Foraging behaviour and population dynamics of northern gannets over a period of environmental change

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Abstract

There is an urgent need to understand better how recent climatic changes and shifting marine environments are affecting the population dynamics and foraging behaviour of marine central-place foragers. I use both single and multi-colony, and single and multi-species approaches to investigate how different aspects of colonial breeding in seabirds impact on parental foraging behaviour under these changing environmental conditions. I combine historical and recent colony counts and trip duration data to consider population-level interactions and relationships for northern gannets *Morus bassanus*. I also consider the role of intra-specific competition in limiting neighbouring colony growth for three additional North Atlantic seabirds, the Atlantic puffin *Fratercula arctica*, European shag *Phalacracorax aristotelis* and black-legged kittiwake *Rissa tridactyla*, with differing population trends over the past three decades. I then proceed to focus on finer-scale effects on individual foraging behaviour and parental care of northern gannets at one colony over a period of 14 years, using direct observations and a variety of bird-borne logging devices.

My findings support models of foraging based on competition for prey around seabird colonies. I also found that annual variation in foraging trip durations was particularly marked at large colonies, making them especially vulnerable to adverse effects of low prey availability at sea. Furthermore, as foraging ranges altered with colony sizes, the scale of apparent interactions between conspecifics at neighbouring colonies also altered, providing novel support for the limiting effect of neighbouring conspecific density on population growth. Gannets also showed annual flexibility in diet, habitat use and finer-scale search strategies, although other aspects of their foraging, such as the mean scale of Area Restricted Search behaviour, appeared less flexible. Further study is now required to understand if gannets have the capacity to alter the scale of their search behaviour under more extreme conditions. Gannets were also flexible within breeding seasons in the foraging and parental effort they expended, suggesting that the chick’s requirements also contribute to adults’ foraging behaviour. Flexibility in foraging and parental behaviour may buffer the potential adverse impacts of variable environments on provisioning and productivity. These findings have implications for the population dynamics and potential resilience of a wide range of seabird species and other central-place foragers.

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Chapter 1: General introduction

1.1. Colonial breeding

Coloniality is typically defined as a form of group living, in which individuals breed within densely distributed nesting territories, and in which no other resources but nest sites are found, but residents regularly depart in search of food or other resources (Perrins and Birkhead, 1983, Wittenberger and Hunt Jr, 1985). The evolution of coloniality is believed to have occurred because of group living enables individuals to exploit the resources in their environment more efficiently (Rolland et al., 1998). Birds have the highest proportion of species that are colonial breeders (ca. 13%) (Lack, 1968, Brown and Brown, 2001, Gill, 2007), coloniality has also evolved in a number of mammals, for example, white-tailed and black-tailed prairie dogs *Cynomys leucurus* and *C. ludovicianus*, and pinnipeds such as elephant seals *Mirounga leonine*, grey seals *Halichoerus grypus* and a number of sealion species, e.g. Galápagos sealions *Zalophus wollebaeki* (Hoogland, 1981, Baldi et al., 1996, Wolf et al., 2007). It is also seen among reptiles, such as marine iguanas (Trillmich and Trillmich, 1984, Doody et al., 2009) and fish, for example three-spined sticklebacks *Gasterosteus aculeatus* (de Fraipont et al., 1993). Coloniality is, however, particularly well developed among seabird species, with 96% of species breeding in dense colonies (Coulson, 2002), making them useful models for investigating the costs and benefits of breeding in such aggregations. In proximate terms, colonial breeding is believed to arise through constraints on the availability of suitable habitat (Brown et al., 1990, Boulinier, 1996) or breeding partners (Wagner, 1998, Danchin et al., 1998), in keeping with the commodity selection hypothesis (Danchin and Wagner, 1997). In evolutionary terms, the persistence of a colony also depends on the balance between the costs and benefits of colonial living.

There are numerous potential costs for individuals breeding in colonies. For example, large groups may attract predators due to increased conspicuousness (Szép and Barta, 1992, Cresswell, 1994). However, this cost may be outweighed by larger groups being more effective at detecting and defending against predators (Robinson, 1985, Cresswell, 1994, Krause and Ruxton, 2002). The ‘many-eyes’ theory proposes that as group size increases, overall vigilance increases but the time each individual spends watching for predators decreases, thereby allowing more time and energy for other activities such as self-maintenance (e.g. preening and grooming), reproduction and foraging (Côté and Gross, 1993, Roberts, 1996, Schädelin et al., 2012).

Other potential costs of colonial breeding include increased risk of transmission of parasites and diseases (Brown and Brown, 1986, Hoi et al., 1998, Mangin et al., 2003). Individuals breeding in dense colonies may also experience more aggression from conspecifics, in some cases resulting in infanticide (Ramos, 2003, Ashbrook et al., 2008, Inoue et al., 2010). Close proximity of nests can also result in misdirected parental care (Møller and Birkhead, 1993, Davies, 2000). However, individuals breeding within a colony can also benefit from energy savings, for example by conserving heat (Kronenberg and Heller, 1982, Ancel et al., 1997, Speakman et al., 2003).

Individuals breeding at colonies are likely to experience intra-specific competition for food resources (Storer, 1952, Ashmole, 1963). However, the behaviour of colony members can be a useful source of information to others searching for food, leading to potential reciprocal benefits through enhanced information transfer (Inglis and Isaacson, 1978, Wilkinson, 1992, Grémillet et al., 2004). Social learning along with social stimulation of young and inexperienced adults can also benefit individuals breeding in colonies (Laland and Williams, 1997, Krause and Ruxton, 2002). While changing environmental conditions may affect any of these factors, coloniality can confer a net benefit to the individuals that form these aggregations.

1.2. Parental investment in offspring

Natural selection should favour individuals maximizing their lifetime reproductive output (Reznick, 1985, Stearns, 1992, McNamara and Houston, 1996). Thus if conditions become severe, theory would predict that individuals of long-lived, iteroparous species should temporarily direct resources away from reproduction, so as not to compromise their survival (Drent and Daan, 1980, Reznick, 1985).

Seabird species are included in this group (Croxall and Rothery, 1991), with most species having deferred maturity, small clutch sizes, extended periods of chick rearing and high annual adult survival (Ricklefs, 1990, Charlesworth, 1994). Individuals raising offspring make decisions based on both intrinsic and extrinsic factors, such as their physiological state and that of their chicks, as well as weather conditions respectively, which affect their investment in parental care and may impact on population dynamics.

1.3. Regulation of seabird populations

Various theories of the key factors believed to limit population size in seabirds have been proposed, many relating to the costs and benefits of breeding in colonies (Rowan, 1965, Birkhead and Furness, 1984, Cairns, 1992, Gaston et al., 2007). These consist of both density-independent and density-dependent factors. Density-independent factors include local marine productivity and prey availability (Österblom et al., 2008, Kitaysky et al., 2010), along with anthropogenic interference or harm, such as pollution or changes in habitat use (Jahncke et al., 2004, Votier et al., 2005).

Cairns (1989) developed a model of population regulation whereby the sizes of colonies were limited only by the extent of foraging habitat closer to each colony than to any other. This ‘hinterland’ model proposed that the locations of potential breeding sites alone may generate observed patterns of distribution and size among populations (Cairns, 1989). Alternatively, density-dependent mortality over the winter was advocated by Lack (1968) as the main factor regulating seabird populations. Additional density-dependent factors believed to contribute to population regulation include the availability and quality of suitable nesting sites (Manuwal, 1974, Kildaw et al., 2005), as well as parasite burden (Duffy, 1983, Mangin et al., 2003). Interference competition on feeding grounds is yet another factor found to play a key function in population size (Hunt Jr et al., 1986, Davoren et al., 2003a). Indeed many researchers have suggested that regulation operates through breeding success. Central to this concept is the hypothesis first proposed by Ashmole (1963), that breeding adults deplete prey stocks around the colony to such an extent that they generate an ‘annulus’ or ‘halo’ of prey surrounding the outer edge of this depleted zone. Accordingly, he predicted intense intra-specific competition for food, such that individuals at larger colonies were forced to feed further away because they had to travel further before encountering profitable prey. Longer trips reduced the rate at which parents could provision their young and the expectation that breeding success would be lower (or chick condition poorer) at larger colonies compared to smaller ones, would hence impact on population size through lower breeding success or recruitment.

This theory of density-dependent regulation through competition for prey received much attention in the 1980s, with studies reporting both behavioural and reproductive parameters linking closely to the availability of prey (Anderson et al., 1982, Birkhead and Furness, 1984). It has been revisited again more recently following the development of bird-borne devices allowing direct and accurate information on species foraging characteristics and ranges, with studies of a wide variety of species’ finding increased foraging effort with greater population sizes (Lewis et al., 2001, Ainley et al., 2003, Grémillet et al., 2004, Ballance et al., 2009, Elliott et al., 2009). Although the limiting effect of population size is difficult to measure directly (Birt et al., 1987), it has been suggested indirectly by testing for relationships between colony size and reproductive output and body condition (Gaston et al., 1983, Hunt Jr et al., 1986, Forero et al., 2002). There is also some evidence that colony size is strongly negatively correlated with the number of putative competitors from neighbouring colonies, within the presumed foraging ranges of colony members (Furness and Birkhead, 1984). This implies that the number of conspecifics competing for prey resources near to the colony limits population size through depletion or interference competition, again supporting the theory that intra-specific competition for prey during the breeding season also limits seabird numbers.

1.4. Changing environmental conditions

Given the speed and magnitude of changes currently occurring in marine systems, it is important to consider the potential influence of extrinsic factors, such as environmental conditions, on population dynamics. Local marine productivity, within species home ranges, can effect seabird populations (Österblom et al., 2008, Kitaysky et al., 2010) and thus changing environmental conditions are likely to influence population size. The impact of global and regional climate change and subsequent shifts in environmental conditions on species' ranges (Hickling et al., 2006, Kelly and Goulden, 2008), timing of life history events (Dolenec, 2006, Jonzen et al., 2006) and behaviour (Peron et al., 2010), have been widely documented in recent years. Much evidence has been provided over the last decade for increasing sea-surface temperatures (IPCC, 2007), reductions in regional ocean primary productivity (Behrenfeld et al., 2006), influencing the trophodynamics of ecosystems (Richardson and Schoeman, 2004, Kirby et al., 2008) and shifts in the abundance and distribution of plankton and fish stocks, including commercially important species (Rindorf and Lewy, 2006, Huse and Ellingsen, 2008). The influence of such shifts, combined with the effects of commercial fisheries activities, has propagated along food chains to higher marine predators (Gjerdrum et al., 2003, Wanless et al., 2007).

