a single Common Tern nest where adults regularly delivered large prey items with high energy contents. We repeated the analysis excluding this nest and still found a significant interaction between species and energy delivery rate per chick ($\chi^2_1 = 15.13$, $p = 0.02$, $n = 40$), hence we can conclude that these outliers did not influence the results of our analysis.

Seven out of 20 hatched Arctic Tern chicks and 10 out of 27 hatched Common Tern chicks died before fledging (35% and 37% respectively). There was no significant interaction between species and chick provisioning rate in explaining the probability of chick survival to fledging (GLMM: $\chi^2_1 = 1.06$, $p = 0.30$, $n = 42$). Probability of survival to fledging was similar for chicks of both species ($\chi^2_1 = 0.31$, $p = 0.58$) and chick provisioning rate had no significant effect on survival ($\chi^2_1 = 1.69$, $p = 0.19$). Hatching order had a significant effect on chick survival with first-hatched chicks being more likely to survive than second and last-hatched chicks ($\chi^2_2 = 12.49$, $p = 0.002$; Table 5. 4). Energy delivery rate per chick also explained a significant amount of variation in chick survival ($\chi^2_1 = 5.38$, $p = 0.02$; Table 5. 4).

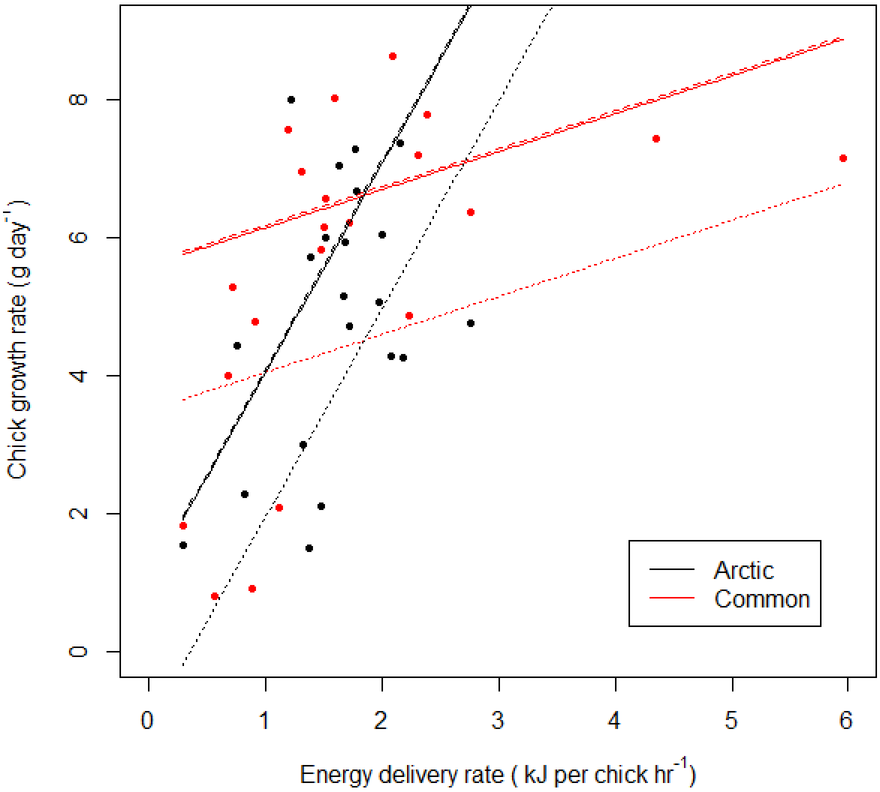

Figure 5. 2 Relationships between chick growth rate (g per chick day^{-1}) and energy delivery rate per chick (kJ per chick h^{-1}) for Arctic (black) and Common Terns (red). Straight lines represent GLMMs fitted for each species and hatching order (solid line = First hatched chick; dashed line = Second hatched chick; dotted line = Last hatched chick)

Table 5. 4 Output from minimum adequate model fitted using restricted maximum likelihood (REML) from a GLMM with a binomial error distribution and complementary log-log link function examining variation in the probability of a chick surviving to fledging. Random factor = Nest ID (*n* = 20). *n* = 42. Random Intercept standard deviation = 0.08 and Residual variance = 0.01.Receiver operating characteristic (ROC) curve showed the model to fit the data satisfactorily (AUC = 0.92)

	Estimate ± SE	**z-value**	**p-value**
Intercept	-0.40 ± 0.85	0.48	0.63
Hatching order:			
Second-hatched	-1.41 ± 0.83	1.71	0.09
Last-hatched	-2.11 ± 0.70	3.00	0.003
Energy delivery rate per chick	1.28 ± 0.67	1.91	0.056

5.5 Discussion

Interspecific variation in diet and provisioning behaviour influence species' vulnerability to changes in the marine environment (Furness and Camphuysen 1997, Furness and Tasker 2000, Diamond and Devlin 2003) and may account for variation in reproductive success of species breeding at the same colony (Uttley et al. 1989, Baird 1990, Inchausti et al. 2003). Despite delivering prey items of different types and sizes to chicks, both Arctic and Common Terns in our study had similar chick growth rates, chick survival and fledging success.

Previous studies have shown that sympatric tern species can reduce interspecific competition by delivering different prey types and sizes to chicks (Duffy 1986, Rock et al. 2007, Robertson et al. 2014a). Arctic and Common Terns in our study delivered significantly different proportions of sandeel, sprat and juvenile fish (Safina 1990a, Safina et al. 1990, Rock et al. 2007). Arctic Terns delivered a higher percentage of sandeel and juvenile fish and fewer sprats than Common Terns, and Figure 5. 1 shows that Common Terns delivered higher percentages of different prey types, which suggests that this species fed on a wider variety of prey items. Sandeel is an important prey species for terns in the

North Sea (Kirkham and Nisbet 1987, Furness and Tasker 2000, Mitchell et al. 2004), but reliance on sandeel varies among species and breeding colonies (Furness and Tasker 2000, Cabot and Nisbet 2013, Robertson et al. 2014a). In general, Arctic Terns rely more heavily on sandeel as a prey source than sympatric Common Tern populations (Monaghan et al. 1989, Uttley et al. 1989), which may explain interspecific variation in reproductive success when sandeel abundance is low (Uttley et al. 1989).

Prey species and size classes vary in energetic content (Harris and Hislop 1978, Hislop et al. 1991). Sprats have a higher energetic content than sandeel and juvenile fish, which also tend to be smaller (Harris and Hislop 1978, Hislop et al. 1991). Prey items delivered to chicks by Arctic Terns were significantly smaller than those delivered to Common Tern chicks. As the energetic content of fish is strongly correlated with length (Hislop et al. 1991), the total amount of energy delivered to Common Tern chicks per hour may be expected to be higher than that delivered to Arctic Tern chicks. However, Arctic Terns delivered prey to chicks at a significantly higher frequency than did Common Terns. Hence, when energy delivery rate per chick was compared between species, no significant difference was found. Although Arctic Terns delivered smaller prey items with lower energy contents to chicks, they maintained similar energy delivery rates to Common Terns by increasing the frequency at which prey items were delivered to each chick.

The provisioning strategy utilised by Arctic Terns appears to be a less efficient than that of Common Terns. Delivering larger more nutritious prey less frequently is more economic for a small seabird with a limited foraging range and energy budget (Pearson 1968, Cabot and Nisbet 2013) hence it is unclear why Arctic Terns consistently delivered small prey items. Due to their small size and limited diving ability, Arctic Terns concentrate their foraging activities at the sea surface and capture prey more regularly by surface-dipping (Shealer 2001, Cabot and Nisbet 2013). As small fish age classes are more often found congregating close to the surface than in deeper waters (Rindorf et al. 2000), Arctic Terns may have encountered smaller prey items regularly during foraging. However, it is possible that Arctic Terns preferentially selected small juvenile fish as they were readily available and easy to catch and transport (Hopkins and Wiley 1972). Being slightly larger with deeper diving capabilities (~0.8 m; Cabot and Nisbet 2013), Common Terns are able to capture and carry larger prey items than Arctic Terns (Nisbet 1981, Snow and Perrins 1998, Shealer 2001). However, there are costs to delivering larger prey items such as transport, increased difficulty in capture and vulnerability to kleptoparasitism (Barrett and Krasnov 1996, Ratcliffe et al. 1997, Dies and Dies 2005).

In our study, Common Terns laid significantly larger clutches than Arctic Terns and raised more chicks to fledging. Interspecific differences in clutch and brood size may reflect the amount of food parents are capable of supplying to chicks (Lack 1968), although brood size in terns has been shown to be limited by the cost of egg production (Heaney and Monaghan 1995) as well as by parental provisioning effort (Robinson and Hamer 2000). Interspecific differences in reproductive output may result from differences in life history traits and migration strategies (Boggs 1992, Egevang et al. 2010, Cabot and Nisbet 2013), but variation in the effectiveness of species' foraging strategies could also influence the amount of energy invested in foraging and reproduction (Uttley et al. 1989). Common Terns may be more capable of fledging larger broods than Arctic Terns due to their wider diet and more flexible foraging behaviour (Uttley et al. 1989, Safina et al. 1990, Robinson et al. 2001b, Cabot and Nisbet 2013). Arctic Terns are more reliant on sandeel during the breeding season, have limited diving capabilities and have more restricted diets than Common Terns, and have therefore been identified as more vulnerable to reductions in food availability (Furness and Ainley 1984, Furness and Tasker 2000). However, chick growth rates during the linear growth phase were similar between species and of the total number of chicks hatched in study nests, a similar proportion survived to fledging in both species. This suggests that Arctic and Common Tern parents were equally successful at providing adequate food to chicks throughout the developmental period.

As Common Terns had larger broods than Arctic Terns, Common Tern parents might have been expected to exhibit greater foraging effort to deliver enough food to each chick in a brood. However, we found there to be no significant difference in brood provisioning rate during the linear growth phase between the two species, which suggests that although individual Arctic Tern chicks within a brood received food deliveries at a higher rate than Common Tern chicks within a brood, parents of both species delivered prey to broods at similar rates. The higher chick provisioning rates of Arctic Terns may have been a consequence of their significantly smaller clutch sizes; food deliveries were distributed among fewer chicks. Although both species had comparable chick energy delivery rates per hour, Common Terns had higher energy delivery rates per brood than Arctic Terns, as they consistently delivered larger prey items to nests. This may be a result of interspecific differences in diet, foraging behaviour and offshore habitat selection (Uttley et al. 1989, Rock et al. 2007, Robertson et al. 2014a).

Although chick growth rate during the linear growth phase was similar between species, beyond a threshold of approximately 1.3 kJ per chick h^{-1}, Arctic Tern chicks had higher growth rates than Common Tern chicks for a given energy delivery rate. Arctic

Terns are smaller than Common Terns and reach asymptotic weight at a younger age (Klaassen et al. 1989, Snow and Perrins 1998). Arctic Tern chicks also require less energy to maintain growth rates than larger tern species (Klaassen et al. 1989, Klaassen et al. 1994). This may explain how Arctic Terns were able to maintain similar chick growth rates to Common Terns while using a less energetically efficient foraging strategy. Energy requirements are 30% higher for Common than for Arctic Tern chicks, and Common Tern chicks spend a greater proportion of their daily energy intake on maintaining body temperature, perhaps because their larger brood sizes reduce the efficiency of parental brooding or because Arctic Terns are better adapted to a more northerly distribution (Robinson et al. 2001b). Chick growth rate of sympatrically breeding tern species has been shown to be differentially affected by changes in weather conditions due to interspecific differences in parental foraging behaviour (Dunn 1975, Uttley et al. 1989). Hence, variation in chick energy requirements and vulnerability to changes in environmental conditions may influence chick growth among species.

There is a tendancy for chicks with higher energy delivery rates to be more likely to survive to fledging than chicks with lower energy delivery rates in both species, although the relationship between chick survival and energy delivery rate was not strong. Previous studies have shown that the energetic value of prey can significantly influence chick survival in seabirds and other marine predators (Rosen and Trites 2000, Wanless et al. 2005b). The ‘junk-food hypothesis’ suggests that declines in seabird productivity can be attributed to a decrease in the nutritional value of the prey items fed to chicks (Romano et al. 2006, Grémillet et al. 2008). Chicks fed prey items of higher energy content are more likely to survive both before and after fledging than those fed on prey items of lower energetic value (Wanless and Harris 1992, Golet et al. 2000, Romano et al. 2006). Both Arctic and Common Tern chicks which were delivered energy at a higher rate were likely to have more available energy to fuel growth and survival than chicks delivered less energy per hour (Massias and Becker 1990, Golet et al. 2000, Litzow et al. 2002).

Diet and chick provisioning behaviour of morphologically similar species breeding at the same colony can differ significantly. Arctic Terns delivered smaller prey of lower energy content to chicks than Common Terns, but there was no significant difference in chick growth rate and survival between species. This is contrary to our initial expectations, as chicks receiving a high proportion of energetically poor prey may be expected to have lower growth rates and survival than those fed on large prey items with high energy contents. However, Arctic Terns in our study were able to compensate for the low energetic value of prey items by increasing the frequency at which prey items were delivered to each chick in a brood. Both tern species delivered prey to broods at similar rates, and Arctic Terns were able to maintain higher chick provisioning rates by laying smaller clutches. Our study shows that sympatrically breeding species vary in their provisioning behaviour and total reproductive output which may be at least partly due to differences in diet and foraging strategies.

Chapter 6

Inter- and intra-year variation in foraging areas of breeding Kittiwakes (*Rissa tridactyla*)

6.1 Abstract

While seabird conservation efforts have largely focused on protection from threats at the colony (e.g. reducing disturbance and predation), attention is increasingly being given to implementing protection measures for foraging areas at sea. For this to be effective, important foraging areas must be identified. Although numerous studies have examined seabird foraging behaviour, information is still lacking on the variability in area utilisation within and among breeding seasons. GPS devices were attached to adult Black-legged Kittiwakes (*Rissa tridactyla*) breeding at an expanding North Sea colony (55º 20' N, 1º 32' W) during both incubation and chick-rearing in 2012 and during chick-rearing in 2011, to determine whether foraging areas remained consistent and to identify the oceanographic characteristics of areas used for foraging. The type and size of prey items consumed at different stages of the breeding cycle was also examined. During incubation (April – May 2012), Kittiwakes foraged substantially further from the colony and fed on larger sandeels than when feeding chicks, and there was significant inter-annual variation in foraging areas used during the chick-rearing period (June – July 2011 and 2012). Foraging areas were characterised by cooler sea surface temperatures (SST) and areas of high chlorophyll *a* concentration, although association with specific oceanographic features changed within the breeding season and between years. These results emphasise the importance of considering how foraging areas and reliance on specific oceanographic conditions change over time when seeking to identify important marine areas for seabirds.

6.2 Introduction

It is becoming increasingly apparent that protection of seabird foraging areas is necessary to mitigate threats caused by human activities at sea such as marine developments, overfishing, fishery bycatch of seabirds and pollution (Monaghan 1996, Lewison and Crowder 2003, Garthe and Hüppop 2004, Votier et al. 2005, Scott et al. 2006, Grecian et al. 2010). Marine Protected Areas (MPAs) are a useful conservation measure to reduce threats to marine life by limiting human activities in important foraging areas (IUCN 1988). For many seabird species data describing the use of offshore areas are limited, making identification of suitable MPAs difficult (Lewison et al. 2012). In recent years, bird-borne GPS devices have been successfully employed to identify foraging areas of a variety of species (Wood et al. 2000, Ryan et al. 2004, Weimerskirch et al. 2005, Kotzerka et al. 2010, Stauss et al. 2012).

Black-legged Kittiwakes (*Rissa tridactyla*, hereafter 'Kittiwakes') are small surface-feeding seabirds widely distributed in temperate and Arctic regions in the northern hemisphere (Harrison 1983). Historically, Kittiwakes have bred in large numbers along the north-western edge of the North Sea (Lloyd et al. 1991) but have recently become a species of conservation concern as their abundance and productivity in the North Sea have declined in the last 30 years (Harris and Wanless 1990, Wanless and Harris 1992, Harris and Wanless 1997, Upton et al. 2000, Mitchell et al. 2004, Eaton et al. 2009). An important factor contributing to this decline is a reduction in food availability due to decreases in the abundance of principal forage fish such as Lesser Sandeel (*Ammodytes marinus*, hereafter 'sandeel') (Harris and Wanless 1990, Rindorf et al. 2000, Daunt et al. 2002, Frederiksen et al. 2004a, 2008b). Kittiwakes are obligate surface-feeders restricted to obtaining food from the top few metres of the water column (Harris and Wanless 1990, Coulson 2011). Previous studies have identified surface-feeding seabird species as being more severely affected by food shortages than diving species (Furness and Ainley 1984, Furness and Tasker 2000). Kittiwakes are especially vulnerable to reductions in prey abundance as they have high foraging costs, restricted diving ability and limited ability to switch to different prey types (Furness and Tasker 2000).

Kittiwakes are useful species in which to examine variation in foraging behaviour for several reasons. Firstly, their foraging areas have been shown to vary depending on environmental conditions and food abundance (Suryan et al. 2000, Scott et al. 2010). Secondly, Kittiwake populations have been shown to fluctuate in synchrony with sandeel abundance (Frederiksen et al. 2004a) and are therefore good indicators of the health of the marine environment (Parsons et al. 2008). Thirdly, understanding foraging distributions of Kittiwake colonies in the North Sea after the closure of the sandeel fishery in the Wee Bankie in 2000 demonstrates the effectiveness of offshore foraging area protection (Daunt et al. 2008). The recent miniaturisation of data loggers has allowed total duration of Kittiwake foraging trips to be recorded and important foraging areas to be identified (Kotzerka et al. 2010, Chivers et al. 2013, Redfern and Bevan 2014).

Despite the large number of tracking studies carried out to date, most have considered only a single breeding phase (Lewis et al. 2002, Weimerskirch et al. 2007, Stauss et al. 2012, Chivers et al. 2013) or breeding season (Weimerskirch et al. 2005, Kotzerka et al. 2010, Votier et al. 2010). As such, few studies have examined spatiotemporal shifts in foraging behaviour at different stages of the breeding cycle, or in different years (Weimerskirch et al. 1993, Hull et al. 1997, Berrow et al. 2000, Stauss et al. 2012, Chivers et al. 2013). Local prey distribution and abundance is strongly influenced by oceanographic conditions, therefore foraging areas used during breeding are likely to change through time (Monaghan et al. 1994, Suryan et al. 2002, Pinaud et al. 2005, Weimerskirch 2007, Chivers et al. 2013). Furthermore, the suitability of different areas is likely to be influenced by other factors such as the costs incurred by being away from the nest or variation in optimal prey size at different stages of the breeding cycle. Adult body condition may also affect an individual's capability to exploit distant foraging areas, and has been shown to vary throughout the breeding season and in different years depending on food availability (Hamer et al. 1993, Kitaysky et al. 1999). Designating protected areas based on data collected only during one year or breeding stage may underestimate the size of foraging areas that need to be protected, but we lack information on variation in area use. Tracking studies carried out over longer temporal periods will improve our understanding of how foraging areas change over time and whether oceanographic conditions facilitate these changes. Such studies will improve our ability to make predictions regarding the distribution of seabirds at sea.

We examined the foraging behaviour of breeding Kittiwakes at a North Sea colony at different stages of the breeding season in the same year and at the same breeding stage (chick-rearing) in two different years. We investigated (1) whether the location of foraging areas or adult condition during chick-rearing varied between the two years, (2) whether prey size, foraging area or adult condition varied with stage of the breeding cycle in the same year and (3) how changes in foraging areas related to variation in specific oceanographic conditions. We discuss the implications of our results for the identification of offshore protected areas for seabirds.

6.3 Methods

6.3.1 GPS Tagging

The study took place on Coquet Island, northeast England (55º 20’ N, 1º 32’ W) during chick-rearing from June to July 2011 and during incubation and chick-rearing from May to July 2012. Tags were deployed on a total of 30 birds in 2012, seven of which were not recaptured, and 15 birds during chick-rearing in 2011, two of which were not recaptured. Hence, we retrieved movement data from adults in 13 nests during chick-rearing in 2011, 10 nests during incubation in 2012 and 13 nests during chick-rearing in 2012. One adult per nest was captured using a pole and noose (Hogan 1985) under a permit issued by the British Trust for Ornithology (BTO). Each tagged bird was captured twice: once to deploy the tag and a second time to retrieve the tag and download the data. Some tags could not be retrieved as we were occasionally unable to recapture birds after deploying tags. No eggs were damaged from deploying or recovering tags during incubation. We ensured that the same nests were not used to capture adults more than once during the study. Body mass and head and bill length were recorded and captured birds were ringed and fitted with GPS tags (Mobile Action Technology GT120, rehoused in heat-shrink tubing and fitted with lighter batteries of lower power) which weighed <14 g, less than 4% of birds’ body mass (Caccamise and Hedin 1985, Hill and Robertson 1987). Tags were attached to the back feathers using thin strips of cloth-backed (TESA®) tape (item model number 56343-00026-02). Four strips of pre-cut tape were attached horizontally to the back feathers so that each overlapped slightly with the preceding strip. The ends of each strip were covered by pieces of grease-proof paper to prevent feathers becoming attached before the tag was in position. The GPS tag was placed in the middle of the four strips and the ends of each strip wrapped around the tag to securely attach it to feathers. Care was taken to ensure that birds’ head, neck and wing feathers were not attached to the strips of tape and could move freely. Birds were processed and tagged within 20 minutes of capture. All flew normally after release and most returned to the nest within 10 – 15 mins. GPS tags were programmed to acquire a position every 100 s and tests indicated they had an accuracy of approximately 20 m when birds were moving. Tags were removed ~2 – 4 days after deployment. Breeding success of birds fitted with GPS tags and a random sample of untagged control birds breeding on the same cliffs were compared in 2012 to determine whether there were any detectable effects of tag deployment on breeding performance. Breeding success of tagged birds was not recorded in 2011 due to conflicts with other studies taking place at the study site. Coquet

Island is a highly sensitive conservation area supporting ~80 pairs of endangered Roseate Terns (*Sterna dougallii*) (Mitchell et al. 2004). In order to visit the Kittiwake colony, researchers had to move through the tern colonies which in 2011 were being studied intensively. Hence, to mitigate disturbance to sensitive species, regular visits to the Kittiwake colony were limited.

Tagging during incubation took place from 23 May – 26 May 2012. During chick-rearing, birds were tagged from 14 June – 17 June 2011 and 17 June – 3 July 2012. The tracking period during chick-rearing in 2012 was longer than that in 2011 as tagging had to be temporarily suspended from 19 June – 25 June 2012 due to poor weather conditions. The difference in tracking start dates between years was caused by a difference in average laying dates at study colonies in 2011 and 2012; dates of first hatching were 31 May 2011 and 5 June 2012. We considered it necessary to ensure that the birds we tracked were feeding chicks of similar ages, since this was likely to be more important than the slight variation in tracking dates between years. Approximate chick age at nests where each adult was tracked was estimated using date of first hatching recorded from a subset of 112 nests in the centre of the Kittiwake colony close to nests which were selected for tagging in both years. Estimates of dates of first hatching and dates on which tags were deployed were used to calculate chick age of tagged nests and were compared between years. Dates of first hatching were similar between tagged nests and the subset of 112 nests used to estimate first hatching dates in 2012 (5 June and 6 June), hence date of first hatching from the subset of nests is likely to provide a useful estimation of date of first hatching for tagged nests in both years. Chicks of tagged birds were likely to be similar ages in 2011 and 2012, as the estimated age of chicks in the study colony, based on first hatching dates for a subset of 112 nests, were 15.5 ± 0.65 and 15.2 ± 1.16 days old when tracking started in 2011 and 2012 respectively. A direct comparison of chick ages when tracking started between the two years was not possible, as hatching dates for tagged nests were not available in 2011 due to conflicts with other studies being carried out on the island. Chick age when tracking began could only be estimated in 2011 using a subsample of 112 nests for which date of first hatching was recorded in both years (as described above). Although this method may not have been entirely accurate, it indicates that chicks should have been of similar ages when tracking began. However, as tracking was carried out over a longer time period in 2012 than in 2011, brood age of tracked adults is likely to have been greater and more variable in 2012 than in 2011. This may have contributed to observed inter-annual differences in foraging behaviour.Chicks of tagged birds were likely to be similar ages in 2011 and 2012, as the estimated age of chicks in the study colony were 15.5 ± 0.65 and 15.2 ± 1.16 days old when tracking started in 2011 and 2012 respectively.

We found no evidence that fitting GPS tags affected breeding performance of Kittiwakes, which we examined in 2012. Number of fledged chicks from nests where one adult was tagged was not significantly different from that of a random sample of 30 untagged pairs breeding on the same cliffs (1.50 ± 0.14, n = 30 and 1.13 ± 0.16, n = 30 respectively; GLM with Poisson error structure: $\chi^2_1 = 1.25$, $p = 0.26$, $n = 60$). Despite being unable to determine the effect of deploying this kind of tag on Kittiwakes in 2011 due to lack of data on breeding success of tagged pairs, previous studies have shown that GPS tags of similar weight and method of attachment had no detrimental effect on Kittiwake reproductive performance (Kotzerka et al. 2010, Chivers et al. 2012a).

6.3.2 Prey Type and Adult Body Condition

In order to obtain information on the main prey type and size utilised during the tracking period, we collected spontaneous regurgitate samples from both adults and chicks while fitting and retrieving GPS tags during incubation and chick-rearing in 2012. Samples were stored in individual plastic containers. A saturated solution of biological washing powder (Biotex$^{®}$) was added to each sample and the container left at approximately 20ºC for 3 – 5 days until all the flesh and soft material had been dissolved. This material was then filtered from the solution leaving only bones (Lewis et al. 2001a, Bull et al. 2004). We identified species composition and estimated fish length from vertebrae. Bones were identified to the lowest taxa possible using a binocular microscope (for small bones x60 magnification and for large bones x12 magnification) and keys in Watt et al. (1997). Anterior caudal bones in each sample were identified, the total horizontal length of bones measured using a calibrated eye piece graticule (x12 magnification) and the corresponding fish length estimated using regression equations in Watt et al. (1997). To examine variation in adult Kittiwake body condition in relation to breeding stage and year, an index (g mm^{-1}) was calculated by dividing body mass (g) by head and bill length (mm) (Chastel et al. 1995, Brinkhof 1997, Mateo et al. 1998, Whitfield et al. 1999, Weimerskirch et al. 2005). Although other methods of calculating a body condition index are available (Johnson et al. 1985), this method was simple and provided useful results. Using weight and head and bill measurements to calculate a body condition index is more accurate than using weight measures alone (Johnson et al. 1985), can perform better than other scaling methods such as wing length which can vary temporally (Ormerod and Tyler 1990), and measurements are quick and easy to collect in the field, which is especially important at a sensitive study site like Coquet Island.

6.3.3 Environmental Variables

To characterise the marine environment around the colony and examine how oceanographic features relate to foraging areas, we extracted 4 km^2 resolution monthly composites of remotely sensed sea surface temperature (SST °C) and chlorophyll *a* concentration (mg m^{-3}) from the MODIS instrument onboard the Aqua (EOS PM) satellite (http://oceancolor.gsfc.nasa.gov/), and 30 x 30 arc second resolution bathymetry data (m) from the GEBCO_08 dataset available from NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS). We used nightime SST data to reduce any bias in daytime estimates due to solar heating. Previous studies have found that SST, chlorophyll *a* concentration and bathymetry correlate with prey distribution and abundance both during the breeding season and during the preceding winter (Lutjeharms 1985, Schneider 1997, Park et al. 2002, Weimerskirch et al. 2004, Pinaud et al. 2005, Hyrenbach et al. 2007). In particular, SST in winter has been found to affect the distribution and abundance of sandeels, known to be an important Kittiwake prey species (Arnott and Ruxton 2002). We also extracted SST and chlorophyll *a* concentration one month before tracking took place to account for potential lag in relationships between these variables and prey abundance. We retrieved mean monthly composites of SST and chlorophyll *a* concentration from concurrent months (May – July 2012 and June 2011 (lag 0)), and from one month previous to tracking commencing (April – June 2012 and May 2011 (lag 1)) as well as from the preceding winters (December – February 2012 and 2011) for use in environmental models.

6.3.4 Data Analyses

Although a previous study on Kittiwake foraging behaviour defined foraging trips as starting 300 m from the colony (Kotzerka et al. 2010), we increased this distance to 1 km in our study to exclude birds observed resting on rocks up to 1 km from Coquet Island (GS Robertson pers. obs.). We therefore classified behaviour at locations within 1 km of the colony or over land as maintenance, resting and nest attendance rather than foraging activities; a trip during which foraging may occur was defined as seaward movement beyond 1 km from the colony. Frequency distributions of flight speeds during incubation and chick-rearing in both years showed slight bimodality at speeds below 1 ms^{-1} and between 9 and 11 ms^{-1}. As Kittiwakes reduce their flight speed to collect food from the sea surface (Coulson 2011), we used periods of reduced flight speeds as indicators of foraging activity (Weimerskirch et al. 2004, Kotzerka et al. 2010). One ms^{-1} was used as a cut off for foraging behaviour as the frequency histogram of flight speeds showed that birds spent a high proportion of time moving at less than 1 ms^{-1}. As foraging and resting on the sea surface are common behaviours in Kittiwakes, this speed was used to represent foraging and/or resting locations. Hence, birds were judged to be engaged in foraging behaviour at locations where instantaneous speed was <1 ms^{-1}. This classification rule cannot discriminate between situations where birds foraged on the sea surface and where they rested between foraging bouts. Kittiwakes are known to rest on the sea surface while collecting food (Cramp and Simmons 1983, Coulson 2011). Without the use of saltwater or stomach temperature switches which record when birds were feeding we could not definitively separate foraging and resting locations (these devices could not be attached to birds in our study due to weight restrictions (Wilson et al. 1995, Benvenuti and Dall'Antonia 2004)). However, this is unlikely to result in misrepresentation of foraging locations as surface-feeders such as Kittiwakes forage primarily during daylight hours (Galbraith 1983, Weimerskirch and Guionnet 2002, Humphreys et al. 2007, Phalan et al. 2007), and locations where birds moved at speeds of <1 ms^{-1} during hours of darkness were removed before carrying out kernel density estimations and examining the effect of environmental variables on foraging, as these locations were likely to be where birds rested during the night.

For each foraging trip we calculated maximum foraging range (most distant point from the colony (km)), total distance travelled (km) and trip duration (h) and examined differences between trip parameters at both breeding stages and in different years using linear mixed models (LMMs) with bird ID as a random factor. Separate models were used to examine how time of day trips were carried out (day or night) affected variation in trip parameters during different breeding stages and years. Four individuals tracked during chick-rearing in both years and one individual tracked during incubation 2012 were excluded from models as their trips included <5 daylight foraging locations. As each individual was only tracked once during the study, and GPS devices were only attached for a limited time, it was possible for birds to be tracked when they were carrying out only brief feeding trips or non-foraging trips for exploration, bathing or resting. Such trips were unusual (only occurred in <14% of tracked individuals), and were therefore not regarded to be part of normal foraging trips, justifying their exclusion. These birds undertook trips with significantly smaller mean maximum foraging ranges (Welch's t-test: $t_{11.28} = -2.71$, $p = 0.02$, $n = 36$) than those of non-excluded individuals, although trip durations were not significantly different ($t_{5.11} = 0.58$, $p = 0.58$). Trips may have been carried out for purposes other than foraging, such as bathing or resting. Number of individuals included in further analyses from each breeding stage and year were as follows: Incubation in 2012 = 9 birds; Chick-rearing in 2012 = 12 birds and Chick-rearing in 2011 = 10 birds. Minimum adequate models were tested for normality by examining residual plots and response variables log-transformed where residuals showed heteroscedasticity. No recorded trips were incomplete.

We examined differences in foraging ranges (95% volume contour) and core foraging areas (25% volume contour) at different breeding stages and in different years using fixed kernel density estimation in a European Albers equal-area conic projection with a smoothing parameter (h) of 2.5 km and a grid size of 1 km² (Suryan 2006). Kernel density plots were calculated in R version 3.2.1 using the adehabitatHR and maptools packages (Calenge 2006). Examination of possible breeding stage and year effects was carried out by quantifying overlap in foraging ranges and core foraging areas between incubation and chick-rearing in 2012 and during chick-rearing in 2011 and 2012. Percentage overlap was calculated by dividing the area of overlap between years/stages by the combined area utilised by foraging birds in both years/stages and multiplying by 100. This quantifies the degree of similarity between foraging areas used in different years and breeding stages. The percentage area of foraging ranges and core foraging areas found within those of another stage or year was also calculated. We used an area saturation curve method (Soanes et al. 2013) to determine whether foraging ranges and core foraging areas calculated for each breeding stage and year were likely to be representative of areas used by the whole colony. Using the statistical software R (R Core Development Team 2014), an increasing sample of individual kittiwakes were randomly selected, and foraging ranges (95% contour) and core foraging areas (25% contour) calculated from each sample using foraging location data. First, one individual was randomly selected from the total number of individuals tracked during each breeding stage/year, and the foraging locations associated with that individual used to calculate kernel density utilisation contours. This was repeated using two individuals and so on until kernel density utilisation contours had been calculated for n - 1 birds for each breeding stage and year. The total number of individuals selected differed for each breeding stage or year, and was defined as the total number of birds tracked - 1 (Incubation 2012 = 1 – 9 birds; Chick-rearing 2012 = 1 – 11 birds; Chick-rearing 2011 = 1 – 9 birds).

Separate binomial generalised linear mixed models (GLMMs) with logit link functions were used to examine how foraging range changed at different stages of the breeding cycle and to identify environmental correlates of foraging locations. GLMMs were also used to examine how the distance that birds foraged from the colony changed during chick-rearing in two different years (2011 and 2012), whether changes could have been caused by the small difference in the timing of tracking studies within and between the two years and whether birds foraged in areas with similar environmental conditions in both years. To reduce interdependency among points, for each model presence data were five randomly selected foraging locations per track and for absence data, five non-foraging locations per individual were randomly selected from a buffer zone around the colony (size of the buffer zone was defined as the maximum foraging range of all tracks in each breeding stage and in each year).

For models examining how environmental variables affected foraging locations we fitted SST (lag 0), chlorophyll *a* concentration (lag 0), bathymetry, SST one month previously (lag 1), chlorophyll *a* concentration one month previously (lag 1), SST and chlorophyll *a* concentration the previous winter and their interactions as fixed effects, and included bird ID as a random factor. Only uncorrelated fixed effects were included in the models (using Pearson's product moment correlation coefficient where $r > 0.7$ was taken to be a significant correlation). We first fitted the fully parameterised models using maximum likelihood (ML), and then removed terms by sequential deletion while testing for significant changes in model variance using likelihood ratio tests (LRTs) (Crawley 2007). We then refitted the minimum adequate model using restricted maximum likelihood (REML) to estimate effect sizes. Models were tested for goodness-of-fit using receiver operating characteristic (ROC) curves and the associated area under the curve (AUC) using the 'ROCR' package in R (Sing et al. 2005). We used a LMM to test for differences in fish length between breeding stages in 2012 with bird ID as a random factor. The body condition indices of adults at different breeding stages and in different years were compared using Welch's t-tests. Analyses were carried out in R version 3.2.1 (R Development Core Team 2014) and ArcGIS version 10.1 (ESRI, USA). Means are presented ± SE throughout.

6.4 Results

6.4.1 Foraging Areas

We obtained data from 106 foraging trips in total (Incubation $n = 15$, Chick-rearing in 2012 $n = 60$, Chick-rearing in 2011 $n = 31$). The amount of time GPS tags were attached to birds (Incubation = 10 birds, Chick-rearing 2012 = 13 birds and Chick-rearing 2011 = 13 birds) did not differ significantly between years and breeding stages (one-way ANOVA: $F_{2,33} = 0.69$, $p = 0.51$, $n = 36$) and the percentage of tags retrieved was also similar between stages and years (Incubation 2012 = 76.92%, Chick-rearing in 2012 = 76.47%, Chick-rearing in 2011 = 86.67%).

In 2012, birds foraged closer to the colony during chick-rearing than during incubation (Figure 6. 1, Table 6. 1); maximum foraging range, total distance travelled and trip duration were all significantly greater during incubation. Despite the longer tracking period, maximum foraging range, total distance travelled and trip duration were significantly smaller during chick-rearing in 2012 compared with chick-rearing in the previous year (Figure 6. 1, Table 6. 1). Models examining the effect of time of day on variation in trip parameters found significant interactions between breeding stage and time of day for all three trip parameters ($\chi^2_1 = 41.78$, $p<0.001$, $n = 75$; $\chi^2_1 = 33.22$, $p<0.001$ and $\chi^2_1 = 34.62$, $p<0.001$ respectively) which suggests that birds travelled further and for longer at night during incubation than during chick-rearing in 2012. Models for chick-rearing in 2011 and 2012 showed that time of day had a significant effect on maximum foraging range ($\chi^2_1 = 7.72$, $p<0.001$, $n = 91$) and trip duration ($\chi^2_1 = 31.93$, $p<0.001$), but no effect on total distance travelled ($\chi^2_1 = 0.10$, $p = 0.75$). There were no significant interactions between year and time of day for maximum foraging range, total distance travelled and trip duration ($\chi^2_1 = 0.75$, $p = 0.39$, $n = 91$; $\chi^2_1 = 0.10$, $p = 0.75$; $\chi^2_1 = 1.45$, $p = 0.23$ respectively).