Considering the apparent importance of intra-specific competition for prey in relation to seabird colony sizes and the implications for population regulation, we may predict that the effect of changing climate should vary between populations of different sizes. Furthermore therefore, their influence on the growth rates of neighbouring colonies, with which members may compete for resources at sea, may also vary with differing population trends. However, to date, longitudinal studies adopting a multi-population approach have been rare. Hence the importance of better understanding the relationships between colony size and competition at the population level, and under varied conditions, becomes evident, along with the potential impacts on breeding success at the individual level, and overall population dynamics.

1.5. Foraging behaviour at sea

Effective foraging is key to success for all species, linking the availability of prey to the reproductive success of the predator. Thus the apparent importance of predator-prey interactions highlights the need for a detailed understanding of the foraging activities of predators in relation to their prey. For seabird species, prey are commonly patchily distributed (Fauchald and Erikstad, 2002), with smaller patches sometimes nested within larger scale patches, forming nested patch hierarchies within a heterogeneous environment (Kotliar and Wiens, 1990, Wu and Loucks, 1995, Fauchald et al., 2000). It is therefore crucial that the movements of marine predators allow them to detect and respond to the presence of prey in patches of different spatial scales. Previously, observations from ship-based surveys have been used to provide information on the foraging characteristics, ranges and behaviours of many seabird species (Camphuysen et al., 1994, Stone and Aps, 1995, Trathan et al., 1998, Louzao et al., 2009), although such surveys do have limitations (Meer and Camphuysen, 1996, Spear et al., 2004). The advent of bird-borne tracking technology has enabled fine-scale foraging behaviour of individuals of known breeding status and origin to be collected for a wide variety of species (Fritz et al., 2003, Pinaud and Weimerskirch, 2006, Hamer et al., 2009). The at-sea distribution of marine birds has been shown to be closely related to both biological and physical aspects of the marine environment over a broad range of spatial scales, with features such as tidal mixing fronts and upwellings often of importance (Pinaud and Weimerskirch, 2007, Bost et al., 2009, Raymond et al., 2010). The development of methods to quantify search effort are relatively recent, and while variation in fine-scale foraging behaviours has been found between species with differing foraging ranges and prey fields, much less is known about how fine-scale foraging characteristics within a species vary under changing environmental conditions (Pinaud & Weimerskich 2007).

1.5.1. Responses to environmental change

Studies of a wide range of marine predators have shown that they respond to shifts in their foraging environment, such as changes in sea-surface temperatures, chlorophyll-α concentration or phytoplankton abundance, which can alter the distribution or abundance of prey (Sims and Quayle, 1998, Oedekoven et al., 2001, Johnston et al., 2005b). In the case of seabirds, these include altering primary feeding locations in accord with shifting prey distributions (Weimerskirch and Lecorre, 2006, Cresswell et al., 2008) and changing foraging effort between seasons, for example with some species recorded travelling over greater distances during seasons with poorer prey availability (Furness, 2007, Hamer et al., 2007, Garthe et al., 2011). Prey switching also occurs when the primary species commonly exploited is in short supply, and other species may be more abundant (Barrett and Krasnov, 1996, Montevecchi and Myers, 1996, Votier et al., 2004); in some cases, this can include utilising discards from commercial fishing vessels (Garthe et al., 1996, Arcos and Oro, 2002, Votier et al., 2010). Such flexibility in foraging behaviour may allow individuals to maintain body condition and provisioning rates of their young when conditions are less favourable, and thus effectively buffer populations against environmental variation (Hamer et al., 2006b). Examples of such flexible species include northern gannets *Morus bassanus* and northern fulmars *Fulmarus glacialis* (Furness and Tasker, 2000). Conversely, such species as black-legged kittiwakes *Rissa tridactyla* and terns, that have more specialised diets and shorter foraging ranges, are more sensitive to the detrimental impacts of variable environments (Furness and Tasker, 2000, Furness, 2007). However, even species with flexible foraging strategies will eventually reach a point where their time or energy budgets (net energy gain per unit of time) can no longer be adjusted to maintain adequate chick provisioning rates, potentially impacting on reproductive success (Hamer et al., 2007).

1.6. Parental care and requirements of the young

Bi-parental care occurs in the majority of bird species (Cockburn, 2006). Among pelagic seabirds, social monogamy is the most common mating system (Hamer et al., 2002), with both sexes contributing to incubation and rearing of nestlings. However, the contribution of each sex may not be equal, with variation in distribution of effort between species and numerous factors influencing the contribution of each sex; e.g. stage of offspring development, number of chicks, relatedness and parent condition (Winkler, 1987). Many seabird species are semi-precocial or altricial, their young hatching in an undeveloped state and totally reliant on parental care during the early stages of development (Starck and Ricklefs, 1998). Reproductive success therefore often requires at least one adult in attendance at all times when chicks are newly hatched. In cases where both adults are away from the nest, the unattended offspring can be vulnerable to prevailing weather conditions, as well as predation and attacks from conspecifics (Hunter, 1984, Nelson, 2002, Ratcliffe and Furness, 2006). Maintaining adequate provisioning rates is also critical for the survival of offspring and their growth (Harris and Wanless, 1997, Gray et al., 2005, Enstipp et al., 2006).

Adults must therefore balance time spent foraging against time spent at the nest with the clutch or brood. Along with the trade-off between travelling costs and prey availability, whereby net gain of prey items needs to be greater than the cost of visiting feeding locations, a cost-benefit scenario also arises between maintaining provisioning rate, and the nutritional benefit of prey caught on longer trips. Foraging strategies, as well as being governed by the nutritional state of the adults (McNamara and Houston, 1996), are also likely to be influenced by the requirements of the young (Weimerskirch et al., 1997, Baduini, 2002, Gaston and Hipfner, 2006b). However, how adults partition foraging effort to meet their own needs and those of their young is poorly understood. Some species, including some procellariiform (tube-nosed) species, adopt a dual-foraging strategy, with foraging trips of different durations taken to permit adults to regulate their offspring's energy expenditures and meet their own requirements (Weimerskirch et al., 1994, Terauds and Gales, 2006, Magalhães et al., 2008). However, many other species do not adopt this strategy (Lewis et al., 2004, Phillips et al., 2009). Phillips et al. (2009) suggests that caution is required when deducing the use of such bimodal foraging by different species; as this behaviour could be facultative rather than obligatory.

1.6.1. Flexibility in diet and provisioning

In addition to maximise adult survival, flexibility in foraging behaviour and breeding effort during poorer feeding conditions can buffer the potential negative impacts on reproductive success (Burger and Piatt, 1990, Pinaud et al., 2005a, Hipfner et al., 2006). While prey switching to more abundant species occurs, this may also require higher provisioning rates or larger meal sizes, which are not always possible, the replacement food stocks having lower nutritional value (Suryan et al., 2000, Österblom et al., 2008). Adults may also feed chicks alternative prey that is difficult for them to digest (Harris et al., 2008). Flexibility in parental time budgets and nest guarding may also buffer the impacts of poor prey availability. For example, when prey are more abundant, adults can spend more of their time guarding chicks and defending nests (Furness and Barrett, 1985, Zador and Piatt, 1999). Conversely, during poor feeding conditions, adults may spend less time at the nest in order to maintain feeding rates (Monaghan et al., 1994a). This can include the time adults spend together at the nest as a pair before changing over. We may predict a greater occurrence of chicks being left unattended when prey abundance is low and foraging trips are long (Harris and Wanless, 1997, Tveraa et al., 1998, Lewis et al., 2004). Adults must balance the risk of leaving a chick unattended with the cost of not maintaining provisioning rates, which can be increased by both parents foraging at the same time. The occurrence of unattendance may be expected to increase as seasons progress and as chicks age, becoming less vulnerable.

1.7. Study species and area

1.7.1. Northern gannets

Northern gannets (hereafter gannets) are the largest member of the family Sulidae, comprising gannets and boobies (Nelson, 1978). Sulids are long lived, medium to large coastal seabirds, found in all areas except the Antarctic. Most sulids breed in dense colonies, often on offshore islands or continental coastlines, and forage by plunge-diving or scooping fish and other prey items from the surface (Nelson, 1978).

Northern gannets currently breed at 21 colonies across the British Isles and southern Ireland, ranging in size from just a few pairs to tens of thousands of breeding pairs, making up a third of the global northern gannet population (Nelson, 2002). This is the most regularly assessed seabird species in Britain, with detailed count data available for the majority of colonies dating back to the turn of the 20th century (Gurney, 1913, Fisher and Vevers, 1943, Wanless et al., 2005). The numbers of breeding pairs at most colonies in the UK have increased over the last century and new colonies have also been established (Wanless et al., 2005). The wide range in individual colony sizes, coupled with the completeness of the count data, make this an excellent species in which to study both density-dependent population change and density-dependent intra-specific competition for prey (Lewis et al., 2001). In addition, a considerable amount of detailed information on the behaviour of northern gannets, both in the colony and at sea, has been collected over the last 10 – 15 years (Garthe et al., 1999, Hamer et al., 2000, Hamer et al., 2007, Lewis et al., 2004, Votier et al., 2010), also making this a good species to investigate parental and foraging behaviour change in response to changing marine environments.

1.7.2. Foraging behaviour

During the breeding season, gannets feed primarily on lipid-rich pelagic shoaling fish, such as mackerel (*Scomber scomber*) and sandeels (mainly *Ammodytes marinus*) (Hamer et al., 2000, Lewis et al., 2003, Hamer et al., 2007). They also compete with other seabird species for discards from commercial fishing vessels (Hamer et al., 2000, Votier et al., 2009). They are medium-ranging foragers, capable of travelling over 1000 km on a single foraging trip in order to locate and obtain food for themselves and their young (Hamer et al., 2007). Typical ranges reached from the colony on these trips have been recorded around 230 km (Thaxter et al., 2012). The finer-scale movement patterns of gannets, namely area-restricted search behaviour, have been found to allow them to detect and respond to prey at a variety of spatial scales (Hamer et al., 2009). They can use a variety of distinct prey capture techniques on locating prey, including vertical plunge-diving and underwater pursuit, as well as scooping certain prey species from the surface (Garthe et al., 2000).

1.7.3. Parental behaviour

Gannets have a single-egg clutch and are an altricial species; their offspring hatch in an undeveloped state, with only sparse neossoptiles and unable to regulate their own body temperature, relying heavily on parental care (Nelson, 1978). Females can replace their egg if lost near the start of the breeding season (Nelson, 2002). Gannets have a relatively long breeding season, with an incubation period of around 6 weeks, followed by 12-13 weeks of chick-rearing (Nelson, 2002). They have biparental care, with males and females taking turns to attend the egg or chick while the other is away from the nest foraging. It is important that chicks are guarded by at least one parent during the first four weeks post-hatching, when they are unable to thermoregulate (Montevecchi et al., 1984) and the risk of attack from conspecifics is greatest (Nelson, 2002). However, brood neglect can occur, with the guarding adult leaving the chick unattended if the foraging adult is away for an extended period (Lewis et al., 2004). Adults feed their chicks on semi-digested fish, which are regurgitated directly into the chick's open bill. As the chick ages, it solicits food from the adult more actively and frequently (Nelson, 2002).

1.7.4. Study sites

During the 2009 breeding season (chapter 2), observational data on nest attendance and changeover rates were collected from 10 gannet colonies across Great Britain and southern Ireland: Great Saltee, Ireland's Eye, Lambay, Bempton Cliffs, Bass Rock, Ailsa Craig, Troup Head, Fair Isle, Noss and Hermaness (Figure 2.1). These colonies are widely distributed across the British Isles, within the Celtic, Irish and North Seas, ranging from Great Saltee on the south-eastern Irish coast, to Hermaness on the northernmost tip of Shetland. Colonies varied in size from 158 breeding pairs (Lambay) to > 50,000 apparently occupied sites (AOS) (Bass Rock; Murray, 2011).

During the 2010 and 2011 breeding seasons, detailed behavioural data were collected from the Bass Rock colony, (56°4.6'N, 2°38.3'W), south-east Scotland. The colony was estimated to hold 52,292 AOS in 2009 making it the second largest colony in the east Atlantic (Murray, 2011). The Bass Rock lies 2 km off the south coast of the Firth of Forth. However, gannets mainly forage further offshore in the North Sea, which is a semi-enclosed shelf sea made up of a mosaic of stratified, mixed and frontal zones (Scott et al., 2006). Gannets on the Bass Rock are both easily caught and later re-caught, facilitating the use of bio-logging devices. Detailed behavioural observations were made in the colony in the 1960s (Nelson, 1966, Nelson, 1978), while bird-borne loggers have been used since the late 1990s to collect detailed data on various aspects of foraging behaviour (Hamer et al., 2000, Hamer et al., 2007, Hamer et al., 2009).

1.7.5. Other species and colonies

While my research primarily focuses on gannets, in chapter 3 I take a multi-species approach and analyze population count data for the Atlantic puffin *Fratercula arctica,* European shag *Phalacracorax aristotelis* and black-legged kittiwake *Rissa tridactyla*. In recent years, these species have shown large annual variation in breeding success at many colonies in the UK (Mavor, 2008). A long history of monitoring British seabird populations means that regular census data for seabird colonies are gathered, such as the Operation Seafarer census of 1969/70 and the Seabird 2000 census. These are available through the Joint Nature Conservation Comittee (JNCC) seabird monitoring program database (JNCC, 2012).

1.8. Aims of thesis

My research uses both single colony and multi-colony, and single species and multi-species approaches to investigate how various aspects of the colonial breeding habit of seabirds impact on parental foraging behaviour under changing environmental conditions. I initially consider population level interactions and relationships and then go on to focus on finer-scale effects on individual foraging behaviour and parental care.

Chapter 2 extends the approach taken by Lewis et al (2001) and examines the influence of colony size on both population growth rates and foraging trip durations of gannets under contrasting environmental conditions in two oceanographic regions. Similarly, chapter 3 extends the approach taken by Furness & Birkhead (1984) and uses data for four species of north temperate seabird with differing feeding ecologies and contrasting population trends over the last 30 years. I test whether there has been a change in the ranges at which neighbouring conspecific density limits colony size as a result of intra-specific competition for prey. Chapter 4 uses data from bird-borne devices to compare foraging locations and fine-scale behaviour of gannets on the Bass Rock over a thirteen-year period, during which feeding conditions varied markedly. In Chapter 5, a combination of GPS tracking and nest observations via a webcam are used to investigate within-season variation in foraging behaviour and parental investment of gannets on the Bass Rock in 2010 and 2011. Finally, chapter 6 discusses these results in the context of seabird life histories and changing environmental conditions, and considers their relevance to the conservation and management of marine environments.

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Chapter 2: Density-dependent foraging and colony growth under varying environmental conditions in a pelagic seabird

Abstract

Intra-specific competition for food resources affects foraging behaviour, chick development, juvenile and adult survival, as well as population growth rates in many species, highlighting a need to understand better how changing environmental conditions affect individuals in populations of different sizes. Using chick-rearing northern gannets as a model, I examined the influence of colony size on per capita population growth rates over two time-periods (1994-2000 and 2000-2009) and on foraging trip durations in each of two years (2000 and 2009) at 10 colonies in two separate regions of the UK and Ireland (the North Sea and the Celtic/Irish Sea). The slope of the relationship between population size and foraging trip duration in 2009 was less than one quarter of that in 2000, suggesting a much weaker influence of population size in 2009, presumably due to less intense intra-specific competition for prey resources at sea. There was also regional variation, with colonies in the Celtic/Irish Sea growing substantially slower for their size over the period between 2000 and 2009 than did colonies bordering the North Sea, whilst observed trip durations in 2009 were on average 13% shorter than predicted from population size at colonies bordering the North Sea but 32% longer than predicted at colonies in the Celtic and Irish Seas. These data suggest less favourable conditions for gannets in the latter region in recent years, and that annual variation in trip durations will be particularly marked at large colonies, making them especially vulnerable to adverse effects of low prey availability at sea.

2.1. Introduction

There is growing concern over impacts of climate change on animal populations (Pearce-Higgins et al., 2010, Rolland et al., 2010, Davey et al., 2011). Recent studies have highlighted that in many cases, climate-related changes depend on population density (Rotella et al., 2009, Votier et al., 2009, Smallegange et al., 2011), but the mechanisms underlying such density-dependence are often unclear (Ahola et al., 2009, Laws and Belovsky, 2010, Linares et al., 2010). In marine environments, the pace and direction of changes in climate over the past five decades have shown marked geographical variation (Burrows et al., 2011) but net warming has had a net negative impact on primary production (Behrenfeld et al., 2006, Boyce et al., 2010). There is also growing evidence that such decreases in production have propagated to other trophic levels (Beaugrand et al., 2002, Behrenfeld et al., 2006), extending in some cases to higher marine predators such as seabirds (Wanless et al., 2007, Dorresteijn et al., 2012, Satterthwaite et al., 2012). Intense fishing pressure can also have cascading effects on marine food webs (Baum and Worm, 2009) and the greatest threat to fish stocks is likely to be the combined effects of climate change and overfishing (Brander, 2007). Recent studies have suggested that these combined effects can also have important consequences for seabird breeding success, survival and population stability (Frederiksen et al., 2004, Ainley and Blight, 2009).

Many seabird species breed in dense colonies, making them potentially powerful models to examine density-dependent responses to changes in prey availability (Kitaysky et al., 2000, Ashbrook et al., 2010). In particular, foraging trip durations of many species are longer if conditions are poor (Hamer et al., 1993, Lewis et al., 2006, Riou et al., 2011) and also increase as a function of colony size, providing strong evidence of intra-specific competition for prey resources at sea (Lewis et al., 2001, Forero et al., 2002, Ainley et al., 2003). Changes in foraging conditions may thus be expected to have greater impacts on trip durations in larger populations (Hamer et al., 2006b), but there are few data to test this prediction.

Within the British Isles, northern gannets *Morus bassanus* (hereafter gannets) breed at colonies differing in size from tens to tens of thousands of pairs (Wanless et al., 2005). They are generalist predators, able to exploit a wide variety of species and sizes of prey, including lipid-rich fish such as mackerel (*Scomber scomber*) and sandeels (mainly *Ammodytes marinus*) in addition to discards from fishing vessels (Hamer et al., 2000, Lewis et al., 2003). Most British colonies are increasing in size, with smaller colonies having higher per capita growth rates (Wanless et al., 2005). In addition, direct observations of nest attendance have revealed a positive relationship between colony size and the mean foraging trip durations of breeding birds, both among colonies of different sizes in the same year and, from the limited longitudinal data available, within individual colonies as they grow (Lewis et al. 2001). However, trip durations and foraging ranges at one of the largest gannet colonies in the UK were found to be much longer in years when sandeel stocks around the colony were low (Hamer et al., 2007), suggesting that impacts of changes in prey availability may outweigh those of changes in population size. Yet it is not known whether birds at colonies of different sizes were similarly affected. Lewis et al. (2006) found that chronically poor conditions resulted in greater foraging effort by Cape gannets *Morus capensis* even at small colonies, highlighting a need to understand better how changing environmental conditions affect birds in populations of varying size.

Here I resample the same colonies as those studied in 2000 by Lewis et al. (2001), after a further nine years of population growth. Lewis et al. (2001) found no evidence of any spatial variation in the effects of population size, but since then, several studies have identified strong regional structure in breeding productivity and population trends of seabirds within Britain and Ireland (Frederiksen et al., 2007, Cook et al., 2011). In particular, for gannets, the Celtic and Irish Sea region was considered ecologically distinct from the North Sea region, including Fair Isle and Shetland, on the basis of consistent variation in abundance at breeding colonies (Fig 3 in Cook et al. 2011). In the North Sea region, several species of seabird have experienced declining breeding success since the mid 1980s (Burthe et al., 2012), but breeding productivity in 2009 was higher than it had been for a number of years including 2000, possibly due to increased availability of sandeels in 2009 (JNCC, 2011). Stocks of mackerel in the southern, western and northern North Sea were also 30% higher in 2009 than in 2000 (4.0×10^3 tonnes and 3.1×10^3 tonnes, respectively; data from ICES 2010). Hence I predicted less intense competition, i.e. a smaller influence of population size on foraging trip durations, at North Sea colonies in 2009 compared to 2000.