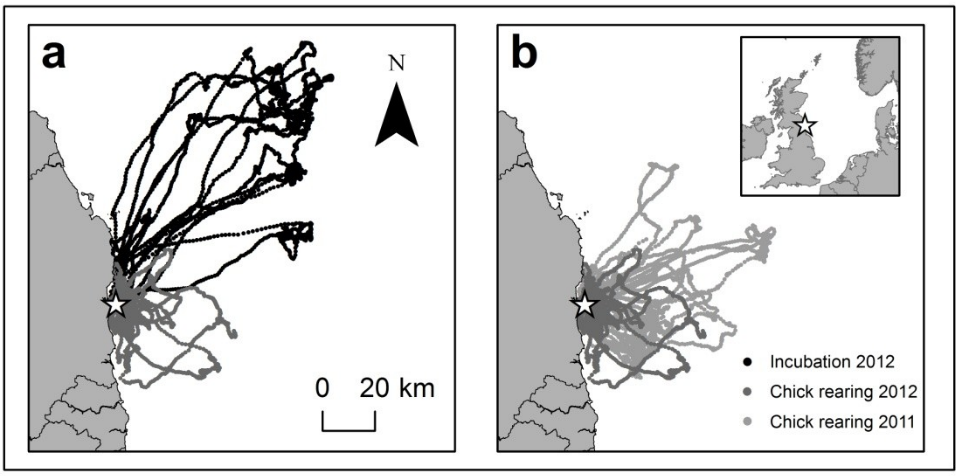

Figure 6. 1 Kittiwake foraging tracks during **a)** Incubation and Chick-rearing in 2012 and **b)** Chick-rearing in 2011 and 2012 recorded from 23 May to 3 July 2012 and 14 June to 17 June 2011. Coquet Island (55° 20’ N, 1° 32’ W) is represented by a star

Table 6. 1 Table comparing trip parameters at different breeding stages and in different years. Mean values are shown ± SE with range given in brackets. Displays results of likelihood ratio tests (LRTs) from LMMs where response variables were log-transformed for models examining differences in max foraging range and total distance travelled between stages/years and where random factor = Bird ID. Incubation and Chick-rearing 2012 $n = 75$, Chick-rearing 2011 and 2012 $n = 91$

Incubation and Chick-rearing 2012

	Incubation ($n = 15$)	Chick-rearing ($n = 60$)	LRTs
Max foraging range (km)	50.95 ± 12.99 (1.16 – 122.55)	9.03 ± 1.17 (2.21 – 47.55)	$\chi^2_1 = 12.99$, $p<0.001$
Total distance travelled (km)	129.62 ± 34.44 (0.22 – 324.84)	20.28 ± 3.24 (1.51 – 153.45)	$\chi^2_1 = 4.90$, $p = 0.03$
Trip duration (h)	10.20 ± 2.55 (0.08 – 25.78)	2.87 ± 0.53 (0.36 – 30.20)	$\chi^2_1 = 16.38$, $p<0.001$

Chick-rearing 2011 and 2012

	Chick-rearing 2011 ($n = 31$)	Chick-rearing 2012 ($n = 60$)	
Max foraging range (km)	28.02 ± 3.88 (1.15 – 77.63)	9.03 ± 1.17 (2.21 – 47.55)	$\chi^2_1 = 17.85$, $p<0.001$
Total distance travelled (km)	64.43 ± 9.19 (0.05 – 182.60)	20.28 ± 3.24 (1.51 – 153.45)	$\chi^2_1 = 9.44$, $p = 0.002$
Trip duration (h)	5.07 ± 0.75 (0.08 – 14.12)	2.87 ± 0.53 (0.36 – 30.20)	$\chi^2_1 = 4.46$, $p = 0.03$

Kernel density plots illustrated clear differences in the extent of foraging ranges at different breeding stages with birds covering a larger area during incubation in 2012 than during chick-rearing in both years (Incubation = 2219.37 km^2, $n = 9$ birds, 964 foraging locations; Chick-rearing in 2012 = 678.48 km^2, $n = 12$ birds, 1539 foraging locations;

Chick-rearing in 2011 = 1962.48 km^2, $n = 10$ birds, 966 foraging locations; Figure 6. 2). The core foraging area was smaller during chick-rearing in 2012 than during incubation in the same year (Incubation = 116.91 km^2, Chick-rearing in 2012 = 32.20 km^2) and showed no overlap between stages (Figure 6. 3). Core foraging areas during chick-rearing in both years showed an overlap of 17.89% and there was a slightly greater degree of overlap in foraging ranges (18.16%; Figure 6. 3). Both foraging ranges and core foraging areas during chick-rearing in 2012 were more restricted than those of chick-rearing in 2011 (Foraging ranges: Chick-rearing in 2012 = 678.48 km^2, Chick-rearing in 2011 = 1962.48 km^2; Core foraging areas: Chick-rearing in 2012 = 32.20 km^2, Chick-rearing in 2011 = 78.74 km^2). As well as examining percentage overlap between foraging areas at different breeding stages and years, we also examined the percentage foraging area from one breeding stage/year which was contained within that of another breeding stage/year. Over half of foraging ranges and core foraging areas of birds foraging during chick-rearing in 2012 were found within those of birds foraging at the same stage in the previous year (Foraging range = 70.70%, Core foraging area = 61.65%).

Area saturation curves showed that chick-rearing 2012 foraging ranges and core foraging areas and chick-rearing 2011 core foraging areas reached asymptote (Figure 6. 4 c, d, f), while those of incubation and chick-rearing 2011 foraging ranges did not. However, increase in foraging area size slowed down as more individuals were included in the sample.

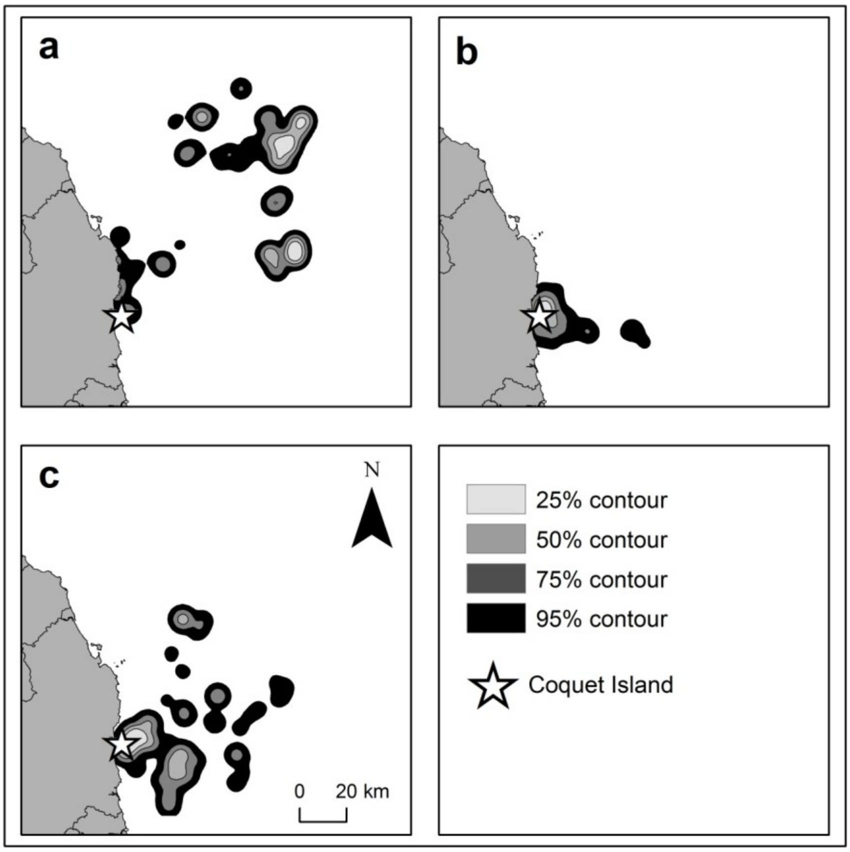

Figure 6. 2 Kernel utilisation distribution of 3469 foraging locations (Incubation 2012 *n* = 964 locations; Chick-rearing 2012 *n* = 1539 locations; Chick-rearing 2011 *n* = 966 locations) using tracks from **a)** 9 incubating birds in 2012, **b)** 12 chick-rearing birds in 2012 and **c)** 10 chick-rearing birds in 2011 foraging off Coquet Island. Contour plots show the density of locations on a 1 km² grid using a 2.5 km smoothing parameter (*h*)

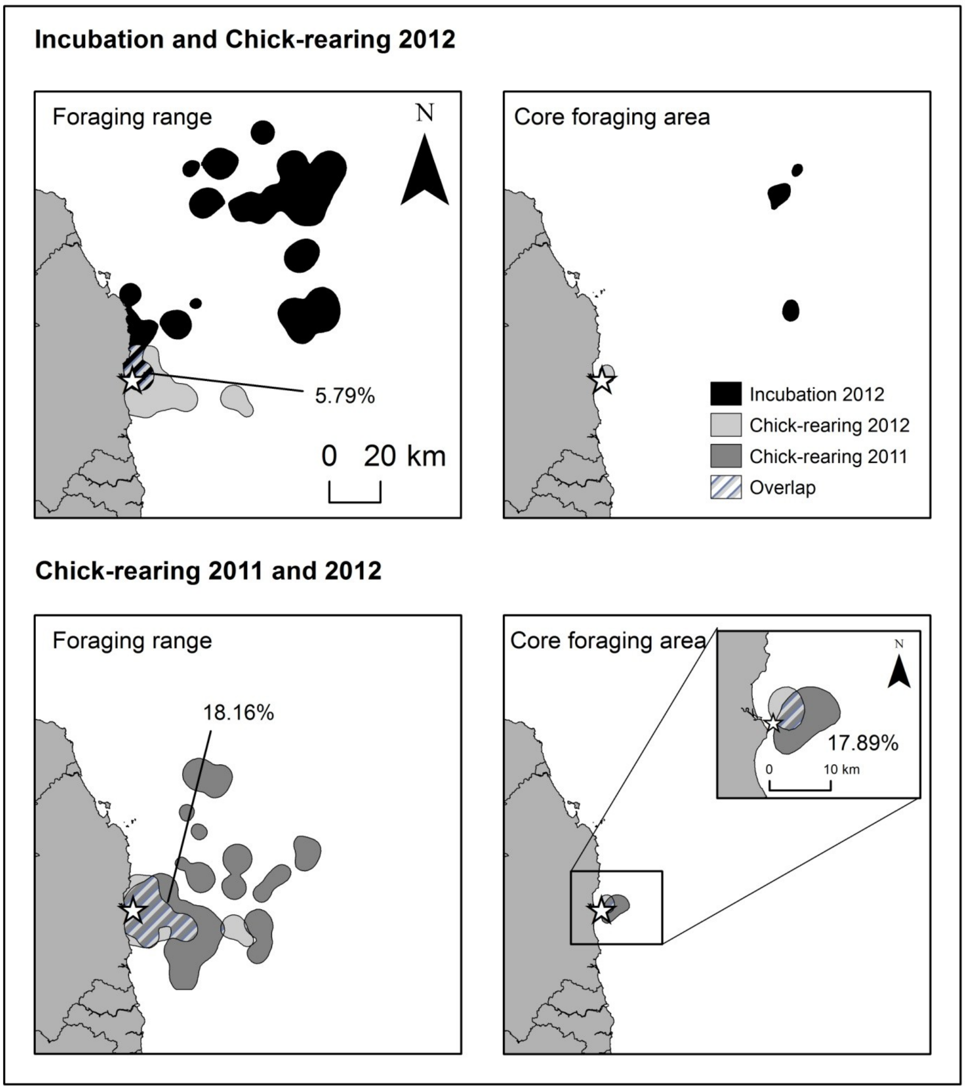

Figure 6. 3 Percentage overlap between foraging ranges (95% contour) and core foraging areas (25% contour) during incubation and chick-rearing in 2012 and during chick-rearing in 2011 and 2012 calculated using a smoothing parameter of 2.5 km and a grid size of 1 km^2. Coquet Island is represented by a star

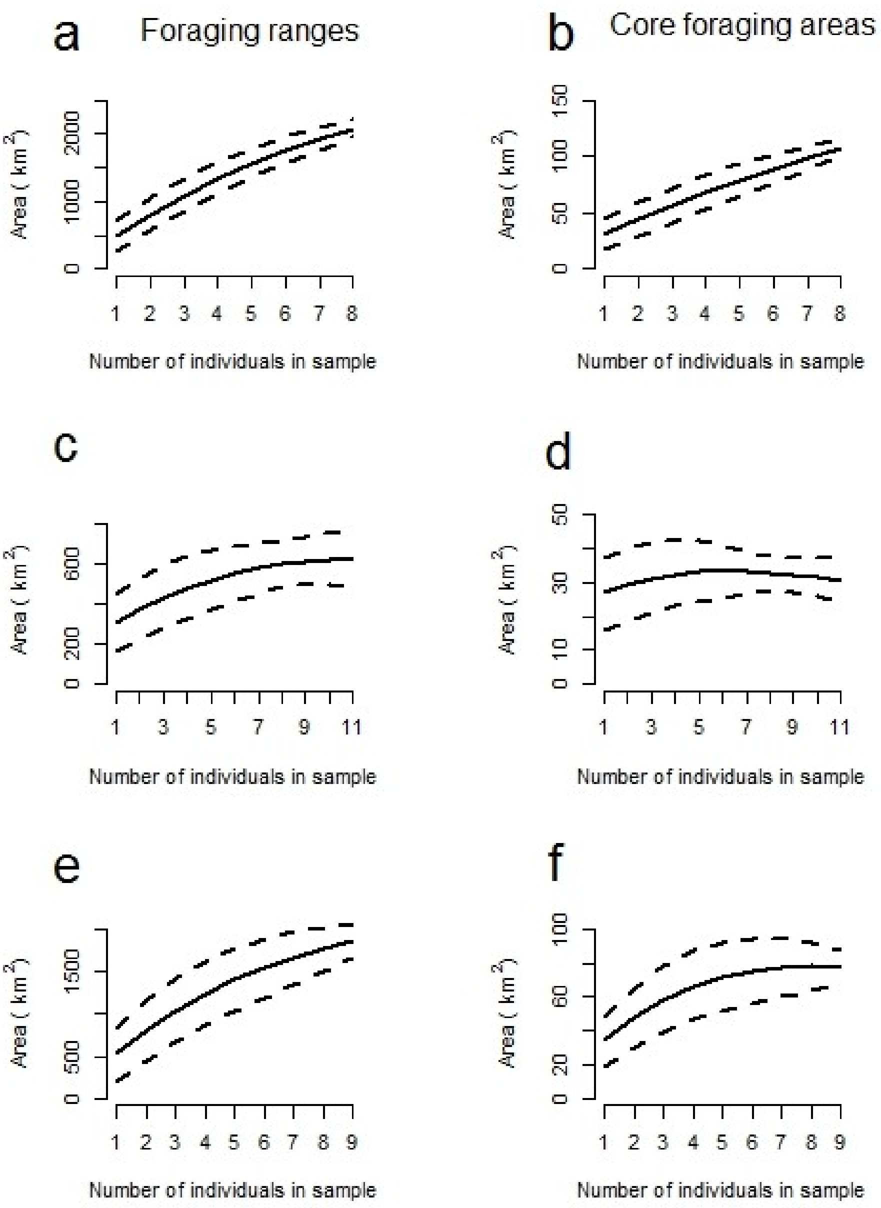

Figure 6. 4 Comparisons of total area (km^2) covered by foraging ranges and core foraging areas estimated using random samples of 1 – 8 individuals (incubation 2012), 1 – 11 individuals (chick-rearing 2012) and 1 – 9 individuals (chick-rearing 2011) for incubation (**a**, **b**), chick-rearing 2012 (**c**, **d**) and chick-rearing 2011 (**e**, **f**). Curved lines were fitted using a loess spline where $\alpha = 1.0$. Standard deviations are represented by dashed lines

6.4.2 Prey Type and Adult Body Condition

A total of 17 regurgitate samples containing 288 vertebrae were collected over the 2012 breeding season (Incubation: adults $n = 8$, vertebrae = 187; Chick-rearing: adults $n = 3$, chicks $n = 6$, vertebrae = 101). In 2012, 94.1% ($n = 16$) of samples contained only sandeel (*Ammodytes* spp) vertebrae; the remaining sample from an adult during incubation contained vertebrae from sprat (*Sprattus sprattus*). Regurgitates collected during incubation in 2012 contained larger fish than those collected during chick-rearing in the same year (Incubation: 165.14 ± 16.70 mm, Chick-rearing: 60.78 ± 43.04 mm; LMM (with sample ID as a random factor): $\chi^2_1 = 10.31$, $p = 0.001$, $n = 288$). Productivity of the whole colony (number of chicks fledged / nest) was slightly higher in 2011 than in 2012 (1.5 and 1.2 respectively from a range of 0.4 – 2.0 on Coquet Island from 1991 – 2012 (RSPB unpubl. data.)). This inter-annual difference did not coincide with variation in body condition. No significant difference in adult body condition index was found between birds foraging during chick-rearing 2012 and 2011 (1.15 ± 0.03 g mm^{-1} and 1.15 ± 0.02 g mm^{-1} respectively; $t_{27.01} = 0.02$, $p = 0.98$, $n = 30$). The body condition index of birds foraging during incubation was significantly higher than that of birds foraging during chick-rearing in 2012 (1.26 ± 0.02 g mm^{-1} and 1.15 ± 0.03 g mm^{-1} respectively; $t_{28.80} = -3.34$, $p = 0.002$, $n = 32$).

6.4.3 Environmental Determinants of Foraging Areas

We used binomial GLMMs with presence/absence data from foraging locations (presence) and randomly selected non-foraging points from a buffer around the colony (absence) to examine how foraging range changed at different stages of the breeding cycle and to identify environmental correlates of foraging locations. Birds foraged further from the colony during incubation than during chick-rearing in 2012 ($\chi^2_1 = 41.51$, $p<0.001$, $n = 220$; Table 6. 2) and while there were some similarities in environmental parameters associated with foraging locations between breeding stages, some environmental parameters associated with foraging locations differed. During incubation, individuals foraged in areas of high chlorophyll *a* concentration, low SST and in areas where chlorophyll *a* concentration had been low the previous winter and in the previous month (Table 6. 3), while during chick-rearing in 2012 individuals foraged in areas of low SST ($\chi^2_1 = 102.98$, $p<0.001$, $n = 120$) and winter chlorophyll *a* concentration ($\chi^2_1 = 5.08$, $p = 0.02$). Birds foraged further from the colony during chick-rearing in 2011 than in 2012 ($\chi^2_1 = 19.56$, $p<0.001$, $n = 220$; Table 6. 4). We found no effect of date on foraging range during the chick-rearing period in 2012 ($\chi^2_1 = 1.04$, $p = 0.31$, $n = 120$) or between chick-rearing in 2011 and 2012 ($\chi^2_1 = 0.89$, $p = 0.34$, $n = 220$). Environmental conditions associated with foraging locations were not consistent between years. During chick-rearing in 2012 birds foraged in areas of low SST (Estimate ± SE = -5.59 ± 0.93, z-value = 5.98, $p<0.001$) and winter chlorophyll *a* concentration (Estimate ± SE = -0.92 ± 0.42, z-value = 2.19, p = 0.03), while during chick-rearing in 2011 foraging locations may have been associated with low SST (Table 6. 5), areas of higher winter chlorophyll *a* concentration ($\chi^2_1 = 19.63$,

$p<0.001$, $n = 100$) and areas of shallow water (Table 6. 5). However, as there was a significant interaction between SST and bathymetry ($\chi^2_1 = 18.24$, $p<0.001$; Table 6. 5) explaining probability of foraging during chick-rearing in 2011, the relationship between foraging locations and SST varied depending on water depth, and the influence of SST alone on foraging location is not clear. Correlated explanatory variables were excluded from models: bathymetry, SST lag 1 and chlorophyll *a* concentration lag 1 from the chick-rearing 2012 model and SST lag 1 from the chick-rearing 2011 model. This is unlikely to have caused the inconsistency in environmental variables observed between breeding stages and years, as including these variables gave qualitatively similar model results. However, we emphasise here that testing for reliance on specific environmental variables using different models does not definitively prove that there is a difference in environmental variables associated with foraging over time.

Table 6. 2 Output from minimum adequate binomial GLMM with a logit link function fitted using restricted maximum likelihood (REML) examining whether birds foraged further from the colony during incubation than during chick-rearing in 2012. Random factor = Bird ID. $n = 210$. ROC curve showed the model to fit the data satisfactorily (AUC = 0.88)

	Estimate ± SE	***z*-value**	***p*-value**
Intercept	4.17 ± 0.85	4.93	<0.001
Distance from colony	-0.13 ± 0.03	5.02	<0.001
Stage:			
Chick-rearing	0	-	-
Incubation	-3.08 ± 0.98	3.13	0.002
Distance from colony x Stage:			
Chick-rearing	0	-	-
Incubation	0.11 ± 0.03	4.29	<0.001

Table 6. 3 Output from minimum adequate binomial GLMM with a logit link function fitted using restricted maximum likelihood (REML) examining environmental variables associated with foraging locations during incubation 2012. Random factor = Bird ID. *n* = 90. ROC curve showed the model to fit the data satisfactorily (AUC = 0.84)

	Estimate ± SE	***z*-value**	***p*-value**
Intercept	19.81 ± 7.16	2.77	0.006
SST lag 0	-2.11 ± 0.78	2.72	0.006
Chlorophyll *a* conc lag 0	0.54 ± 0.17	3.13	<0.002
Chlorophyll *a* conc winter	-0.84 ± 0.42	2.01	0.04
Chlorophyll *a* conc lag 1	-0.46 ± 0.24	1.94	0.05

Table 6. 4 Output from minimum adequate binomial GLMM with a logit link function fitted using restricted maximum likelihood (REML) examining whether birds foraged further from the colony during chick-rearing in 2011 than during chick-rearing in 2012. Random factor = Bird ID. *n* = 220. ROC curve showed the model to fit the data satisfactorily (AUC = 0.91)

	Estimate ± SE	***z*-value**	***p*-value**
Intercept	1.86 ± 0.48	3.86	<0.001
Distance from colony	-0.05 ± 0.01	4.37	<0.001
Year:			
Chick-rearing 2011	0	-	-
Chick-rearing 2012	2.10 ± 0.89	2.37	0.02
Distance from colony x Year:			
Chick-rearing 2011	0	-	-
Chick-rearing 2012	-0.10 ± 0.03	3.64	<0.001

Table 6. 5 Output from minimum adequate binomial GLMM with a logit link function fitted using restricted maximum likelihood (REML) examining environmental variables associated with foraging locations during chick-rearing in 2011. Random factor = Bird ID. *n* = 100. ROC curve showed the model to fit the data satisfactorily (AUC = 0.85)

	Estimate ± SE	***z*-value**	***p*-value**
Intercept	144.09 ± 32.92	4.38	<0.001
SST lag 0	-14.49 ± 3.26	3.26	<0.001
Chlorophyll *a* conc winter	1.16 ± 0.32	3.66	<0.001
Bathymetry	2.05 ± 0.50	4.13	<0.001
SST lag 0 x Bathymetry	-0.20 ± 0.05	4.18	<0.001

6.5 Discussion

To protect at-sea foraging areas over an appropriate time scale, temporal changes in foraging behaviour must be considered if important areas are to be fully captured. Previous studies have identified foraging areas used by a range of seabird species including Kittiwakes from tracking data collected during only one breeding stage (examples from recent studies include Kotzerka et al. 2010, Stauss et al. 2012, Chivers et al. 2013, Edwards et al. 2013) or year (e.g. Weimerskirch et al. 2005, Votier et al. 2010). However, there are some studies which have tracked birds from the same colony in multiple years and breeding stages (Anderson et al. 2003, Guilford et al. 2008, Louzao et al. 2009), although such studies are relatively rare. Using tracking data over restricted time periods to recommend suitable locations for long term MPAs is likely to result in seabird foraging areas being underrepresented. Our findings show that foraging areas can change significantly within the breeding season and between years and that environmental variables associated with foraging locations also change over time.

The Kittiwake colony on Coquet Island comprised 215 breeding pairs in 2012, which is typical of a smaller colony in the UK where the median colony size is 301 pairs (data from http://jncc.defra.gov.uk/page-4460 and RSPB unpub. data. 2012). Intra-specific competition for food may regulate seabird foraging behaviour (Hunt et al. 1986, Lewis et al. 2001b, Grémillet et al. 2004), with individuals breeding in smaller colonies having shorter foraging ranges than those from large colonies. Whilst such relationships have not been demonstrated for Kittiwakes in the UK, it is possible that birds from larger colonies range more widely than the birds tracked here. The effect of breeding stage on foraging range of Kittiwakes nesting in larger colonies is unknown, although one study has examined inter-annual variation in foraging range at larger colonies than that on Coquet Island (Chivers et al. 2012b). Chivers et al. (2012b) examined foraging behaviour of Kittiwakes breeding at two UK and Irish colonies (Rathlin Island and Lambay Island) using GPS loggers. Trip parameters such as foraging range, distance travelled and trip duration increased significantly in 2010 for birds breeding at Rathlin Island. The authors postulated that birds increased their foraging effort to compensate for reduced food availability close to the colony in 2010. A corresponding decline in breeding success was observed for Kittiwakes on Rathlin Island during this year.

Foraging areas exhibited very little overlap between breeding stages. Important foraging areas were situated further to the north of the colony during incubation while birds foraged close to the colony during chick-rearing in 2012, to the west and south. During incubation, birds made longer foraging trips further from the colony presumably to areas with more predictable resources compared with during chick-rearing when birds made shorter trips to areas closer to the colony. Studies on a variety of different species have found a similar effect with birds foraging further from the colony during incubation than during chick-rearing (Cairns 1988 (Common Murres *Uria aalge*); Weimerskirch et al. 1993 (Wandering Albatross *Diomedea exulans*); Jouventin et al. 1994 (King Penguins *Aptenodytes patagonicus*)). Chicks require regular food provisioning shortly after hatching (Weimerskirch et al. 1993, Suryan et al. 2002) and chick demand for food may explain the reduction in trip length we observed during early chick-rearing compared with the incubation period, when adults were less restricted (Weimerskirch et al. 1993, Ojowski et al. 2001). Although studies have shown that adults respond to changing chick demands by varying diet and foraging areas (Williams and Rothery 1990, Robertson et al. 2014a), these changes may also be facilitated by changes in food availability over time (Uttley et al. 1994, Myksvoll et al. 2013).

More foraging trips contained overnight components during incubation than during chick-rearing in 2012. Birds may have been less restricted to foraging close to the colony during incubation than during chick-rearing (Weimerskirch et al. 1993, Ojowski et al. 2001) which may have allowed them to undertake longer trips, requiring overnight resting periods, to exploit distant foraging areas.

While there were some similarities in environmental variables explaining variation in foraging locations between breeding stages, our results suggest that the importance of specific environmental variables linked to foraging change throughout the breeding season. During incubation birds foraged in areas of higher chlorophyll *a* concentration, while during chick-rearing in 2012 chlorophyll *a* concentration had no effect on foraging location and birds foraged in areas of lower SST and where chlorophyll *a* concentration had been low the previous winter. Sandeel have been shown to aggregate in areas of high chlorophyll *a* concentration (Eliasen et al. 2011) and lower SST has been correlated with increased sandeel recruitment and growth (Arnott and Ruxton 2002, Frederiksen et al. 2004a, 2011).

North Sea Kittiwakes feed almost exclusively on sandeel during the breeding season (Harris and Wanless 1997, Lewis et al. 2001a, Coulson 2011) but change their feeding habits according to breeding stage. During incubation in May, adults concentrate on older sandeel (1+ year group) to feed themselves and switch to juvenile sandeel (0 year group) to feed both themselves and their chicks during the chick-rearing period in June and July (Wright 1996, Harris and Wanless 1997, Lewis et al. 2001a). Kittiwake breeding success has been shown to correlate with abundance of both 0 group and 1+ group sandeel in the North Sea (Harris and Wanless 1990, 1997, Rindorf et al. 2000) which suggests that both these age classes are necessary for successful reproduction. We found significantly larger (and therefore older) sandeel in adult regurgitates during incubation in May 2012 and smaller sandeel in both adult and chick regurgitates during chick-rearing in June 2012. Juvenile sandeel are readily available in surface waters in June while older sandeel start to move deeper into the water column at this time (Rindorf et al. 2000), hence temporal changes in diet may reflect variation in abundance of different sandeel age classes (Montevecchi and Myers 1996, Coulson 2011).

While birds travelled further from the colony during incubation, the size corrected mass of birds tracked at this breeding stage was higher than that of birds tracked during chick-rearing in 2012. Previous studies have shown that adult body mass declines during chick-rearing as birds must work harder to supply both themselves and their chicks with enough food (Weimerskirch 1990, Tveraa et al. 1998a, Lormée et al. 2003). Adults can compensate for weight loss during chick-rearing by accumulating fat reserves during incubation and initially feed on large energy-rich prey before switching to smaller prey items to feed chicks (Kitaysky et al. 1999). Birds in our study may have targeted large prey items to accumulate fat reserves prior to chicks hatching when they had to increase their energy expenditure, although it has been suggested that weight loss during chick-rearing is a deliberate strategy by adults to improve flight efficiency (Croll et al. 1991).

Environmental variables such as SST and chlorophyll *a* concentration can change significantly over the course of the breeding season (Pingree 1975, Sharples et al. 2001, Hyrenbach et al. 2002, Peck et al. 2004). Such changes have the potential to affect the distribution and abundance of sandeel of different age classes. Zero group sandeel are smaller than older age classes and are therefore more vulnerable to predation and cannibalism (Arnott and Ruxton 2002). They also have higher metabolic rates and are differentially affected by physical features such as ocean currents, upwellings and temperature (Hayward 1997, Hollowed et al. 2001). Sandeel in the North Sea mainly prey on *Calanus* species, the abundance and distribution of which also depends on oceanographic conditions (Mackas et al. 2001). Prey preference and habitat selection vary among fish of different age classes (Werner and Gilliam 1984), hence 0 group sandeel may utilise different feeding areas to 1+ group sandeel. As Kittiwakes in our study exploited sandeels of different age classes between breeding stages, variation in habitat preference (e.g. sediment size) among sandeel age classes may explain differences in environmental variables associated with Kittiwake foraging locations we observed during incubation and chick-rearing (Wright et al. 2000, Holland et al. 2005).

We show that foraging areas of birds breeding at the same colony can change significantly during chick-rearing in two consecutive years confirming the results of previous studies (Wanless et al. 1991, Suryan et al. 2000, Chivers et al. 2012a). A study comparing Kittiwake foraging behaviour in years of varying food availability showed that trip length and duration increased in years of low food availability resulting in decreased breeding success (Chivers et al. 2012a). Both foraging range and core foraging area were larger during chick-rearing in 2011 than in 2012 and birds were more likely to forage further from the colony during chick-rearing in 2011. This was despite tracking being carried out over a longer period in 2012, which might have been expected to result in more variable foraging areas. On the contrary, foraging areas used in 2012 were smaller than those used in 2011 despite the longer tracking period, and the greater variation in brood age among individuals tracked in 2012, emphasising the importance of areas close to the colony during chick-rearing in 2012. While there was limited overlap in foraging areas between years, over half of the chick-rearing 2012 foraging range and core foraging area were found within those of chick-rearing 2011. Hence, although birds foraged further from the colony in 2011, birds in both years shared some important foraging areas. Time of day trips were carried out affected duration and maximum foraging range during chick-rearing in both years. However, the percentage of trips which took place at night was similar during chick-rearing in 2011 and 2012 (29.0% and 22.0% respectively) hence this is unlikely to explain inter-annual variation in trip parameters.

While tracking dates did not overlap between the two years (birds were tracked from 14 – 17 June 2011 and from 17 June – 3 July 2012), we found no effect of date on the distance birds foraged from the colony between years. Therefore, the difference in foraging range between chick-rearing in 2011 and 2012 is very unlikely to result from seasonal effects. Our analysis shows that birds foraged in areas associated with different environmental variables during chick-rearing in consecutive years. In 2012 birds foraged in areas of lower SST and areas where winter chlorophyll *a* concentrations had been low. While SST and winter chlorophyll *a* concentrations were also significant in 2011, birds were found to forage in areas of deeper water and winter chlorophyll *a* concentration was shown to have the opposite effect on probability of foraging than during chick-rearing in 2012. These changes may reflect differences in oceanographic conditions between years affecting prey abundance and distribution. In 2012, conditions close to the colony appear to have supported a high abundance of small sandeel, while models and kernel density plots suggest that prey was distributed in patches of productive areas further from the colony in 2011. Productivity of the whole colony was relatively high in 2011 and 2012 suggesting that adequate prey was available in both years (Chivers et al. 2012a). Size corrected mass measurements taken from adults during chick-rearing in both years suggest that adult condition was similar during chick-rearing in 2011 and 2012. Hence, while prey distribution may have differed between the two years, there is no evidence to suggest that low food availability affected foraging locations of birds in 2011. Previous studies have shown that foraging behaviour of species breeding at the same colony varies between years (Watanuki et al. 1993, Monaghan et al. 1994, Chivers et al. 2012b) making it necessary to undertake tracking studies over several years of differing food availability to identify useful foraging areas.

While this study suggests that foraging parameters can change significantly even within a single breeding season and between consecutive years, other studies on various species have shown that foraging locations used by individuals can remain consistent throughout the breeding season and also between years (Kittiwakes (Irons 1998), Imperial Shags *Phalacrocorax atriceps* (Harris et al. 2014) and Northern Gannets (Patrick et al. 2014)). Such behavoiour suggests that oceanographic conditions and prey availability in areas surrounding the breeding colony remain relatively stable during the breeding season and over several years. However, some seabird prey species are highly mobile and can be difficult to locate in the environment. Seabirds sometimes rely on information transferred among individuals at gathering places, allowing birds to locate unpredictable foraging patches (Weimerskirch et al. 2010, Machovsky-Capuska et al. 2013). Our study shows that birds travelled further from the colony during incubation than duing chick-rearing in 2012. However, a recent study by Ponchon et al. (2014) found that Kittiwakes breeding at a colony in the southern Barents Sea did the opposite; birds travelled further during early chick-rearing than during incubation. The authors also noted a dramatic decline in the proportion of successful breeding pairs in early chick-rearing, which was related to an increase in foraging range and trip duration. This change in foraging and reproductive behaviour was thought to be related to a decrease in prey availability during early chick-rearing. These results emphasise the difficulty in disentangling the effects of changes in reproductive demands at different stages of the breeding cycle with intra-seasonal variation in food availability. Without local data on fish abundance, we cannot disregard the possibility that the change in foraging behaviour at different breeding stages we observed in our study was caused by coincidental variation in prey availability.

Area saturation curves showed that number of individuals included in kernel density estimations affected the estimated size of foraging areas. As curves for foraging ranges and core foraging areas reached asymptote for chick-rearing 2012, this suggests that an adequate number of birds were tracked to accurately represent foraging areas for the whole colony during this breeding stage. However, foraging ranges during incubation 2012 and chick-rearing 2011 did not reach asymptote hence differences in extent of foraging areas used by the whole colony between breeding stages and years may have been even larger area than estimated by this study (Soanes et al. 2013). We recognise that while our study suggests that foraging areas can differ significantly throughout the breeding season and in different years, data were collected for a very limited period during each stage and year. Considerably more data are needed before definitive differences in foraging areas and association with specific environmental conditions at different stages of the breeding season and in different years may be determined. Therefore our results must be treated with caution when applied over longer time periods.

The protection of foraging areas to enhance the prey resources on which seabirds depend for successful reproduction would be expected to result in higher levels of breeding productivity. Previous studies have attempted to estimate probable seabird foraging areas using correlations between known foraging locations and associated oceanographic features (Huettmann and Diamond 2001, Nur et al. 2011, Grecian et al. 2012, Lascelles et al. 2012). Prey aggregations for seabirds occur where oceanographic features combine to enhance phytoplankton abundance and hence zooplankton and fish availability, or where currents force prey species to aggregate (Hunt et al. 1999). Features such as chlorophyll *a* concentration and SST vary spatially and temporally (Hunt et al. 1999, Hyrenbach et al. 2000) affecting the location of potential foraging areas. Our study shows how oceanographic features associated with foraging areas vary throughout the breeding season and between years. This has significant implications for the designation of potential MPAs based on habitat suitability as the usefulness of specific areas for foraging will change over time. To designate useful long-term MPAs for seabirds, temporal changes in foraging areas and variation in preference for oceanographic features must be considered. The UK Government is a signatory to international agreements including the EU Birds Directive, Convention on Biological Diversity and the OSPAR Convention whose aims include establishing a network of MPAs and Special Protection Areas (SPAs) incorporating foraging areas used by seabirds, seaducks, waders and divers (Stroud et al. 2001, www.jncc.gov.uk/page-4549). This network is unlikely to adequately represent a significant proportion of seabird foraging areas, as areas useful for foraging are highly variable. The development of dynamic MPAs which vary depending on breeding stage and the location of optimal foraging habitat would complement current proposed sites (Game et al. 2009).

It is becoming increasingly apparent that protection of seabird foraging areas is necessary to prevent population declines brought about by a decrease in food availability. Examining foraging behaviour throughout the breeding season and in more than one year, results in the identification of larger potential foraging areas than by examining foraging behaviour only during a single breeding stage or year. Our study emphasises the importance of carrying out seabird tracking and examining associated environmental variables during extended time periods when attempting to identify sites for designation as MPAs for seabirds.

Chapter 7

Parental priorities vary with increasing brood age in Black-legged Kittiwakes; second-hatched chicks come to the fore

7.1 Abstract

In species with asynchronously hatching young, parents usually allocate resources to older chicks at the expense of younger chicks. While resource allocation between parents and offspring has been examined, few studies have considered how intra-brood parental resource allocation varies throughout the developmental period. We examine how parental investment and intra-brood resource allocation change with increasing brood age, and how differential allocation of feeds affects chick growth rate and fledging success in Black-legged Kittiwakes (*Rissa tridactyla*). Kittiwake nests were observed during chick-rearing at a North Sea colony. Contrary to our expectations, we found no difference in growth or feeding rates between chicks of different hatching order. However, while the growth rate of first-hatched chicks was not related to how frequently they were fed by parents, our results suggest that for second-hatched chicks there was a significant negative relationship between growth and feeding rate. Both overall parental investment and intra-brood resource allocation varied according to brood age. Feeding rate per brood per hour and nest attendance decreased nonlinearly as brood age increased. First-hatched chicks were more frequently fed at the beginning of multiple feed bouts and received a higher proportion of feeds delivered to broods during early chick-rearing. This pattern of prioritising the feeding of first-hatched chicks did not persist into the later phases of chick-rearing; second-hatched chicks then received proportionally more feeds and chicks of different hatching order were fed at the beginning of multiple feeds equally often. These results illustrate how parental resource allocation can change throughout the developmental period and may explain similarities in growth rate and fledging success between chicks of different hatching order.

7.2 Introduction

Iteroparous individuals balance limited resources among offspring during a reproductive event (Royle et al. 2002, Royle et al. 2004). The amount of parental resources allocated to offspring can vary depending on number of offspring (Rogowitz and McClure 1995, Rogowitz 1996), parental condition (Tveraa et al. 1998b) and resource availability (Braun and Hunt 1983, Erikstad et al. 1998). While it was originally thought that parents control the amount of food allocated to each offspring, recent empirical studies have suggested that resource allocation can be influenced by offspring through sibling competition and begging stategies (Kacelnik et al. 1995, Krebs and Magrath 2000, Royle et al. 2002, Royle et al. 2004). However, it is still unclear which of these mechanisms influence how resources are allocated to each offspring throughout chick-rearing. Allocation decisions may be expected to vary throughout the developmental period as offspring demand and foraging conditions change (Tveraa et al. 1998b, Granadeiro et al. 2000).

Theoretical models predict that parents should invest more resources in offspring with the greatest need, usually the smallest (Godfray 1995). While some studies have shown that older offspring tend to solicit food from parents more frequently than younger chicks (Drummond 2002, Royle et al. 2002), others have reported that parents consistently feed larger offspring more often than their smaller siblings, even when not signalling the greatest need (Price and Ydenberg 1995, Price et al. 1996). In bird species with asynchronously hatching young, parents preferentially allocate resources to older, larger chicks, which are of higher value to parents than younger offspring that are less likely to survive to fledging (Parker et al. 2002). First-hatched chicks in asynchronous broods are generally larger than second-hatched chicks and are fed at a higher rate (Braun and Hunt 1983, Price and Ydenberg 1995). As feeding rate is generally positively correlated with growth rate (Braun and Hunt 1983, Donazar and Ceballos 1989), older chicks may be expected to have higher growth rates and therefore be more likely to survive to fledging than younger chicks (Hahn 1981, Kersten and Brenninkmeijer 1995).

It is difficult to predict how parental resource allocation will vary with offspring age. Increasing reproductive value of offspring over time should favour an increase in parental investment, while changes in the benefit of parental care to offspring survival and the requirement of parents to replenish their own depleted resources are likely to favour a reduction (Sargent and Gross 1986, Redondo and Carranza 1989, Pugesek 1990). Studies on birds have shown that parents match feeding rates to increasing chick energy requirements over time (Ricklefs et al. 1985, Bertram et al. 1991). The energy demands of chicks peak at period of maximum growth (Ricklefs and White 1981) hence chicks generally require more food during maximum growth and less as they approach fledging age (Cairns 1987, Emms and Verbeek 1991, Roby 1991). Adults usually decrease the amount of energy delivered to chicks prior to fledging (Cairns 1987, Emms and Verbeek 1991), either to match declining energy demands of chicks or as a strategy to induce fledging (Emms and Verbeek 1991, Roby 1991). Hence, parental investment may be expected to vary throughout the chick developmental period as energetic demands of offspring change.

As timing of maximum growth and peak energy demand vary among offspring of different hatching order (Drent and Daan 1980, Mock and Schwagmeyer 1990) and as reproductive value of offspring increases with age (Redondo and Carranza 1989), parents may be expected to increase the proportion of resources allocated to younger chicks in a brood later in the developmental period (Kloskowski 2001, Shizuka and Lyon 2009). It has been previously shown that greater cooperation among siblings can be expected later in development as energy demands decline (O'Connor 1978, Kloskowski 2001). While resource allocation between parents and offspring and among offspring have been examined in several species (Ricklefs 1987, Jodice et al. 2002, Royle et al. 2002), fewer studies have examined how food distribution varies among offspring throughout the developmental period and how this affects reproductive success (but see Seddon and van Heezik 1991, Kloskowski 2001, Shizuka and Lyon 2009).

We investigate intra-brood parental resource allocation in broods of two Black-legged Kittiwake (*Rissa tridactyla* hereafter 'Kittiwake') chicks on Coquet Island, northeast England. We expect: 1) first-hatched chicks to be fed more frequently and have higher growth rates and fledging success than second-hatched chicks, 2) parental investment to increase until chicks reach maximum growth and decrease as they approach fledging age and 3) the proportion of resources allocated to first and second-hatched chicks to become more equal as brood age increases. We discuss how our results contribute to the understanding of parental resource allocation in species with asynchronously hatching offspring.

7.3 Methods

7.3.1 Study Species

Kittiwakes are a suitable species in which to examine parental resource allocation as they are easy to observe on breeding cliffs and, provided due care is taken, allow close approach without disturbance having an effect on breeding success (Sandvik and Barrett 2001, Brewer et al. 2008). Each nest is a separate structure from which chicks generally do not stray until a few days prior to fledging allowing observations of individual broods to be made (Galbraith 1983). Feeding rate and trip duration can be deduced for large numbers of nests through colony observations. Mean and mode trip duration is relatively short for Kittiwakes foraging during chick-rearing (mean ± SE = 2.87 ± 0.53 h and mode = 1.17 h for 13 birds tracked on Coquet Island during mid chick-rearing in 2012; Robertson et al. 2014b) compared to other offshore foraging seabirds such as Northern Fulmars *Fulmaris glacialis* (median = 6 h at a colony on Foula in 1981; Furness and Todd 1984) and Northern Gannets *Morus bassanus* (mean ± SE = 31.3 ± 2.67 h at a colony on Bass Rock in 1999; Hamer et al. 2001). Hence, numerous nest deliveries can be recorded during a few hours of observation. Mean trip duration of birds in this study was estimated as 1.08 ± 0.06 h, perhaps due to prey availability close to the breeding colony in June – July. This was smaller than the mean trip duration calculated from birds tracked using GPS devices in the same year on Coquet (Robertson et al. 2014b) and may be a consequence of the larger sample size or greater extent of the data collection period utilised during this study (30 nests were observed continually for 28 days compared with 13 birds tracked for 16 days during the previous study on Coquet).

Kittiwake broods vary in size from 1 – 3 chicks (Coulson 2011), depending on parental body condition, breeding experience and food availability (Coulson and White 1961, Coulson and Porter 1985, Jacobsen et al. 1995). In our study, the majority of pairs had broods of two, hence broods of three and single broods (either from single clutches or from broods which lost chicks during the study period) were excluded from analyses (a total of 9 nests). Chicks (usually first-hatched) close to fledging would occasionally leave the nest during observations towards the end of the developmental period, leaving a single chick (usually second-hatched) in the nest. Occasions where one chick left the nest during an observation period occurred in 16% of nests. As A chicks tend to leave the nest before B chicks, this could cause an apparent increase the proportion of feeds allocated to B chicks later in the chick-rearing period. Therefore, while these chicks invariably returned before subsequent observations, occasions when one chick was left at the nest were excluded from analyses.

7.3.2 Nest Observations

The study took place on Coquet Island, northeast England (55º 20' N, 1º 32' W) during chick-rearing from June – July 2012. To produce an adequate sample size for analyses, 30 study nests were selected from an area close to the centre of the Kittiwake colony by assigning a unique number to each nest and using a random number generator (R version 3.0.1) to randomly select nests. The position of nests within Kittiwake colonies has been shown to affect reproductive success and survival (Coulson and Thomas 1985, Aebischer and Coulson 1990). Hence, nests positioned at the edge of the colony, and those which were difficult to reach for the purpose of marking chicks, were excluded from the selection process. Study nests had a mean clutch size of 2.2 ± 0.1 (n = 30). Study nests were checked every 2 – 3 days allowing the hatching date of each chick to be recorded. First-hatched (A) chicks hatched ~0.9 ± 0.2 (mean ± SE) days before second-hatched (B) chicks, and were 10.36 ± 4.77 g heavier than second-hatched chicks when broods were weighed 2 – 4 days after hatching at the beginning of the study period. Approximately 2 – 4 days after hatching, A chicks in each nest were marked (under a permit issued by the British Trust for Ornithology (BTO)) using a small amount of water-soluble nontoxic Tippex® on the tip of the beak which was clearly visible from the ground using binoculars (8 x 10 magnification). As the position and size of the Tippex® mark was similar to the fecal spots which regularly appeared on both chicks in a brood, we did not expect the marking of A chicks to influence parental provisioning behaviour. Tippex® has been used successfully to mark chicks in previous studies (Cook 2000, Skórka et al. 2012) and had no observable effect on chick behaviour or survival in this study (GS Robertson pers. obs.). B chicks were differentiated from A chicks both by size, B chicks always being visibly smaller than A chicks, and by Tippex® marks. As chicks were weighed as close to hatching as possible, it is unlikely that incidences of asymmetry reversals among broods were missed. Kittiwake chicks solicit food from parents by begging (defined as frequent vertical movements of the head accompanied by vocalisations; Kitaysky et al. 2001). We were unable to collect solicitation behaviour data in this study due to difficulties in effectively recording begging of each chick in 30 nests simultaneously.

Observations of study nests took place from a portable hide to minimise disturbance to breeding birds. The hide was positioned ~10 – 15 m from the base of cliffs (maximum distance at which chicks could be conclusively identified) during observations from 17 June – 17 July 2012. Hatching dates were relatively synchronous (6 – 13 June) hence chicks were of similar ages when observations began (4 – 10 days old). Three-hour watches included every time period from 0400 – 2100 h for each tidal state (low, high, rising, falling). For each nest, we recorded time of arrival of an adult with food, time of departure of either adult, whether or not an adult was attending the nest when its partner returned with food, which chick was fed during feeding bouts, how many times an adult regurgitated food to each chick and the order in which chicks were fed during multiple feed bouts. A feed was defined as an occasion during which an adult regurgitated food to a chick. A feeding bout was defined as a period during which either attending adults or those returning to the nest from a foraging trip delivered food on one or more occasions to at least one chick in a brood.

Trip duration was quantified by recording the time of adult departure and return to the nest during each observation period. Although adults were not marked, trip duration prior to food delivery could be deduced on occasions when an adult was recorded leaving the nest and returning to feed at least one chick while the second member of the pair continuously attended the nest. Trip duration could not be deduced on occasions when both adults were absent from the nest simultaneously. Mean trip duration calculated from GPS-tracked birds at the same colony was <3 h (Robertson et al. 2014b) which suggests that three hour observation periods can be used to record whole foraging trips.

7.3.3 Data Analyses

Adults began feeding chicks within 15 minutes of returning to the nest which was also the maximum time period for which an adult was observed continually feeding chicks during a feeding bout (GS Robertson pers.obs.). Hence, separate feeding bouts were regarded as those where chick feeds occurred >15 minutes apart. Feeding bouts which began close to the end of the observation period may not have been completed before the observation period ended; hence feeding bouts which began within 15 minutes of the end of the observation period were excluded from analyses. A total of 686 feeding bouts were observed from 30 nests over a total of 135 h of observations.

Kittiwakes deliver meals to chicks by regurgitating food stored in a crop hence adults can make multiple regurgitations while feeding chicks (Coulson 2011). A multiple feed bout refers to feeding bouts during which an adult regurgitated food more than once to at least one chick within 15 minutes of the first initial feed. The order in which A and B chicks were fed during a multiple feed bout was recorded and the number of times A and B chicks were fed first compared. To compare the number of feeds allocated to A and B chicks during both single and multiple feed bouts, the number of feeds received by the A chick in a brood was expressed as a proportion of the total number of feeds delivered to both chicks. The mass and total energy content of regurgitates could not be determined due to limitations placed on regular chick handling by reserve managers.

Two metrics of feeding rate were calculated, one to examine how number of feeds delivered to each chick per hour differed between chicks of different hatching order and how this affected growth rate (hourly feeding rate per chick, hereafter 'chick feeding rate'), and another to determine how number of feeds delivered to each brood per hour varied with increasing brood age (hourly feeding rate per brood, hereafter 'brood feeding rate'). Chick feeding rate was calculated by dividing the number of times a chick received food from an adult during the linear growth phase by the total number of hours for which that chick was observed. Brood feeding rate was defined as the number of feeds delivered to each brood per hour of observation throughout the developmental period.

In order to limit disturbance to the colony, chick weights were recorded on two occasions during the linear growth phase (Coulson and Porter 1985). Each chick in a study nest was weighed twice to the nearest 0.1 g using electronic scales (SATRUE SA-500), first when chicks were 2 – 8 days old and again when the same chicks were 16 – 20 days old. A and B chicks from the same brood were weighed as close together in time as possible, usually on the same day. Chick growth rate (g day^{-1}) was calculated for each chick using the following equation (Coulson and Porter 1985, Nisbet et al. 1995):

$$Growth\,rate = \frac{(W2 - W1)}{(D2 - D1)}$$

Where: $W1$ = Weight (g) at first measurement (2 < chick age < 8 days old)

$W2$ = Weight (g) at second measurement (16 < chick age < 20 days old)

$D1$ = Date of first measurement

$D2$ = Date of second measurement

Growth rate and chick feeding rate were both calculated during the linear growth phase and are therefore directly comparable. Chick skeletal measurements (such as tarsus and wing length) were not recorded in this study to reduce chick handling time and disturbance to the colony. Previous studies have also calculated chick growth rate using weight measurements recorded during the linear growth phase (Coulson and Porter 1985, Coulson and Thomas 1985). Fledging success (%) was calculated as the percentage of hatched chicks observed leaving the nest at the end of the developmental period (Spahn and Sherry 1999).

Linear mixed models (LMMs) were used to examine differences in growth rate and chick feeding rate between chicks of different hatching order and to examine how much variation in growth rate could be explained by chick feeding rate. Unless otherwise stated LMMs were fitted with normal error distributions and identity link functions, and included nest ID as a random factor. A GLMM with a Poisson error distribution, a log link function and with nest ID as a random factor was used to compare how often A and B chicks were fed first during multiple feed bouts throughout the chick-rearing period. The total number of occasions A and B chicks were fed first was calculated for each brood over the whole study period.

Change in parental investment throughout the chick-rearing period was determined by examining variation in brood feeding rate, trip duration and nest attendance (whether or not study nests were already attended by a parent each time an adult returned to the nest to feed at least one chick) with increasing brood age. Brood age (in days after hatching) was defined as the difference between the date on which an observation was made and date of first hatching within a brood. Brood age was separated into eight five day categories from 0 – 40 days. For each category, mean brood feeding rate ± SE was calculated and plotted against brood age. The percentage of occasions study nests were already attended by a parent when a foraging adult returned with food was calculated for each brood age category in one day intervals from 9 – 40 days old (broods less than nine days old were continually attended by an adult) and were plotted against brood age category. Variation in brood feeding rate and trip duration with increasing brood age was examined using LMMs, while changes in nest attendance with increasing brood age was examined using a generalised linear mixed model (GLMM) with a binomial error distribution. GLMMs used the logit link function and included nest ID as a random factor unless otherwise stated. Date of first hatching was not included in models as this was included within calculations of brood age.

Variation in parental resource allocation among offspring was examined with increasing brood age using a GLMM with a binomial error distribution and a logit link function. The response variable was the hatching order of the chick fed first (A or B) for a given multiple feed bout, where A chick fed was defined as 0 and B chick fed was defined as 1. Changes in the proportion of total feeds delivered to a brood that were received by A chicks during both single and multiple feed bouts were also examined. GLMMs with

Poisson error distributions and log link functions were used to compare the number of times A and B chicks in each nest were fed first during multiple feed bouts in early and late chick-rearing periods. A GLMM with a binomial error distribution was used to determine how much variation in the proportion of feeds received by A chicks was explained by brood age.

For each LMM and GLMM, we first fitted a fully parameterised model using maximum likelihood (ML) and removed terms by sequential deletion while testing for significant changes in model variance using likelihood ratio tests (LRTs) (Crawley 2007). We then refitted the minimum adequate model using restricted maximum likelihood (REML) to estimate effect sizes. Where necessary, brood feeding rate was log-transformed to reduce heteroscedasticity in the residuals and improve the fit of the model. Models were tested for goodness-of-fit using residual plots, receiver operating characteristic (ROC) curves and associated area under the curve (AUC) using the 'ROCR' package in R (Sing et al. 2005). LMMs were fitted using the 'nlme' R package (Pinheiro et al. 2014) and GLMMs using the 'lme4' R package (Bates et al. 2013). Analyses were carried out in R version 3.1.2 (R Core Development team 2014). Means are presented ± SE throughout.

7.4 Results

7.4.1 Effect of Differential Resource Allocation on Growth Rate and Fledging Success

There was no significant difference between chick feeding rates (in feeds h^{-1}) calculated during the linear growth phase for A and B chicks (0.85 ± 0.09 and 0.75 ± 0.08 respectively; LMM: $\chi^2_1 = 2.30$, $p = 0.13$, $n = 42$) and no difference between growth rates (g day^{-1}) of chicks of different hatching order (15.62 ± 0.46 and 15.31 ± 0.52 for A and B chicks respectively; LRT from LMM: $\chi^2_1 = 0.39$, $p = 0.53$, $n = 42$). There was a significant difference in the mean number of occasions chicks of different hatching order were fed first per nest during multiple feed bouts for all brood ages (81.04% of feeding bouts throughout the chick-rearing period contained multiple feeds), with A chicks being fed first significantly more often than B chicks (5.33 ± 0.45 and 3.71 ± 0.36 respectively; GLMM with Poisson error distribution: $\chi^2_1 = 6.12$, $p = 0.01$, $n = 42$).

Table 7. 1 Output from minimum adequate model fitted using restricted maximum likelihood (REML) from LMM with a normal error distribution and identity link function examining the effect of chick feeding rate (feeds h^{-1}) on chick growth rate (g day^{-1}). Random factor = Nest ID. n = 42

	Estimate ± SE	***t*-value**	***p*-value**
Intercept	15.70 ± 1.05	14.94	<0.001
Chick feeding rate	-0.08 ± 1.10	0.08	0.94
Hatching order:			
A chicks	0	-	-
B chicks	2.02 ± 1.18	1.71	0.10
Chick feeding rate x Hatching order:			
A chicks	0	-	-
B chicks	-3.13 ± 1.37	2.28	0.035

A 2-way interaction between chick feeding rate and chick hatching order explained a significant amount of variation in growth rate ($\chi^2_1 = 5.25$, $p = 0.02$, $n = 42$) and for B chicks, growth rate declined with increasing chick feeding rate (Table 7. 1, Figure 7. 1). However, Figure 7. 1 suggests that the significance of this interaction may be influenced by one B chick data point. A Grubbs test (carried out using the 'outliers' package in R version 3.1.2 (Komsta 2014)) showed that this point was significantly different from other values of growth rate for B chicks ($G = 2.79$, $p = 0.02$). When the LMM was repeated excluding this data point no significant interaction between chick feeding rate and hatching order was found ($\chi^2_1 = 1.30$, $p = 0.26$, $n = 41$). However, as there was no obvious biological reason to exclude data collected from the B chick or its brood from the analysis, the data point was retained. Overall fledging success was high (94.92%), and only a slightly higher percentage of A chicks survived to fledge (93.33%) than B chicks (89.65%).

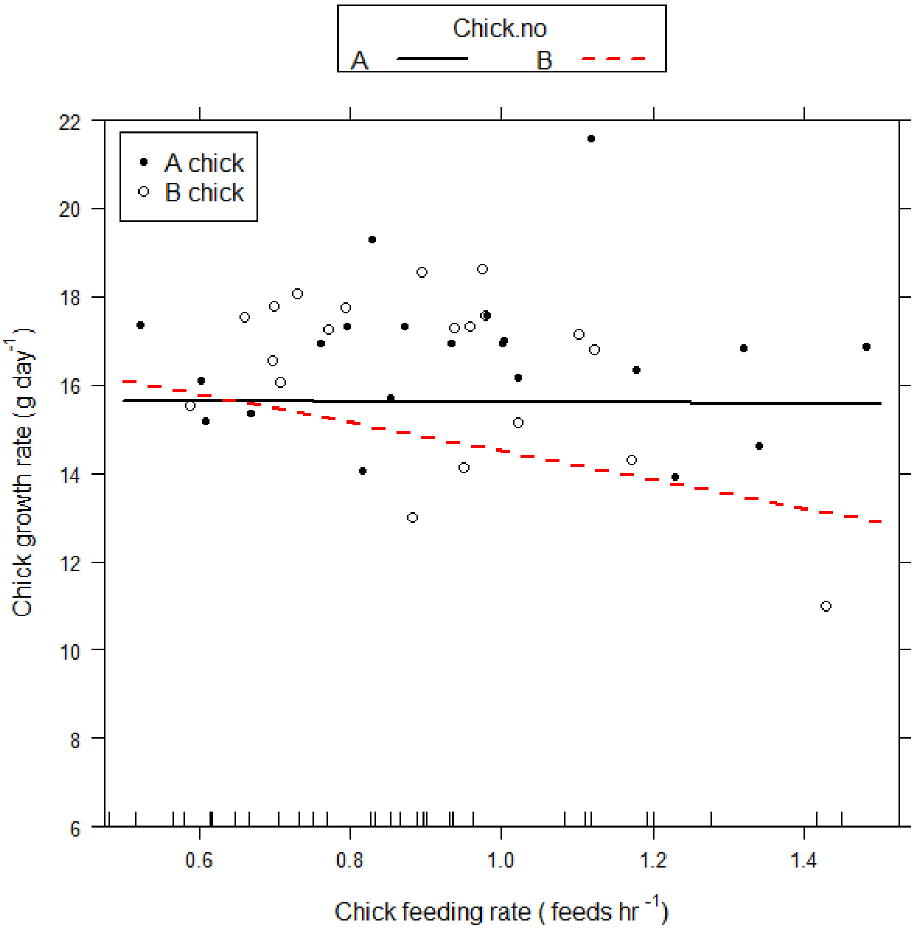

Figure 7. 1 Relationship between chick growth rate (g day^{-1}) and chick feeding rate (feeds h^{-1}) during the linear growth phase for chicks of different hatching order. Straight lines were derived from coefficients of LMMs fitted for chicks of each hatching order

7.4.2 Variation in Parental Investment with Increasing Brood Age

Brood feeding rate appeared to increase slowly with brood age before declining as chicks approached fledging (Figure 7. 2). Due to the apparent quadratic relationship between brood feeding rate and brood age, brood age squared was included in an LMM examining how feeding rate changes with increasing age. Both brood age and brood age squared explained a significant amount of variation in feeding rate (results of LRTs from LMMs: $\chi^2_1 = 29.38$, $p<0.001$, $n = 483$ and $\chi^2_1 = 25.14$, $p<0.001$ respectively), brood age had a positive effect on brood feeding rate and brood age squared a negative effect (Table 7. 2). This confirms that the quadratic relationship between brood feeding rate and brood age was significant and that feeding rate increased with brood age to reach a peak when chicks were ~21 – 25 days old, before decreasing as they approached fledging age (Figure 7. 2).

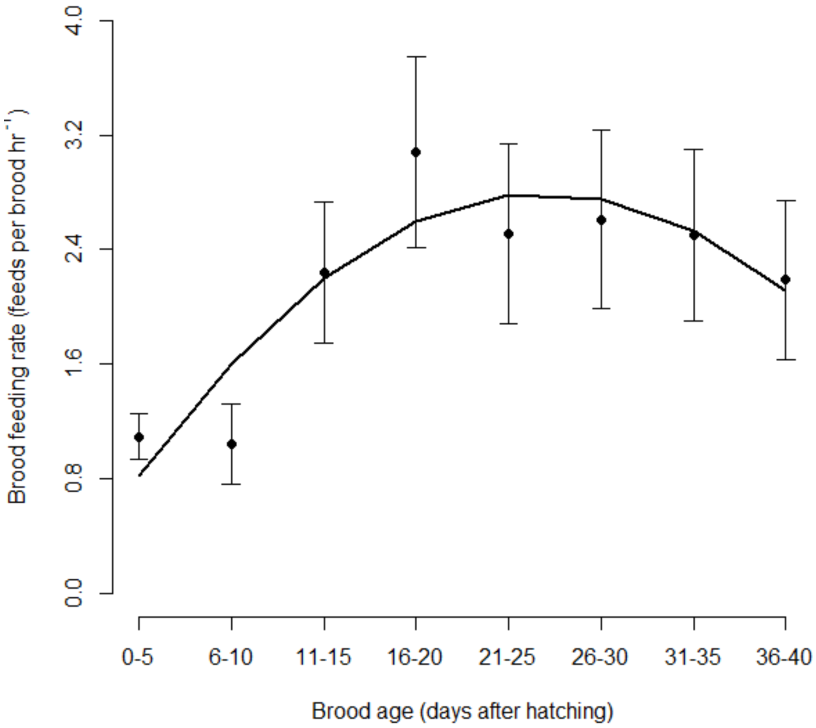

Figure 7. 2 Relationship between mean brood feeding rate (feeds per brood h^{-1}) ± SE and brood age category (days after hatching). Curved line was fitted using a loess-smoothed spline with a second-degree polynomial where span (α) = 1.5. Broods contained two chicks throughout the chick-rearing period

Table 7. 2 Output from minimum adequate model fitted using restricted maximum likelihood (REML) from LMM with a normal error distribution and identity link function examining the effect of increasing brood age on log(brood feeding rate; feeds per brood h^{-1}). Random factor = Nest ID. *n* = 482

	Estimate ± Std error	***t*-value**	***p*-value**
Intercept	-0.73 ± 0.24	3.02	0.003
Brood age	0.13 ± 0.02	5.51	<0.001
Brood age^2	-0.003 ± 0.0005	5.09	<0.001

Nest attendance appeared to vary nonlinearly with increasing brood age, declining as brood age increased (Figure 7. 3). Brood age had a significant negative effect on the probability of a nest being attended by a parent when an adult returned with food and attendance declined as brood age increased ($\chi^2_1 = 275.89$, $p<0.001$, $n = 446$; Estimate ± SE

= -0.33 ± 0.03, *z*-value = -11.21, p<0.001). There was no effect of increasing brood age on trip duration ($\chi^2_1 = 0.06$, $p = 0.81$, $n = 79$).

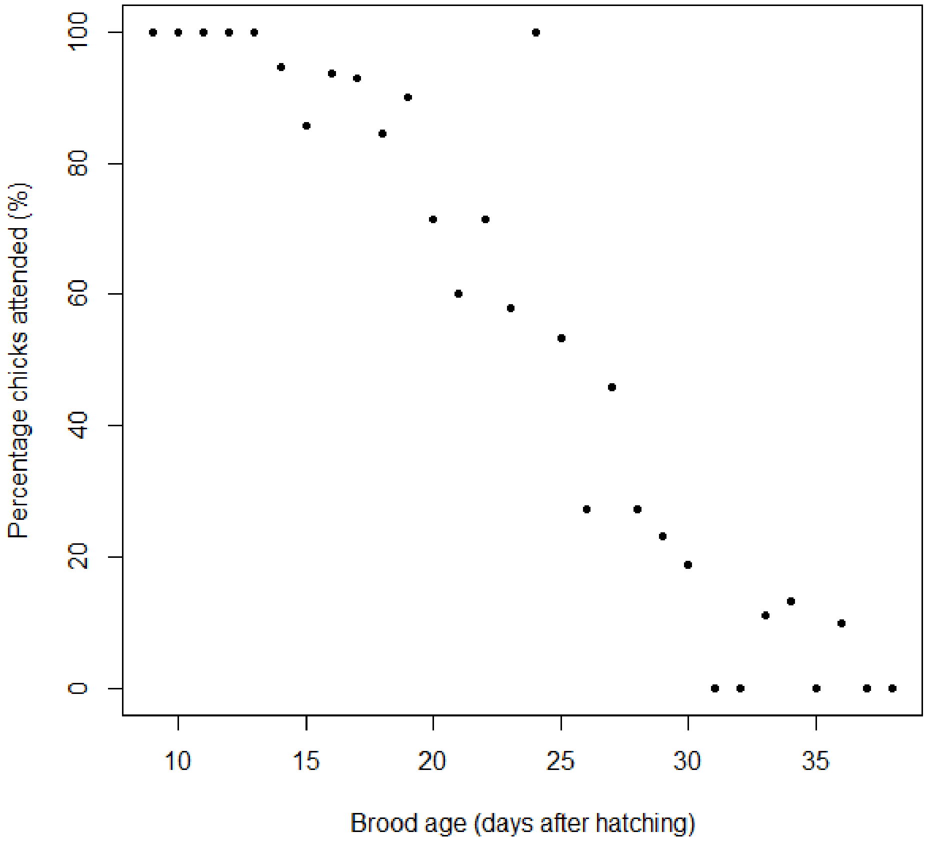

Figure 7. 3 Relationship between percentage of occasions a nest was attended when an adult returned with food and brood age category (days after hatching) for broods aged 9 – 40 days old

7.4.3 Variation in Intra-brood Resource Allocation with Increasing Brood Age

Variation in the likelihood of second-hatched chicks being fed first during multiple feed bouts with increasing brood age was examined using a GLMM. The likelihood of second-hatched chicks being fed first during multiple feed bouts was found to increase significantly with brood age ($\chi^2_1 = 5.02$, $p = 0.03$, $n = 190$; Estimate ± SE = 0.05 ± 0.02, *z*-value = 2.20, $p = 0.03$). Figure 7.4 illustrates the difference in the number of occasions where A and B chicks were fed first during early chick-rearing (4 < brood age < 20 days old) and late chick-rearing (20 < brood age < 35 days old).

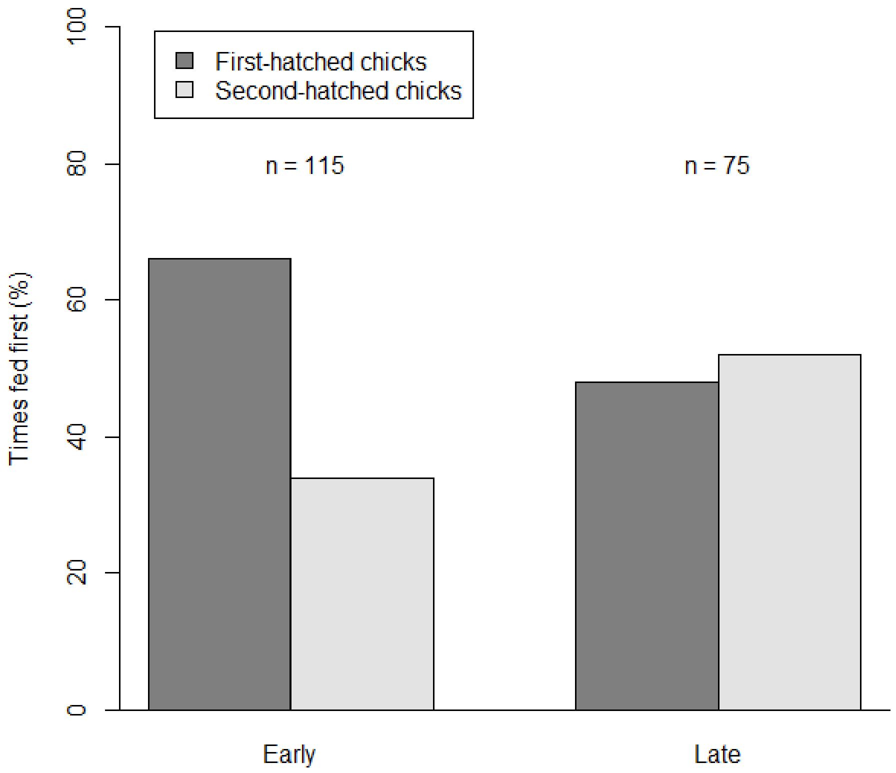

Figure 7. 4 Barplot showing the percentage of occasions first-hatched and second-hatched chicks were fed first during multiple feed bouts during early (4 < brood age < 20 days old) and late (20 < brood age < 35 days old) chick-rearing. Few data were available on which chick was fed first for brood ages > 35 days old as size differences between chicks were less clear

There appeared to be slight increase in the proportion of feeds received by A chicks out of the total number of feeds delivered to chicks when broods were >10 days old, however this proportion began to decline when brood were >30 days old (
Figure 7. 5). A GLMM showed that the proportion of times A chicks were fed in comparison with B chicks decreased with increasing brood age (χ^2_1 =6.44, p = 0.01, n = 446; Estimate ± SE = -0.02 ± 0.006, z-value = 2.54, p = 0.01).

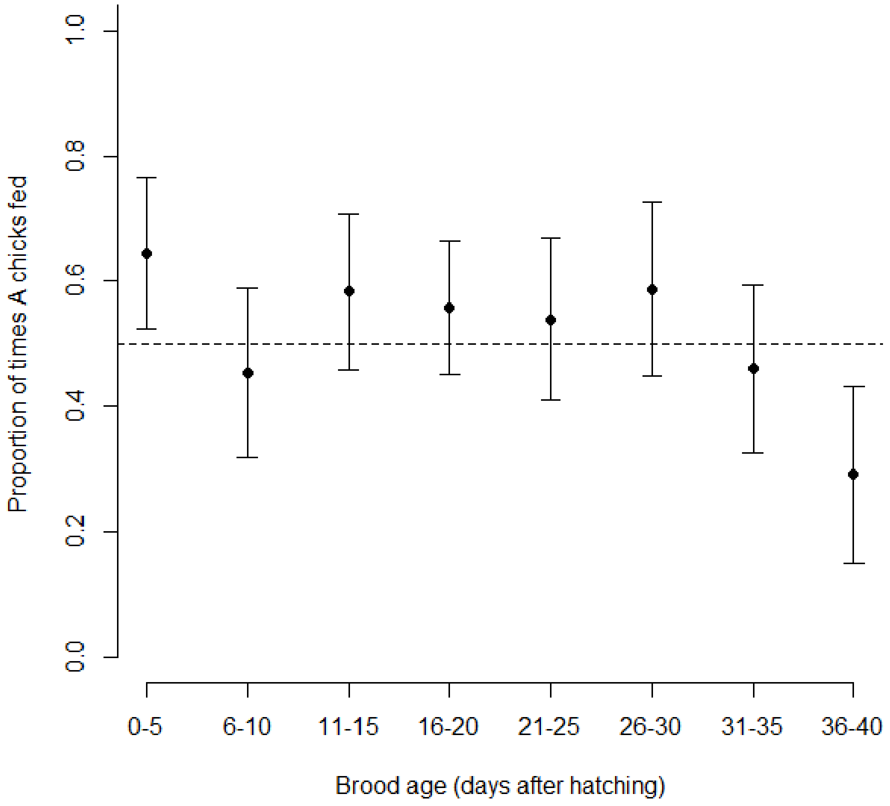

Figure 7. 5 Mean proportion of feeds received by A chicks out of the total number of feeds delivered to broods ± SE with increasing brood age category (days after hatching). A horizontal line at y = 0.5 emphasises departure from equivalent feeds between chicks

7.5 Discussion

Previous studies have shown that older offspring tend to receive food from parents more often than younger offspring, regardless of individual requirements (Price and Ydenberg 1995, Price et al. 1996). This is especially apparent in bird species with asynchronously hatching young, where older, larger chicks are fed more frequently and are more likely to survive to fledging than younger chicks (Braun and Hunt 1983, Parker et al. 2002). However, parental investment may be expected to vary throughout the breeding season as energetic demands of offspring change. Our study shows how parental investment and allocation of resources between offspring in broods of two varies throughout the chick-rearing period.

Asynchronous hatching has been observed in many different bird species, including Kittiwakes (Braun and Hunt 1983, Magrath 1990, Stenning 1996). It was suggested that asynchronous hatching is a deliberate strategy to induce brood reduction during periods of food shortage by producing a competitive hierarchy within broods (Lack 1947, 1954, Ricklefs 1965). However, experimental evidence suggests that asynchronous hatching could be a consequence of external drivers such as predation risk, temperature control and embryo viability, which facilitate the need for immediate incubation and introduce brood hierarchy (Clark and Wilson 1981, Stenning 1996, Hillström et al. 2000, Gilby et al. 2011, Aldredge et al. 2014). The effect of brood hierarchy on the allocation of resources to chicks has been examined in several species (Ricklefs 1987, Jodice et al. 2002, Royle et al. 2002); however few studies have compared food distribution among offspring throughout the developmental period (but see Seddon and van Heezik 1991, Kloskowski 2001, Shizuka and Lyon 2009). Our study examined differences in feeding rates, growth rates and fledging success among chicks of different hatching order and determined whether parental provisioning behaviour and intra-brood resource allocation varied over time.

While previous studies have shown that first-hatched Kittiwake chicks in a brood tend to receive food from parents significantly more frequently than younger offspring (Braun and Hunt 1983), we found no significant difference in the feeding rates or growth rates of A and B chicks during the linear growth phase. This is contrary to what we initially expected, as studies have shown that parents usually allocate resources to older, larger chicks (Parker et al. 2002), which facilitates variation in growth rates between chicks of different hatching order (Barrett and Runde 1980, Braun and Hunt 1983, Coulson 2011).

Competition for food can result in brood reduction in asynchronously hatching species, either directly due to older chicks attacking and sometimes killing younger chicks, or from unequal food distribution (Mock and Parker 1997, White et al. 2010). Although physical contact between Kittiwake chicks is unusual, its incidence increases during periods of low food availability (White et al. 2010). No incidence of physical conflict between siblings was observed in our study perhaps because adequate food was available for both chicks in a brood.

Field research suggests that the benefit of hatching asynchrony and brood reduction varies depending on environmental conditions and resource availability (Stenning 1996, Hillström et al. 2000). Although there were no available data on prey abundance around Coquet Island in the year of our study, productivity of the whole colony was generally high (number of chicks fledged per nest = 1.2 (taken from a random sample of 30 nests); Productivity range on Coquet Island 1991 – 2011 = 0.4 – 2.0 (www.jncc.defra.gov.uk/page-4460)) when compared with other colonies and years (productivity = 0.02 – 0.97 chicks per nest on the Isle of May, southeast Scotland; Lewis et al. 2001a; mean productivity 1986 – 2004 for colonies in east England = 1.02 chicks per nest; Frederiksen et al. 2007a). Trip duration of birds in our study was short which suggests that prey availability was adequate close to the colony (Monaghan et al. 1994, Croxall et al. 1999). Also, fledging success of both first and second-hatched chicks was high, indicative of a good feeding environment (Cairns 1988). Good feeding conditions in the area surrounding the colony in 2012 may also explain similarity in feeding frequencies between chicks of different hatching orders, as adults are more likely to be able to deliver adequate food to both chicks in a brood when prey availability is good.

Although we found growth rate during the linear growth phase to be comparable for chicks of different hatching order, there was a significant negative relationship between growth rate and chick feeding rate for B chicks, while no relationship was evident for A chicks. Hence, B chicks with high feeding rates appeared to have significantly lower growth rates than A chicks fed at the same rate. This is contrary to the results of previous studies which show that feeding rate and growth rate are positively correlated in seabird chicks (Huin et al. 2000, Roby et al. 2000). However, other studies have suggested that the size and energy content of regurgitates fed to chicks varies depending on hatching order, and that younger chicks receive less energy per regurgitate than older chicks (Galbraith 1983, Golet et al. 2000).

Mass and energy content of prey can explain more variation in seabird chick growth rate and pre-fledging survival than feeding frequency (Weimerskirch et al. 1997, Golet et al. 2000, Wanless et al. 2005b). Birds are able to vary the proportion of their stomach contents regurgitated to each chick (Meyer et al. 1997) and are able to gauge a chick's nutritional status by its solicitation behaviour (Phillips and Croxall 2003). While we were unable to regularly collect regurgitate samples from chicks due to imposed limits to colony disturbance on Coquet Island, we speculate that variation in regurgitate content may explain why B chicks with high feeding rates had significantly lower growth rates than A chicks fed at the same rate. B chicks may have received frequent small regurgitations of lower energy content than A chicks, which received larger, higher quality meals. Although the relationship between chick feeding rate and growth rate was significant for B chicks, the effect was not strong due to large amounts of variation in chick feeding rates and growth rates.

Parental resource allocation may be expected to vary throughout the developmental period in response to changing offspring energy requirements and environmental conditions (Ricklefs et al. 1985, Emms and Verbeek 1991, Low et al. 2012). While increasing reproductive value of offspring with age should favour an increase in parental investment, changes in the benefit of parental care and the requirement of parents to replenish depleted resources later in the breeding season may favour a reduction (Sargent and Gross 1986, Redondo and Carranza 1989, Pugesek 1990). In our study both brood feeding rate and nest attendance changed nonlinearly with increasing brood age. Brood feeding rate increased until chicks were 21 – 25 days old, before declining as chicks approached fledging age at ~40 – 43 days old (Maunder and Threlfall 1972, Coulson 2011).

The seasonal deterioration hypothesis (Bertram et al. 1991) states that declines in feeding rates in the latter stages of chick-rearing are caused by a seasonal decline in food abundance around the breeding colony (Burger 1980). While brood feeding rates in our study declined after chicks reached a certain age, there was no change in trip duration with increasing brood age. This suggests that food availability in surrounding waters remained adequate throughout the chick-rearing period as parents showed no increase in foraging effort later in the breeding season (Abrams 1991, Petersen et al. 2006). Hence, this hypothesis is not likely to explain the changes in feeding rate we observed. An alternative hypothesis suggests that a decline in feeding rates later in the breeding season reflects decreasing energy demands of nestlings. Studies on various seabirds have shown that chick energy budgets peak in the middle of the developmental period and fall as chicks approach fledging age (Simons and Whittow 1984, Cairns 1987, Coulson 2011). Kittiwake chick growth rate increases linearly until chicks are ~20 days old (Coulson and Porter 1985) after which growth rate decreases. Chicks require less food after the period of maximum growth which is reflected by a decline in energy demand (Coulson and Porter 1985, Cairns 1987).