In contrast to the North Sea, there was little evidence for any increase in prey availability or quality within the Celtic or Irish Seas in 2009 and some evidence of recent declines in prey biomass in this region (JNCC, 2011, Riou et al., 2011). As a result of this difference between the two regions in 2009, I predicted less difference between years in the relationship between population size and trip duration at colonies in the Celtic and Irish Seas than in the North Sea, resulting in significant interactions between the effects of population size, year and region on trip duration. I also examined the per capita growth rates of our study colonies over the periods 1994-2000 and 2000-2009. I assessed whether the relationship between population size and growth rate was similar in each time-period or whether it was affected by changing environmental conditions, resulting in significant two-way or three-way interactions between the effects of population size, time-period and region on per capita growth rate.

2.2. Materials and methods

Fieldwork took place from June to August 2000 and 2009 at nine gannet colonies around the coast of Britain and Ireland. A tenth colony (Lambay, established in 2007) was also sampled in 2009 (Fig 2.1). Counts of Apparently Occupied Sites (AOS), made from aerial photographs combined with visits to colonies, both with a maximum sampling error of around 5-10% (Wanless et al., 2005), were obtained from the literature (Murray and Wanless, 1997, Wanless et al., 2005, Murray, 2011), together with more recent unpublished data for some colonies (see acknowledgements). Five of the nine colonies sampled in 2000 were counted that year. Population sizes for the other four colonies (two counted in 1999, one in 1998 and one in 1995) were adjusted using colony-specific per capita growth rates recorded between 1994 and 2004 (Murray and Wanless, 1997, Lewis et al., 2001, Wanless et al., 2005) to estimate the additional increase in population size since the most recent count (in practice these increments were < 3% of population size). Six of the 10 colonies sampled in 2009 were counted that year. The other four were last counted in 2004 (n=2) or 2008 (n=2) and population sizes for these colonies in 2009 were estimated by assuming that per capita growth rates recorded between 1994 and 2004 or 2008 were maintained until 2009. The remaining colony (Ailsa Craig) decreased slightly in size between 1994 and 2004 (Wanless et al., 2005) but has shown no further decreases since then (B. Zonfrillo pers comm.) and so I assumed the same size in 2009 as in 2004.

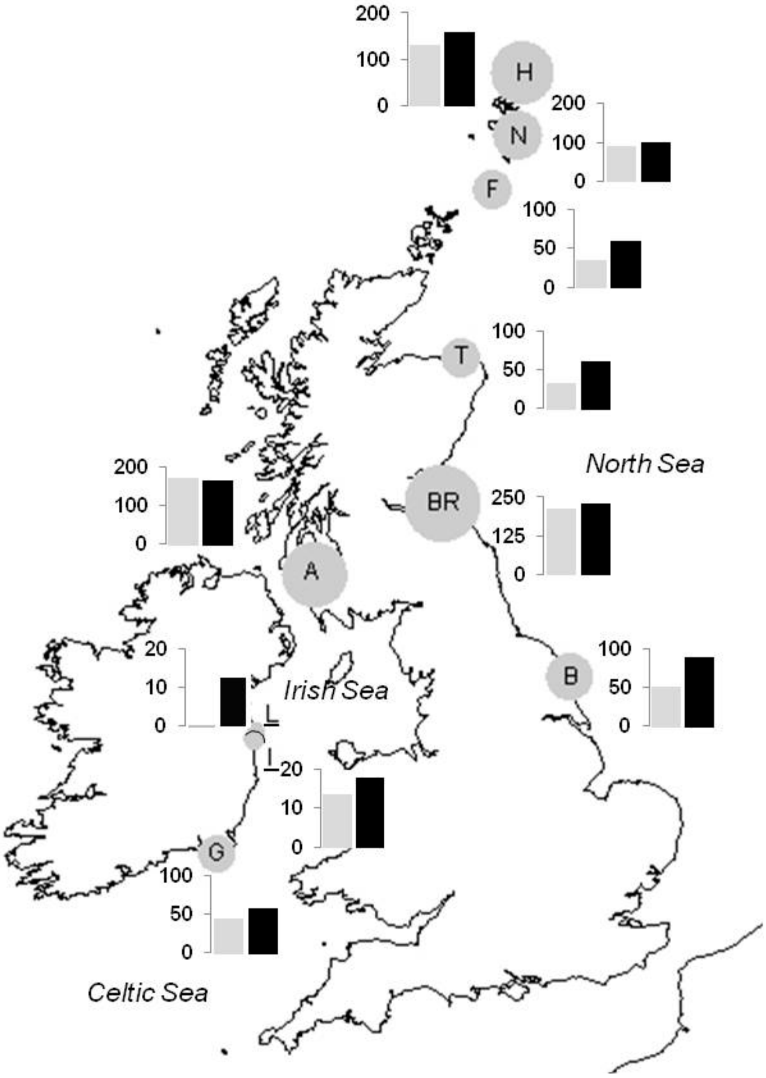

Figure 2.1. Locations and sizes of the ten gannet colonies studied in 2000 and 2009 (A, Ailsa Craig; BR, Bass Rock; B, Bempton Cliffs; F, Fair Isle; G, Great Saltee; H, Hermaness; I, Ireland’s Eye; L, Lambay; N, Noss; T, Troup Head). Colony sizes (number of apparently occupied sites, square-root transformed) are shown for 2000 (grey bars) and 2009 (black bars). The area of each circle is proportional to colony size in 2009. Scales on the y axes differ among colonies.

To determine foraging trip durations, around 20 chick-rearing pairs at each colony (2000, 18-24 pairs; 2009, 19-30 pairs) were observed during daylight hours (sunrise to sunset) for an average of 41 hours each (2000, 16-60hrs; 2009, 16-64hrs). Following Hamer et al. (1993) and Lewis et al. (2001), the arrival and departure times of foraging adults were recorded to the nearest minute and used to calculate a daily changeover rate at each colony (number of changeovers observed divided by the nest-days of observation). The mean trip duration at each colony was then calculated by dividing the time available per day for undertaking foraging trips (24 hours minus the mean time adults spent together at the nest) by the estimated changeover rate. Chicks were aged using a combination of observed hatch dates and plumage characteristics (Nelson, 2002). The median age of all chicks observed was 7 weeks in 2000 and 5 weeks 2009.

All statistical analyses were carried out using R version 2.12.1 (R-Development-Core-Team, 2010). I used a linear mixed effects model (LME) (Pinheiro and Bates, 2000) using the package ‘nlme’ to examine whether the relationship between natural log (Log_e) population size (log-transformed to normalize the data and because population growth is a multiplicative rather than additive effect) and per capita growth rate differed over the periods 1994-2000 and 2000-2009. This model included region (North Sea or Celtic/Irish Sea, as defined by Cook et al. 2011) as a fixed effect and colony identity as a random effect to account for repeated measures (see Fig 1 for locations of colonies; the model had the form: per capita growth rate ~ initial $\log_e$ colony size + (initial $\log_e$ colony size * time period) + (initial $\log_e$ colony size * time period * region) + random =(~1| colony), with a Gaussian error distribution). I then used an additional LME to examine how the relationship between square root colony size and foraging trip duration differed between years. This model also included two potential confounding effects (median chick age and total number of nest-hours of observation at each colony) and had the form: trip duration (hours) ~ square-root colony size + (square-root colony size * year) + (square-root colony size * region) + chick age + nest-hours + random =(~1| colony), with a Gaussian error distribution. Colony size was square-root transformed for this second analysis, following Lewis et al. (2001), because the area covered by birds at sea increases with the square of the mean foraging radius. To check the robustness of our analyses, I compared each full model with the minimum adequate model (Crawley, 2007) following serial deletion of non-significant terms (Mundry and Nunn, 2009). To check that our analysis was not affected by errors in estimating population sizes, I also re-ran each model using extreme population sizes, assuming no further growth of any colonies since the most recent counts. This had no qualitative effect on our results in either case, and so I am confident that any errors in estimating population sizes did not affect our conclusions.

In contrast to foraging trip durations, mean travel speeds at sea show remarkable consistency between different colonies and years (Grémillet et al., 2006, Hamer et al., 2007, Votier et al., 2010). Hence, in addition to trip durations, I also estimated foraging ranges each year, using telemetry data to calibrate foraging range against trip duration, following Hamer et al. (2001).

2.3. Results

2.3.1. *Population sizes and per capita growth rates*

Study colonies differed in size from 188 AOS (Ireland's Eye) to 45,569 AOS (Bass Rock) in 2000 and from 158 AOS (Lambay) to 52,292 AOS (Bass Rock) in 2009. With the exception of Ailsa Craig (see Methods), all colonies increased in size between 2000 and 2009 (Fig 1). Per capita population growth rates between 1994 and 2000 and between 2000 and 2009 were significantly negatively related to population size in 1994 and 2000, respectively (LME; $F_{1,7} = 27.3$, $P = 0.001$) with no difference in this relationship over the two time-periods (two-way interaction; $F_{1,7} = 1.0$, $P > 0.05$; 1994-2000: $b = -1.953$, 2000-2009: $b = -3.675$; Fig 2). However, colonies in the Celtic/Irish Sea region (I, G and A) grew substantially and significantly more slowly for their size over the period between 2000 and 2009 than did colonies bordering the North Sea (three-way interaction; $F_{2,6} = 9.2$, $P < 0.05$; Fig 2.2).

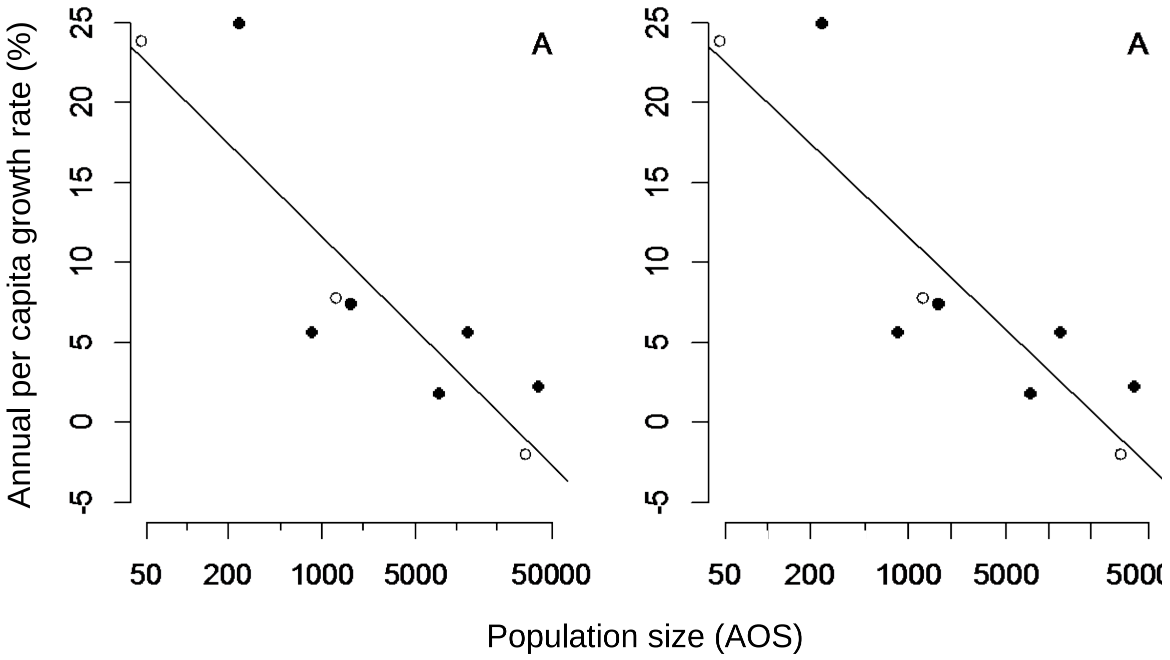

Figure 2.2. The relationship between initial $\log_e$ population size and percentage per capita population growth rate from 1994 to 2000 (A) and from 2000 to 2009 (B). North Sea colonies: filled circles, Celtic/Irish Sea colonies: open circles. In 2000-2009, there was a significant difference between colonies in the North Sea (solid regression line) and the Celtic/Irish Sea (dashed regression line).

2.3.2. *Foraging trip durations*

There was a significant positive relationship between current population size (square root transformed AOS) and mean trip duration (TD) during chick rearing in both 2000 and 2009 (LME; $F_{1,5} = 28.97$, $P = 0.01$) but with a much steeper slope, indicating a much stronger influence of population size, in 2000 (TD (hours) = [0.069*Sqrt colony size(AOS)] + 6.39) than in 2009 (TD (hours) = [0.011*Sqrt colony size(AOS)] + 8.08); two-way interaction between square-root colony size and year; $F_{1,5} = 8.73$, $P < 0.05$; Fig 3). Population size also explained much more of the variation in trip duration among colonies in 2000 ($R^2 = 0.76$) than in 2009 ($R^2 = 0.43$). Despite the increases in population sizes over the study period, birds at all but the two smallest colonies studied in 2000 (Ireland's Eye and Troup Head) made shorter trips in 2009 than in 2000 (Fig 2.3), suggesting that in most cases, changes in environmental conditions had a stronger effect on trip durations than did the increases in colony size.

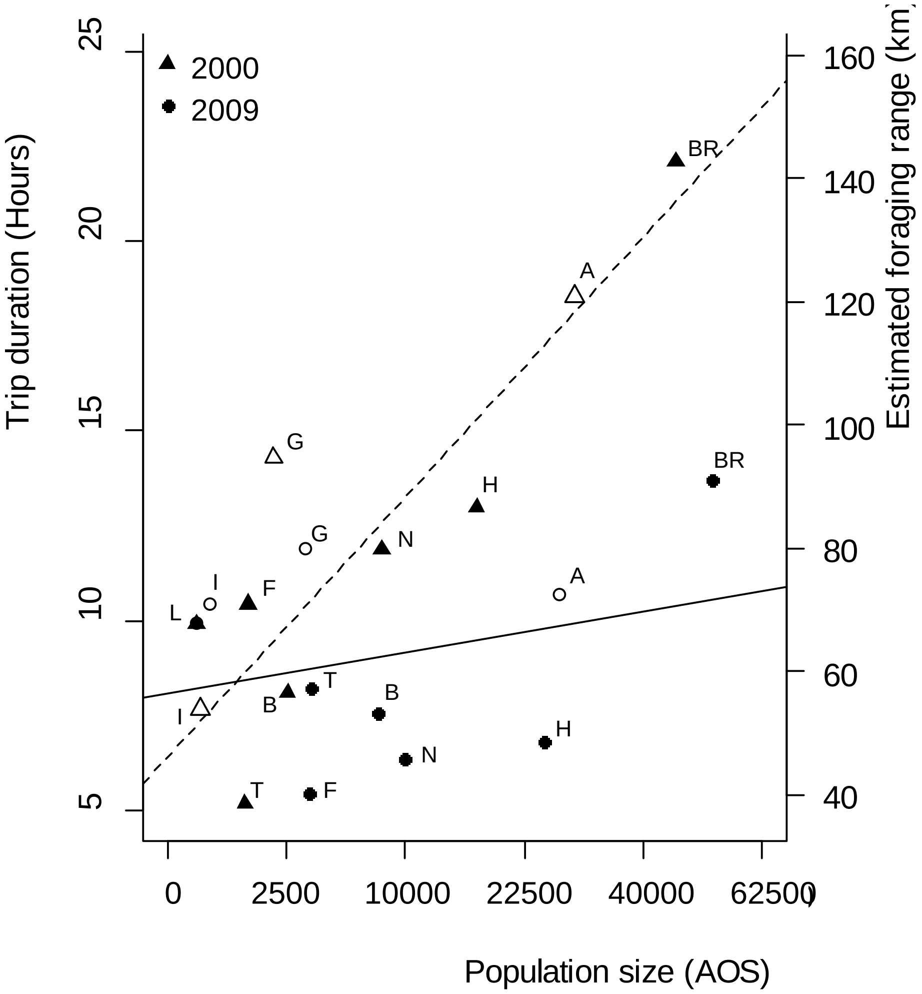

Figure 2.3. The relationship between mean foraging trip duration (hours) and population size (square-root transformed) in 2000 (open symbols) and 2009 (filled symbols). Triangles, Irish/Celtic Sea colonies; Circles, North Sea colonies (A, Ailsa Craig; BR, Bass Rock; B, Bempton Cliffs; F, Fair Isle; G, Great Saltee; H, Hermaness; I, Ireland’s Eye; L, Lambay; N, Noss; T, Troup Head).

There was also a significant effect of region in the model ($F_{1,8} = 7.36$, $P < 0.05$), with observed trip durations in 2009 on average 32% longer than predicted from colony size (i.e. above the fitted regression line for 2009) at colonies in the Celtic and Irish Seas, but 13% shorter than predicted (i.e. below the regression line) at colonies bordering the North Sea (Fig 2.3). This difference between regions was confirmed by running separate linear models for each year; there was a significant two-way interaction between square-root colony size and region in 2009 ($F_{2,7} = 7.56$, $P < 0.05$) but not in 2000 ($F_{2,6} = 2.82$, $P = 0.1$). There was a small but significant additional effect of chick age ($F = 13.83$, $P = 0.03$) but no effect of the number of nest-hours of observation (ns).

To assess further the difference between years and regions in the influence of colony size, I used the relationship between colony size and trip durations found in 2000 to predict trip durations from colony sizes in 2009. Observed trip durations in 2009 were shorter than predicted at all six colonies bordering the North Sea but longer than predicted at three of the four study colonies in the Celtic and Irish Sea, the exception being the colony on Ailsa Craig (Fig 2.4).

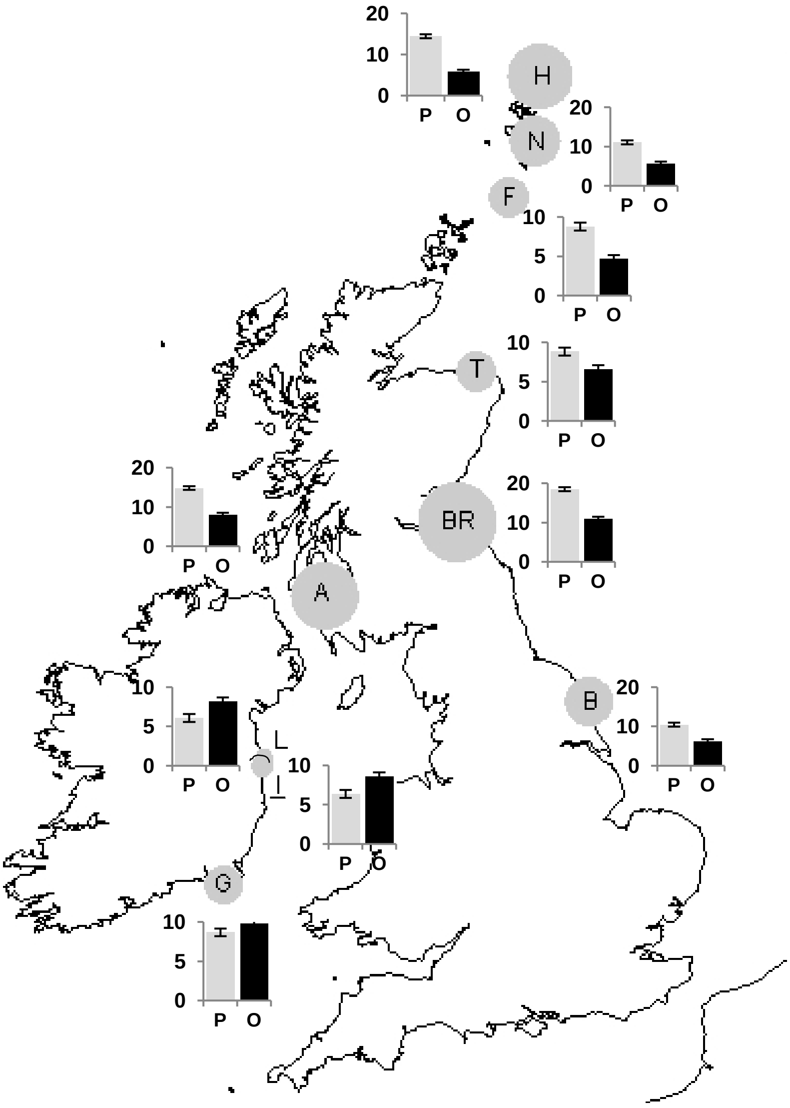

Figure 2.4. Observed (O) and predicted (P) trip durations (hours), with associated standard errors, at different colonies in 2009. Predictions were based on population sizes in 2009, using the relationship between square-root population size and trip duration that was observed in 2000 (A, Ailsa Craig; BR, Bass Rock; B, Bempton Cliffs; F, Fair Isle; G, Great Saltee; H, Hermaness; I, Ireland's Eye; L, Lambay; N, Noss; T, Troup Head).