Some studies have suggested that both chick energy demand and changing environmental conditions affect seabird foraging behaviour during the breeding season. Environmental conditions influence prey availability with important effects on foraging and reproductive success for Kittiwakes and other seabirds (Hamer et al. 1993, Harding et al. 2007). It is thought that prey availability is linked nonlinearly to reproductive success (Cairns 1988) such that beyond a given threshold it has no effect on feeding rate and breeding success (Burger and Piatt 1990, Phillips et al. 1996). Hence, when food availability is good, Kittiwake parents are able to adjust foraging effort to chick energy demand (Suryan et al. 2002). This was likely to have been the case in the year of our study, as productivity and trip duration suggest that food abundance was good.

Seabird nest attendance has been related to temporal changes in food availability and chick demand (Gaston and Nettleship 1982, Coulson and Johnson 1993). The probability of one Kittiwake parent attending a nest when an adult returned with food declined as brood age increased in our study; the probability of a nest being attended was

~50% when broods were 25 days old. Previous studies have also shown Kittiwake nest attendance to decline throughout the chick-rearing period (Coulson and Johnson 1993, Cadiou and Monnat 1996) although the age at which chicks are first left alone at the nest varies among individuals (Coulson and Johnson 1993) and is dependent on annual food availability (Hamer et al. 1993). Seabird chicks require less brooding as they get older (Barrett 1978) and energy demand declines after the period of maximum growth (Cairns 1987). Seabird chicks also tend to be larger and less vulnerable to predatory attacks later in the breeding season (Andersson 1976, Davies and McCaffrey 1986). Hence, adults are able to decrease time spent at the nest and increase self-maintenance activities such as replenishing depleted body reserves, and to prospect for future nest sites (Boulinier et al. 1996, Cadiou and Monnat 1996, Weimerskirch et al. 2001).

The order in which chicks received food from parents varied between chicks of different hatching order. A chicks were fed at the beginning of multiple feed bouts significantly more often than B chicks in each brood. This confirms results of previous studies on several species which showed that older chicks were fed first following an adult’s return to the nest more frequently than younger chicks, regardless of begging intensity (Price and Ydenberg 1995, van Heezik and Seddon 1996). Being larger, older chicks are able to stretch higher (Teather 1992), gape wider and are better able to position themselves at the edge of the nest, closer to the approaching adult than younger chicks (McRae 1993, Kacelnik et al. 1995). In these ways, older chicks are better equipped to obtain food from adults before younger chicks, although adults have been shown to be capable to some extent of manipulating the quantity and quality of food each chick receives per delivery (Hudson 1979, Weimerskirch et al. 1997). A previous study has suggested that the first few feeds delivered to seabird chicks by a returning adult are larger and therefore contain more energy than subsequent feeds (Anderson and Ricklefs 1992). Hence, by receiving the first feed in a multiple feed bout more frequently than B chicks, A chicks may be expected to obtain more energy and sustain higher growth rates (Golet et al. 2000, Romano et al. 2006). However, in our study no variation in feeding or growth rates was found between chicks of different hatching order.

When considering data collected during different chick-rearing stages, A chicks were fed first significantly more often than B chicks during early chick-rearing, but there was no difference in the order in which A and B chicks were predominantly fed during late chick-rearing. As timing of peak growth differs between seabird chicks in asynchronous broods (Braun and Hunt 1983, Moreno et al. 1994), B chicks might be expected to be smaller and lighter than A chicks prior to reaching peak mass, and therefore be less competitive. During this period, younger chicks consistently adopt a submissive posture when confronted by older siblings and are more likely to lose competitive interactions (Galbraith 1983, Drummond and Osorno 1992). As intra-brood variation in weight declines as seabird chicks approach fledging age (Williams and Croxall 1991), competitive abilities of younger chicks should more closely match those of their older siblings later in the developmental period. Change in intra-brood resource allocation could explain the similarities in growth rates observed between chicks of different hatching order.

Our results show that initially, A chicks received a higher proportion of feeds delivered to broods during early chick-rearing, but this proportion declined steadily as brood age increased, resulting in a higher proportion of B chicks receiving feeds later in the chick-rearing period. It is unclear whether this change in intra-brood resource allocation is the result of an increase in competitive abilities of younger chicks later in the developmental period, whether younger chicks' demand for food surpasses that of older chicks after peak growth, or whether parents allocate a higher proportion of resources to younger chicks as their reproductive value increases (Kacelnik et al. 1995, Parker et al. 2002). Whichever mechanism is responsible, variation in intra-brood resource allocation may explain similarities in overall chick feeding rates, growth rates and pre-fledging survival of A and B chicks. As mortality of larid chicks is highest in the first week of life (Langham 1972, Bollinger et al. 1990), changes in resource allocation later in the chick-rearing period are only likely to positively influence fledging success of younger chicks if conditions allow them to survive this long. Likelihood of younger Kittiwake chicks surviving to late chick-rearing decreases in years of poor food availability, when sibling competition for food causes mortality rates of younger offspring to increase prior to reaching peak growth rate (Braun and Hunt 1983, Wanless and Harris 1992). Our results may have been influenced by A chicks leaving the nest for short periods of time during observations which were carried out towards the end of the study period. A chicks, being older, were more likely to leave the nest than B chicks. This meant that the B chicks was left in the nest alone on some occasions and was able to fully exploit deliveries made by parents. Although we were careful to exclude occasions when one chick was absent from the nest, it is possible that some occasions were missed which may partially explain the increase in proportion of feeds received by B chicks later in the chick-rearing period. Previous studies have suggested that the presence of artificial marks can affect parent-offspring and offspring-offspring interactions (Calvo and Furness 1992). Hence, consistently applying Tippex® marks to the first-hatched chick in each brood may also have influenced our results.

While A chicks received feeds at the beginning of multiple feed bouts more frequently than B chicks and received a greater proportion of feeds delivered to broods during early chick-rearing, this pattern of allocation did not persist into the latter stages of the developmental period when parental resource allocation switched to favouring younger chicks. Our study provides evidence of changing parental intra-brood resource allocation within the chick development period, which may explain similarities in growth and survival between chicks of different hatching order. Only by considering resource allocation throughout the developmental period can we gain a more complete understanding of differential parental investment in asynchronous broods and its effect on offspring survival. We recommend that the mass and energy content of regurgitates fed to chicks in asynchronously hatching broods be examined throughout the developmental period to determine the influence of regurgitate content on parental resource allocation and chick growth rate and survival.

Chapter 8

General Discussion

Changing environmental conditions are known to affect the population dynamics of most organisms in marine and terrestrial habitats. However, some species are easier to study and more sensitive to changes than others, and as such can provide useful indicators of ecosystem health over different spatial scales. Studying seabird foraging and breeding behaviour contributes to our understanding of how marine ecosystems change over time (Cairns 1988, Monaghan 1996, Lewis et al. 2006). In recent years the miniaturisation of electronic devices and the development of novel tracking methods have allowed seabird species to be tracked to and from foraging areas and for environmental conditions in distant pelagic areas to be sampled. This thesis investigated temporal changes in foraging behaviour and demographic parameters of terns and Kittiwakes breeding sympatrically at a North Sea colony, and examined how interspecific differences in foraging behaviour influences reproductive parameters. Long-term population abundance and productivity data in conjunction with colony-based and offshore observational data were used to examine how seabird populations reflect changes in the marine ecosystem. The implications of the results can now be discussed in the context of predicting and understanding changes in the marine environment and in developing marine conservation policy.

8.1 Seabirds as Indicators of the Marine Environment

Environmental changes and ecological disturbances, due to both natural phenomena and anthropogenic effects, can significantly influence population dynamics of marine organisms. There is a need to develop reliable indicators of the ecological state of the marine environment in order to track changes in biodiversity and maintain essential ecosystem services (Rice and Rochet 2005, Worm et al. 2006). Numerous long-term studies examining the response of organisms to changes in marine ecosystems have been carried out for species at different trophic levels (Reid and Croxall 2001, Beaugrand et al. 2002, Perry et al. 2005). While species at lower trophic levels have been identified as more responsive to environmental change than those at upper trophic levels (Perry et al. 2005, Walther 2010), data can be more difficult and more costly to obtain for species at lower trophic levels, such as forage fish, than more visible species such as marine predators (Edgar et al. 2004, Agnew et al. 2009). Fishery catch statistics and transect sampling for phytoplankton and zooplankton can be used to estimate abundance of lower trophic level species (Durbin and Durbin 1981, Bannerot and Austin 1983, Rozas and Minello 1997), but these methods can be labour intensive, expensive and logistically challenging (Cairns 1992b, Rice and Rochet 2005, Agnew et al. 2009, Einoder 2009).

The selection of informative biological indicators can be difficult due to the complexity of marine trophic interactions (Cairns 1988), and current uncertainty regarding relationships between physical and biological components of the marine environment (Freon et al. 2005). Selection of appropriate indicator species can also be dependent on the feasibility and accuracy with which demographic parameters can be measured. Seabirds and other marine predators have been shown to be useful biological indicators of the health of marine ecosystems and can be used to assess a range of information about the environment (Diamond and Devlin 2003, Piatt et al. 2007). Marine predators tend to forage over large areas, locate prey quickly and efficiently and sample prey at multiple trophic levels. They are sensitive to changes in food abundance and distribution, are highly visible in the environment, are relatively easy to study and are charismatic species with a high public profile (Cairns 1988, Montevecchi 1993, Sydeman et al. 2006). Seabirds tend to be more useful indicators of environmental change than marine mammals, which are more difficult to observe and census (Zacharias and Roff 2001). Seabird-based data are cheaper and easier to collect than other measures of prey abundance and ecosystem status such as fishery data, and seabird populations can be used to estimate fish abundance in areas where fishery data are unavailable (Cairns 1988, Cairns 1992b, Monaghan 1996).

There are various examples illustrating direct associations between seabird demographics and changes in oceanographic conditions and anthropogenic activities. Cyclical changes in oceanic temperatures in the Pacific Ocean are known to strongly influence seabird populations over wide areas, by affecting primary production and the abundance of prey species (Hodder and Graybill 1985, Ainley et al. 1988, Chavez et al. 2003). Seabird productivity has been shown to vary with temporal changes in sea surface temperatures (Decker et al. 1995, Guinet et al. 1998, Frederiksen et al. 2004a) as well as with local variation in anthropogenic fishing activities (Daunt et al. 2008), both of which affect prey availability. Where long-term seabird monitoring studies coincide with changes in fishing effort they can provide a means of assessing the relative importance of anthropogenic and environmental factors in influencing marine organisms (Frederiksen et al. 2004a, Scott et al. 2006).

Examinations of trends in seabird demographic parameters such as breeding population abundance, productivity and adult mortality can provide an index of prey abundance and distribution, and can identify regime shifts in the marine environment (Cairns 1988, Frederiksen et al. 2007b, Newman et al. 2007, Piatt et al. 2007). However, demographic parameters vary in their sensitivity to changes in food supply (Cairns 1988), and previous studies have suggested that behavioural parameters are more accurate indicators of changes in local prey density and distribution (Monaghan 1996, Harding et al. 2007). Seabird foraging and chick provisioning behaviour have been shown to reflect environmental change, as species vary these behaviours in response to changes in prey availability and foraging conditions during the breeding season (Montevecchi 1993, Monaghan 1996, Kitaysky et al. 2000, Pinaud et al. 2005, Harding et al. 2007).

8.2 Examining Variation in Seabird Foraging Behaviour

Comparing parameters such as foraging range, trip duration and habitat and dietary preference among sympatrically breeding seabirds can address important ecological questions regarding interspecific competition and resource partitioning, and can provide information on the state of the local environment. Interspecific comparisons of dietary and foraging behaviour in sympatric species allow changes in abundance and distribution of different prey types and size classes surrounding the breeding colony to be determined (Croxall and Prince 1980, Diamond and Devlin 2003, González-Solís et al. 2007, Iverson et al. 2007, Montevecchi et al. 2012, Thaxter et al. 2012). Changes in the availability of prey species and size classes at critical stages of the breeding season can be indicative of regime shifts in the surrounding environment and can facilitate reductions in productivity at local seabird colonies (Rindorf et al. 2000, Lewis et al. 2001a).

For many seabird species, data describing foraging behaviour and the use of offshore areas are limited (Lewison et al. 2012). In recent years, novel seabird tracking methods have been developed to identify both foraging areas and oceanographic variables associated with foraging (Weimerskirch et al. 2005, Kotzerka et al. 2010, Perrow et al. 2011, Stauss et al. 2012). However, many previous seabird tracking studies have been temporally restricted or have examined foraging behaviour in only a limited number of species (Mori and Boyd 2004, Lance and Thompson 2005, Votier et al. 2010, Chivers et al. 2013). In Chapter 4 I compared foraging area use, diet and chick provisioning behaviour in three morphologically similar sympatric tern species and showed that species reduce interspecific competition by varying diet, foraging areas or both. I also found that foraging area use and chick provisioning behaviour changed throughout the chick-rearing period in two tern species. Chapter 5 showed that although two sympatrically breeding tern species fed chicks on different prey types and sizes, both delivered comparable amounts of energy to each chick in a brood. Common Terns (*Sterna hirundo*) delivered larger prey items to chicks than Arctic Terns (*S. paradisaea*), but Arctic Terns were able to match energy delivery rates of Common Terns by increasing the frequency at which prey was delivered to each chick. However, Common Terns laid larger clutches and fledged more chicks in total than Arctic Terns. Hence, foraging behaviour of morphologically similar species can differ significantly with important consequences for total reproductive output. Temporal variation in foraging behaviour was examined further in Chapter 6 and 7 by comparing foraging areas utilised by Black-legged Kittiwakes (*Rissa tridactyla*) at different stages of the breeding season and in two consecutive years, and by examining chick provisioning behaviour throughout the developmental period. Diet, foraging areas, oceanographic variables associated with foraging and parental resource allocaton changed throughout the breeding season and between years. These results demonstrate how seabird behavioural data can be used to track temporal changes in the marine environment and in chick demand.

8.3 Problems with using Seabirds as Environmental Indicators

Despite the advantages of using seabird demographic and behavioural data over more conventional methods of sampling the marine environment, such as vessel-based surveys and fishery catch statistics (Bannerot and Austin 1983, Diamond and Devlin 2003), there are uncertainties regarding the extent to which seabird populations indicate change in the local environment (Frederiksen et al. 2007b, Piatt et al. 2007, Parsons et al. 2008). Previous studies have suggested that seabird species vary in their response to changes in food availability depending on their foraging ecology and life history (Montevecchi 1993, Furness and Tasker 2000). Estimating prey abundance and distribution based on seabird population dynamics or behavioural observations depends on species' sensitivity to food reductions and requires a comprehensive understanding of species-specific relationships between demographic or behavioural parameters and food supply.

As seabirds are long-lived, they are likely to reduce reproductive effort in response to declining foraging conditions in order to increase their long-term survival (Stearns 1992, Montevecchi 1993). This is evident in most seabird species, especially those with limited ability to increase foraging effort during periods of low food availability (Monaghan et al. 1989, Furness and Tasker 2000, Kitaysky et al. 2000). Hence, seabirds may be less responsive to environmental variability than short-lived species (Morris et al. 2008, Sandvik and Erikstad 2008) and seabird productivity and behavioural parameters are likely to provide more accurate information on the state of the marine ecosystems than adult mortality data. Some of the problems associated with using seabirds as biological indicators can be mitigated by careful species and parameter selection, which I discuss further below.

8.4 Selecting Appropriate Indicator Species and Parameters

Seabird breeding success, chick growth, colony attendance and activity budgets have been shown to vary with prey availability (Cairns 1988, Monaghan et al. 1989, Montevecchi and Myers 1995, Diamond and Devlin 2003), although changes in these parameters with food supply can occur at different temporal scales (Cairns 1988, Hyrenbach and Veit 2003). Some parameters convey information on daily or monthly food availability, while others reflect feeding conditions over longer temporal scales, over years or decades (Cairns 1992b, Montevecchi 1993, Einoder 2009). Short-term parameters such as foraging and breeding behaviour are useful when examining abundance and age structure of prey populations (Montevecchi 1993), while parameters such as annual population abundance and productivity are useful for gauging the effects of long-term environmental change (Piatt et al. 2007, Crawford et al. 2008).

Selected indicator species must reflect environmental conditions at an appropriate spatial scale, which depends on the extent of foraging activities. Pelagic seabirds which forage over wide areas are likely to be useful indicators of environmental conditions throughout the ocean basin, while coastal seabirds are likely to reflect conditions at a more local scale (Cairns 1988, Montevecchi and Myers 1995).

Dietary preferences and foraging behaviour are known to influence the sensitivity of seabird species to perturbations in food supply and foraging conditions (Furness and Ainley 1984, Furness and Tasker 2000). Generalist feeders are able to switch to different prey types when the abundance of preferred prey declines, whereas species with more restricted diets are less capable of prey switching (Furness and Nettleship 1991, Furness and Tasker 2000). Smaller bodied species also tend to be more sensitive to declines in prey availability due to their more restricted energy budgets (Furness and Camphuysen 1997, Furness and Tasker 2000). Small species already forage close to their maximum rate when food availability is good and are therefore less able to increase their foraging effort during periods of reduced food supply (Monaghan 1992, Piatt et al. 2007). In contrast, larger species are able to buffer breeding parameters when food abundance is low by increasing their foraging effort (Hamer et al. 1993, Uttley et al. 1994, Hamer et al. 2001, Carscadden et al. 2002, Litzow and Piatt 2003). Hence, variation in food availability is better reflected in breeding and behavioural parameters of small bodied specialist species (Hamer et al. 2006). During small to moderate food shortages, the breeding success of sensitive species has been shown to decline significantly, while that of more resistant species remains unaffected (Montevecchi 1993, Furness and Tasker 2000). Hence, when monitoring small-scale changes in food supply, seabird species such as terns and Kittiwakes that are more sensitive to changes in food supply may provide the most accurate information.

Studies have shown that sympatrically breeding surface-feeding and diving seabirds respond in different ways to changes in local prey availability (Monaghan et al. 1992, Monaghan et al. 1996, Carscadden et al. 2002, Enstipp et al. 2006). Hence, only by examining changes in demographic parameters and foraging behaviour among various sympatric seabird species can we gain a more complete understanding of conditions in the local environmental (Carscadden et al. 2002). Chapter 3 and 5 show that even among ecologically similar species with broadly similar diets and foraging behaviour, demographic parameters and reproductive output can vary significantly, which may be due to interspecific variation in diet and foraging behaviour. Chapters 4, 6 and 7 show how foraging behaviour of different species can vary inter-annually and within a single breeding season. Examining variation in demographic parameters and foraging behaviour in a suite of seabird species over extended temporal scales can contribute to a greater understanding of changes in the marine environment than by examining single species over a limited time period.

8.5 Implications and Recommendations for Marine Conservation

Population trends have varied significantly among UK seabird species in recent decades (Mitchell et al. 2004). Threats from declines in food abundance (especially sandeel; *Ammodytes marinus*), human disturbance at breeding colonies and predation have led to declines in abundance and productivity of many species since the 1980s, although some have exhibited greater population changes than others (Mitchell et al. 2004, Mavor et al.

2008). Terns and Kittiwakes have been identified as particularly vulnerable to reductions in prey availability (Furness and Tasker 2000) and have exhibited significant declines in population abundance and productivity in recent years (Mitchell et al. 2004).

Population trends can vary among tern species breeding sympatrically at the same colony. Coquet Island supports breeding populations of four tern species, one of which, the Roseate Tern (*Sterna dougallii*), is among the most endangered seabird species breeding in the UK (Mitchell et al. 2004, Cabot and Nisbet 2013). By comparing diet and foraging behaviour among sympatrically breeding tern species on Coquet, we showed that Roseate Terns consistently foraged in a specific area close to the mainland shore and exhibited less variation in prey selection than other tern species (see Chapter 4). This confirms the results of studies on Roseate Terns in the tropics and the US and may explain the limited abundance of this species throughout its range (Nisbet and Spendelow 1999, Safina et al. 1990, Shealer 1996). No protection is currently given to the foraging areas used by Roseate Terns breeding on Coquet (www.jncc.defra.gov.uk/mczmap), although in light of new data, JNCC are currently making recommendations to the UK Government on the protection of areas identified by tracking work.

While legal protection is afforded to seabird breeding colonies in the UK to mitigate threats from human disturbance and predation (Nettleship 1991, Mitchell et al. 2004), at-sea foraging areas are currently provided with little legal protection. The UK Government is a signatory to international agreements including the EU Birds Directive, Convention on Biological Diversity and the OSPAR Convention whose aims include establishing a network of Marine Protected Areas (MPAs) and Special Protection Areas incorporating foraging areas used by seabirds, as well as other aquatic bird species (Stroud et al. 2001; www.jncc.gov.uk/page-4549). For many species, few data are available on the location of important foraging areas making protection of offshore foraging areas difficult (Lewison et al. 2012).

In recent years, bird-borne GPS devices have been successfully employed to record complete foraging trips to and from foraging grounds and to identify foraging areas of a variety of seabird species (Weimerskirch et al. 2005, Kotzerka et al. 2010, Stauss et al. 2012). Seabird tracking data can be used to accurately identify foraging locations and associated oceanographic variables and inform the designation of useful offshore protected areas (Weimerskirch et al. 2005, Kotzerka et al. 2010, Grecian et al. 2012, Lascelles et al. 2012, Stauss et al. 2012). Previous studies have attempted to estimate probable seabird foraging areas over wider areas using correlations between known foraging locations and associated oceanographic features (Huettmann and Diamond 2001, Nur et al. 2011, Grecian et al. 2012, Lascelles et al. 2012).

There are various limitations to using GPS devices to track seabirds. Sample sizes are usually restricted due to difficulties in fitting and recovering devices (Soanes et al. 2013), there may be adverse effects of fitting devices on bird foraging behaviour and flight efficiency (Wilson et al. 2002, Phillips et al. 2003), monetary cost of devices can be high (Ropert-Coudert and Wilson 2005) and the duration of the tracking periods tend to be limited. Most tracking studies have been carried out over restricted time scales, either during a single breeding season (Kotzerka et al. 2010, Votier et al. 2010) or breeding phase (Stauss et al. 2012, Chivers et al. 2013). Chapter 6 shows that both foraging areas and oceanographic variables associated with foraging locations vary intra- and inter-annually. This has significant implications for the designation of potential MPAs based on habitat suitability as the usefulness of specific areas for foraging are likely to change over time. To designate useful long-term MPAs for seabirds, temporal changes in foraging areas and variation in preference for oceanographic features must be considered. The development of MPAs for seabirds that are dynamic in space and time may account for temporal variation in foraging area utilisation. MPAs with flexible borders that change depending on the stage of the breeding cycle (being larger during incubation) and on annual environmental conditions, such as SST, primary productivity and oceanic stratification, are likely to be more effective at representing important seabird foraging areas than MPAs with intransigent borders. However, this method may not be viable over longer time periods as it does not prevent areas from being overexploited when protection is temporally rescinded. Also, tracking enough individuals in order to accurately determining home range areas of whole colonies can be difficult, due to the cost and effort required (Burger and Shaffer 2008, Soanes et al. 2013).

The development of smaller, more accurate tracking devices and of novel methodologies such as visual tracking is likely to increase the value of seabirds as remote sensors of the marine environment. An extension in the number of individuals, colonies, populations and species included in studies will lead to a corresponding increase in knowledge and understanding of coastal and pelagic environments, with positive implications for the conservation and protection of offshore areas.

8.6 Concluding Remarks

In this thesis it has been shown firstly, that variation in seabird foraging behaviour and demographic parameters can reflect changes in the local environment, such as prey availability and oceanographic conditions. Secondly, that prey selection, foraging areas and chick provisioning behaviour can vary temporally and among morphologically similar sympatrically breeding species. Finally, these results provide evidence that seabird demographic and behavioural data can be used effectively to indicate the state of the marine environment and can inform marine conservation policy designating effectual offshore protected areas for marine predators.

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Appendix

Impacts of climate change on a marine apex predator: sea temperature and stratification within seabird foraging areas influence breeding success and could drive future declines

Matthew J. Carroll[1*], Adam Butler[2], Ellie Owen[3], Steven R. Ewing[4], Tessa Cole[4], Jonathan A. Green[5], Louise M. Soanes[5], John P. Y. Arnould[6], Stephen F. Newton[7], Julia Baer[7,8], Francis Daunt[9], Sarah Wanless[9], Mark A. Newell[9], Gail S. Robertson[10], Roddy A. Mavor[11] & Mark Bolton[1]

Abstract

Species at higher trophic levels are likely to be vulnerable to impacts of climate change acting indirectly, via changes to their supporting food webs. As apex predators in marine ecosystems, seabirds may primarily experience such indirect climate change impacts. Declines in UK black-legged kittiwake (*Rissa tridactyla*) populations have been linked to oceanographic and food web changes possibly associated with climate change, but relationships have often been derived from relatively few colonies and consider only sea surface temperature (SST), meaning that other important oceanographic drivers, and spatial variation in these drivers, may remain undetected. Further, explicit projections of the consequences of climate change for kittiwakes have rarely been made, meaning that the extent of longer-term impacts remains unclear. Here, we use tracking data to estimate foraging areas for eleven kittiwake colonies in the UK and Ireland, thus reducing reliance on single colonies and allowing calculation of colony-specific oceanographic conditions. We then use mixed models to consider how SST, the potential energy anomaly (a metric indicating the strength of density stratification) and the timing of seasonal density stratification influence kittiwake productivity. Models including data from all colonies indicated that higher breeding success was associated with weaker ocean stratification before the breeding season and lower SSTs during the breeding season. Eight colonies with ≥10 years of data were also modelled individually: three showed higher productivity with later stratification, two showed higher productivity with weaker stratification, one showed higher productivity with lower SSTs, and two showed no relationship with any variable, indicating that primary drivers of productivity varied amongst colonies. Finally, fitted models were used to make climate change projections. Results indicated that breeding success could decline by 21–43% between 1961-90 and 2070-99, suggesting that climate change poses a substantial longer-term threat to UK kittiwake populations, and potentially to other marine apex predators.

Introduction

Ecological impacts of climate change are becoming increasingly well-understood, with changes in geographical ranges and the timing of important life-history events predicted and observed in both terrestrial and marine environments (Parmesan, 2006; Walther, 2010; Bellard *et al.*, 2012; Doney *et al.*, 2012). Climate change impacts acting via food chains or community composition are also becoming better-understood (e.g., Pearce-Higgins *et al.*, 2005; Pearce-Higgins, 2010; Pearce-Higgins *et al.*, 2010), but for many ecosystems such impacts may be hard to predict and observe (Tylianakis *et al.*, 2008; Gilman *et al.*, 2010; Walther, 2010). These "indirect" impacts may be relatively widespread and bring with them substantial extinction risks (Cahill *et al.*, 2013; Ockendon *et al.*, 2014), but they also pose considerable conservation challenges: whilst species near the top of food webs often attract most conservation attention (Sergio *et al.*, 2006; Sergio *et al.*, 2008), successful conservation may require consideration of the multiple lower trophic levels and abiotic drivers that combine to influence their population trajectories.

Seabirds are the world's most threatened group of birds, with around 50% of species declining (Croxall *et al.*, 2012). Although seabirds face various direct threats, such as introduced predators and fishery practices, as apex predators in marine ecosystems they could also experience "indirect" climate change impacts through their supporting food webs (Croxall *et al.*, 2012; Sydeman *et al.*, 2012; Burthe *et al.*, 2014). Their populations are sensitive to changes in breeding success (Sandvik *et al.*, 2012), which may be influenced by food availability or quality during the breeding season (Wanless & Harris, 1992; Wanless *et al.*, 2004; Wanless *et al.*, 2005). Under conditions of low food availability or quality, seabird adults and chicks are in poorer condition, nest attendance falls, and chicks may starve, thus reducing productivity (Wanless & Harris, 1992; Frederiksen *et al.*, 2004b; Vincenzi & Mangel, 2013). Hence, environmental changes that affect seabird food webs could impact productivity. Identifying the underlying mechanisms can be challenging, particularly in light of relatively poor information on local prey availability, but it can be informative to examine relationships between physical ocean conditions and seabird population parameters (e.g., Frederiksen *et al.*, 2004b; Wanless *et al.*, 2007), as these can indicate the ultimate drivers of declines.

Some of the best examples of impacts of changing oceanographic conditions on seabirds come from the UK and Ireland, where populations of several species have declined since the mid-1980s (JNCC, 2013). Some declines have been linked to rising sea surface temperatures (SSTs) (e.g., Frederiksen *et al.*, 2004b; Frederiksen *et al.*, 2007a).

Possible mechanisms behind the relationship include reduced prey accessibility due to fish behavioural responses, reduced prey nutritional value due to changing zooplankton communities, or increased predation of key prey species (Arnott & Ruxton, 2002; Frederiksen *et al.*, 2007b; van Deurs *et al.*, 2009). However, although strong SST relationships have been derived for individual colonies (e.g., Frederiksen *et al.*, 2004b), the importance of temperature may vary between regions and colonies (Frederiksen *et al.*, 2007a; Lauria *et al.*, 2012). Further, SST may not be the only important variable, with thermohaline stratification potentially having a strong effect (Scott *et al.*, 2006). Stratification occurs when temperature or salinity differences cause density differences between deep and shallow waters. Associated changes in nutrient availability and light regimes lead to increased phytoplankton growth and subsequent increases in zooplankton abundance, in turn influencing fish activity and growth (Scott *et al.*, 2006; Sharples *et al.*, 2006). Under earlier seasonal stratification, key fish species may be less nutritious or be available too early in the seabird breeding season (Wright & Bailey, 1996; Wanless *et al.*, 2004; Scott *et al.*, 2006; van der Kooij *et al.*, 2008), whilst under stronger stratification, abundance of key zooplankton and accessibility of key fish species may decline (Beare *et al.*, 2002; Jensen *et al.*, 2003). To improve our understanding of the physical drivers of seabird productivity and the threats posed by climate change, it may therefore be necessary to consider multiple colonies and multiple oceanographic variables.

With a more complete understanding of the physical drivers of seabird productivity, longer-term climate change impacts can be considered more explicitly. Whilst longer-term impacts have been implied from observed changes (e.g., Frederiksen *et al.*, 2004b; Wanless *et al.*, 2007), few studies have made explicit climate change projections (but see, e.g., Frederiksen *et al.*, 2013). A clearer understanding of future impacts is essential to establish appropriate conservation strategies in a changing climate, especially in light of legislative frameworks that consider seabird productivity under prevailing climatic conditions (HM Government, 2012). Therefore, examining both observed relationships and explicit climate change projections provides a more complete understanding of the influences of oceanographic change on seabird populations, allowing consideration of both immediate and longer-term impacts.

In this study, we examine drivers of productivity for multiple colonies of a seabird species, considering both temperature and stratification variables. We use the black-legged kittiwake (*Rissa tridactyla*, hereafter “kittiwake”) as a model, as it has been well-studied throughout its range and is considered to be a sensitive indicator of the condition of the marine environment (Wanless *et al.*, 2007; Cook *et al.*, 2014). We focus on the UK and

Ireland, which support around 14% of the biogeographic kittiwake population and for which population and productivity data are routinely collected (JNCC, 2013). Specifically, we consider the following hypotheses:

1) higher SSTs are associated with reduced kittiwake breeding success;
2) strong, early ocean stratification is associated with reduced kittiwake breeding success;
3) modelled kittiwake productivity will be reduced in future scenarios due to the impacts of climate change.

Materials and methods

Study species

Kittiwakes are one of the most abundant seabirds in the UK and Ireland, with approximately 400,000 pairs (Mitchell *et al.*, 2004; Coulson, 2011). However, populations have declined by around 60% since 1986 (JNCC, 2013). They nest on steep cliffs in colonies of up to tens of thousands of pairs, with egg-laying usually occurring from April to June (Mitchell *et al.*, 2004; Coulson, 2011). Kittiwakes feed primarily on fish during the breeding season, with sandeels (particularly the lesser sandeel, *Ammodytes marinus*) a key prey species (Furness & Tasker, 2000; Wanless *et al.*, 2007). However, diet may vary temporally and spatially: in the Irish Sea, clupeids (e.g., herring, sardine, sprat) are locally important (Chivers *et al.*, 2012), whilst capelin, gadids (e.g., cod, pollock) and krill are important elsewhere in the kittiwake's range and outside of the main breeding season (e.g., Lewis *et al.*, 2001; Barrett, 2007). At finer scales, the importance of sandeels may vary between colonies (Bull *et al.*, 2004) and throughout the breeding season (Lewis *et al.*, 2001; Suryan *et al.*, 2002). Although colonies with diverse diets may be somewhat buffered from variations in prey availability (Coulson, 2011), many colonies are heavily dependent upon a single species, often sandeels, during the breeding season (e.g., Harris & Wanless, 1997; Lewis *et al.*, 2001; Bull *et al.*, 2004), thus are more likely to experience impacts of climatic variability.

Oceanographic data sources

Oceanographic data were acquired from two sources: one covered recent years (hereafter 'hindcast'), whilst the other covered 30-year periods for the mid 20th Century and late 21st Century (hereafter 'projections'). Both datasets were produced from the Atlantic Margin Model of the Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS), which simulates ocean hydrodynamics as driven by atmospheric inputs and oceanic boundary conditions (Holt & James, 2001). The model operates on a $^1/_6$° long × $^1/_9$° lat grid (approximately 12 km × 12 km), and divides the vertical dimension into layers, with an increased vertical resolution nearer the surface. Outputs acquired consisted of monthly mean values for temperature and salinity in each vertical layer.

Hindcast data were acquired from the MyOcean web portal (http://www.myocean.eu; product NORTHWESTSHELF_REANALYSIS_PHYS_004_005; accessed 23/04/2013). For this dataset, POLCOMS was driven by the 'ERA-40' climate reanalysis dataset (Uppala *et al.*, 2005) until 2001, then the European Centre for Medium-Range Weather Forecasting operational analysis dataset until 2004; these are climatic reconstructions based on observed climate data, so represent an estimate of actual conditions experienced between 1967 and 2004. This dataset could therefore be used to establish relationships with observed kittiwake productivity. Further information on this dataset is provided by Holt *et al.* (2012).

Projection data were acquired from the British Atmospheric Data Centre (http://badc.nerc.ac.uk/data/link; accessed 01/03/2013; data access provided by the UK Met Office). For this dataset, POLCOMS was driven by UKCP09 climate projections for a baseline period (1961-90) and a future period (2070-99) under the A1B SRES scenario. Projections account for inter-annual variability but do not correspond to conditions in specific years, thus could only be used to predict breeding success under average conditions in each time period. Further information on this dataset is provided by Lowe *et al.* (2009).

Oceanographic variables

Three key oceanographic variables were selected for use in analysis: SST (e.g., Frederiksen *et al.*, 2004b; Frederiksen *et al.*, 2007a), the strength of ocean stratification and the timing of seasonal stratification onset (e.g., Scott *et al.*, 2006; Scott *et al.*, 2010). Variables were calculated for winter and spring time periods. The winter period, defined as December, January and February, approximately corresponded to that important for sandeel recruitment and, consequently, for kittiwake breeding success (Arnott & Ruxton, 2002; Frederiksen *et al.*, 2004b). The spring period, defined as March, April, May and June, approximately corresponded to the period in which kittiwakes commence breeding, and in which sandeel eggs hatch, larvae metamorphose and abundance peaks (Wright & Bailey, 1996; Coulson, 2011; Lynam *et al.*, 2013). SST was calculated for these periods by extracting the top layer of temperature outputs for each month.

The strength of stratification was expressed using the potential energy anomaly (PEA; Equation 1), as defined by Holt *et al.* (2010). PEA indicates the amount of energy per unit depth required to mix the water column completely. Hence, the higher the value, the greater the energy input required to achieve mixing, and therefore, the stronger the stratification. PEA was calculated as

$$\varphi = -\frac{g}{h}\int_{z=-h}^{0} z\left(\rho\big(T(z), S(z)\big) - \rho(\bar{T}, \bar{S})\right) dz \qquad (1).$$

Here, φ = PEA, g = gravitational acceleration, h = water depth (or 400 m if the depth exceeds this, after Holt *et al.* (2010)), z = the vertical coordinate (with 0 indicating the surface, and with larger negative values indicating deeper water), ρ = density (calculated here using a deterministic polynomial function defined by Jackett *et al.* (2006)), T = temperature, S = salinity, and the overbar indicates the quantity is averaged from h to the surface. As temperature and salinity data were only available for a discrete set of depths, the integral was evaluated numerically using Simpson's rule.

The timing of seasonal stratification onset was calculated in a similar way to previous analyses of POLCOMS data (Lowe *et al.*, 2009; Holt *et al.*, 2010), but as daily outputs were unavailable, additional assumptions were made. Stratification onset was defined to be the first day of the year on which the mixed layer depth (MLD) was shallower than 50 m (or, if the total water depth was <50 m, shallower than the water depth). MLD was defined as the depth at which density differed from surface density by an amount equivalent to a 0.5°C reduction in temperature. Only monthly outputs were available, so daily MLD values were interpolated by fitting a cubic spline with 365 knots through monthly values; note that this interpolation retains the overall seasonal pattern of MLD, but could lead to some error around the 'true' MLD, and will likely lead to underestimation of the true variability in stratification onset. Hence, the stratification onset metric is relatively coarse, but variability between years and sites should still be adequately described. For a small number of cells, MLD was never <50 m, so were assigned a 'no data' value; as these were only a small fraction of all cells, it was determined that this should not unduly bias subsequent estimates of mean stratification onset date.

Bird foraging areas

Previous analyses linking kittiwake productivity to oceanographic conditions have extracted conditions from arbitrarily-sized boxes or broad-scale regions (e.g., Frederiksen *et al.*, 2004b; Frederiksen *et al.*, 2007a; Burthe *et al.*, 2012; Lauria *et al.*, 2013; Sandvik *et al.*, 2014). However, seabird tracking studies have indicated substantial variability in the size, shape and location of the areas used by different colonies (e.g., Wakefield *et al.*, 2013). This implies that the area of sea influencing productivity is also likely to vary among colonies. To account for such variability here, data from kittiwake tracking studies were used to define colony-specific areas.

Data were acquired for 11 colonies where kittiwake tracking was carried out during the 2010-12 breeding seasons and for which productivity data were available (Table 1; Fig. 1). Tracked birds had high-resolution GPS tags (modified IgotU GT 120, Mobile Action, Taiwan) attached with waterproof adhesive tape to back feathers whilst at the colony. Tags recorded a location fix accurate to around 20 m approximately every 100 seconds, and remained attached for two to five days. Kittiwake tracking occurred from May to July, with most tracking occurring in June, primarily covering the late incubation and chick rearing period.