2.4. Discussion

The slope of the relationship between population size and foraging trip duration in 2009 was less than one quarter of that in 2000 (Fig 2.3), suggesting a much weaker influence of population size in 2009, presumably due to less intense intra-specific competition for prey resources at sea. Gannets compete mainly through passive interference due to prey disturbance rather than by depleting prey (Lewis et al., 2001, Camphuysen, 2011), but lower prey abundance can nonetheless lead to greater competition through fewer, smaller and/or shorter-lasting occurrences of prey close to the surface within the vertical foraging ranges of birds (Lewis et al., 2002a). Gannets may also compete directly for discards from fishing vessels, which comprise about 15% of the diet at colonies in the UK (Hamer et al. 2007; Votier et al. 2010). Changes in prey availability can result in birds altering their activity at sea (e.g. the proportion of time spent resting on the water; (Monaghan et al., 1994b, Litzow and Piatt, 2003) without any effect on trip durations (Lescroël and Bost, 2005, Garthe et al., 2011), but large reductions in prey availability are likely to exceed this buffering capacity, resulting in longer trips, especially at large colonies where birds have less flexibility in their time/activity budgets owing to their greater foraging effort (Lewis et al., 2004, Hamer et al., 2007).

Trips at most colonies were shorter in 2009 than in 2000, despite all but one of these colonies increasing in size since 2000. Hence the impact of changes in prey availability between years exceeded that of changes in colony sizes in most cases. However, trips at the two smallest colonies studied in 2000 (Troup Head and Ireland’s Eye) were longer in 2009, because annual variation in density-dependence had little effect on trip durations at these small colonies (Fig 2.3). Hence the main influence on trip duration in these two cases was from colony growth. This has important implications for the use of trip durations to monitor marine environments (Furness and Camphuysen, 1997a, Hamer et al., 2006b), because even large changes in prey availability will have relatively little effect on trip durations at small colonies.

A recent analysis of seabird monitoring data for the UK identified two separate ecologically coherent regions for gannets, corresponding with the North Sea and the Celtic/Irish Sea, within which trends in abundance varied in a consistent fashion (Cook et al., 2011). In support of this distinction, I found that colonies in the Celtic/Irish Sea region grew significantly more slowly for their size over the period between 2000 and 2009 than did colonies bordering the North Sea. I also found that observed trip durations in 2009 were shorter than predicted at colonies bordering the North Sea, but longer than predicted at colonies in the Celtic and Irish Seas. These data suggest less favourable environmental conditions in the latter region over recent years, similar to the impacts of low food availability on trip durations and population trajectories of Cape gannets *Morus capensis* in southern Africa (Lewis et al., 2006). This suggestion is also supported by recent data showing longer trips than expected from population size at a gannet colony in Brittany (Grémillet et al., 2006), long foraging trips and poor chick growth of Manx shearwaters *Puffinus puffinus* since 2007 at a colony in SW Wales (Riou et al., 2011) and decreases in overwinter survival of adult guillemots *Uria aalge* and razorbills *Alca torda* breeding in Wales (Votier et al., 2005).

At Ailsa Craig, in the northern Irish Sea, population size decreased slightly between 1995 and 2004 (Wanless et al., 2005) but mean trip duration in relation to population size was lower in 2009 than at more southerly colonies (Fig 4). I have no data on diets of birds or prey biomasses in this region but this difference suggests more favourable environmental conditions within the northern Irish Sea in more recent years. This corresponds with both a suspected northerly shift in the foraging areas of Manx shearwaters from the south of the region (Guilford et al., 2008) and large increases in populations of guillemots and razorbills at nearby Rathlin Island, following steep declines between 1999 and 2007 (Allen et al., 2011).

In contrast to gannets, which have maintained consistently high breeding success over this period (Hamer et al., 2007, JNCC, 2011), several species of seabird at colonies in the North Sea have experienced declining breeding success since the mid 1980s (Burthe et al., 2012) and greatly reduced adult survival since the mid-2000s (Lahoz-Monfort et al., 2011). This difference partly reflects the greater flexibility of gannets in terms of diet and foraging ranges (Hamer et al., 2007, Hamer et al., 2009) and may also be linked to recent increases in North Sea stocks of mackerel (ICES, 2010), which are too large to be taken by most other seabirds in the region and may compete with them for prey species such as sandeels (Furness, 2002, Frederiksen et al., 2007, Langoy et al., 2012), but have been the main component in the diet of gannets at the large colony on Bass Rock in recent years (> 80% by frequency in 2010; Chapter 4).

The consistency between different colonies and years in the mean travel speeds of gannets at sea (Grémillet et al., 2006, Hamer et al., 2007, Votier et al., 2010) can be used in conjunction with the relationship between colony size and trip duration to project foraging ranges and hence at-sea distributions for additional colonies (Grecian et al., 2012); Fig 2.3). However, the results of this study highlight the importance of accounting for temporal variation in the latter relationship to avoid mismatches between observed and predicted foraging ranges.

The observed difference between years in the effect of population size on gannet foraging behaviour means that annual variation in trip durations will be particularly marked at large colonies, making them especially vulnerable to adverse effects of low prey availability. Long foraging trips result in chicks receiving less food per unit time, assuming food loads are no larger after long trips (Lewis et al., 2006), and also increase the likelihood of adults leaving chicks unattended and at risk of being washed from the nest during poor weather, exposed to cold temperatures or attacked by conspecifics (Nelson, 2002, Lewis et al., 2004). There is no evidence to date of a relationship between colony size and breeding success in gannets (Lewis et al. 2001), but such a relationship has been observed in some other species (Hunt et al., 1986, Kitaysky et al., 2000) and evidence from one large gannet colony suggests that in years of poor food availability, adults have very little leeway to increase foraging effort any further without likely adverse effects on chick survival (Hamer et al., 2007).

Finally, there is evidence that gannets from large colonies recruit into smaller colonies (Moss et al., 2002, Votier et al., 2011), so it is possible that trip durations and provisioning rates play a role in influencing where birds choose to breed for the first time (Lewis et al. 2001). Our data indicate that the difference in trip durations between large and small colonies is most marked during adverse foraging conditions, and so differences in recruitment rate may have contributed towards both the observed negative density-dependent growth of populations and the lower per capita growth rates since 2000 at colonies in the Celtic and Irish Sea (Fig 2).

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Chapter 3: Dynamics of seabird colony distributions over 30 years suggest competition for food during the breeding season

Abstract

The role of intra-specific competition in limiting population growth has been hotly debated for over 50 years. In the case of seabirds, there is mounting evidence for density-dependent competition for food, both between conspecifics from the same colony (positive relationships between population size and foraging range) and those breeding at different colonies (inverse relationships between population size and number of conspecifics breeding in neighbouring colonies). The spatial scale at which the latter effect operates varies between species, generally being greater in pelagic species compared to in-shore feeders. Similarly, within species, the scale at which it occurs is predicted to vary with overall population size, i.e. between-colony effects should occur over greater distances if local population size increases and over smaller distances if it declines. Over the past 30 years, UK seabirds have shown highly variable population trends; some species have increased, while others have declined markedly. I use this opportunity to test whether there has been a concomitant change in the distance over which neighbouring conspecific density limits population size. I found significant changes in spatial structure since the 1980s, with population sizes dependent on neighbouring conspecific density over a much larger distance than previously noted for northern gannets, which have almost doubled their population in the study area, but over much shorter distances than previously identified for shags and kittiwakes, whose populations have greatly declined. For puffins, whose population has remained relatively unchanged, structuring occurred over the same distance as before. My results provide strong support for the limiting effect of competition between conspecifics breeding in adjacent colonies.

3.1. Introduction

The relative importance of different factors regulating seabird population sizes has been hotly debated for well over 50 years (Rowan, 1965, Cairns, 1992, Gaston et al., 2007). Potential factors include parasitism or disease (Duffy, 1983, Mangin et al., 2003); intra-specific competition for food between sympatric breeders (Storer, 1952, Ashmole, 1971); availability of suitable nesting habitat (Thompson and Furness, 1991, Kildaw et al., 2005) and density-dependent winter mortality (Lack, 1966, Lack, 1968), or density-independent mortality, i.e. through food availability. All but the last of these factors are made more acute because seabirds are generally colonial breeders. Clearly therefore, there must also be benefits associated with coloniality, including information transfer, predator avoidance and access to mates (Birkhead, 1977, Clode, 1993). Of the potentially limiting factors, competition for prey among sympatric conspecifics has received most attention; it has been shown that the foraging range of breeding seabirds is positively related to population size in a wide range of marine biomes and in species with different foraging strategies e.g. Adélie penguins *Pygoscelis adeliae*, northern gannet *Morus bassanus*, common guillemot *Uria aalge*, thick-billed guillemot *Uria lomvia*, lesser noddy *Anous minutus* and sooty tern *Onychoprion fuscatus* (Lewis et al., 2001, Davoren et al., 2003a, Ballance et al., 2009, Elliott et al., 2009). This implies that parental foraging effort increases and brood provisioning rates decrease with increasing population size, placing a density-dependent limitation on breeding success and therefore population growth (Lewis et al., 2001, Davoren et al., 2003a, Ballance et al., 2009, Elliott et al., 2009). It is less clear what effect competition between breeders from neighbouring colonies (i.e. neighbouring conspecifics) has on population size. Furness and Birkhead (1984) found that in four species of UK breeding seabirds (northern gannet, Atlantic puffin *Fratercula arctica*, European shag *Phalacracorax aristotelis* and black-legged kittiwake *Rissa tridactyla*; hereafter gannet, puffin, shag and kittiwake), population size was strongly and negatively correlated with the number of conspecifics breeding in neighbouring colonies. The spatial scale (i.e. the distance within which colonies were considered neighbours) over which these relationships were strongest varied between species (gannets 100 km; puffins, 150 km; shags 30 km; and kittiwakes 40 km). This variation was thought to reflect inter-specific differences in foraging ranges and was therefore taken as evidence that competition for food between birds from adjacent colonies limits population size (Furness and Birkhead, 1984). However, nesting habitat constraints have also been found to contribute to spatial structuring of population sizes in a number of species (Forbes et al., 2000). Indeed, Cairns (1989) suggested that colony location is limited by geology and topography, and that population size is then a function of foraging habitat available from those locations. To date, no study has tested between these competing hypotheses. However, if the spatial relationships found by Furness and Birkhead (1984) were due mainly to geology, they would be expected to remain unchanged regardless of overall population size, since topographical features change at a far slower rate than seabird populations.