It was assumed that as oceanographic changes would primarily affect kittiwake productivity via the food web, the most relevant areas from which to extract oceanographic conditions would be those associated with foraging. GPS records were therefore filtered to remove records unlikely to be associated with foraging. Records within 1 km of the colony centre were removed to exclude GPS fixes associated with behaviours at or around the nest, which may not be associated with foraging in some colonies (e.g., Irons, 1998;

Suryan *et al.*, 2002). Then, travel speeds between points were calculated; the distribution of speeds formed a bimodal distribution, with only the lower speeds likely to be associated with foraging (e.g., Kotzerka *et al.*, 2010). Based on preliminary analysis of a subset of the data, a threshold of 14 km h^{-1} was selected (Appendix S1); records associated with higher speeds were removed. This filtering left 192,638 individual GPS records. Although filtering did not exclude behaviours such as resting on the sea, the range of kittiwake foraging behaviours (Coulson, 2011) makes it hard to apply a set of criteria to describe all foraging, so it was determined that this more inclusive approach was preferable. A sensitivity analysis (Appendix S1) indicated that the speed threshold chosen made little difference to mean environmental variable values extracted from the resulting foraging area (Pearson correlations between threshold values ranging 11– 20 km h^{-1} all > 0.999). The distance threshold had a larger effect, but resulting environmental variable values were still highly correlated (correlations between threshold values ranging 0.2 – 2 km all ≥ 0.929). Therefore, analyses using environmental data at this relatively coarse scale should be robust to threshold specification within the ranges considered.

Kernel density estimates were calculated to convert GPS records into estimated foraging areas. Foraging areas were computed separately for each colony, with data pooled across all years and birds to produce an estimate of the ‘core’ area for that colony. Although the size of foraging kernels is sensitive to the number of birds included in estimation, all colonies here had at least the number of birds required to describe >50% of the ‘true’ foraging area, with many including the number required to describe >95% (Soanes *et al.*, 2013). Kernel densities were evaluated on a regular 30 arc-second by 30 arc-second rectangular grid. The limits of the grid were defined to be 1.25 degrees away from the most extreme observed foraging location in each direction.

Kernel density estimates were based on a bivariate Gaussian kernel, and were evaluated the 'ks' R package (Duong, 2013). Two possible methods for choosing the degree of smoothing were considered: 1) a bivariate plug-in bandwidth estimator (Duong & Hazelton, 2003); and 2) an estimator selected using a simple rule-of-thumb (Silverman, 1986). The rule-of-thumb approach involved taking the kernel bandwidth to be $1.06 \cdot \sigma_x \cdot n^{(-1/5)}$ and $1.06 \cdot \sigma_y \cdot n^{(-1/5)}$, where n denotes the sample size and σ_x and σ_y denote the standard deviations of the longitudes and latitudes of GPS record locations. This rule-of-thumb is derived in a univariate setting, under an assumption of normality, and so should be interpreted with some caution in the bivariate setting. However, the plug-in estimation approach was highly computationally intensive for datasets of this size. The two approaches were therefore compared using a subset of sites: foraging area shapes differed slightly between the two methods, but locations were highly similar, hence resulting oceanographic variable values were highly correlated ($r \geq 0.99$). The rule-of-thumb approach was therefore used for all remaining sites. Foraging areas were defined by the 90% density contour, which has been recommended for home range estimates (Börger *et al.*, 2006). Resulting kernels are presented in Appendix S2.

Bird population data

Kittiwake breeding success data were acquired from the seabird monitoring programme (SMP; http://www.jncc.defra.gov.uk/smp; Walsh *et al.* (1995)). The SMP is an annual sample survey of seabird abundance and breeding success in the UK and Ireland, which started in 1986 and is coordinated by the Joint Nature Conservation Committee (JNCC). Data from an associated study on the Isle of May National Nature Reserve were acquired from the Centre for Ecology & Hydrology (http://gateway.ceh.ac.uk; accessed 12/04/2013). Productivity data were not available for all years for all colonies, leaving 142 site-by-year combinations (Table 1).

SMP breeding success is often analysed as the mean number of fledged chicks per nest (e.g., Mavor *et al.*, 2008). However, it was preferable here to avoid modelling productivity as a Gaussian variable: if predicting outside the range of current climates, a Gaussian variable could become negative, and the number of nests monitored varied between colonies and years (minimum 21, maximum 1446), so there was unequal variance associated with observations. Therefore, numbers of fledged and failed chicks were modelled directly in a binomial error framework, with fledged chicks taken from the raw data, and failed chicks estimated as ((2 × nests) - fledged), based on the mean and modal UK kittiwake clutch size of 2 eggs (range 1 - 3; Coulson & Porter, 1985; Harris & Wanless, 1997; Coulson, 2011; Cook *et al.*, 2014). Consequently, breeding success was modelled as the young produced *per egg* (Cook *et al.*, 2014), thus preventing the response becoming negative, and allowing prior weights to account for variation in surveyed nests. To ensure results were robust to these assumptions, modelling was also carried out in a Poisson error framework using the raw number of fledged chicks as the response variable, and containing an offset of log(nests) to reflect unequal sampling; results were highly similar to those from the binomial analysis, so are only presented in Appendix S3.

Statistical analysis

Analyses were conducted in R v. 3.1.0 (R Core Team, 2014). Oceanographic data were extracted from estimated foraging areas using the ‘raster’ R package (Hijmans, 2013). The mean of each variable within each foraging area was calculated; for SST and PEA, spring and winter means were calculated; for stratification onset, only an annual mean could be defined. Before inclusion in productivity models, oceanographic variables were tested for collinearity and trends over time (Appendix S4). Further, PEA values appeared to display a heavily skewed distribution, so logged and untransformed PEA values were compared in productivity models (Appendix S4). Akaike information criterion (AIC) values indicated that logged PEA performed better, so all further models used log(PEA).

Breeding success data were analysed in a Generalised Linear Mixed Model (GLMM) framework, using a binomial error distribution and logit link function. The response was a two-column matrix containing the numbers of fledged chicks and estimated numbers of failed chicks. All models were fitted via maximum likelihood in the ‘lme4’ R package (Bates *et al.*, 2014).

Models of breeding success were fitted with time as a predictor variable to identify temporal trends (Appendix S4), and then with oceanographic predictor variables to explore drivers of breeding success variation. Models including all sites were fitted with ‘site’, ‘region’, ‘year’, ‘site*year’ and ‘region*year’ random effects; the site*year random effect was an observation-level factor included to model overdispersion (e.g., Browne *et al.*, 2005); the ‘region’ random effect was based on the kittiwake population regions identified by Frederiksen *et al.* (2005). For single-site models, only colonies with ≥10 years of overlapping breeding success and oceanographic data were analysed; these models were fitted with only a ‘year’ random effect, which at this scale constituted an observation-level factor to model overdispersion.

For single-site models, which had a minimum of 12 and a maximum of 19 data points, only models with single predictor variables were considered as the data were deemed inadequate to include multiple explanatory variables. The influence of each variable was assessed by comparing the sample-size-corrected AIC (AICc) value to that from a null model fitted with intercept and random effects only; models with ΔAICc ≤ 0 were considered to show some support over the null model, with ΔAICc ≤ -2 taken to show substantial support. AICc was used in favour of QAICc because overdispersion was already accounted for by inclusion of observation-level random effects. Equivalent models were also constructed including data from all sites to examine independent impacts of each variable; due to the larger sample size, these models were assessed with uncorrected AIC. Previous analyses have indicated that SST with a 1-year lag provided the best predictor of kittiwake productivity, but that unlagged SST still had some effect (Frederiksen *et al.*, 2004b). Therefore, both lagged and unlagged variables were trialled. Lagged and unlagged variables produced similar relationships, but unlagged variables produced lower AICs, so further analyses only considered unlagged variables, and results from analyses with lagged variables are presented in Appendix S4.

Models including data from all sites were then fitted with multiple predictor variables. Interactions between variables were not considered, as this would lead to overfitting and reduce interpretability of results in models containing high-order interactions. Model comparison was conducted using the 'MuMIn' R package (Barton, 2014), with model performance determined by comparing AIC values to that from the model with lowest AIC. Models with ΔAIC ≤ 2 relative to the best model were considered to show similar support.

Climate change impacts were estimated from the models with multiple predictor variables. To account for model uncertainty, all 32 candidate models were used in a randomisation procedure; for each randomisation run, one model was picked with probability of selection proportional to its Akaike weight. To account for parameter uncertainty within models, new parameter estimates were simulated. Fixed effect estimates were simulated from a multivariate normal distribution, with mean and covariance matrix equal to those from the chosen model, using the 'mvtnorm' R package (Genz & Bretz, 2009; Genz *et al.*, 2014). As the sites and regions used for projections were the same as those in model fitting, 'site' and 'region' random effect estimates were extracted directly from the fitted model. As years in projections differed from those in model fitting, 'year', 'site*year' and 'region*year' estimates were simulated from normal distributions with mean = 0 and standard deviations equal to those from the chosen model.

Simulated parameters were applied to UKCP09 oceanographic projection data for the 'baseline' period of 1961-90 and the future period of 2070-99 to produce breeding success estimates. Estimates were calculated for all years within each period, but as these periods represented average conditions, the mean across all years was calculated. The randomisation process was carried out 1,000,000 times, giving 1,000,000 estimates of 30-year mean breeding success for each time period. To estimate climate change impacts, the two periods were compared to one another; proportional change in breeding success was calculated as ((future - baseline)/baseline); probability of decline was estimated by calculating the difference between the periods for each randomisation run, and then calculating the proportion of these differences that did not show a decline. Finally, to understand which variables influenced projected breeding success trends, differences in oceanographic predictor variables between periods were tested using Wilcoxon rank sum tests.

Results

Temporal trends and correlations in oceanographic variables

Across all sites, breeding success showed no significant trend over time ($P = 0.141$; Appendix S4). Spring SST increased significantly ($P = 0.026$), and winter SST increased but did not attain significance ($P = 0.054$). Winter PEA showed a weakly significant increase over time ($P = 0.046$), but spring PEA ($P = 0.173$) and stratification onset ($P = 0.096$) showed no significant change over time.

For individual site models, the direction and strength of temporal trends varied (Appendix S4). Breeding success decreased at Flamborough Head, Fowlsheugh and St Abb's Head, but increased at Bardsey Island; other than at Flamborough Head ($P = 0.003$) these trends were only weakly significant ($0.023 \leq P \leq 0.047$). Spring and winter SST increased at every site; winter increases were either weakly significant or non-significant ($0.029 \leq P \leq 0.192$), and spring increases were significant for Bardsey Island, Flamborough Head and Puffin Island ($P < 0.01$) but non-significant elsewhere. Increases in winter PEA were only significant at Isle of May ($P = 0.016$) and St Abb's Head ($P = 0.048$). Spring PEA showed no significant changes over time. Stratification onset showed significant changes only at Boddam to Collieston, Fowlsheugh and Isle of May ($0.014 \leq P \leq 0.020$), becoming earlier over time.

Correlations between unlagged variables were moderate or weak (Appendix S4), with the highest those between winter and spring PEA ($\rho = 0.669$), winter and spring SST ($\rho = 0.672$), and stratification onset date and PEA (spring $\rho = -0.559$; winter $\rho = -0.485$). Strong or moderate correlations were found between lagged and unlagged forms of stratification onset ($\rho = 0.815$), spring SST ($\rho = 0.647$), winter SST ($\rho = 0.673$) and winter PEA ($\rho = 0.825$). Overall, it was considered acceptable to include multiple predictor variables in the same model, but that it was preferable to avoid including lagged and unlagged forms of the same variable.

Models with single predictor variables

Relationships between breeding success and oceanographic predictor variables differed between sites, but some overall patterns emerged (Table 2; Appendix S5). Stratification onset provided the best model at Isle of May and St Abb's Head, and showed some support at Bardsey Island, with higher productivity associated with later stratification. Spring PEA provided the best model at Flamborough Head and showed some support at Fair Isle; both indicated that higher productivity was associated with lower spring PEA. The best model at Bardsey Island showed that breeding success was higher when winter PEA was lower; the winter PEA parameter estimate attained significance at Coquet Island and approached significance at St Abb's Head but displayed no support over the null model. Spring SST provided the best model at Fair Isle and received some support at Flamborough Head, showing higher breeding success was associated with lower spring SSTs. Winter SST did not perform better than the null model or approach significance at any site. Boddam to Collieston and Fowlsheugh showed no variable to perform better than the null model. When lagged variables were considered, the only relationships that were better-supported than unlagged equivalents were negative relationships with spring SST at Isle of May and St Abb's Head (Appendix S4).

The best all-sites model with a single predictor variable showed breeding success to be higher when winter PEA was lower (Table 2; Fig. 2). A similar relationship was found with spring PEA, but a smaller ΔAIC value indicated weaker support. There was also strong support for a negative relationship with spring SST and a positive relationship with stratification onset date (Table 2). Models including lagged variables showed similar patterns, but with lower AICs than the unlagged equivalents (Appendix S4). Therefore, as in single-site models, breeding success was typically higher under lower SSTs, when stratification occurred later and when the water column was better mixed early in the year.

Models with multiple predictor variables

The best model with multiple predictor variables (Table 3; Supporting Information 5) contained significant, negative coefficients for winter PEA (-0.602, $P = 0.002$) and spring SST (-0.539, $P = 0.027$), indicating that higher breeding success was associated with weaker stratification the winter before breeding and lower SSTs in early spring of the preceding year. Only three other models had strong empirical support ($\Delta AIC \leq 2$ relative to the best model; Table 4). The second-ranked model ($\Delta AIC = 1.649$) contained significant, negative coefficients for winter PEA (-0.609, *P* = 0.001) and spring SST (-0.674, *P* = 0.045), but also a non-significant positive effect of winter SST (0.173, *P* = 0.556), contrasting with the negative impact of winter SST found in the single predictor case, but possibly reflecting the moderate collinearity between winter and spring SST. The third-ranked model (ΔAIC = 1.861) contained significant negative coefficients for spring SST (-0.544, *P* = 0.027) and winter PEA (-0.566, *P* = 0.008), but also a non-significant positive coefficient for stratification onset (0.003, *P* = 0.712), in line with the single predictor models. The fourth-ranked model (ΔAIC = 1.926) showed significant negative effects of spring SST (-0.541, *P* = 0.027) and winter PEA (-0.574, *P* = 0.008), and included a non-significant negative effect of spring PEA (-0.090, *P* = 0.786). Therefore, multiple predictor variable models again highlighted the importance of lower spring SSTs and lower winter PEAs for kittiwake breeding success.

Climate change projections

Projections of breeding success in the climatic baseline period of 1961-90 and a future scenario of 2070-99 indicated that substantial productivity declines could be driven by changing oceanography under climate change (Table 4; Fig. 3). For the climatic baseline period, mean projected breeding success across all sites was 0.560, corresponding to around 1.12 chicks per pair; by 2070-99, this had declined by 32.6% to 0.377, corresponding to approximately 0.754 chicks per pair. Only 3.0% of simulations of breeding success across all sites did not predict a decline.

Projections differed slightly between sites, but all sites showed declines (Table 4). The largest proportional decline was for Fair Isle (43.2%), followed by Bardsey Island (42.4%); the smallest proportional decline projected was at Coquet Island (21.4%). The largest absolute decline projected was at Flamborough Head (-0.214), and the smallest absolute decline projected was at Boddam to Collieston (-0.161). The proportion of simulations predicting a decline also varied between sites; at Bardsey Island and Fair Isle, only 1.8% and 1.1% of simulations respectively did not predict a decline, whilst for Boddam to Collieston, Coquet Island, Fowlsheugh, Isle of May and St Abb's Head, 7.9 – 16.9% of simulations did not predict a decline. Therefore, both the magnitude and probability of declines varied between sites.

Neither stratification onset date (Wilcoxon rank sum test, W = 48309, *P* = 0.692) nor winter PEA (W = 45255.5, *P* = 0.325) changed significantly between periods. Spring PEA increased significantly (W = 39562, *P* < 0.001), but the absolute change was small

(1961-90 mean 10.02 Jm^{-3} (log scale 2.034); 2070-99 mean 12.13 Jm^{-3} (log scale 2.215)) and spring PEA coefficients in high-ranking models were small. Hence, these three variables changed too little or had too little an effect on productivity estimates to have contributed substantially to the projected productivity declines. SST increased significantly in both spring (1961-90 mean 7.95°C; 2070-99 mean 10.46°C; W = 2470, $P < 0.001$) and winter (1961-90 mean 7.08°C; 2070-99 mean 9.58°C; W = 4736, $P < 0.001$); model coefficients for spring SST were large and negative, whilst those for winter SST were either small and positive or large and negative. Hence, due to the larger differences between the two periods and the larger model coefficients, rising SSTs appeared to be the major driver of projected productivity declines.

Discussion

Here, seabird productivity has been related to multiple oceanographic variables from colony-specific foraging areas for multiple colonies, with derived relationships subsequently used to produce explicit projections of climate change impacts. This approach has reduced reliance on individual colonies, allowed examination of spatial variation in the importance of different drivers, and considered both short-term and longer-term effects of changing conditions, thus providing a more complete examination of physical drivers of kittiwake productivity.

Across all colonies, lower SSTs and weaker, later stratification were associated with higher kittiwake productivity. At eight colonies modelled individually, stratification timing provided the best model at two, PEA provided the best model at three, and SST provided the best model at one, indicating spatial variation in primary drivers of kittiwake productivity. Future projections indicated that rising SSTs could drive productivity declines, suggesting that climate change is a longer-term threat. Together, these results provide an example of how changing physical conditions, presumably acting via supporting food webs, can influence apex predators, leading to substantial “indirect” climate change impacts.

Use of estimated foraging areas

Previous analyses have extracted oceanographic data from generic boxes or large regions (e.g., Frederiksen *et al.*, 2004a; Frederiksen *et al.*, 2007a; Lauria *et al.*, 2013) but here, GPS tracking data were used to estimate colony-specific foraging areas. Although this allowed the regions of interest around focal colonies to reflect observed variation in habitat use, the approach brings caveats that must be considered when interpreting results. It was assumed that colonies use foraging areas consistently, but foraging locations may vary somewhat over time (e.g., Ainley *et al.*, 2003; Robertson *et al.*, 2014). However, given the narrow habitat requirements of sandeels (Holland *et al.*, 2005), a key prey species for many colonies, some areas where prey resources are concentrated are likely to remain important, presumably explaining previous findings of foraging site fidelity (Irons, 1998). A further consideration is that foraging area estimates are sensitive to the number of birds included in calculations (Soanes *et al.*, 2013; Bogdanova *et al.*, 2014), so the true 'whole colony' foraging area may not be well-represented. Here, however, all colonies passed the threshold required to estimate >50% of the core foraging area (Soanes *et al.*, 2013). These issues could be resolved by collecting more tracking data, allowing increased understanding of foraging location variability and providing more robust foraging kernel estimates. Even with these caveats, the use of tracking data to identify areas of sea relevant to individual colonies will provide new opportunities to understand interactions between the marine environment and seabirds.

Physical oceanography as a driver of kittiwake productivity

As in previous analyses (e.g., Frederiksen *et al.*, 2004b; Frederiksen *et al.*, 2007a; Lauria *et al.*, 2013) a negative relationship between productivity and SST was found, but the strongest relationship across all sites showed a negative relationship with winter PEA. This confirms that examination of multiple oceanographic variables can provide a more complete understanding of the system, with the relationships identified allowing underlying mechanisms to be considered.

The onset of stratification is linked to the occurrence of the spring plankton bloom, which can cause sandeels to emerge from the sediment (Greenstreet *et al.*, 2006) and other fish to move towards surface waters to feed (e.g., Buren *et al.*, 2014). Therefore, stratification itself is unlikely to be detrimental to foraging seabirds. Instead, it is likely that stratification timing and strength interact to determine the suitability of feeding conditions. In particular, early stratification could lead to a mismatch between peak fish availability and the bird breeding season (Rindorf *et al.*, 2000; Scott *et al.*, 2006; Burthe *et al.*, 2012), possibly explaining the positive relationship between stratification onset date and kittiwake productivity.

The strong negative relationship with winter PEA may reflect variation in stratification timing, with high PEA values simply indicating areas likely to stratify early. However, there may be more direct mechanisms: kittiwakes avoid foraging in the most strongly stratified areas (Scott *et al.*, 2010), indicating that feeding conditions are less suitable somehow. In areas where sandeels are an important food resource, this may be linked to accessibility or abundance, as sandeel larvae are more abundant in surface waters in areas with weaker stratification (Jensen *et al.*, 2003), and strong stratification can cause oxygen deficits in underlying sediments, thus reducing habitat suitability (Behrens *et al.*, 2009). More widely, stronger stratification is associated with lower abundance of the copepod *Calanus finmarchicus* (Beare *et al.*, 2002). This is a key prey item for many forage fish species (e.g., Prokopchuk & Sentyabov, 2006), so reduced abundance may lead to decreased size of the seabirds' prey (e.g., van Deurs *et al.*, 2014). Given that stratification is likely to become stronger and earlier under climate change (Lowe *et al.*, 2009) investigating relationships between stratification, forage fish and seabirds seems to be a priority for further research.

It has been suggested that relationships between SST and seabird productivity could reflect stratification conditions (Scott *et al*., 2006), but the best models here included both PEA and SST, indicating that temperature has an independent effect. For sandeels, increased metabolic costs at higher temperatures may inhibit growth or cause them to remain buried in the sediment (Greenstreet *et al*., 2006), possibly explaining observations of reduced presence and abundance of sandeels at high temperatures (van der Kooij *et al.*, 2008). Higher temperatures also cause changes in plankton communities, with smaller, less nutritious species replacing larger, cold-adapted species, and affecting energy flow through the food web (Beaugrand *et al*., 2002; van Deurs *et al*., 2009; Morán *et al*., 2010; Doney *et al*., 2012); such changes could reduce survival or growth of forage fish more generally. Results therefore support suggestions that higher temperatures may reduce food availability or quality, leading to declining kittiwake productivity under rising temperatures.

Examination of single-site models allowed some consideration of local and regional differences in drivers of productivity. Primary drivers varied between colonies, but where foraging areas overlapped, similar patterns were observed. At Isle of May and St. Abb's Head, which showed some overlap (Appendix S2), stratification onset was the strongest driver of productivity, whilst at Boddam to Collieston and Fowlsheugh, which showed substantial overlap, no variable showed a strong relationship with productivity. This therefore supports the idea that spatial clustering of kittiwake population trends is driven by local food webs and oceanographic conditions (Frederiksen *et al.*, 2005). At many colonies, and across all colonies, variables with a 1-year lag showed similar relationships to unlagged variables, but received less support. Only Isle of May and St Abb's Head showed a lagged variable to perform better than the unlagged equivalent, with both sites showing negative relationships with lagged spring SST. This result replicates a previous result from Isle of May, which was taken to show that 1-group sandeels influenced productivity more than 0-group (Frederiksen *et al.*, 2004b). However, the absence of lagged effects elsewhere implies that other areas may rely on 0-group sandeels or other species, or that oceanographic conditions may affect availability of all prey items. Therefore, further examination of seabird diets, and how they vary between colonies, is required to improve understanding of such spatial differences.

Climate change impacts

Climate change projections indicated that kittiwake productivity could decline by 21 – 43% between the mid 20th Century and late 21st Century, driven by rising sea temperatures. The largest absolute decline was projected for Flamborough Head, likely reflecting the greater warming forecast in that region (Lowe *et al.*, 2009). Smaller declines, with lower probabilities of occurrence, were projected for colonies further up the east coast, suggesting that climate change impacts may be slightly weaker there. However, the largest proportional decline occurred at Fair Isle, indicating that more severe impacts will not necessarily be limited to southerly colonies. Indeed, as dramatic declines have already been observed in northern Scottish colonies (JNCC, 2013), it may be these colonies where climate change poses the greatest threat.

Between 1986 and 2008, UK kittiwake productivity declined by 31% (Cook & Robinson, 2010; JNCC, 2013), making observed declines comparable to those projected over longer timescales. This does not, however, indicate that productivity declines have reached their maximum. Instead, projections simply indicate that climate change could drive substantial productivity declines, with realised extents determined by factors such as density dependence (Massaro *et al.*, 2001; Frederiksen *et al.*, 2005), anthropogenic influences (e.g., Furness & Tasker, 2000; Frederiksen *et al.*, 2004b), and adult condition (Frederiksen *et al.*, 2004a). Methodological differences also limit comparison with observations: projections describe 30-year means that obscure 'bad' or 'good' years, and are based on only 11 colonies (c.f. >50 colonies in Cook & Robinson, 2010) that did not show significant declines over the observation period. Therefore, although realised impacts will differ from projections, results strongly suggest that climate change is expected to reduce kittiwake productivity.

Global SSTs are projected to increase by 1 – 3°C by the end of the 21st Century (Collins *et al.*, 2013), meaning that further impacts on seabirds may be unavoidable. However, if reduced food availability or quality underlies the impacts, appropriate management may ameliorate some negative effects. Sandeel fisheries reduce kittiwake productivity (Furness & Tasker, 2000; Frederiksen *et al.*, 2004b), so any action that reduces prey abundance in key foraging areas is also likely to have some effect. With improved knowledge of foraging locations, it may be possible to identify important areas to be granted enhanced environmental protection; this is in line with previous recommendations for climate change adaptation in marine ecosystems (Mawdsley *et al.*, 2009). Indeed, abundance of some fish species may even increase under warmer temperatures (Rijnsdorp *et al.*, 2009; Edwards *et al.*, 2013). Therefore, ensuring that populations of potential prey species can be supported in sensitive areas may provide the best approach for conserving kittiwakes and other apex predators under uncertain future conditions.

Conclusions

Results presented here suggest that lower SSTs and weaker, later stratification are beneficial for kittiwake productivity, with both likely to act via changes to abundance, quality or accessibility of key prey resources during the breeding season. Kittiwakes are surface-feeding apex predators, so some findings may be primarily relevant to species occupying this foraging niche: if stronger stratification simply reduces availability of prey near the surface, this may explain why surface feeders such as kittiwakes and Arctic terns (*Sterna paradisaea*) appear to be more susceptible to changes than do diving species such as common guillemots (*Uria aalge*) (Monaghan, 1996; Enstipp *et al.*, 2006). If, however, changes to stratification conditions and rising temperatures lead to reduced prey nutritional value or decreased abundance throughout the water column, it is feasible that all marine apex predators could be affected. Indeed, widespread declines have been observed in North Sea harbour seal (*Phoca vitulina*) populations (Lonergan *et al.*, 2007), increased starvation of harbour porpoises may be linked to reduced sandeel availability (MacLeod *et al.*, 2007), and productivity of both guillemots and razorbills (*Alca torda*) has declined (JNCC, 2013), suggesting that changing physical conditions could be affecting more than just surface-feeding birds. Climate change could therefore have substantial ecosystem-wide impacts, but further examination of links between prey populations and physical conditions is needed to assess the true extent of possible impacts.

More widely, this study provides an example of possible "indirect" climate change impacts, with the variables tested likely to influence productivity via changes to supporting food webs rather than a direct physiological response. Although the relationships identified over the observed period are not evidence in themselves of climate change impacts, the explicit projections indicated that climate change is likely to drive substantial declines in productivity by the late 21st Century. Such "indirect" impacts are possible whenever predators rely heavily on prey species that are themselves susceptible to more direct climate change impacts (e.g., Pearce-Higgins *et al.*, 2010), and may be a more frequent and serious concern than previously understood (Cahill *et al.*, 2013; Ockendon *et al.*, 2014). Given the complexity associated with identifying and understanding these impacts, there is a great need to identify drivers and investigate the biotic mechanisms that link the physical environment to higher consumers. By improving our understanding of these relationships, we may be able to identify appropriate conservation actions. If appropriate management allows apex predators to maintain high productivity in some years, it may still be possible to ameliorate population-level impacts of climate change.

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Supporting information

Appendix S1: Sensitivity analysis of threshold values used to define foraging areas

Appendix S2: Maps of foraging area kernels used in analyses

Appendix S3: Results from generalised linear mixed models with Poisson error structure

Appendix S4: Results from models testing for trends over time, and from models trialling different forms of input variables

Appendix S5: Full model results from main analysis

Table 1. Descriptions of sites included in analyses. Site refers to the name in the SMP database. Map site number refers to location on Fig. 1. Oceanographic data were available up to 2004, whilst productivity data were available from 1986, meaning that the maximum possible overlap was 19 years. Regions listed were based on those specified by Frederiksen *et al.* (2005); if a region was not stated for a specific site, the region of the next nearest site was used.

Site	Map site number	Region based on Frederiksen *et al.* (2005)	Coordinates	Years of breeding success data overlapping oceanography	Years of tracking data	Total birds tracked
Fair Isle	1	Shetland	-1.65° long, 59.52° lat	19	3	11
Boddam to Collieston	2	East Scotland	-1.85° long, 57.42° lat	15	1	25
Fowlsheugh	3	East Scotland	-2.20° long, 56.92° lat	17	1	15
Isle of May NNR	4	East Scotland	-2.57° long, 56.18° lat	18	1	17
St Abb's Head NNR	5	East Scotland	-2.13° long, 55.91° lat	18	1	15
Coquet Island	6	East England	-1.52° long, 55.34° lat	12	2	36
Flamborough Head and Bempton Cliffs	7	East England	-0.08° long, 54.12° lat	18	3	51
Bardsey Island NNR	8	Irish Sea	-4.83° long, 52.76° lat	17	1	8
Puffin Island	9	Irish Sea	-4.03° long, 53.32° lat	1	3	70
Lambay	10	Irish Sea	-6.03° long, 53.50° lat	1	2	14
Isle of Colonsay	11	West Scotland	-6.21° long, 56.08° lat	6	3	59

Table 2. Results from models relating breeding success to single oceanographic predictor variables. See text for model fitting details. Parameter estimates (± SE) are given, along with ΔAIC (for all-sites models) or ΔAICc (for individual site models) relative to a null model fitted with intercept and random effects only. Parameter estimates significantly different from 0 at $P < 0.05$, as indicated by Wald Z tests, are bold; results approaching but not attaining significance with $0.05 \leq P < 0.1$ are italic. Full model details are given in Supporting Information 5.

	Bardsey Island	Boddam to Collieston	Coquet Island	Fair Isle	Flamborough Head and Bempton Cliffs	Fowlsheugh	Isle of May	St Abb's Head	All sites
Null model	AICc = 187.621	AICc = 178.476	AICc = 103.824	AICc = 278.788	AICc = 225.489	AICc = 214.311	AICc = 254.784	AICc = 230.539	AIC = 1803.730
Winter SST	0.928 (± 0.579), ΔAICc = 0.516	0.175 (± 0.498), ΔAICc = 3.059	-0.075 (± 0.315), ΔAICc = 3.610	**-3.661 (± 1.474), ΔAICc = -2.561**	-0.434 (± 0.393), ΔAICc = 1.733	-0.270 (± 0.366), ΔAICc = 2.453	-0.283 (± 0.535), ΔAICc = 2.636	-0.122 (± 0.328), ΔAICc = 2.777	-0.240 (± 0.231), ΔAIC = 0.994
Winter PEA	**-1.645 (± 0.693), ΔAICc = -2.090**	-0.141 (± 0.488), ΔAICc = 3.099	**-0.697 (± 0.346), ΔAICc = 0.109**	-0.942 (± 1.295), ΔAICc = 2.336	0.253 (± 0.509), ΔAICc = 2.668	-0.388 (± 0.451), ΔAICc = 2.263	-1.478 (± 1.192), ΔAICc = 2.738	*-1.085 (± 0.613), ΔAICc = 0.029*	**-0.641 (± 0.201), ΔAIC = -11.502**
Spring SST	1.311 (± 0.877), ΔAICc = 0.807	0.057 (± 0.593), ΔAICc = 3.172	-0.061 (± 0.351), ΔAICc = 3.636	**-4.280 (± 1.189), ΔAICc = -8.679**	**-0.663 (± 0.300), ΔAICc = -1.416**	-0.239 (± 0.407), ΔAICc = 2.647	-0.488 (± 0.601), ΔAICc = 2.264	-0.024 (± 0.361), ΔAICc = 2.910	**-0.700 (± 0.264), ΔAIC = -5.242**
Spring PEA	-1.719 (± 2.266), ΔAICc = 2.420	-0.123 (± 1.414), ΔAICc = 3.174	1.228 (± 0.968), ΔAICc = 2.140	**-13.414 (± 5.332), ΔAICc = -3.316**	**-2.502 (± 0.909), ΔAICc = -3.417**	-1.176 (± 1.244), ΔAICc = 2.117	0.689 (± 2.371), ΔAICc = 2.830	-1.177 (± 1.241), ΔAICc = 2.034	**-0.602 (± 0.285), ΔAIC = -2.668**
Strat. onset	**0.041 (± 0.019), ΔAICc = -1.356**	0.024 (± 0.018), ΔAICc = 1.561	0.018 (± 0.014), ΔAICc = 1.992	0.042 (± 0.058), ΔAICc = 2.348	-0.023 (± 0.029), ΔAICc = 2.321	0.013 (± 0.020), ΔAICc = 2.561	**0.092 (± 0.030), ΔAICc = -4.855**	**0.034 (± 0.013), ΔAICc = -2.665**	*0.014 (± 0.007), ΔAIC = -3.383*

Table 3. Top-ranked models from the all-sites analysis relating breeding success to oceanographic variables; those shown have ΔAIC ≤ 4 relative to the best model; the null model, fitted with intercept and random effects only, is shown for comparison. See text for details of model fitting. Parameter estimates (± SE) are given, along with the ΔAIC value relative to the best model. Parameter estimates significantly different from 0 ($P < 0.05$), as indicated by Wald Z tests, are bold; results with $0.05 \leq P < 0.1$ are italic. Full model details are given in Supporting Information 5.

Intercept	Spring PEA	Spring SST	Stratification onset date	Winter PEA	Winter SST	AIC	ΔAIC	Weight
4.429 (± 2.181)	-	**-0.539 (± 0.244)**	-	**-0.602 (± 0.190)**	-	1789.734	0	0.263
4.308 (± 2.185)	-	**-0.674 (± 0.336)**	-	**-0.609 (± 0.192)**	0.173 (± 0.295)	1791.383	1.649	0.115
4.206 (± 2.269)	-	**-0.544 (± 0.245)**	0.003 (± 0.008)	**-0.566 (± 0.214)**	-	1791.595	1.861	0.104
4.706 (± 2.408)	-0.090 (± 0.333)	**-0.541 (± 0.244)**	-	**-0.574 (± 0.217)**	-	1791.659	1.926	0.100
-0.322 (± 0.263)	-	-	-	**-0.641 (± 0.201)**	-	1792.228	2.495	0.076
4.521 (± 2.416)	-0.070 (± 0.335)	**-0.670 (± 0.336)**	-	**-0.586 (± 0.220)**	0.167 (± 0.296)	1793.340	3.606	0.043
1.283 (± 1.076)	-	-	-	**-0.622 (± 0.198)**	-0.212 (± 0.222)	1793.342	3.609	0.043
4.211 (± 2.264)	-	*-0.662 (± 0.344)*	0.001 (± 0.008)	**-0.591 (± - 0.591)**	0.155 (± 0.316)	1793.354	3.621	0.043
-0.677 (± 0.268)	-	-	-	-	-	1803.730	15.336	0.000

Table 4. Projected breeding success for the UKCP09 climatic baseline period of 1961-90 and for 2070-99 under the SRES A1B scenario. Reported breeding success values are the mean of 100,000 randomisation runs, where each run produces a mean breeding success across all years in the time period; breeding success is here defined as the proportion of successfully fledged chicks. The standard deviation of the 1,000,000 projections is also given. Percentage change is calculated as ((future - baseline)/baseline)*100, based on the mean for each period. To indicate the probability of decline, the difference between the baseline and future projections was calculated for each run, and the proportion of these differences > 0 (i.e. those not showing a decline) was calculated. See Methods for randomisation procedure details.

Site	Mean predicted 1961 – 1990 breeding success (± st. dev.)	Mean predicted 2070 – 2099 breeding success (± st. dev.)	Absolute change	Percentage change	Proportion of projections not showing decline
Bardsey Island	0.426 (± 0.090)	0.246 (± 0.121)	-0.181	-42.4%	0.018
Boddam to Collieston	0.578 (± 0.109)	0.418 (± 0.107)	-0.161	-27.8%	0.169
Coquet Island	0.776 (± 0.077)	0.610 (± 0.123)	-0.166	-21.4%	0.125
Fair Isle	0.431 (± 0.091)	0.245 (± 0.068)	-0.186	-43.2%	0.011
Flamborough Head and Bempton Cliffs	0.591 (± 0.108)	0.378 (± 0.112)	-0.214	-36.1%	0.028
Fowlsheugh	0.606 (± 0.106)	0.442 (± 0.109)	-0.164	-27.0%	0.168
Isle of Colonsay	0.535 (± 0.101)	0.350 (± 0.104)	-0.185	-34.6%	0.035
Isle of May	0.492 (± 0.097)	0.308 (± 0.084)	-0.183	-37.3%	0.098
Lambay	0.500 (± 0.077)	0.318 (± 0.139)	-0.182	-36.4%	0.087
Puffin Island	0.633 (± 0.106)	0.437 (± 0.158)	-0.197	-31.0%	0.026
St Abb’s Head	0.592 (± 0.088)	0.401 (± 0.097)	-0.191	-32.2%	0.079
Across all sites	0.560 (± 0.074)	0.377 (± 0.095)	-0.183	-32.6%	0.030

Figure legends

Figure 1. Map indicating locations of kittiwake colonies included in analyses. Numbers refer to colony descriptions in Table 1.

Figure 2. Plots of breeding success against oceanographic predictor variables with no lag, along with fitted lines from binomial GLMMs including the 'site' and 'region' random effects. Each point represents one site-by-year observation; point sizes are scaled by log(nests surveyed) to reflect weightings of observations in models.

Figure 3. Boxplots comparing oceanographic variables and projected breeding success between 1961-90 and 2070-99. For oceanographic variables plots, input values were 30 years of projection data for each foraging area used in all-sites analyses; for breeding success, input values were 1,000,000 annual breeding success projections (see text for details of randomisation). Boxes indicate interquartile range and median; whiskers indicate 1.5×IQR; outliers indicate points outside 1.5×IQR. Letters above boxes indicate whether difference between time periods was significant (see text for relevant methods); if letters are the same, there was no significant difference between time periods.