Seabird populations in the British Isles have shown contrasting trends over the past 30 years (JNCC, 2011). I take advantage of this opportunity to determine whether relationships shown by Furness & Birkhead (1984), between population size and numbers of conspecifics breeding at neighbouring colonies (hereafter, neighbouring conspecific density), have changed in response to population change. Foraging range increases with population size (Lewis et al. 2001; Elliott et al. 2009; but see Chapter 2). Therefore, the hypothesis that neighbouring conspecific competition limits population size implies that in a growing population, the negative relationship between population size and neighbouring conspecific density will become stronger at larger spatial scales. Conversely, if population size decreases, the spatial scale at which the relationship is strongest will decrease. Such changes would not be seen if population size were limited solely by breeding and foraging habitat availability *sensu* Cairns (1989). Of the four species included in Furness and Birkhead's (1984) analysis, recent count data indicate that the gannet population has increased, the kittiwake and shag populations have declined and the puffin population has remained relatively unchanged (JNCC, 2011). Here I show concomitant changes in the scales at which population size is related most strongly to neighbouring conspecific density, providing strong support for the hypothesis that competition between conspecifics from neighbouring colonies plays an important role in regulating seabird population sizes.

3.2. Methods

In their original study, Furness and Birkhead (1984) analysed gannet population sizes (apparently occupied sites) estimated during the 1970s (Nelson, 1978, Murray, 1981, Dennis, 1979-83), puffins in the early 1970s (Harris, 1976), shags in 1969/70 (Cramp, 1974) and kittiwakes in 1982 (Richardson, 1983) (Fig 3.1). In order to examine the effects of overall population changes I compiled recent population count data for each of these species following the same protocols as Furness and Birkhead (1984). Population count data for gannets were for the 2003/04 census from Wanless et al. (2005), count data for the other three species were from Mitchell et al. (2004) and the Seabird 2000 census counts in 2000/01 from the JNCC Seabird Monitoring Program online database (http://jncc.defra.gov.uk/smp/). I used the same core colony areas as Furness & Birkhead (1984): i) gannet colonies throughout the British Isles and Republic of Ireland, excluding the Channel Islands, ii) puffin colonies of > 1000 pairs in Scotland north of 57°30’N, iii), shag colonies of ≥ 40 pairs in Orkney and Shetland and iv) all kittiwake colonies in Shetland (Fig 3.2). Furness and Birkhead (1984) did not consider gannet colonies established after 1960, regarding them to be “too young to have increased beyond a very small number of pairs”. Similarly I include only colonies established before 1990. For each species I calculated the overall percentage change at each colony between the count used by Furness & Birkhead (1984) and the contemporary count data. In addition, because gannet colonies have been counted approximately every decade, I was also able to examine counts for this species using data from 1984 (Murray and Wanless, 1986, Lloyd et al., 1991) and 1994 (Murray and Wanless, 1997, Mitchell et al., 2004).

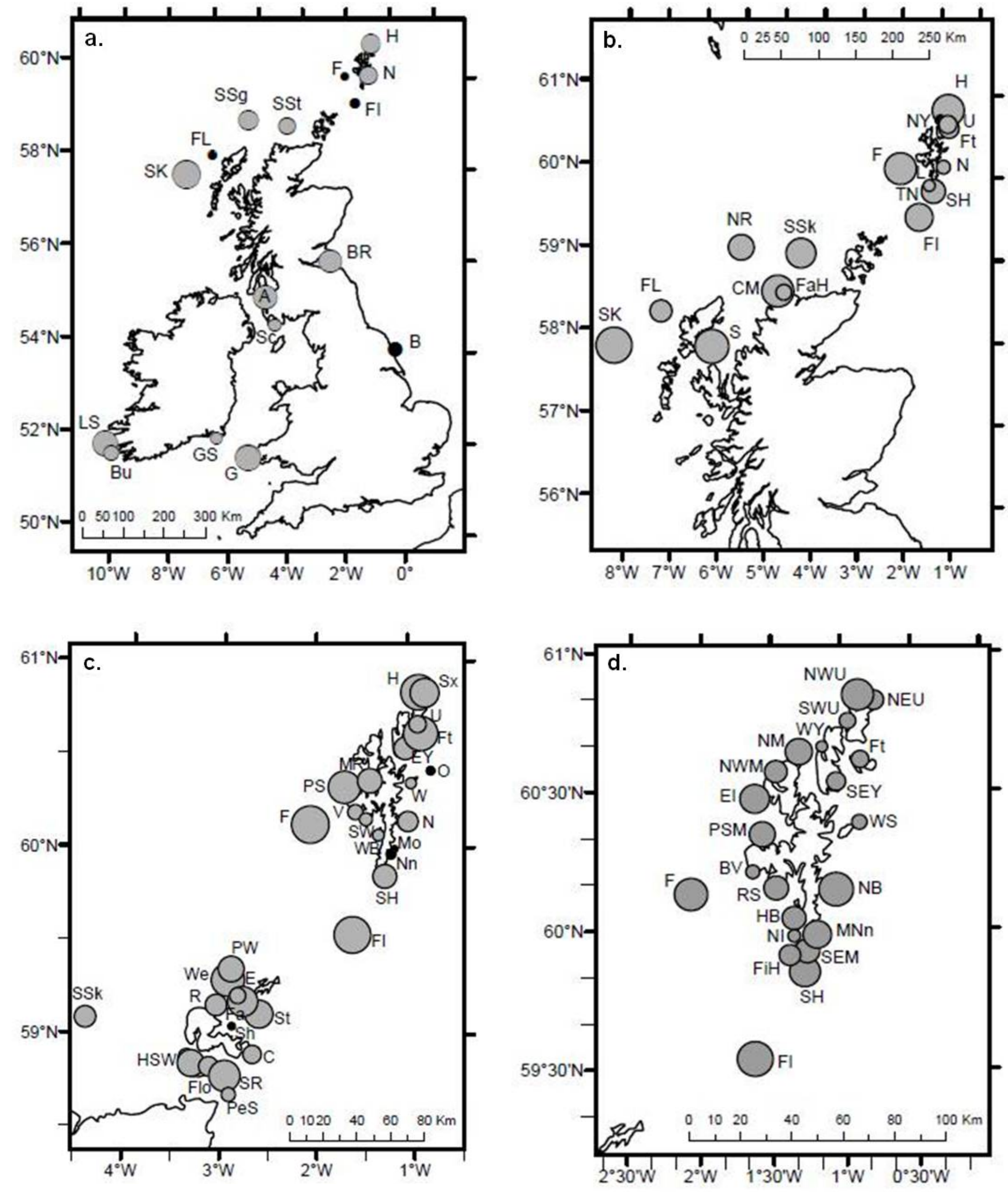

Figure 3.1. Locations of seabird colonies used in the Furness and Birkhead (1984) analysis **a.** Gannets (all colonies in the British Isles and southern Ireland) in the 1970s, **b.** Puffins breeding in the UK, north of 57°30'N (1969-75), **c.** Shags breeding in Orkney and Shetland (1969-70) and **d.** Kittiwakes breeding in Shetland in 1982. Symbols are proportional to population size (number of pairs). Grey symbols are established colonies. Black symbols indicate very small or newly established colonies. Colony codes refer to Table A.1 in Appendix A.