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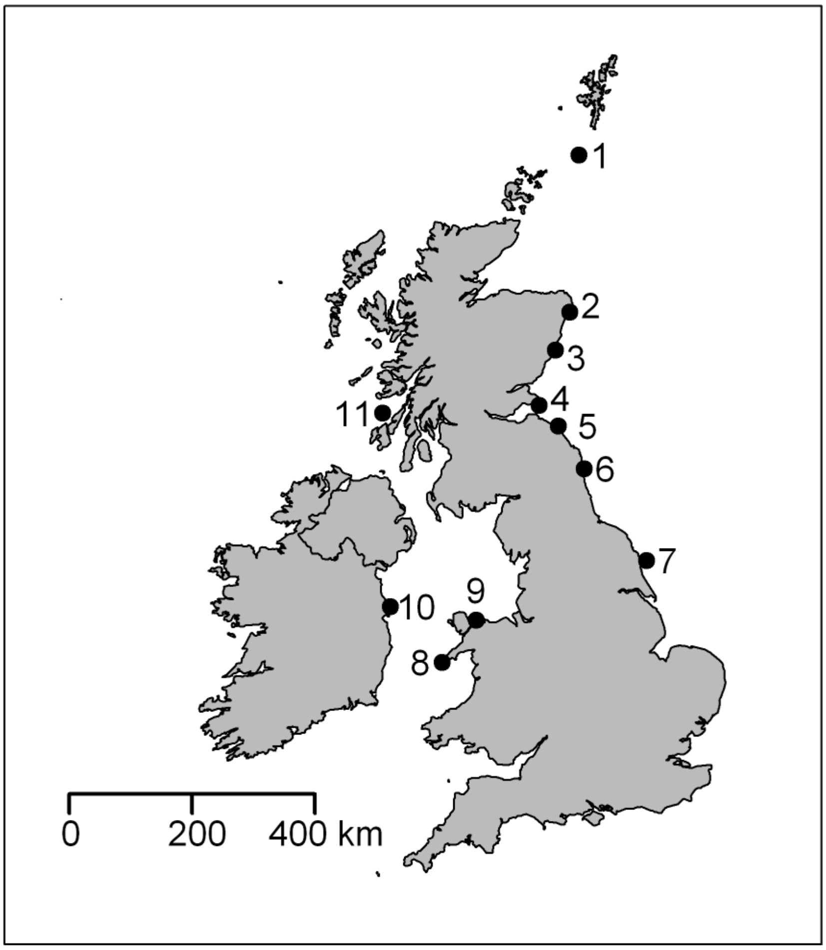

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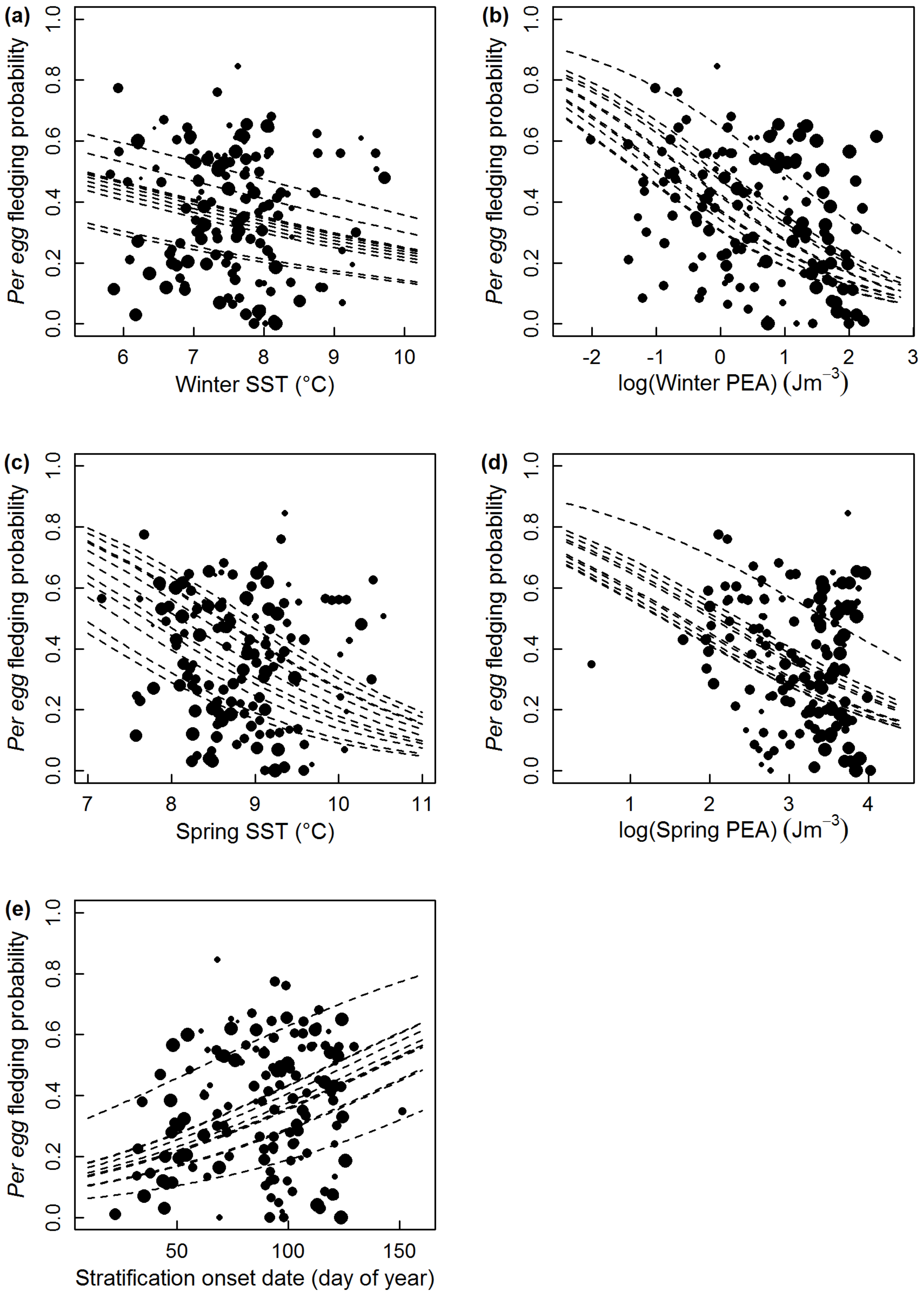

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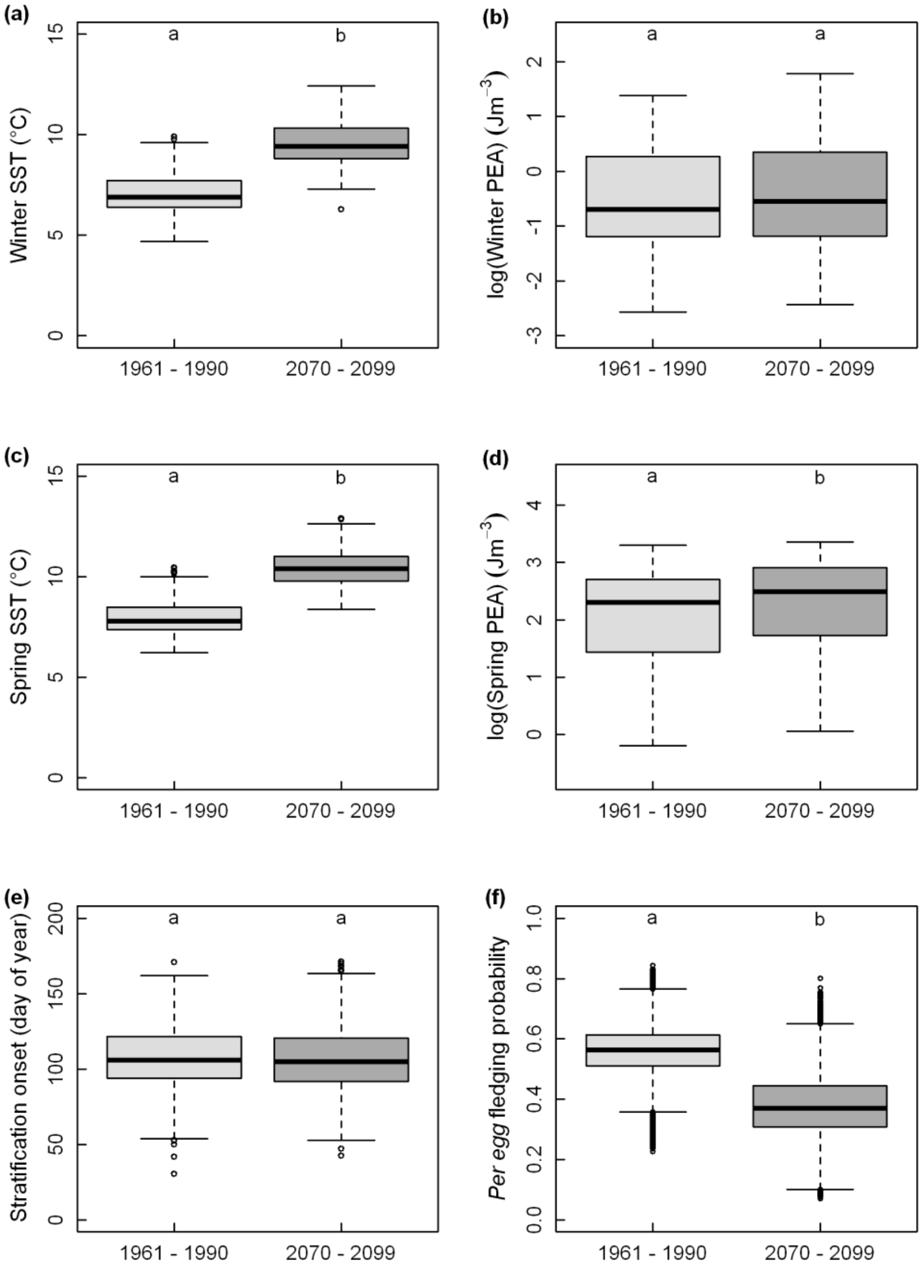


Appendix S1: sensitivity analysis of threshold values used to define foraging areas

As part of the process of turning raw GPS fixes into estimated foraging areas, thresholds had to be applied to remove records unlikely to be associated with foraging behaviour. As these thresholds influence which GPS fixes are taken into account for kernel density estimation, it was necessary to examine whether subsequent analyses would be sensitive to the exact threshold value. Therefore, an initial threshold value was selected for both travel speed and distance from colony, and then three other values for each threshold were trialled in a sensitivity analysis to determine threshold selection would impact subsequent analyses.

A threshold based on distance from colony was applied to remove records associated with behaviours at or around the nest. A distance threshold of 1 km was used, as kittiwakes are very rarely observed foraging within 1 km of the nest (Irons, 1998). Values of 0.2, 0.5 and 2 km were trialled in the subsequent sensitivity analysis. Hence, the distance to the colony centre was calculated for each GPS record, and all records with a distance smaller than the threshold values were discarded.

A travel speed threshold was also applied to remove records associated with commuting. Previous analyses have shown that speed between GPS records may follow a bimodal distribution, with the two parts of the distribution representing different behaviours (e.g., Weimerskirch *et al.*, 2002; Guilford *et al.*, 2008); for kittiwakes, the slower speeds are likely to be associated with foraging (Kotzerka *et al.*, 2010). A preliminary analysis of FAME project data from 2010 and 2011, covering colonies at Bardsey Island, Flamborough Head and Bempton Cliffs, Isle of Colonsay, Fair Isle, Orkney (Copinsay, Muckle Skerry and Swona), Puffin Island and the Isles of Scilly, indicated that the trough between the two modes was wide, and that a speed of 14 km h^{-1} represented a reasonable threshold (Fig. S1.1; A. Butler & E. Owen, *unpublished*). As the distribution of speed values in the full dataset was highly similar to that from this earlier analysis (Fig. S1.2), 14 km h^{-1} was selected as the primary threshold in the full analysis; values of 11, 17 and 20 km h^{-1} were trialled in the sensitivity analysis. Hence, travel speed was calculated for all records, and those records with speeds above the threshold values were discarded.

The sensitivity analysis involved applying each threshold in turn to the data and calculating relevant values from the resulting records. First, the proportion of points found in each POLCOMS grid cell (the grid on which all environmental data were based) was calculated under each threshold condition: this was designed to indicate whether areas would be over- or under-represented in subsequent extraction of environmental data. Second, the environmental variables used in the full analyses (surface temperature, stratification onset date and potential energy anomaly) were extracted from the point locations and a mean was calculated across all points: this was designed to indicate whether environmental variables included in analyses would be biased by threshold selection. In each case, the resulting values were correlated against those produced by using the 1 km and 14 km h^{-1} thresholds (Figs. S1.3 – S1.6); Pearson correlations were calculated for each comparison.

In all cases, the selection of the speed threshold made little or no difference to resulting values; Pearson correlations for both the proportion of time in each cell and for all three environmental variables were > 0.999, indicating that there was substantial robustness to the threshold value specified (Figs. S1.3 – S1.6, parts a, c, e). The distance threshold had a greater impact on the proportion of time spent in each cell, with the correlation dropping to 0.873 when a 200 m threshold was used, and 0.751 when a 2 km threshold was used (Fig. S1.3, parts b, d, f), presumably implying that individual well-used grid cells near the colony were being included or excluded depending on the threshold value. However, mean environmental variables were still very highly correlated (Figs. S1.4 – S1.6, parts b, d, f), with Pearson correlation coefficients ranging from 0.929 to 0.999. Therefore, whilst the distance threshold had a greater impact than did the speed threshold, resulting environmental variable values were still robust to the value selected.

In conclusion, the speed threshold had almost no impact on the analysis, and although the distance threshold had a slightly greater impact, its effect on mean environmental variables was minimal and, further, there is biological support for a 1 km threshold (Irons, 1998). Therefore, it was concluded that further analyses would be sufficiently robust to threshold specification, and that the thresholds of 14 km h^{-1} and 1 km would be suitable for use in the full analysis. It must be noted, however, that the findings of this analysis are only relevant to the grid from which the environmental data are drawn; if environmental data were at a finer resolution or analyses conducted at a finer spatial scale, impacts of threshold specification could increase.

Figure S1.1. Distribution of speed values from initial analysis of subset of tracking data (see text for details of sites and years), showing a) full histogram, and b) histogram with truncated y axis for improved view of second distribution mode. Vertical line indicates 14 km h^{-1} speed threshold used in subsequent analyses.

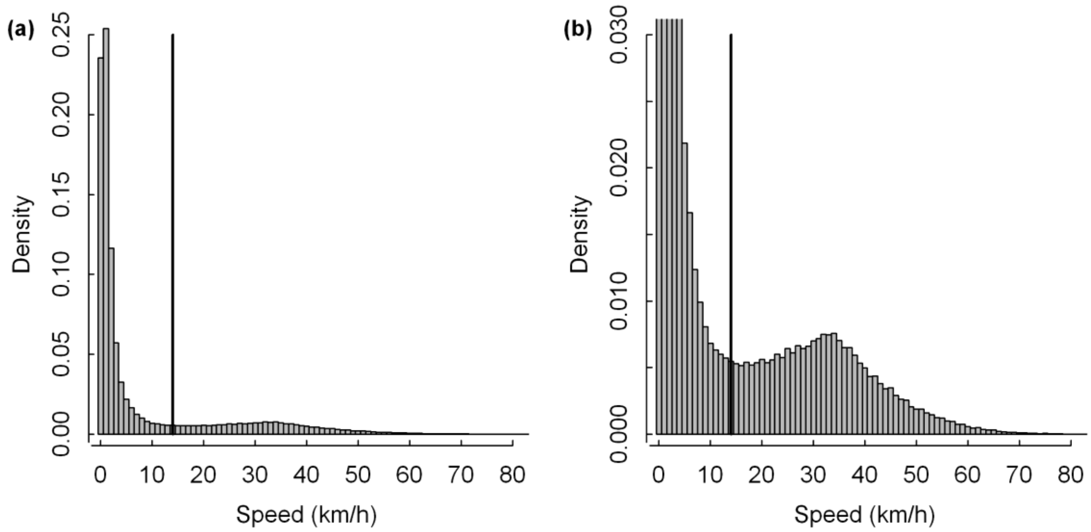


Figure S1.2. Distribution of speed values from full dataset used in analysis showing a) full histogram, and b) histogram with truncated y axis for improved view of second distribution mode. Vertical lines indicate thresholds used (solid line = 14 km h^{-1}) and trialled in the sensitivity analysis (dashed lines = 10, 17 and 20 km h^{-1})

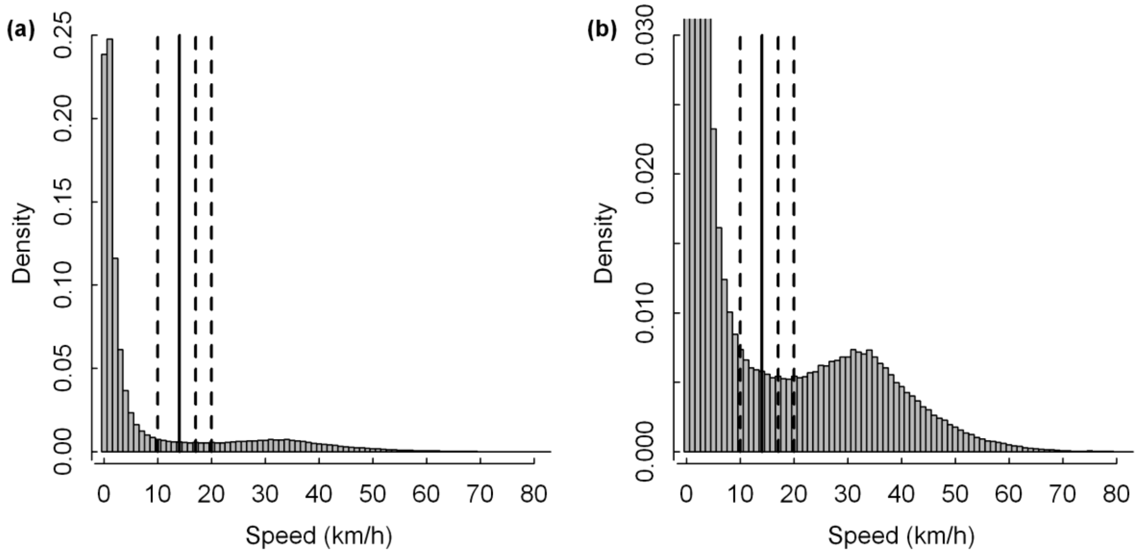


Figure S1.3. Comparison of the proportion of time spent in each POLCOMS grid cell for the standard distance and speed thresholds (i.e., 1 km and 14 km h^{-1}), and that for different possible speed threshold values ((a) 11 km h^{-1}; (c) 17 km h^{-1}; (e) 20 km h^{-1}) and distance threshold values ((b) 200 m; (d) 500 m; (f) 2 km). Plots show Pearson correlation coefficient between the two sets of values.

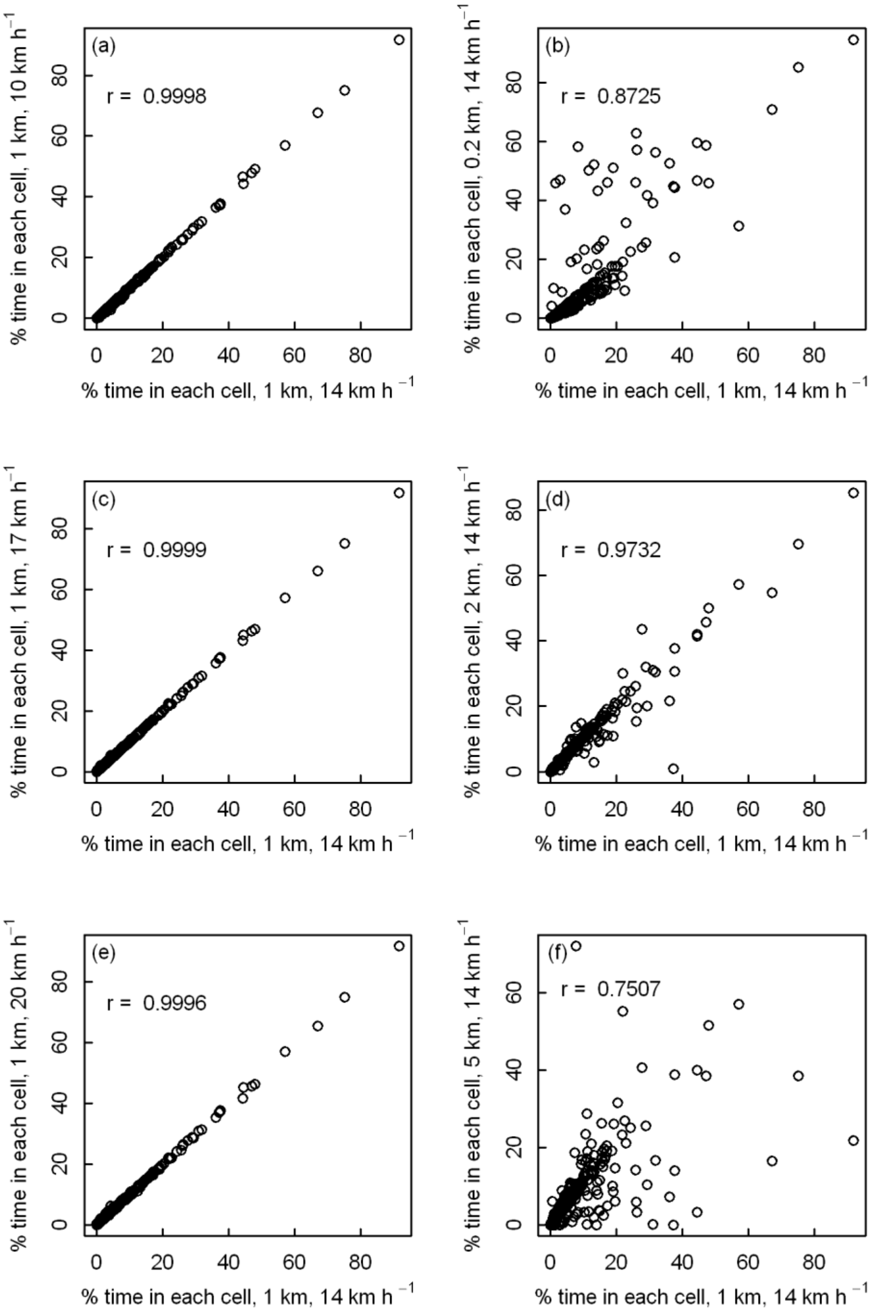


Figure S1.4. Comparison of the mean sea surface temperature extracted from filtered points for the standard distance and speed thresholds (i.e., 1 km and 14 km h^{-1}), and that for different possible speed threshold values ((a) 11 km h^{-1}; (c) 17 km h^{-1}; (e) 20 km h^{-1}) and distance threshold values ((b) 200 m; (d) 500 m; (f) 2 km). Plots show Pearson correlation coefficient between the two sets of values.

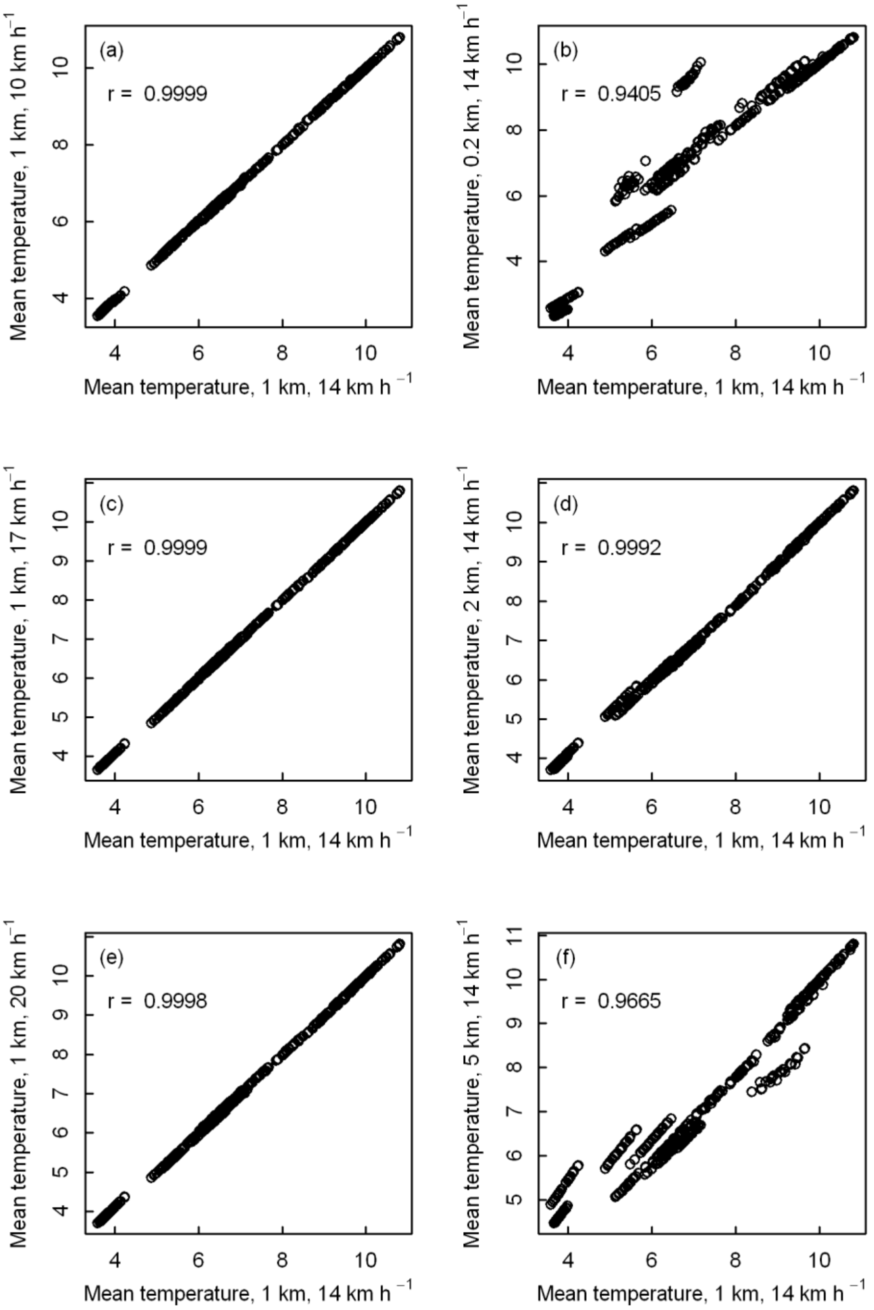


Figure S1.5. Comparison of the mean potential energy anomaly extracted from filtered points for the standard distance and speed thresholds (i.e., 1 km and 14 km h^{-1}), and that for different possible speed threshold values ((a) 11 km h^{-1}; (c) 17 km h^{-1}; (e) 20 km h^{-1}) and distance threshold values ((b) 200 m; (d) 500 m; (f) 2 km). Plots show Pearson correlation coefficient between the two sets of values.

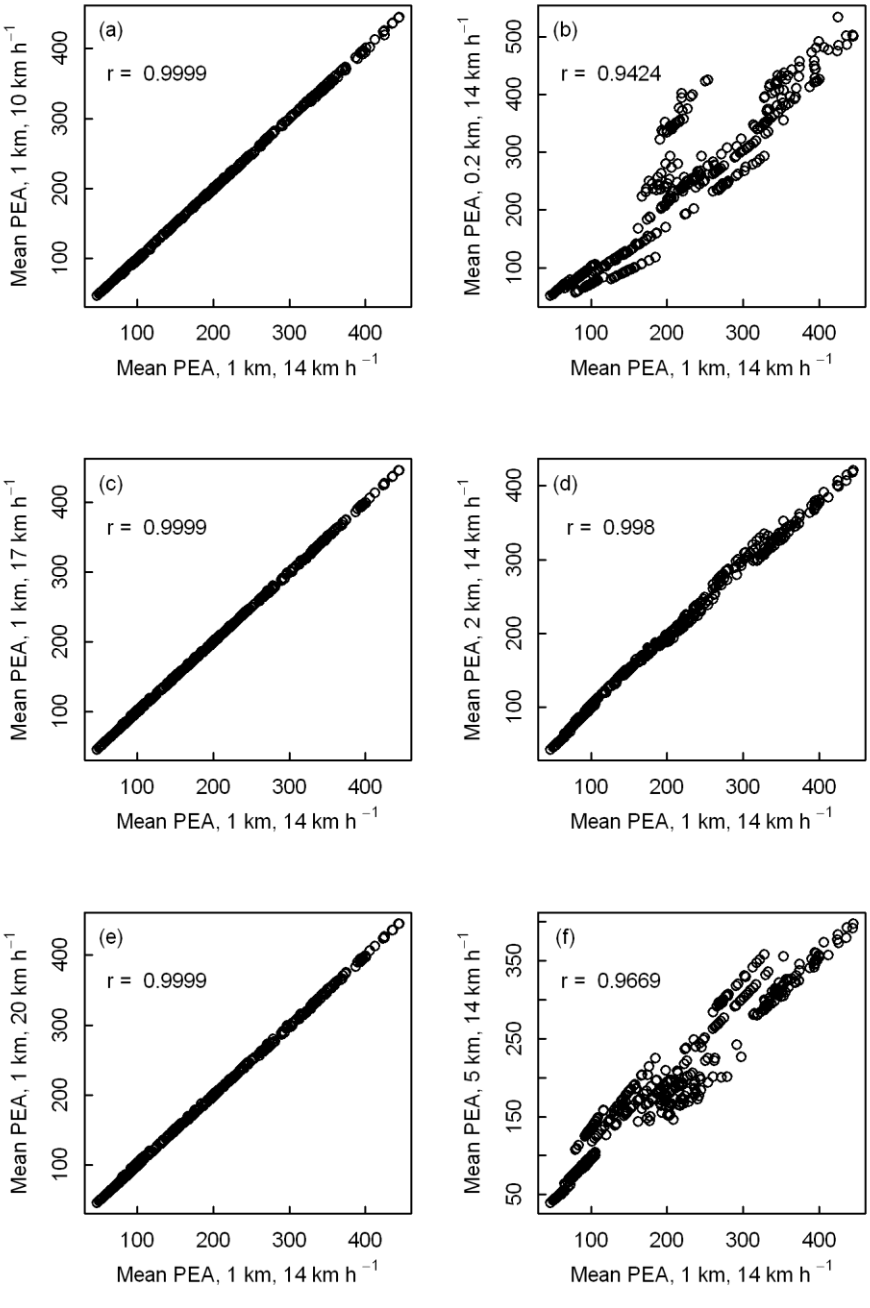
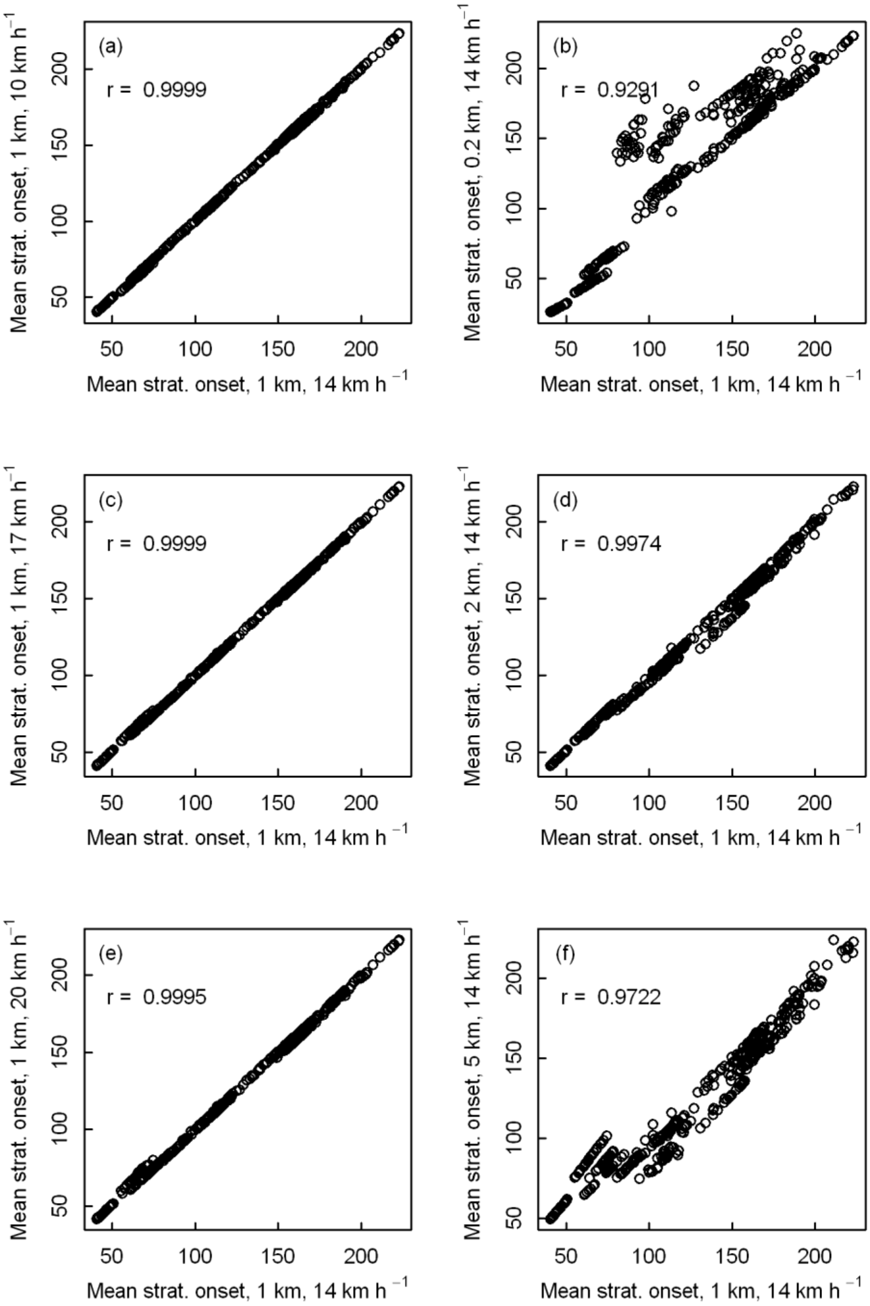


Figure S1.6. Comparison of the mean stratification onset date extracted from filtered points for the standard distance and speed thresholds (i.e., 1 km and 14 km h^{-1}), and that for different possible speed threshold values ((a) 11 km h^{-1}; (c) 17 km h^{-1}; (e) 20 km h^{-1}) and distance threshold values ((b) 200 m; (d) 500 m; (f) 2 km). Plots show Pearson correlation coefficient between the two sets of values.



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Guilford TC, Meade J, Freeman R *et al.* (2008) GPS tracking of the foraging movements of Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis,* **150**, 462-473.

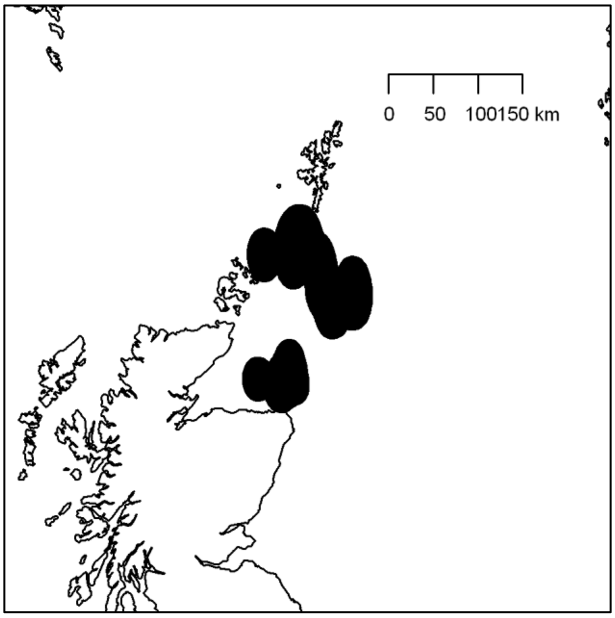
Irons DB (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology,* **79**, 647-655.

Kotzerka J, Garthe S & Hatch S (2010) GPS tracking devices reveal foraging strategies of black-legged kittiwakes. *Journal of Ornithology,* **151**, 459-467.

Weimerskirch H, Bonadonna F, Bailleul F, Mabille G, Dell'Omo G & Lipp H-P (2002) GPS tracking of foraging albatrosses. *Science,* **295**, 1259.

Appendix S2: maps of foraging area kernels used in analyses

Fair Isle



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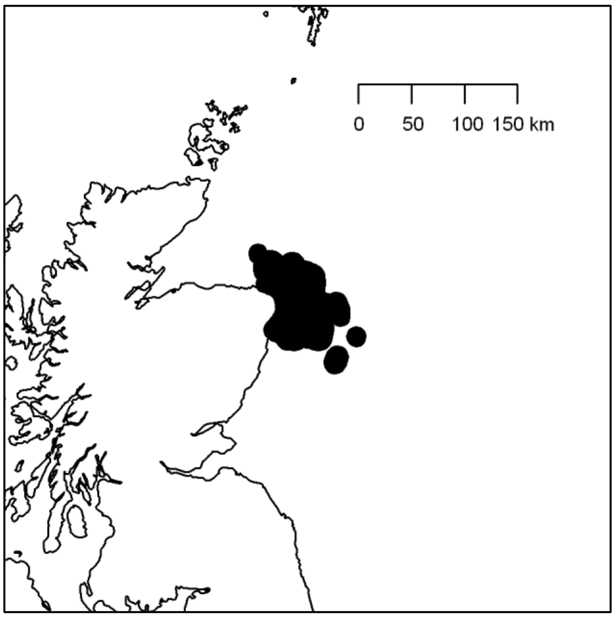
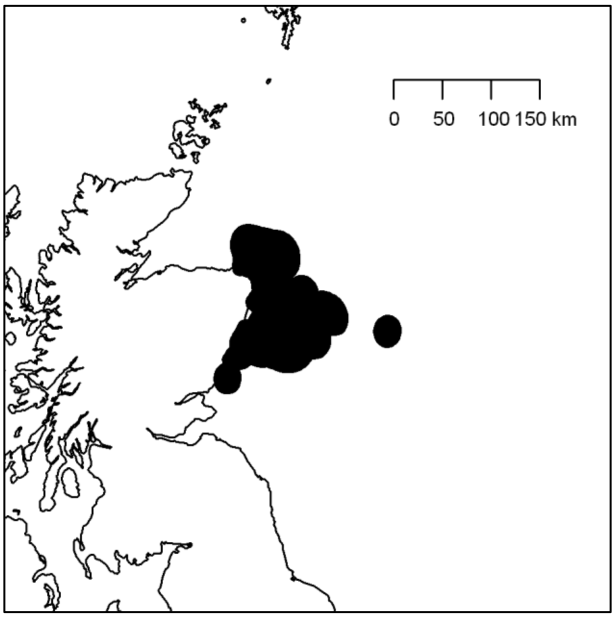
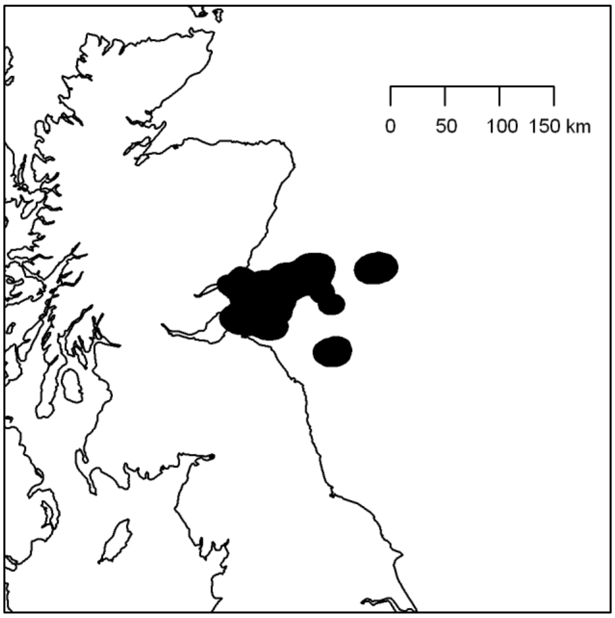


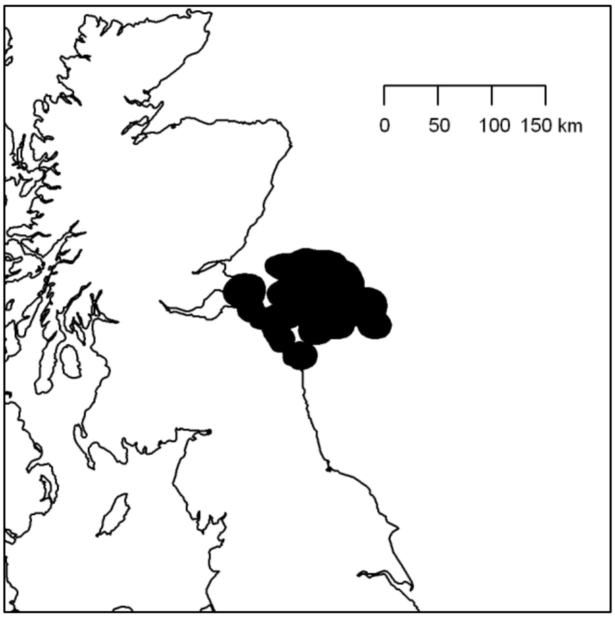
Fowlsheugh



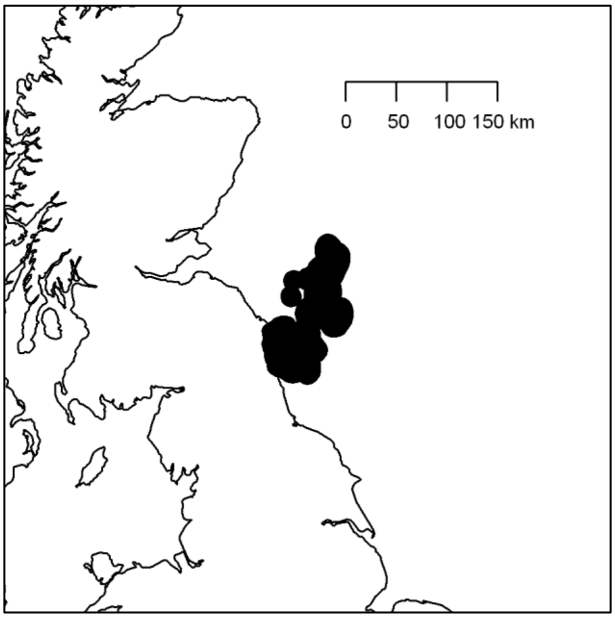
Isle of May NNR



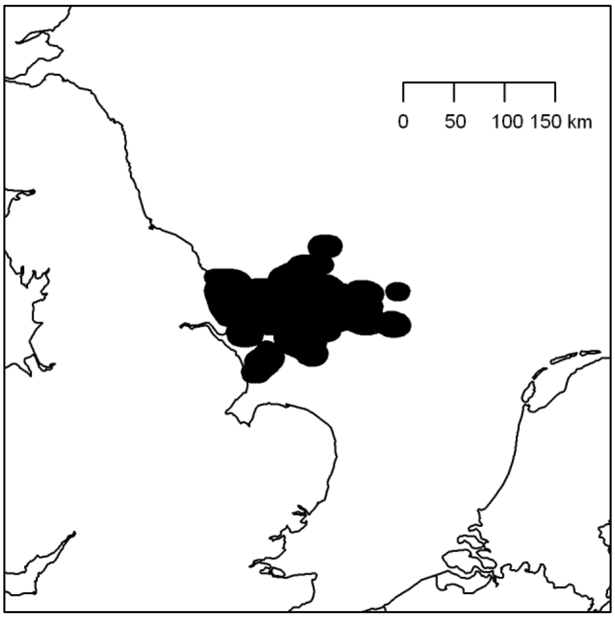
St Abb's Head NNR



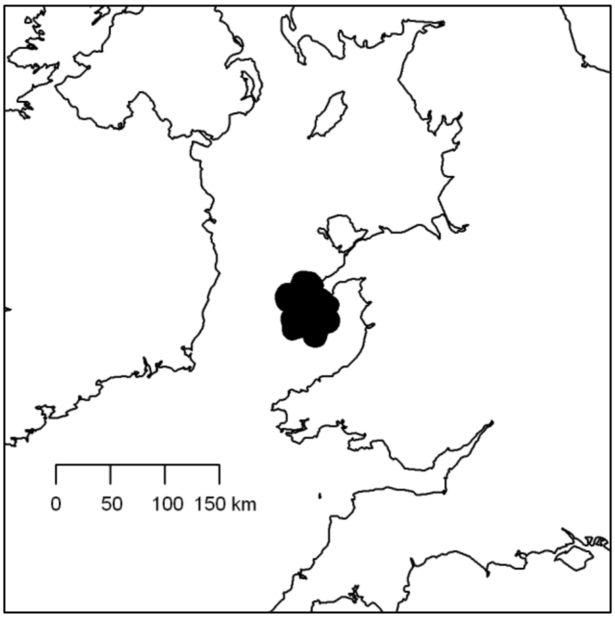
Coquet Island



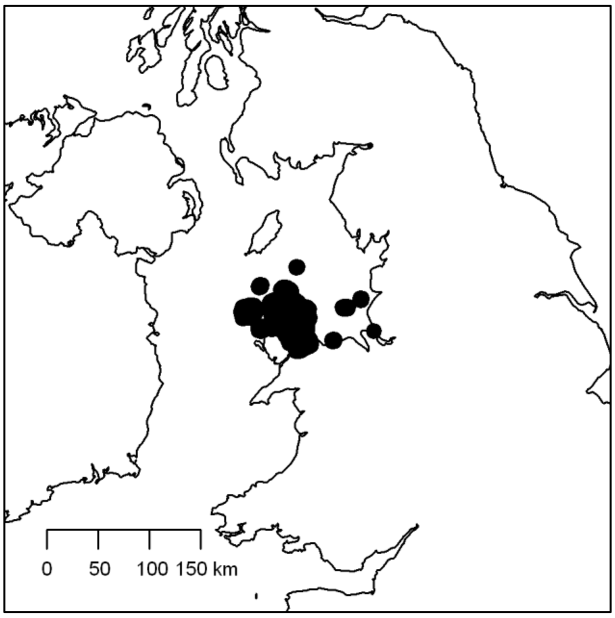
Flamborough Head and Bempton Cliffs



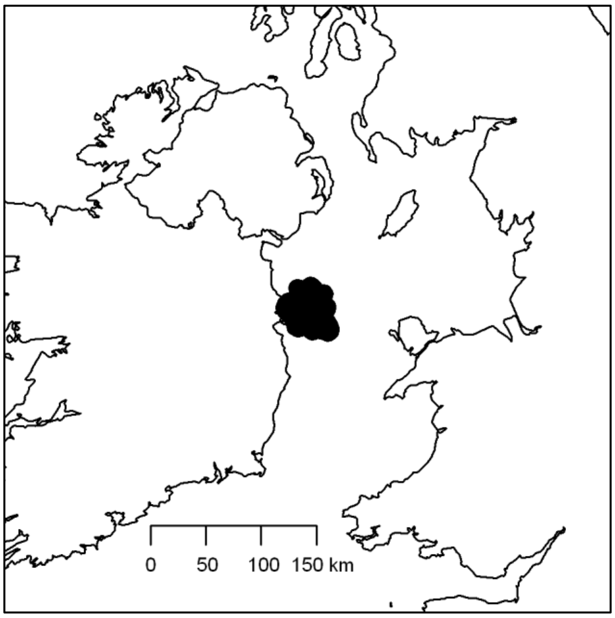
Bardsey Island NNR



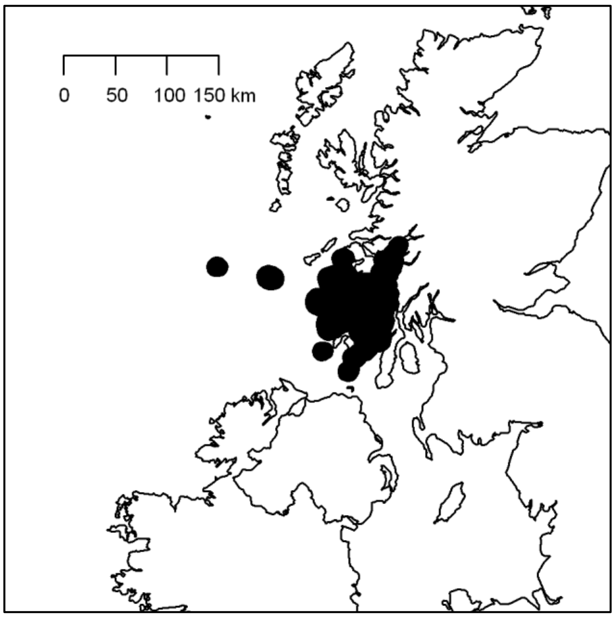
Puffin Island



Lambay



Isle of Colonsay



Appendix S3: results from generalised linear mixed models with Poisson error structure

Methods

Models used in main analyses were generalised linear mixed models (GLMMs) with binomial error structure and logit link, for which the response variable was a matrix of the number of fledged chicks and the estimated number of failed chicks. In this, failed chicks were estimated as ((2 × nests) - fledged), because although 1-egg and 3-egg clutches are possible, the mean and modal clutch size in the UK is 2 (Coulson & Porter, 1985; Harris & Wanless, 1997; Coulson, 2011; Cook *et al.*, 2014). This approach was preferred over modelling the number of fledged chicks as the response, with a Poisson error structure and log(nests) offset, because when predicting from the models under new climate scenarios, the number of fledged chicks would not be an inherently meaningful value without reference to the number of nests, unlike the proportional response from the binomial model. Therefore, it was decided that the binomial error models provided a better approach. However, to examine whether this assumption and error specification substantially affected the results of analyses, GLMMs were specified with the number of fledged chicks as the response, with a Poisson error distribution, log link function, and an offset of log(nests).

Results from single predictor variable models for single sites are presented in Table S3.1 (comparable to results presented in Table S5.1). Models were fitted with a single predictor variable, with a ‘year’ random effect to model overdispersion. Effects of variables were assessed by comparing AICc from each model to AICc from a null model, fitted with intercept and random effect only. These models were only fitted for sites with ≥10 years of overlapping oceanographic and breeding success data.

Results from all-sites models (i.e. including all sites, regardless of number of years of data) with single predictor variables are presented in Table S3.2; those with multiple predictor variables are presented in Table S3.3 (comparable to results presented in Table S5.2). All-sites models were fitted with up to five predictor variables, with no interactions between main effects considered; random effects were ‘site’, ‘region’, ‘year’, ‘site*year’ and ‘region*year’; ‘site*year’ was an observation-level random effect included to model overdispersion. Models were assessed using AIC: single predictor variable models had

AIC compared to that from the null model, and multiple predictor variable models were evaluated by comparing AIC to that from the best model.

Results

Local-scale models showed the same patterns as those analysed in the binomial error framework. All sites showed the best model to be the same as that identified in the main analysis, and other variables identified as important via ΔAICc were the same as those in binomial models. Fixed effect parameter estimates were similar to those from the binomial models, indicating similar relationships in both approaches. The best model with multiple predictor variables was the same in both frameworks, with strong negative effects of both spring temperature and winter PEA; ΔAIC of the best model relative to the null model was highly similar in both cases. When considering other models with some empirical support ($\Delta AIC \leq 2$ relative to the best model), there were some differences between approaches, with the order of the top-ranked models differing somewhat. The 4th-ranked model under the binomial framework (spring PEA, spring temperature, winter PEA) becoming 3rd-ranked under the Poisson framework. However, the other highly-ranked models appeared to retain their relative rankings. Outside of the top-ranked models, there was further variation in relative model performance, but the strong negative effects of spring temperature and winter PEA remained the main feature of all highly-ranked models. Climate change projections from models fitted with Poisson error structure, indicated similar patterns to those found from the binomial analysis, with projected declines across all sites (Table S3.4). However, the scale of declines was projected to be larger, and the proportion of simulations not showing a decline was projected to be larger, meaning that the magnitude and significance of decline projections differed from the binomial analysis.

Given the high similarities between results from the two different approaches, it can be concluded that in the present analyses there is little impact of modelling breeding success in a binomial framework instead of a Poisson framework. The best models were the same in both analyses, and relationships identified were highly similar; the only differences were in the ranking of some all-sites models and the magnitude of climate change driven productivity declines. Therefore, the results identified in the main analyses appear to be robust to the error specification used.

Table S3.1. Parameter estimates, AIC and ΔAIC from model fitting for single-site models with a Poisson error and log link. Fixed effects are reported as estimate (± standard error); the 'year' random effect is reported as the standard deviation of the effect. ΔAIC and ΔAICc were calculated relative to the null model for each site. Fixed effects highlighted in bold are those for which Wald Z tests indicated the parameter estimate was significantly different from 0; italics highlight marginally non-significant parameter estimates ($0.05 \leq P < 0.1$). See text for model fitting details.

Site	Predictor variable	Intercept	Parameter estimate	Year RE	AIC	ΔAIC	AICc	ΔAICc
Bardsey Island	Null model	**-0.680 (± 0.282)**	-	1.134	196.679	-		-
	Spring PEA	2.299 (± 4.549)	-1.124 (± 1.715)	1.120	198.252	1.573	200.098	2.562
	Lagged spring PEA	6.800 (± 4.954)	-2.837 (± 1.880)	1.051	196.526	-0.153	198.372	0.836
	Spring SST	*-11.027 (± 6.575)*	1.044 (± 0.662)	1.070	196.222	-0.457	198.068	0.532
	Lagged spring SST	1.668 (± 5.087)	-0.239 (± 0.517)	1.129	198.466	1.787	200.312	2.776
	Stratification onset	**-3.986 (± 1.646)**	**0.031 (± 0.015)**	1.025	194.573	-2.106	196.419	-1.117
	Lagged strat. onset	2.183 (± 2.710)	-0.025 (± 0.024)	1.100	197.571	0.892	199.417	1.881
	Winter PEA	-0.104 (± 0.339)	**-1.217 (± 0.528)**	0.975	193.776	-2.903	195.622	-1.914
	Lagged winter PEA	-0.073 (± 0.385)	**-1.614 (± 0.800)**	1.022	194.768	-1.911	196.614	-0.922
	Winter SST	*-6.915 (± 3.859)*	0.713 (± 0.439)	1.060	196.108	-0.571	197.954	0.418
	Lagged winter SST	-0.262 (± 4.162)	-0.048 (± 0.477)	1.135	198.669	1.990	200.515	2.979
Boddam to Collieston	Null model	**-0.787 (± 0.194)**	-	0.742	180.033	-	181.033	-
	Spring PEA	-1.064 (± 3.123)	0.094 (± 1.059)	0.742	182.025	1.992	184.207	3.174
	Lagged spring PEA	-4.468 (± 2.731)	1.239 (± 0.917)	0.701	180.302	0.268	182.484	1.450
	Spring SST	-1.193 (± 3.806)	0.047 (± 0.443)	0.742	182.022	1.989	184.204	3.170
	Lagged spring SST	-1.187 (± 3.896)	0.046 (± 0.453)	0.742	182.023	1.989	184.205	3.171
	Stratification onset	*-2.528 (± 1.431)*	0.017 (± 0.014)	0.707	180.596	0.562	182.777	1.744
	Lagged strat. onset	0.745 (± 1.501)	-0.015 (± 0.014)	0.717	181.010	0.977	183.192	2.159
	Winter PEA	**-0.789 (± 0.193)**	-0.149 (± 0.364)	0.738	181.867	1.833	184.048	3.015
	Lagged winter PEA	**-0.787 (± 0.194)**	-0.028 (± 0.402)	0.742	182.029	1.995	184.210	3.177
	Winter SST	-1.454 (± 2.907)	0.086 (± 0.374)	0.741	181.981	1.947	184.163	3.129

	Lagged winter SST	2.508 (± 2.939)	-0.423 (± 0.377)	0.713	180.818	0.785	183.000	1.967

Table S3.1 (cont.)

Site	Predictor variable	Intercept	Parameter estimate	Year RE	AIC	ΔAIC	AICc	ΔAICc
Coquet Island	Null model	0.081 (± 0.074)	-	0.214	102.258	-	103.592	-
	Spring PEA	-1.796 (± 1.483)	0.515 (± 0.405)	0.199	102.713	0.454	105.713	2.121
	Lagged spring PEA	-1.253 (± 1.578)	0.368 (± 0.434)	0.201	103.585	1.326	106.585	2.993
	Spring SST	0.655 (± 1.322)	-0.065 (± 0.149)	0.214	104.070	1.811	107.070	3.478
	Lagged spring SST	0.428 (± 1.343)	-0.040 (± 0.153)	0.214	104.192	1.933	107.192	3.600
	Stratification onset	-0.482 (± 0.401)	0.008 (± 0.006)	0.198	102.253	-0.006	105.253	1.661
	Lagged strat. onset	-0.067 (± 0.432)	0.002 (± 0.006)	0.214	104.137	1.879	107.137	3.545
	Winter PEA	**0.266 (± 0.118)**	*-0.256 (± 0.142)*	0.182	101.308	-0.950	104.308	0.716
	Lagged winter PEA	0.005 (± 0.153)	0.100 (± 0.174)	0.209	103.939	1.680	106.939	3.347
	Winter SST	0.440 (± 1.030)	-0.048 (± 0.138)	0.214	104.137	1.878	107.137	3.545
	Lagged winter SST	-0.155 (± 1.024)	0.032 (± 0.139)	0.214	104.205	1.947	107.205	3.613
Fair Isle	Null model	**-1.564 (± 0.603)**	-	2.586	292.324	-	293.074	-
	Spring PEA	**43.710 (± 17.285)**	**-11.908 (± 4.557)**	2.204	287.716	-4.609	289.316	-3.759
	Lagged spring PEA	32.916 (± 20.510)	*-9.112 (± 5.427)*	2.422	291.513	-0.811	293.113	0.039
	Spring SST	**29.875 (± 8.858)**	**-3.661 (± 1.037)**	1.934	283.073	-9.252	284.673	-8.401
	Lagged spring SST	**21.916 (± 10.217)**	**-2.755 (± 1.202)**	2.291	289.155	-3.169	290.755	-2.319
	Stratification onset	-6.145 (± 5.706)	0.041 (± 0.050)	2.557	293.680	1.356	295.280	2.206
	Lagged strat. onset	-7.820 (± 5.889)	0.055 (± 0.052)	2.517	293.212	0.888	294.812	1.738
	Winter PEA	-0.589 (± 1.659)	-0.705 (± 1.128)	2.548	293.942	1.618	295.542	2.468
	Lagged winter PEA	0.577 (± 1.569)	-1.526 (± 1.053)	2.447	292.302	-0.022	293.902	0.828
	Winter SST	**21.915 (± 10.082)**	**-3.023 (± 1.300)**	2.232	289.485	-2.839	291.085	-1.989
	Lagged winter SST	12.997 (± 11.566)	-1.883 (± 1.495)	2.493	292.770	0.446	294.370	1.296

Table S3.1 (cont.)

Site	Predictor variable	Intercept	Parameter estimate	Year RE	AIC	ΔAIC	AICc	ΔAICc
Flamborough Head and Bempton Cliffs	Null model	-0.182 (± 0.137)	-	0.577	233.190	-	233.990	-
	Spring PEA	**3.389 (± 1.332)**	**-1.519 (± 0.565)**	0.485	229.072	-4.119	230.786	-3.205
	Lagged spring PEA	1.868 (± 1.520)	-0.882 (± 0.652)	0.551	233.436	0.245	235.150	1.160
	Spring SST	**3.489 (± 1.597)**	**-0.423 (± 0.184)**	0.506	230.504	-2.686	232.218	-1.772
	Lagged spring SST	1.060 (± 1.871)	-0.145 (± 0.218)	0.571	234.752	1.561	236.466	2.476
	Stratification onset	1.247 (± 1.733)	-0.015 (± 0.018)	0.566	234.518	1.327	236.262	2.242
	Lagged strat. onset	-0.929 (± 1.796)	0.008 (± 0.018)	0.575	235.018	1.827	236.732	2.741
	Winter PEA	-0.018 (± 0.325)	0.174 (± 0.313)	0.572	234.883	1.692	236.597	2.607
	Lagged winter PEA	-0.303 (± 0.325)	-0.122 (± 0.298)	0.575	235.023	1.833	236.737	2.747
	Winter SST	1.750 (± 1.618)	-0.289 (± 0.241)	0.556	233.806	0.616	235.520	1.530
	Lagged winter SST	0.427 (± 1.773)	-0.092 (± 0.266)	0.576	235.072	1.881	236.786	2.796
Fowlsheugh	Null model	**-0.472 (± 0.132)**	-	0.539	215.509	-	216.366	-
	Spring PEA	2.117 (± 2.534)	-0.829 (± 0.811)	0.523	216.490	0.982	218.336	1.971
	Lagged spring PEA	-0.865 (± 2.598)	0.126 (± 0.833)	0.538	217.486	1.977	219.332	2.966
	Spring SST	1.014 (± 2.282)	-0.173 (± 0.266)	0.532	217.088	1.579	218.934	2.568
	Lagged spring SST	1.677 (± 2.261)	-0.252 (± 0.265)	0.524	216.627	1.118	218.473	2.107
	Stratification onset	-1.338 (± 1.261)	0.009 (± 0.013)	0.531	217.038	1.529	218.884	2.518
	Lagged strat. onset	0.223 (± 1.236)	-0.007 (± 0.013)	0.534	217.192	1.683	219.038	2.672
	Winter PEA	**-0.495 (± 0.131)**	-0.261 (± 0.294)	0.526	216.737	1.228	218.583	2.217
	Lagged winter PEA	**-0.495 (± 0.133)**	-0.210 (± 0.277)	0.530	216.943	1.434	218.789	2.423
	Winter SST	0.965 (± 1.842)	-0.187 (± 0.239)	0.530	216.906	1.398	218.753	2.387
	Lagged winter SST	0.962 (± 1.889)	-0.188 (± 0.247)	0.529	216.940	1.431	218.786	2.420

Table S3.1 (cont.)

Site	Predictor variable	Intercept	Parameter estimate	Year RE	AIC	ΔAIC	AICc	ΔAICc
Isle of May	Null model	**-1.034 (± 0.236)**	-	0.997	258.389	-	259.189	-
	Spring PEA	0.141 (± 6.755)	-0.337 (± 1.939)	0.995	260.359	1.970	262.073	2.884
	Lagged spring PEA	0.712 (± 6.779)	-0.503 (± 1.953)	0.995	260.322	1.934	262.037	2.848
	Spring SST	2.700 (± 4.233)	-0.432 (± 0.489)	0.977	259.622	1.233	261.336	2.148
	Lagged spring SST	**7.168 (± 2.976)**	**-0.960 (± 0.348)**	0.831	254.011	-4.377	255.726	-3.463
	Stratification onset	**-4.353 (± 1.072)**	**0.076 (± 0.024)**	0.800	252.328	-6.061	254.042	-5.147
	Lagged strat. onset	-1.516 (± 1.309)	0.011 (± 0.029)	0.992	260.249	1.860	261.963	2.774
	Winter PEA	1.402 (± 1.830)	-1.297 (± 0.967)	0.952	258.666	0.277	260.380	1.191
	Lagged winter PEA	-0.679 (± 1.877)	-0.189 (± 0.993)	0.995	260.353	1.964	262.067	2.878
	Winter SST	0.758 (± 3.067)	-0.256 (± 0.437)	0.989	260.048	1.659	261.762	2.573
	Lagged winter SST	1.161 (± 2.974)	-0.316 (± 0.427)	0.980	259.850	1.461	261.564	2.376
St Abb's Head	Null model	**-0.502 (± 0.116)**	-	0.485	231.157	-	231.957	-
	Spring PEA	2.416 (± 2.910)	-0.829 (± 0.826)	0.472	232.176	1.019	233.890	1.933
	Lagged spring PEA	0.865 (± 3.046)	-0.390 (± 0.869)	0.482	232.956	1.799	234.670	2.714
	Spring SST	-0.155 (± 2.137)	-0.039 (± 0.240)	0.485	233.130	1.974	234.845	2.888
	Lagged spring SST	*2.783 (± 1.621)*	**-0.375 (± 0.185)**	0.437	229.428	-1.729	231.142	-0.815
	Stratification onset	**-1.998 (± 0.587)**	**0.023 (± 0.009)**	0.412	227.447	-3.709	229.162	-2.795
	Lagged strat. onset	-0.741 (± 0.679)	0.004 (± 0.010)	0.483	233.029	1.872	234.743	2.786
	Winter PEA	0.351 (± 0.487)	*-0.730 (± 0.408)*	0.445	230.208	-0.948	231.922	-0.034
	Lagged winter PEA	0.112 (± 0.495)	-0.528 (± 0.415)	0.464	231.607	0.450	233.321	1.365
	Winter SST	0.333 (± 1.594)	-0.115 (± 0.219)	0.482	232.882	1.725	234.596	2.639
	Lagged winter SST	0.702 (± 1.557)	-0.167 (± 0.216)	0.477	232.566	1.409	234.280	2.323

Table S3.2. Parameter estimates, AIC and ΔAIC from all-sites models with single predictor variables, fitted with Poisson error and log link. Fixed effects are reported as estimate (± standard error); random effects are reported as the standard deviation of the effect. ΔAIC was calculated relative to the null model for each site. Fixed effects highlighted in bold are those for which Wald Z tests indicated the parameter estimate was significantly different from 0; italics highlight marginally non-significant parameter estimates ($0.05 \leq P < 0.1$). See text for model fitting details.

Predictor variable	Intercept	Parameter estimate	Site RE	Region RE	Year RE	Site ∗ year RE	Region ∗ year RE	AIC	ΔAIC
Null model	**-0.532 (± 0.202)**	-	0.244	0.263	0.182	0.601	0.904	1885.454	-
Spring PEA	0.960 (± 0.674)	-0.485 (± 0.213)	0.332	0.000	0.114	0.574	0.932	1881.685	-3.769
Lagged spring PEA	0.836 (± 0.676)	**-0.446 (± 0.214)**	0.326	0.000	0.119	0.577	0.934	1882.769	-2.685
Spring SST	**4.323 (± 1.865)**	**-0.546 (± 0.207)**	0.244	0.429	0.000	0.574	0.907	1880.231	-5.223
Lagged spring SST	**3.793 (± 1.746)**	**-0.491 (± 0.196)**	0.247	0.398	0.000	0.582	0.901	1880.978	-4.477
Stratification onset	**-1.536 (± 0.546)**	*0.011 (± 0.006)*	0.326	0.338	0.134	0.558	0.939	1881.849	-3.605
Lagged strat. onset	-0.751 (± 0.458)	0.002 (± 0.004)	0.223	0.304	0.190	0.601	0.901	1887.186	1.731
Winter PEA	-0.284 (± 0.195)	**-0.444 (± 0.147)**	0.355	0.000	0.217	0.539	0.920	1874.959	-10.495
Lagged winter PEA	**-0.355 (± 0.176)**	**-0.354 (± 0.129)**	0.303	0.280	0.197	0.580	0.880	1878.297	-7.157
Winter SST	0.926 (± 1.311)	-0.188 (± 0.168)	0.303	0.173	0.000	0.594	0.920	1886.337	0.883
Lagged winter SST	0.302 (± 1.437)	-0.108 (± 0.185)	0.282	0.199	0.116	0.601	0.910	1887.133	1.678

Table S3.3 Parameter estimates, AIC, ΔAIC and Akaike weights from all-sites models fitted with multiple predictor variables, using Poisson error distribution and log link. Fixed effects are reported as estimate (± standard error); random effects are reported as the standard deviation of the effect. Fixed effects highlighted in bold are those for which Wald Z tests indicated the parameter estimate was significantly different from 0; italics highlight marginally non-significant parameter estimates (0.05 ≤ P < 0.1). See text for model fitting details.

Intercept	Spring PEA	Spring temperature	Stratification onset	Winter PEA	Winter temperature	Site RE	Region RE	Year RE	Site ∗ year RE	Region ∗ year RE	AIC	delta	weight
3.320 (± 1.685)	-	**-0.408 (± 0.189)**	-	**-0.424 (± 0.140)**	-	0.372	0.000	0.000	0.532	0.922	1872.433	-	0.243
3.245 (± 1.686)	-	*-0.507 (± 0.260)*	-	**-0.429 (± 0.141)**	0.125 (± 0.225)	0.385	0.001	0.000	0.531	0.918	1874.117	1.684	0.105
3.753 (± 1.863)	-0.138 (± 0.252)	**-0.412 (± 0.189)**	-	**-0.379 (± 0.163)**	-	0.380	0.000	0.000	0.531	0.923	1874.130	1.696	0.104
3.135 (± 1.744)	-	**-0.415 (± 0.190)**	0.003 (± 0.006)	**-0.392 (± 0.159)**	-	0.398	0.001	0.003	0.528	0.923	1874.236	1.803	0.099
-0.284 (± 0.195)	-	-	-	**-0.444 (± 0.147)**	-	0.355	0.000	0.217	0.539	0.920	1874.959	2.526	0.069
3.627 (± 1.865)	-0.127 (± 0.253)	*-0.498 (± 0.258)*	-	**-0.386 (± 0.165)**	0.113 (± 0.225)	0.388	0.001	0.004	0.531	0.920	1875.869	3.436	0.044
0.962 (± 1.276)	-	-	-	**-0.432 (± 0.143)**	-0.164 (± 0.166)	0.345	0.000	0.154	0.539	0.927	1875.999	3.566	0.041
3.540 (± 1.954)	-0.125 (± 0.258)	**-0.415 (± 0.189)**	0.002 (± 0.006)	**-0.358 (± 0.174)**	-	0.398	0.001	0.004	0.528	0.924	1876.009	3.576	0.041
3.145 (± 1.741)	-	*-0.495 (± 0.266)*	0.002 (± 0.006)	**-0.408 (± 0.013)**	0.103 (± 0.242)	0.400	0.001	0.001	0.529	0.920	1876.053	3.620	0.04
0.034 (± 0.773)	-0.110 (± 0.258)	-	-	**-0.412 (± 0.165)**	-	0.368	0.000	0.208	0.538	0.923	1876.774	4.340	0.028
-0.445 (± 0.629)	-	-	0.002 (± 0.006)	**-0.428 (± 0.160)**	-	0.377	0.000	0.208	0.535	0.926	1876.885	4.452	0.026
3.068 (± 1.896)	-	**-0.505 (± 0.201)**	*0.009 (± 0.005)*	-	-	0.302	0.430	0.000	0.548	0.918	1877.424	4.991	0.020
0.910 (± 1.297)	-	-	0.004 (± 0.006)	**-0.377 (± 0.167)**	-0.212 (± 0.180)	0.385	0.000	0.097	0.531	0.940	1877.537	5.104	0.019
1.441 (± 1.577)	-0.138 (± 0.260)	-	-	**-0.391 (± 0.163)**	-0.175 (± 0.168)	0.362	0.000	0.136	0.537	0.930	1877.713	5.279	0.017
3.545 (± 1.948)	-0.119 (± 0.258)	*-0.492 (± 0.264)*	0.001 (± 0.007)	**-0.375 (± 0.179)**	0.099 (± 0.242)	0.398	0.000	0.000	0.529	0.921	1877.841	5.407	0.016

4.880 (± 1.813)	**-0.480 (± 0.206)**	**-0.444 (± 0.189)**	-	-	-	0.343	0.001	0.000	0.559	0.926	1878.006	5.573	0.015

Table S3.3 (cont.)

Intercept	Spring PEA	Spring temperature	Stratification onset	Winter PEA	Winter temperature	Site RE	Region RE	Year RE	Site ∗ year RE	Region ∗ year RE	AIC	delta	weight
3.882 (± 1.976)	-0.344 (± 0.241)	**-0.451 (± 0.191)**	0.007 (± 0.006)	-	-	0.408	0.000	0.000	0.544	0.930	1878.248	5.815	0.013
-0.116 (± 1.026)	-0.105 (± 0.261)	-	0.001 (± 0.006)	**-0.399 (± 0.176)**	-	0.384	0.000	0.201	0.535	0.927	1878.722	6.289	0.010
1.337 (± 1.587)	-0.124 (± 0.263)	-	0.004 (± 0.006)	*-0.343 (± 0.183)*	-0.217 (± 0.180)	0.393	0.000	0.079	0.531	0.941	1879.313	6.880	0.008
3.063 (± 1.894)	-	*-0.525 (± 0.272)*	*0.009 (± 0.005)*	-	0.027 (± 0.240)	0.299	0.436	0.000	0.548	0.918	1879.412	6.979	0.007
4.765 (± 1.817)	**-0.473 (± 0.021)**	**-0.502 (± 0.253)**	-	-	0.08 (± 0.216)	0.343	0.008	0.003	0.559	0.926	1879.866	7.432	0.006
4.322 (± 1.865)	-	**-0.545 (± 0.207)**	-	-	-	0.244	0.429	0.000	0.574	0.907	1880.231	7.798	0.005
3.881 (± 1.977)	-0.343 (± 0.241)	-0.435 (± 0.266)	0.007 (± 0.006)	-	-0.021 (± 0.239)	0.407	0.001	0.000	0.544	0.930	1880.241	7.807	0.005
0.690 (± 1.321)	-	-	**0.013 (± 0.005)**	-	*-0.313 (± 0.173)*	0.421	0.000	0.000	0.548	0.944	1880.814	8.381	0.004
1.898 (± 1.560)	-0.332 (± 0.242)	-	*0.009 (± 0.006)*	-	*-0.296 (± 0.173)*	0.403	0.000	0.000	0.547	0.943	1880.926	8.492	0.003
4.023 (± 1.855)	-	**-0.688 (± 0.251)**	-	-	0.203 (± 0.209)	0.216	0.465	0.000	0.574	0.904	1881.323	8.889	0.003
0.959 (± 0.674)	**-0.485 (± 0.213)**	-	-	-	-	0.332	0.000	0.114	0.574	0.932	1881.685	9.252	0.002
-1.536 (± 0.546)	-	-	*0.011 (± 0.006)*	-	-	0.326	0.338	0.134	0.558	0.939	1881.849	9.416	0.002
-0.094 (± 1.078)	-0.362 (± 0.244)	-	0.008 (± 0.006)	-	-	0.408	0.000	0.089	0.552	0.951	1881.870	9.437	0.002
2.645 (± 1.487)	**-0.504 (± 0.215)**	-	-	-	-0.213 (± 0.164)	0.343	0.000	0.000	0.571	0.930	1881.973	9.540	0.002

-0.532 (± 0.202)	-	-	-	-	-	0.244	0.263	0.182	0.601	0.904	1885.454	13.021	0.000
0.926 (± 1.311)	-	-	-	-	-0.188 (± 0.168)	0.303	0.172	0.000	0.594	0.920	1886.337	13.904	0.000

Table S3.4. Projections of mean fledged chicks under the UKCP09 climatic baseline period of 1961-90 and for 2070-99 under the SRES A1B scenario. Reported values are the mean of 100,000 randomisation runs, where each run produces a mean number of fledged chicks across all years in the time period. The standard deviation of the 100,000 projections is also given. Proportional change is calculated as ((future - baseline)/baseline), based on the mean for each period. To indicate the probability of decline, the difference between the baseline and future projections was calculated for each run, and the proportion of these differences > 0 (i.e. those not showing a decline) was calculated.

Site	Mean predicted 1961 – 1990 fledged chicks (± st. dev.)	Mean predicted 2070 – 2099 fledged chicks (± st. dev.)	Proportional change	Proportion of projections not showing decline
Bardsey Island	1.498 (± 0.818)	0.665 (± 0.543)	-55.6%	0.032
Boddam to Collieston	2.875 (± 1.728)	1.369 (± 0.772)	-52.4%	0.136
Coquet Island	6.506 (± 3.883)	2.768 (± 1.778)	-57.5%	0.100
Fair Isle	1.407 (± 0.718)	0.557 (± 0.246)	-60.4%	0.016
Flamborough Head and Bempton Cliffs	3.087 (± 1.900)	1.141 (± 0.678)	-63.0%	0.056
Fowlsheugh	3.256 (± 1.927)	1.539 (± 0.875)	-52.7%	0.143
Isle of Colonsay	2.674 (± 1.747)	1.097 (± 0.672)	-59.0%	0.054
Isle of May	1.953 (± 1.042)	0.798 (± 0.374)	-59.2%	0.088
Lambay	1.882 (± 0.811)	0.899 (± 0.704)	-52.3%	0.079
Puffin Island	3.990 (± 3.126)	1.783 (± 1.748)	-55.3%	0.035
St Abb’s Head	3.047 (± 1.542)	1.262 (± 0.617)	-58.6%	0.082
Across all sites	2.925 (± 1.290)	1.261 (± 0.638)	-56.9%	0.063

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Appendix S4: results from models testing for trends over time, and from models trialling different forms of input variables

Breeding success and oceanographic variables were tested for trends over time (Table S4.1). Breeding success trends were tested using generalised linear mixed models with binomial error and logit link, with 'year' as a continuous predictor, and with the response a matrix with the number of fledged chicks as successes and the estimated number of failed chicks as failures; random factors were 'site', 'region', 'year', 'site*year' and 'region*year' in models including all colonies, and 'year' for single colony models. Trends in oceanographic variables were modelled in the same framework but with Gaussian error structure, and with observation-level random factors removed (i.e., 'site*year' and 'year' for all-sites and single-site models respectively); therefore, no random factors were required for local-scale models, meaning that they were fitted as standard linear models. Breeding success models showed convergence problems when fitted with raw 'year' input, so 'year' was scaled and centred. This reduced convergence problems, but means that parameters are not strictly comparable with those from oceanographic trend models.

Results of Spearman correlations to test for collinearity between predictor variables are presented in Table S4.2. Correlation coefficients were typically weak to moderate; see the main text for discussion of stronger correlations.

Models of productivity were fitted using both log-transformed and untransformed PEA (Table S4.3). For both spring and winter PEA, models with log-transformed PEA were associated with smaller AIC values than were models with untransformed PEA.

Productivity models were fitted with variables with a 1-year lag (Table S4.4; Fig. S4.1) for comparison with those without a lag (main text Table 2 and Fig. 2). Lagged spring SST showed support over the null model at Fair Isle, Isle of May and St Abb's Head; as with the unlagged form, higher productivity was associated with lower SSTs. The relationships at Isle of May and St Abb's Head were not found with the unlagged form, but the relationship at Fair Isle was weaker than the unlagged equivalent. The only other models that performed better than the null model were negative relationships with winter PEA at Bardsey Island and spring PEA at Fair Isle; both were less well supported than the unlagged equivalents. For models including data from all colonies, relationships were similar to those without lags, but ΔAIC was always greater for the unlagged form, indicating that unlagged variables performed better. Therefore, with the exception of spring SST at Isle of May and St Abb’s Head, lagged variables performed worse than unlagged equivalents.

Table S4.1 Results from models of breeding success and oceanographic variables against time. Results presented indicate the parameter estimate of the predictor variable, along with its associated *P*-value; bold indicates that the parameter estimate is significantly different from 0; italics indicate the estimate is marginally non-significantly different from 0 (i.e., $0.05 \leq P < 0.1$). Models of breeding success in Lambay and Puffin Island could not be fitted due to limited years of data. To aid model convergence, breeding success models were fitted using scaled and centred year; see text for further details of model fitting.

	Breeding success	Winter SST	Winter PEA	Spring SST	Spring PEA	Stratification onset
Across all sites	-0.235 (± 0.159), P = 0.141	0.038 (± 0.019), P = 0.054	0.020 (± 0.010), P = 0.046	0.044 (± 0.018), P = 0.026	0.006 (± 0.004), P = 0.173	-0.316 (± 0.180), P = 0.096
Bardsey Island	**0.724 (± 0.348), *P* = 0.038**	**0.052 (± 0.023), *P* = 0.035**	-0.011 (± 0.020), *P* = 0.588	**0.057 (± 0.020), *P* = 0.009**	-0.002 (± 0.007), *P* = 0.782	0.026 (± 0.769), *P* = 0.973
Boddam to Collieston	-0.179 (± 0.312), *P* = 0.567	*0.040 (± 0.021), P = 0.073*	*0.039 (± 0.022), P = 0.092*	*0.037 (± 0.018), P = 0.057*	0.005 (± 0.008), *P* = 0.589	**-1.285 (± 0.491), *P* = 0.018**
Coquet Island	0.336 (± 0.276), *P* = 0.224	**0.046 (± 0.021), *P* = 0.043**	0.003 (± 0.021), *P* = 0.904	*0.048 (± 0.024), P = 0.061*	0.007 (± 0.006), *P* = 0.264	-0.102 (± 0.522), *P* = 0.848
Fair Isle	-0.970 (± 0.706), *P* = 0.170	0.026 (± 0.017), *P* = 0.133	0.028 (± 0.022), *P* = 0.224	*0.039 (± 0.019), P = 0.052*	*0.009 (± 0.005), P = 0.076*	*-0.956 (± 0.475), P = 0.061*
Flamborough Head and Bempton Cliffs	**-0.560 (± 0.186), *P* = 0.003**	**0.047 (± 0.021), *P* = 0.037**	0.013 (± 0.018), *P* = 0.482	**0.069 (± 0.023), *P* = 0.008**	0.013 (± 0.008), *P* = 0.129	0.184 (± 0.322), *P* = 0.576
Fowlsheugh	**-0.361 (± 0.181), *P* = 0.047**	*0.040 (± 0.021), P = 0.070*	0.035 (± 0.020), *P* = 0.101	*0.038 (± 0.019), P = 0.067*	0.006 (± 0.007), *P* = 0.407	**-1.043 (± 0.381), *P* = 0.014**
Isle of Colonsay	-0.379 (± 0.432), *P* = 0.381	0.031 (± 0.023), *P* = 0.192	0.020 (± 0.017), *P* = 0.260	*0.043 (± 0.024), P = 0.086*	-0.002 (± 0.008), *P* = 0.801	-0.851 (± 0.529), *P* = 0.126
Isle of May	-0.190 (± 0.310), *P* = 0.541	0.035 (± 0.023), *P* = 0.138	**0.023 (± 0.009), *P* = 0.016**	0.032 (± 0.024), *P* = 0.194	0.002 (± 0.005), *P* = 0.670	**-0.767 (± 0.299), *P* = 0.020**
Lambay	-	**0.050 (± 0.021), *P* = 0.029**	-0.001 (± 0.024), *P* = 0.982	0.037 (± 0.025), *P* = 0.164	-0.002 (± 0.005), *P* = 0.659	0.458 (± 0.530), *P* = 0.400
Puffin Island	-	*0.045 (± 0.023), P = 0.064*	0.008 (± 0.012), *P* = 0.507	**0.056 (± 0.019), *P* = 0.008**	0.001 (± 0.008), *P* = 0.917	0.634 (± 0.515), *P* = 0.235
St. Abb’s Head	**-0.380 (± 0.167), *P* = 0.023**	*0.042 (± 0.022), P = 0.069*	**0.022 (± 0.010), *P* = 0.048**	*0.041 (± 0.023), P = 0.092*	0.007 (± 0.006), *P* = 0.255	-0.513 (± 0.462), *P* = 0.282

Table S4.2 Spearman rank correlations between predictor variables, and associated *P*-values. Correlations were tested at the national scale (i.e. across all sites).

	Strat. onset	**Lagged strat. onset**	**Spring PEA**	**Lagged spring PEA**	**Spring SST**	**Lagged spring SST**	**Winter PEA**	**Lagged winter PEA**	**Winter SST**
Lagged strat. onset	ρ = 0.815 *P* < 0.001	-							
Spring PEA	ρ = -0.559 *P* < 0.001	ρ = -0.529 *P* < 0.001	-						
Lagged spring PEA	ρ = -0.537 *P* < 0.001	ρ = -0.558 *P* < 0.001	ρ = 0.169 *P* = 0.006	-					
Spring SST	ρ = -0.210 *P* < 0.001	ρ = -0.199 *P* = 0.001	ρ = 0.212 *P* < 0.001	ρ = 0.174 *P* = 0.005	-				
Lagged spring SST	ρ = -0.229 *P* < 0.001	ρ = -0.209 *P* < 0.001	ρ = 0.169 *P* = 0.006	ρ = 0.208 *P* = 0.001	ρ = 0.647 *P* < 0.001	-			
Winter PEA	ρ = -0.485 *P* < 0.001	ρ = -0.411 *P* < 0.001	ρ = 0.669 *P* < 0.001	ρ = 0.681 *P* < 0.001	ρ = 0.165 *P* = 0.007	ρ = 0.148 *P* = 0.016	-		
Lagged winter PEA	ρ = -0.428 *P* < 0.001	ρ = -0.465 *P* < 0.001	ρ = 0.681 *P* < 0.001	ρ = 0.681 *P* < 0.001	ρ = 0.112 *P* = 0.069	ρ = 0.166 *P* = 0.007	ρ = 0.825 *P* < 0.001	-	
Winter SST	ρ = 0.197 *P* = 0.001	ρ = 0.183 *P* = 0.003	ρ = 0.070 *P* = 0.257	ρ = 0.340 *P* = 0.059	ρ = 0.672 *P* < 0.001	ρ = 0.481 *P* < 0.001	ρ = 0.093 *P* = 0.131	ρ = 0.052 *P* = 0.395	-
Lagged winter SST	ρ = 0.162 *P* < 0.008	ρ = 0.212 *P* < 0.001	ρ = 0.072 *P* < 0.241	ρ = 0.061 *P* = 0.320	ρ = 0.488 *P* < 0.001	ρ = 0.655 *P* < 0.001	ρ = 0.051 *P* = 0.411	ρ = 0.097 *P* = 0.116	ρ = 0.673 *P* < 0.001

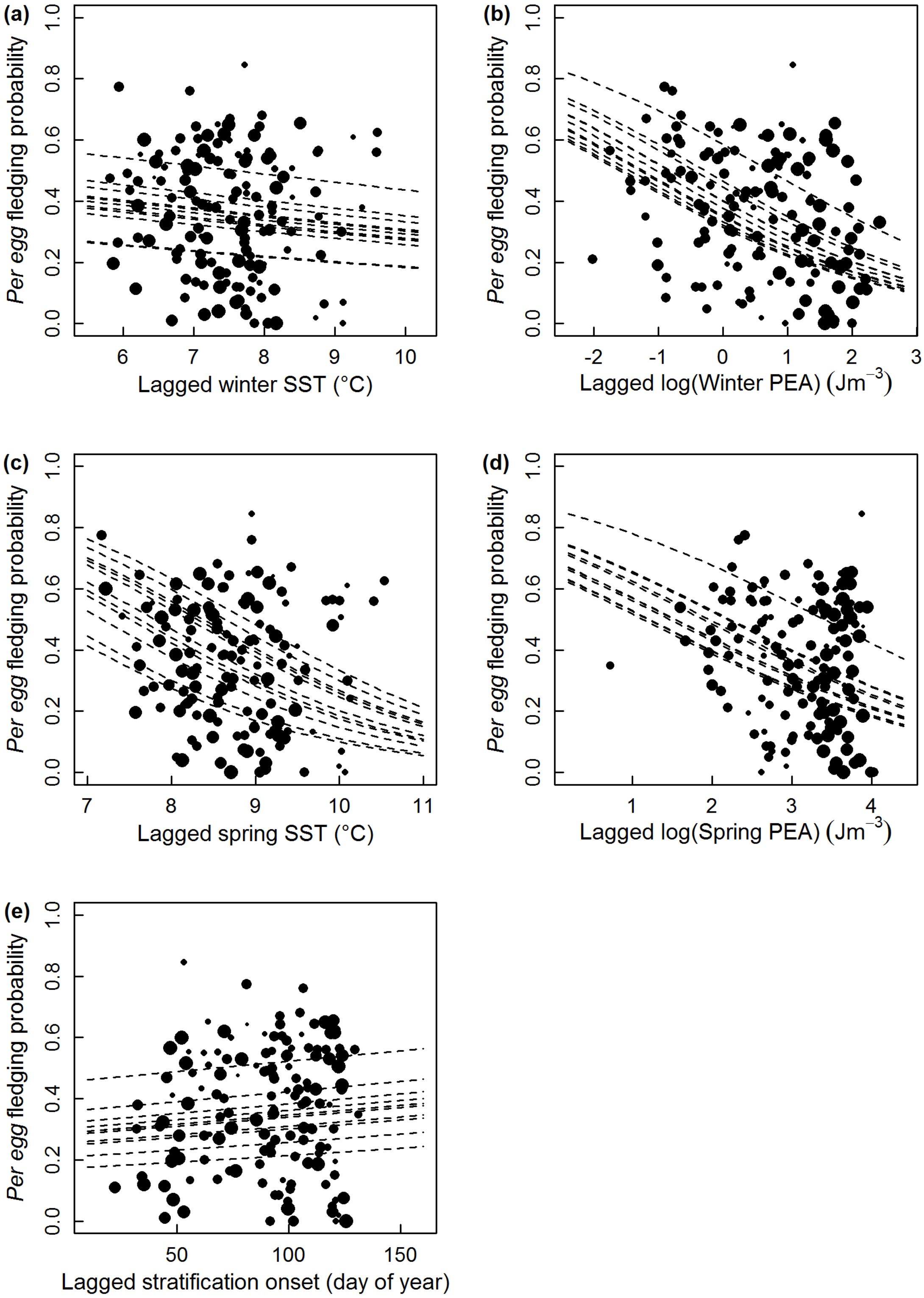
Table S4.3. Results from models of breeding success with log-transformed and untransformed PEA as predictors, fitted to data from all sites. Models were GLMMs with binomial error distribution, logit link function and 'year', 'site', 'region', 'site*year' and 'region*year' random effects. ΔAIC values are calculated relative to the null model, fitted with only intercept and random effects.

Variable	Parameter estimate (± SE)	*P* value	AIC	ΔAIC
Null model	-	-	1803.730	-
Spring PEA	-0.024 (± 0.014)	0.104	1803.181	-0.549
Log(spring PEA)	-0.602 (± 0.285)	0.035	1801.062	-2.669
Winter PEA	-0.217 (± 0.070)	0.002	1793.519	-10.211
Log(winter PEA)	-0.641 (± 0.201)	0.001	1792.228	-11.502

Table S4.4. Results from models relating breeding success to single oceanographic predictor variables with a 1-year lag. See main text for details of model fitting. Parameter estimates (± SE) are given, along with the ΔAIC (for all-sites models) or ΔAICc (for individual site models) value relative to a null model fitted with intercept and random effects only. Parameter estimates significantly different from 0 at $P < 0.05$, as indicated by Wald Z tests, are bold; results approaching but not attaining significance with $0.05 \leq P < 0.1$ are italic. Full model details are given in Supporting Information 5.

	Bardsey Island	Boddam to Collieston	Coquet Island	Fair Isle	Flamborough Head and Bempton Cliffs	Fowlsheugh	Isle of May	St Abb's Head	All sites
Null model	AICc = 187.621	AICc = 178.476	AICc = 103.824	AICc = 278.788	AICc = 225.489	AICc = 214.311	AICc = 254.784	AICc = 230.539	AIC = 1803.730
Lagged winter SST	0.037 (± 0.632), ΔAICc = 2.986	-0.496 (± 0.508), ΔAICc = 2.257	0.124 (± 0.326), ΔAICc = 3.522	-2.052 (± 1.732), ΔAICc = 1.473	-0.068 (± 0.433), ΔAICc = 2.889	-0.281 (± 0.378), ΔAICc = 2.445	-0.429 (± 0.523), ΔAICc = 2.254	-0.251 (± 0.324), ΔAICc = 2.323	-0.105 (± 0.248), ΔAIC = 1.827
Lagged winter PEA	**-2.133 (± 1.052), ΔAICc = -0.886**	-0.130 (± 0.536), ΔAICc = 3.123	0.244 (± 0.425), ΔAICc = 3.343	-1.880 (± 1.203), ΔAICc = 0.524	-0.110 (± 0.484), ΔAICc = 2.863	-0.376 (± 0.421), ΔAICc = 2.209	-0.510 (± 1.212), ΔAICc = 2.738	-0.862 (± 0.619), ΔAICc = 1.074	**-0.483 (± 0.175), ΔAIC = -7.091**
Lagged spring SST	-0.234 (± 0.689), ΔAICc = 2.874	0.017 (± 0.605), ΔAICc = 3.181	-0.043 (± 0.366), ΔAICc = 3.653	**-3.115 (± 1.399), ΔAICc = -2.046**	-0.221 (± 0.353), ΔAICc = 2.526	-0.425 (± 0.404), ΔAICc = 1.916	**-1.192 (± 0.425), ΔAICc = -3.636**	*-0.541 (± 0.280), ΔAICc = -0.502*	**-0.621 (± 0.250), ΔAIC = -4.247**
Lagged spring PEA	-3.720 (± 2.478), ΔAICc = 0.873	1.644 (± 1.225), ΔAICc = 1.478	1.013 (± 1.051), ΔAICc = 2.778	*-10.901 (± 6.243), ΔAICc = -0.191*	-1.140 (± 1.072), ΔAICc = 1.817	0.244 (± 1.274), ΔAICc = 2.952	-0.279 (± 2.398), ΔAICc = 2.901	-0.451 (± 1.311), ΔAICc = 2.796	*-0.528 (± 0.283), ΔAIC = -1.381*
Lagged stratification onset	-0.031 (± 0.032), ΔAICc = 2.047	-0.019 (± 0.019), ΔAICc = 2.258	0.002 (± 0.015), ΔAICc = 3.647	0.068 (± 0.059), ΔAICc = 1.572	0.004 (± 0.030), ΔAICc = 2.893	-0.008 (± 0.020), ΔAICc = 2.831	0.019 (± 0.036), ΔAICc = 2.632	0.007 (± 0.016), ΔAICc = 2.713	0.003 (± 0.005), ΔAIC = 1.756

Figure S4.1. Plots of breeding success against oceanographic predictor variables with a 1-year lag, along with fitted lines from binomial GLMMs including the ‘site’ and ‘region’ random effects. Each point represents one site-by-year observation; point sizes are scaled by log(nests surveyed) to reflect weightings of observations in models.



Appendix S5: full model results from main analysis

Full details of models relating breeding success to single oceanographic predictor variables for single sites are given in Table S5.1. Only sites with ≥ 10 years of overlapping oceanographic and breeding success data were selected for this analysis. Models were generalised linear mixed models with binomial error structure and logit link. Only one predictor variable was entered into each model to avoid overfitting. The response variable was a matrix with number of fledged chicks as success and estimated number of failed chicks as failures. Only a 'year' random factor was fitted, which in these models represented an observation-level factor used to model overdispersion. The effect of each predictor variable was assessed by comparing each model's AICc to that from a null model, fitted with intercept and random effect only.

Full details of models relating breeding success to oceanographic predictor variables across all sites are given in Tables S5.2 (single predictor variable models) and S5.3 (multiple predictor variable models). Models were generalised linear mixed models with binomial error structure and logit link. For multiple predictor models, up to 5 predictor variables were fitted in each model, with no interaction terms considered. The response variable was a matrix with number of fledged chicks as successes and estimated number of failed chicks as failures. Random effects were 'site', 'region', 'year', 'site*year' and 'region*year', with the 'site*year' effect an observation-level factor used to model overdispersion. Single predictor variable models were assessed by comparing each model's AIC to that from a null model. Multiple predictor variable models were ranked by AIC, allowing all models to be compared to the best single model.

Table S5.1. Parameter estimates, AIC and ΔAIC from model fitting for single-site models with single predictor variables. Fixed effects are reported as estimate (± standard error); the 'year' random effect is reported as the standard deviation of the effect. ΔAIC was calculated relative to the null model for each site. Fixed effects highlighted in bold are those for which Wald Z tests indicated the parameter estimate was significantly different from 0; italics highlight marginally non-significant estimates ($0.05 \leq P < 0.1$). See text for model fitting details.

Site	Predictor variable	Intercept	Parameter estimate	Year RE	AIC	ΔAIC	AICc	ΔAICc
Bardsey Island	Null model	**-0.888 (± 0.373)**	-	1.507	186.764	-	187.621	-
	Spring PEA	3.668 (± 6.012)	-1.719 (± 2.266)	1.483	188.195	1.431	190.042	2.420
	Lagged spring PEA	8.924 (± 6.534)	-3.720 (± 2.478)	1.401	186.648	-0.116	188.494	0.873
	Spring SST	-13.877 (± 8.707)	1.311 (± 0.877)	1.431	186.582	-0.182	188.428	0.807
	Lagged spring SST	1.411 (± 6.776)	-0.234 (± 0.689)	1.504	188.649	1.885	190.495	2.874
	Stratification onset	**-5.369 (± 2.133)**	**0.041 (± 0.019)**	1.351	184.420	-2.345	186.266	-1.356
	Lagged strat. onset	2.628 (± 3.609)	-0.031 (± 0.032)	1.470	187.822	1.058	189.668	2.047
	Winter PEA	-0.111 (± 0.449)	**-1.645 (± 0.693)**	1.295	183.685	-3.079	185.531	-2.090
	Lagged winter PEA	-0.086 (± 0.511)	**-2.133 (± 1.052)**	1.359	184.889	-1.875	186.735	-0.886
	Winter SST	*-8.998 (± 5.082)*	0.928 (± 0.579)	1.412	186.291	-0.473	188.137	0.516
	Lagged winter SST	-1.213 (± 5.513)	0.037 (± 0.632)	1.506	188.761	1.997	190.607	2.986
Boddam to Collieston	Null model	**-1.113 (± 0.259)**	-	0.995	177.476	-	178.476	-
	Spring PEA	-0.751 (± 4.170)	-0.123 (± 1.414)	0.994	179.468	1.992	181.650	3.174
	Lagged spring PEA	-5.996 (± 3.648)	1.644 (± 1.225)	0.940	177.772	0.296	179.953	1.478
	Spring SST	-1.606 (± 5.092)	0.057 (± 0.593)	0.995	179.466	1.991	181.648	3.172
	Lagged spring SST	-1.260 (± 5.207)	0.017 (± 0.605)	0.995	179.475	1.999	181.657	3.181
	Stratification onset	*-3.579 (± 1.902)*	0.024 (± 0.018)	0.942	177.855	0.380	180.037	1.561
	Lagged strat. onset	0.837 (± 2.014)	-0.019 (± 0.019)	0.964	178.552	1.076	180.733	2.258
	Winter PEA	**-1.115 (± 0.258)**	-0.141 (± 0.488)	0.992	179.393	1.917	181.574	3.099
	Lagged winter PEA	-1.111 (± 0.258)	-0.130 (± 0.536)	0.993	179.417	1.941	181.599	3.123
	Winter SST	-2.474	0.175	0.99	179.35	1.87	181.53	3.059

	(± 3.875)	(± 0.498)	0	3	7	4	
Lagged winter SST	2.744 (± 3.960)	-0.496 (± 0.508)	0.965	178.551	1.075	180.732	2.257

Table S5.1 (cont.)

Site	Predictor variable	Intercept	Parameter estimate	Year RE	AIC	ΔAIC	AICc	ΔAICc
Coquet Island	Null model	0.233 (± 0.178)	-	0.579	102.490	-	103.824	-
	Spring PEA	-4.245 (± 3.532)	1.228 (± 0.968)	0.541	102.964	0.473	105.964	2.140
	Lagged spring PEA	-3.445 (± 3.819)	1.013 (± 1.051)	0.552	103.601	1.111	106.601	2.778
	Spring SST	0.775 (± 3.109)	-0.061 (± 0.352)	0.578	104.460	1.970	107.460	3.636
	Lagged spring SST	0.612 (± 3.224)	-0.043 (± 0.366)	0.578	104.477	1.986	107.477	3.653
	Stratification onset	-0.999 (± 0.940)	0.018 (± 0.014)	0.538	102.816	0.325	105.816	1.992
	Lagged strat. onset	0.088 (± 1.040)	0.002 (± 0.015)	0.578	104.470	1.980	107.470	3.647
	Winter PEA	**0.742 (± 0.297)**	**-0.697 (± 0.346)**	0.493	100.933	-1.558	103.933	0.109
	Lagged winter PEA	0.047 (± 0.369)	0.244 (± 0.425)	0.569	104.167	1.676	107.167	3.343
	Winter SST	0.791 (± 2.343)	-0.075 (± 0.315)	0.577	104.433	1.943	107.433	3.610
	Lagged winter SST	-0.679 (± 2.402)	0.124 (± 0.326)	0.575	104.346	1.856	107.346	3.522
Fair Isle	Null model	**-1.815 (± 0.695)**	-	2.985	278.038	-	278.788	-
	Spring PEA	**49.179 (± 20.227)**	**-13.414 (± 5.332)**	2.586	273.871	-4.166	275.471	-3.316
	Lagged spring PEA	*39.437 (± 23.595)*	*-10.901 (± 6.243)*	2.780	276.997	-1.041	278.597	-0.191
	Spring SST	**34.932 (± 10.162)**	**-4.280 (± 1.189)**	2.225	268.509	-9.529	270.109	-8.679
	Lagged spring SST	**24.732 (± 11.892)**	**-3.115 (± 1.399)**	2.671	275.142	-2.896	276.742	-2.046
	Stratification onset	-6.486 (± 6.587)	0.042 (± 0.058)	2.962	279.535	1.498	281.135	2.348
	Lagged strat. onset	-9.526 (± 6.744)	0.068 (± 0.059)	2.892	278.760	0.722	280.360	1.572
	Winter PEA	-0.513 (± 1.905)	-0.942 (± 1.295)	2.929	279.523	1.486	281.123	2.336
	Lagged winter PEA	0.823 (± 1.795)	-1.880 (± 1.203)	2.800	277.712	-0.326	279.312	0.524
	Winter SST	**26.625 (± 11.439)**	**-3.661 (± 1.474)**	2.535	274.626	-3.411	276.226	-2.561
	Lagged winter SST	14.057 (± 13.397)	-2.052 (± 1.732)	2.894	278.661	0.623	280.261	1.473

Table S5.1 (cont.)

Site	Predictor variable	Intercept	Parameter estimate	Year RE	AIC	ΔAIC	AICc	ΔAICc
Flamborough Head and Bempton Cliffs	Null model	-0.166 (± 0.222)	-	0.938	224.689	-	225.489	-
	Spring PEA	**5.717 (± 2.146)**	**-2.502 (± 0.909)**	0.785	220.357	-4.332	222.072	-3.417
	Lagged spring PEA	2.484 (± 2.502)	-1.140 (± 1.072)	0.910	225.591	0.902	227.306	1.817
	Spring SST	**5.594 (± 2.613)**	**-0.663 (± 0.300)**	0.831	222.359	-2.330	224.073	-1.416
	Lagged spring SST	1.730 (± 3.036)	-0.221 (± 0.353)	0.928	226.301	1.612	228.015	2.526
	Stratification onset	2.014 (± 2.816)	-0.023 (± 0.029)	0.922	226.096	1.407	227.810	2.321
	Lagged strat. onset	-0.589 (± 2.926)	0.004 (± 0.030)	0.937	226.668	1.979	228.382	2.893
	Winter PEA	0.072 (± 0.527)	0.253 (± 0.509)	0.931	226.443	1.754	228.157	2.668
	Lagged winter PEA	-0.275 (± 0.527)	-0.110 (± 0.484)	0.937	226.637	1.948	228.351	2.863
	Winter SST	2.735 (± 2.635)	-0.434 (± 0.393)	0.907	225.508	0.819	227.222	1.733
	Lagged winter SST	0.287 (± 2.883)	-0.068 (± 0.433)	0.937	226.664	1.975	228.378	2.889
Fowlsheugh	Null model	**-0.685 (± 0.202)**	-	0.827	213.453	-	214.311	-
	Spring PEA	2.986 (± 3.889)	-1.176 (± 1.244)	0.806	214.582	1.128	216.428	2.117
	Lagged spring PEA	-1.445 (± 3.975)	0.244 (± 1.274)	0.826	215.417	1.963	217.263	2.952
	Spring SST	1.368 (± 3.499)	-0.239 (± 0.407)	0.819	215.111	1.658	216.957	2.647
	Lagged spring SST	2.936 (± 3.446)	-0.425 (± 0.404)	0.801	214.380	0.927	216.226	1.916
	Stratification onset	-1.951 (± 1.935)	0.013 (± 0.020)	0.816	215.025	1.572	216.872	2.561
	Lagged strat. onset	0.069 (± 1.903)	-0.008 (± 0.020)	0.823	215.296	1.842	217.142	2.831
	Winter PEA	**-0.718 (± 0.201)**	-0.388 (± 0.451)	0.809	214.72	1.274	216.574	2.263

					8			
	Lagged winter PEA	**-0.725 (± 0.202)**	-0.376 (± 0.421)	0.808	214.674	1.220	216.520	2.209
	Winter SST	1.388 (± 2.818)	-0.270 (± 0.366)	0.814	214.917	1.464	216.763	2.453
	Lagged winter SST	1.462 (± 2.895)	-0.281 (± 0.378)	0.813	214.910	1.456	216.756	2.445

Table S5.1 (cont.)

Site	Predictor variable	Intercept	Parameter estimate	Year RE	AIC	ΔAIC	AICc	ΔAICc
Isle of May	Null model	**-1.408 (± 0.289)**	-	1.223	253.984	-	254.784	-
	Spring PEA	0.990 (± 8.263)	-0.689 (± 2.371)	1.219	255.900	1.916	257.614	2.830
	Lagged spring PEA	-0.439 (± 8.325)	-0.279 (± 2.398)	1.222	255.971	1.986	257.685	2.901
	Spring SST	2.810 (± 5.200)	-0.488 (± 0.601)	1.202	255.334	1.350	257.049	2.264
	Lagged spring SST	**8.777 (± 3.636)**	**-1.192 (± 0.425)**	1.017	249.434	-4.550	251.148	-3.636
	Stratification onset	**-5.411 (± 1.316)**	**0.092 (± 0.030)**	0.988	248.215	-5.769	249.929	-4.855
	Lagged strat. onset	-2.247 (± 1.599)	0.019 (± 0.036)	1.212	255.702	1.718	257.416	2.632
	Winter PEA	1.367 (± 2.256)	-1.478 (± 1.192)	1.175	254.505	0.520	256.219	1.435
	Lagged winter PEA	-0.452 (± 2.292)	-0.510 (± 1.212)	1.216	255.808	1.824	257.522	2.738
	Winter SST	0.575 (± 3.757)	-0.283 (± 0.535)	1.214	255.705	1.721	257.420	2.636
	Lagged winter SST	1.567 (± 3.635)	-0.429 (± 0.523)	1.199	255.323	1.339	257.038	2.254
St Abb's Head	Null model	**-0.754 (± 0.174)**	-	0.731	229.739	-	230.539	-
	Spring PEA	3.391 (± 4.370)	-1.177 (± 1.241)	0.714	230.859	1.120	232.573	2.034
	Lagged spring PEA	0.825 (± 4.595)	-0.451 (± 1.311)	0.729	231.621	1.882	233.335	2.796
	Spring SST	-0.540 (± 3.211)	-0.024 (± 0.361)	0.731	231.735	1.996	233.449	2.910
	Lagged spring SST	3.993 (± 2.457)	*-0.541 (± 0.280)*	0.665	228.323	-1.416	230.037	-0.502
	Stratification onset	**-2.972 (± 0.881)**	**0.034 (± 0.013)**	0.625	226.160	-3.579	227.875	-2.665
	Lagged strat. onset	-1.205 (± 1.018)	0.007 (± 0.016)	0.727	231.538	1.799	233.252	2.713
	Winter PEA	0.513 (± 0.733)	*-1.085 (± 0.613)*	0.674	228.853	-0.886	230.568	0.029
	Lagged winter PEA	0.248 (± 0.738)	-0.862 (± 0.619)	0.695	229.898	0.159	231.613	1.074
	Winter SST	0.133 (± 2.396)	-0.122 (± 0.328)	0.729	231.602	1.863	233.316	2.777
	Lagged winter SST	1.057 (± 2.342)	-0.251 (± 0.324)	0.719	231.148	1.409	232.862	2.323

Table S5.2. Parameter estimates, AIC and ΔAIC from all-sites models with single predictor variables. Fixed effects are reported as estimate (± standard error); random effects are reported as the standard deviation of the effect. ΔAIC was calculated relative to the null model for each site. Fixed effects highlighted in bold are those for which Wald Z tests indicated the parameter estimate was significantly different from 0; italics highlight marginally non-significant parameter estimates ($0.05 \leq P < 0.1$). See text for model fitting details.

Predictor variable	Intercept	Parameter estimate	Site RE	Region RE	Year RE	Site * year RE	Region * year RE	AIC	ΔAIC
Null model	-0.677 (± 0.268)	-	0.315	0.373	0.263	0.790	1.146	1803.730	-
Spring PEA	1.174 (± 0.895)	**-0.602 (± 0.285)**	0.461	0.000	0.183	0.754	1.189	1801.062	-2.669
Lagged spring PEA	0.945 (± 0.889)	*-0.528 (±0.283)*	0.447	0.000	0.176	0.759	1.194	1802.349	-1.381
Spring SST	**5.554 (± 2.371)**	**-0.700 (± 0.264)**	0.323	0.545	0.000	0.756	1.154	1798.488	-5.242
Lagged spring SST	**4.792 (± 2.227)**	**-0.621 (± 0.250)**	0.326	0.509	0.000	0.766	1.150	1799.483	-4.247
Stratification onset	**-1.964 (± 0.709)**	*0.014 (±0.007)*	0.432	0.448	0.221	0.736	1.186	1800.347	-3.383
Lagged strat. onset	-0.941 (± 0.592)	0.003 (± 0.005)	0.298	0.406	0.267	0.790	1.142	1805.486	1.756
Winter PEA	-0.322 (± 0.263)	**-0.641 (± 0.201)**	0.517	0.000	0.320	0.694	1.177	1792.228	-11.502
Lagged winter PEA	*-0.436 (±0.235)*	**-0.483 (± 0.175)**	0.430	0.000	0.285	0.756	1.123	1796.639	-7.091
Winter SST	1.184 (± 1.801)	-0.240 (± 0.231)	0.388	0.276	0.093	0.781	1.170	1804.724	0.994
Lagged winter SST	0.134 (± 1.927)	-0.105 (± 0.248)	0.350	0.323	0.218	0.789	1.152	1805.557	1.827

Table S5.3. Parameter estimates, AIC, ΔAIC and Akaike weights from all-sites models with multiple predictor variables. Fixed effects are reported as estimate (± standard error); random effects are reported as the standard deviation of the effect. Fixed effects highlighted in bold are those for which Wald Z tests indicated the parameter estimate was significantly different from 0. See text for model fitting details.

Intercept	Spring PEA	Spring SST	Stratification onset	Winter PEA	Winter SST	Site RE	Region RE	Year RE	Site ∗ year RE	Region ∗ year RE	AIC	ΔAIC	Weight
4.429 **(± 2.181)**	-	**-0.539** **(± 0.244)**	-	**-0.602** **(± 0.190)**	-	0.526	0.000	0.000	0.687	1.185	1789.734	0	0.263
4.308 **(± 2.185)**	-	**-0.674** **(± 0.336)**	-	**-0.609** **(± 0.192)**	0.173 (± 0.295)	0.542	0.000	0.000	0.687	1.180	1791.383	1.649	0.115
4.206 *(± 2.269)*	-	**-0.544** **(± 0.245)**	0.003 (± 0.008)	**-0.566** **(± 0.214)**	-	0.551	0.000	0.000	0.685	1.185	1791.595	1.861	0.104
4.706 *(± 2.408)*	-0.090 (± 0.333)	**-0.541** **(± 0.244)**	-	**-0.574** **(± 0.217)**	-	0.533	0.000	0.000	0.687	1.185	1791.659	1.926	0.100
-0.322 (± 0.263)	-	-	-	**-0.641** **(± 0.201)**	-	0.517	0.000	0.320	0.694	1.177	1792.228	2.495	0.076
4.521 *(± 2.416)*	-0.070 (± 0.335)	**-0.670** **(± 0.336)**	-	**-0.586** **(± 0.220)**	0.167 (± 0.296)	0.545	0.000	0.000	0.687	1.180	1793.34	3.606	0.043
1.283 (± 1.076)	-	-	-	**-0.622** **(± 0.198)**	-0.212 (± 0.222)	0.502	0.000	0.249	0.694	1.186	1793.342	3.609	0.043
4.211 *(± 2.264)*	-	*-0.662* *(± 0.344)*	0.001 (± 0.008)	**-0.591** **(± - 0.591)**	0.155 (± 0.316)	0.554	0.000	0.001	0.686	1.180	1793.354	3.621	0.043
4.441 *(± 2.543)*	-0.070 (± 0.341)	**-0.545** **(± 0.245)**	0.003 (± 0.008)	**-0.548** **(± 0.232)**	-	0.553	0.000	0.000	0.685	1.185	1793.553	3.819	0.039
-0.501 (± 0.806)	-	-	0.002 (± 0.008)	**-0.621** **(± 0.219)**	-	0.537	0.000	0.312	0.690	1.182	1794.172	4.439	0.029
-0.156 (± 1.023)	-0.057 (± 0.342)	-	-	**-0.626** **(± 0.222)**	-	0.525	0.000	0.315	0.693	1.178	1794.200	4.467	0.028
1.200 (± 1.725)	-	-	0.005 (± 0.008)	**-0.557** **(± 0.226)**	-0.262 (± 0.237)	0.538	0.000	0.206	0.688	1.196	1794.994	5.260	0.019
1.611 (± 2.096)	-0.093 (± 0.344)	-	-	**-0.596** **(± 0.221)**	-0.219 (± 0.224)	0.514	0.000	0.239	0.693	1.188	1795.268	5.534	0.017
4.414	-0.062	*-0.658*	0.001	**-0.573**	0.148	0.554	0.001	0.001	0.686	1.181	1795.322	5.588	0.016

(± 2.536)	(± 0.341)	*(± 0.344)*	(± 0.008)	**(± 0.238)**	(± 0.316)								
3.962 (± 2.428)	-	**-0.650** **(± 0.257)**	*0.012* *(± 0.007)*	-	-	0.408	0.540	0.000	0.723	1.167	1795.925	6.191	0.012
-0.348 (± 1.360)	-0.048 (± 0.346)	-	0.002 (± 0.008)	**-0.609** **(± 0.235)**	-	0.541	0.000	0.309	0.690	1.182	1796.153	6.419	0.011

Table S5.3 (cont.)

Intercept	Spring PEA	Spring SST	Stratification onset	Winter PEA	Winter SST	Site RE	Region RE	Year RE	Site * year RE	Region * year RE	AIC	ΔAIC	Weight
1.453 (± 2.112)	-0.072 (± 0.348)	-	0.005 (± 0.008)	**-0.539** **(± 0.244)**	-0.265 (± 0.238)	0.544	0.000	0.199	0.687	1.197	1796.950	7.217	0.007
4.877 *(± 2.565)*	-0.396 (± 0.319)	**-0.592** **(± 0.247)**	0.010 (± 0.007)	-	-	0.558	0.000	0.000	0.716	1.183	1797.241	7.507	0.006
6.310 **(± 2.345)**	**-0.589** **(± 0.273)**	**-0.584** **(± 0.244)**	-	-	-	0.471	0.000	0.000	0.736	1.182	1797.277	7.543	0.006
3.956 (± 2.425)	-	**-0.692** **(± 0.353)**	*0.012* *(± 0.007)*	-	0.054 (± 0.315)	0.401	0.556	0.000	0.723	1.165	1797.895	8.162	0.004
5.554 **(± 2.372)**	-	**-0.700** **(± 0.264)**	-	-	-	0.323	0.545	0.000	0.756	1.154	1798.488	8.755	0.003
6.199 **(± 2.355)**	**-0.580** **(± 0.275)**	**-0.666** **(± 0.331)**	-	-	0.107 (± 0.285)	0.471	0.008	0.001	0.736	1.183	1799.137	9.403	0.002
4.877 *(± 2.565)*	-0.394 (± 0.319)	*-0.569* *(± 0.346)*	0.010 (± 0.008)	-	-0.030 (± 0.311)	0.557	0.002	0.000	0.716	1.183	1799.232	9.498	0.002
0.925 (± 1.711)	-	-	**0.017** **(± 0.007)**	-	*-0.408* *(± 0.224)*	0.556	0.000	0.000	0.722	1.203	1799.428	9.694	0.002
5.139 **(± 2.366)**	-	**-0.901** **(± 0.322)**	-	-	0.285 (± 0.272)	0.278	0.604	0.000	0.757	1.149	1799.440	9.707	0.002
2.331 (± 2.046)	-0.387 (± 0.321)	-	*0.013* *(± 0.007)*	-	*-0.391* *(± 0.224)*	0.546	0.000	0.000	0.720	1.202	1799.950	10.217	0.002
-1.964 **(± 0.709)**	-	-	*0.014* *(± 0.007)*	-	-	0.432	0.448	0.221	0.736	1.186	1800.347	10.614	0.001
-0.325 (± 1.422)	-0.423 (± 0.324)	-	0.011 (± 0.008)	-	-	0.561	0.000	0.174	0.726	1.206	1800.959	11.226	0.001
1.174 (± 0.895)	**-0.602** **(± 0.285)**	-	-	-	-	0.461	0.000	0.183	0.754	1.189	1801.062	11.328	0.001
3.430 *(± 1.948)*	**-0.627** **(± 0.287)**	-	-	-	-0.285 (± 0.214)	0.472	0.000	0.000	0.750	1.190	1801.295	11.562	0.001
-0.677	-	-	-	-	-	0.315	0.373	0.263	0.790	1.146	1803.730	13.996	0

(± 0.268)													
1.184 (± 1.801)	-	-	-	-	-0.240 (± 0.231)	0.388	0.276	0.093	0.781	1.170	1804.724	14.991	0