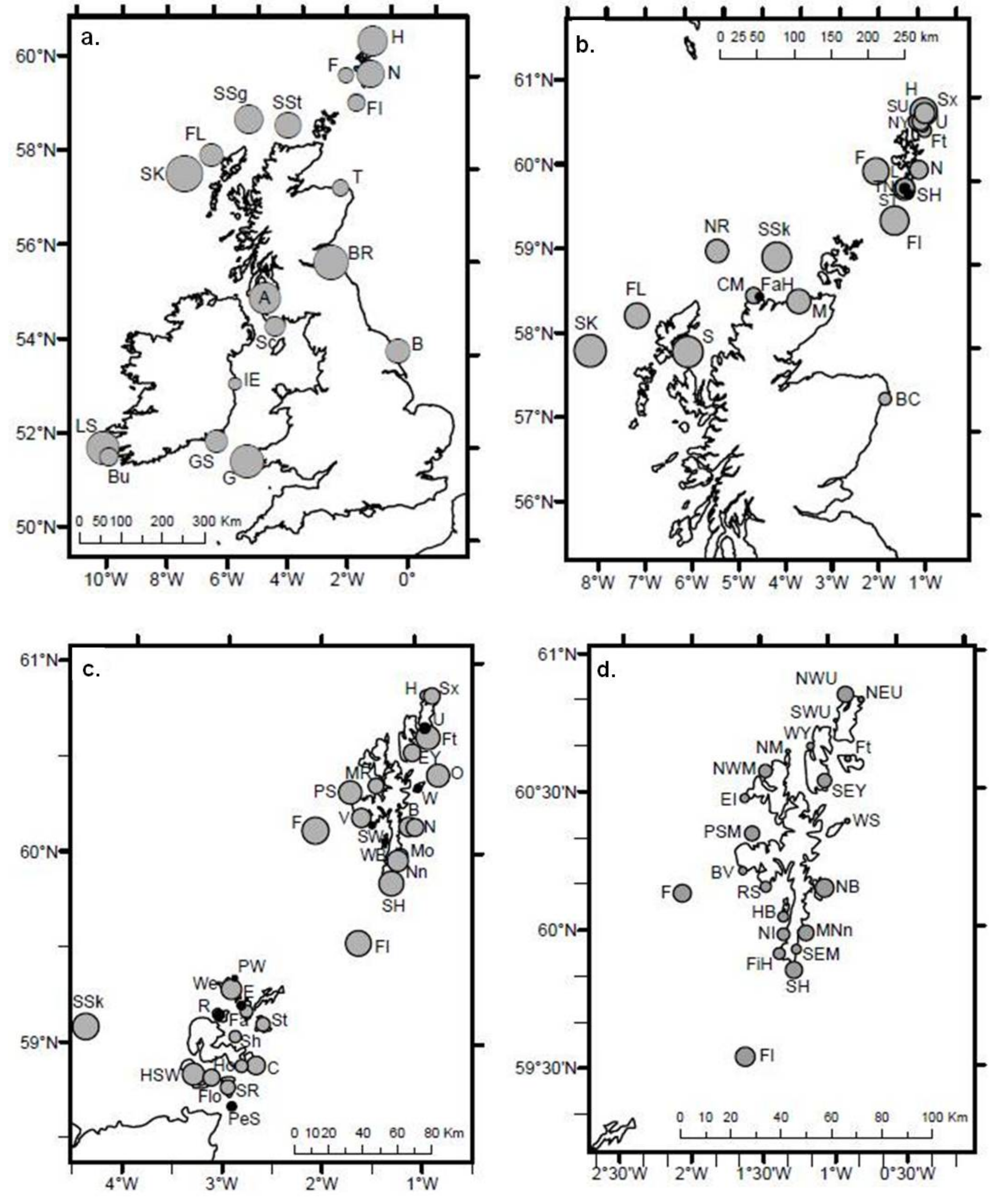

Figure 3.2. Locations of seabird colonies used in the update of the Furness and Birkhead (1984) analysis **a.** Gannets (all colonies in the British Isles and southern Ireland) in 2003/04, **b.** Puffins breeding in the UK, north of 57°30'N in 2000/01, **c.** Shags breeding in Orkney and Shetland in 2000/01 and **d.** Kittiwakes breeding in Shetland in 2000/01. Symbols are proportional to population size (number of pairs). Grey symbols are established colonies. Black symbols indicate very small or very newly established colonies. Colony codes refer to Table A.1 in Appendix A.

For comparison with Furness and Birkhead (1984), I tested for correlations (Pearson's r) between population size and neighbouring conspecific density (i.e. number of conspecific pairs breeding at neighbouring colonies within the species' maximum putative foraging range, obtained using the census counts described above). I used four, five, seven and six distances within the putative foraging range of gannets, puffins, shags and kittiwakes respectively. I also examined this relationship within the putative foraging distances using linear models. The additional counts of gannet colonies enabled me to compare relationships between population sizes and neighbouring conspecific density during the 1980s (Murray and Wanless, 1986, Lloyd et al., 1991) and 1990s (Murray and Wanless, 1997, Mitchell et al., 2004).

None of the species considered routinely fly over land. Hence, throughout my analysis, distance refers to the shortest distance by sea. Putative foraging ranges were the average and maximum foraging ranges recently estimated for each species using tracking technology (Harris et al., 2012, Thaxter et al., 2012). The earlier count data were also analysed as described above to ensure the results from Furness & Birkhead (1984) could be replicated. Population sizes and number of neighbouring conspecifics were square-root transformed to be proportional to the putative density of birds at sea (Furness and Birkhead, 1984, Lewis et al., 2001) and to improve normality. Following the previous study, I used permutation tests to determine whether the observed correlations could have occurred by chance. I randomly relabelled colonies 1000 times for each species and time period considered, calculating the correlation coefficient at each permutation. I then compared observed correlation coefficients with the null distribution using Wilcoxon signed-rank tests. In addition, I used semi-variograms (Cressie, 1993) to examine spatial autocorrelation within observed population sizes and the linear model residuals.

3.3. Results

Between the late 1970s and the early 2000s all of the original gannet colonies increased in size and six new colonies were established prior to 1990 (Fig 3.3). Overall, the gannet population in the study area nearly doubled (92% increase) during this period. Of the 15 puffin colonies that were larger than 1000 pairs in the early 1970s, 9 decreased and 6 increased in size by the early 2000s (Fig 3.4). A further 7 were newly established or grew to greater than 1000 pairs. However, there was little change in the overall numbers of puffins in the study area during this period (net 5% decrease).

Of the 33 shag colonies studied, 22 decreased in size while 5 increased. An additional 6 colonies were established or grew to > 40 pairs (Fig 3.5). Overall, the breeding population of shags in Orkney and Shetland decreased by 47%. All 22 of the Shetland kittiwake colonies studied decreased in size between the 1981 and 2000 censuses and no new colonies were established. Overall, the breeding population decreased by 69% (Fig 3.6).

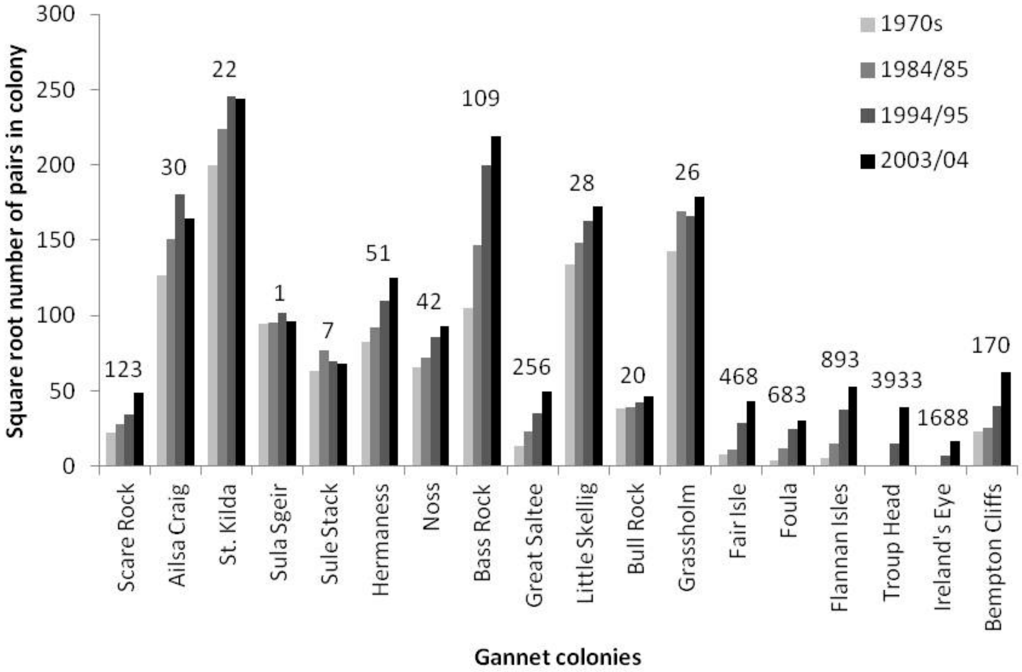

Figure 3.3. Size of gannet colonies (square-root pairs) in the British Isles in the 1970s (light grey bars), 1984/85 (medium grey bars), 1994/95 (dark grey bars), and 2003/04 (black bars). This includes 6 colonies established prior to 1990 and not included in the analysis by Furness and Birkhead (1984) (Fair Isle, Foula, Flannan Isles, Troup Head, Ireland's Eye and Bempton Cliffs). The percentage increase at each colony between the 1970s and 2003/04 is shown above each bar.

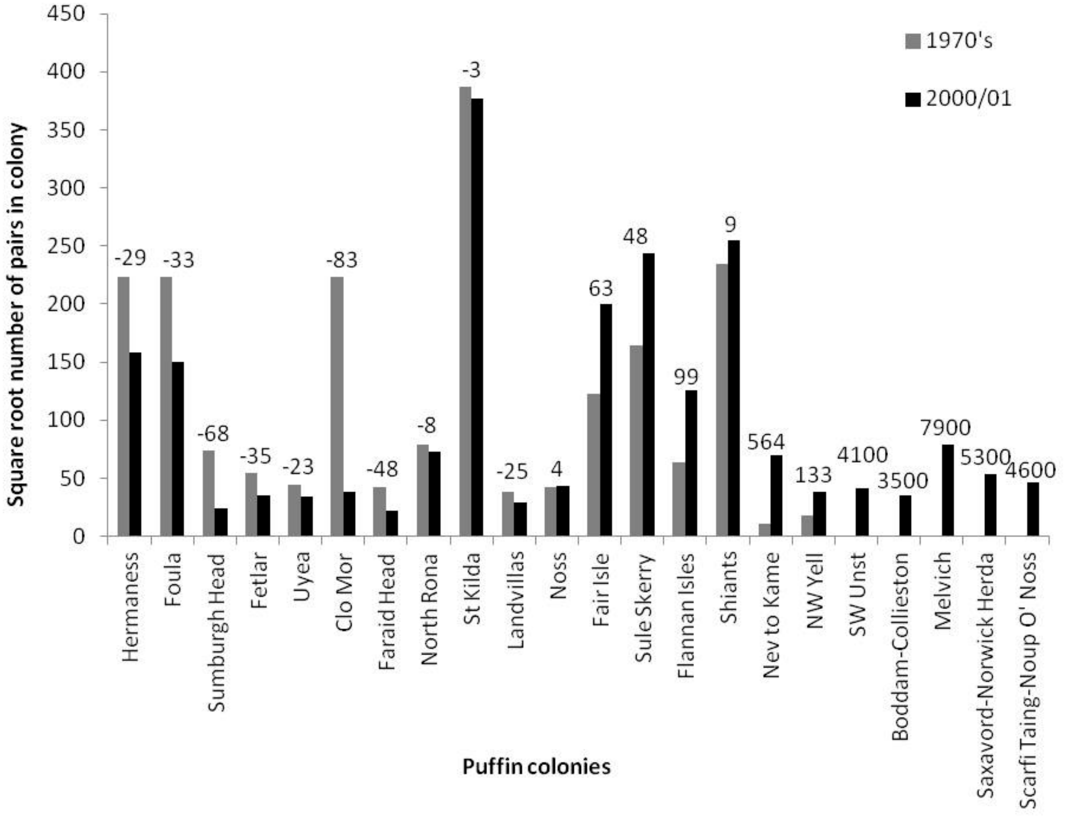

Figure 3.4. Size of puffin colonies (square-root number of pairs) north of 57°30'N in the early 1970s (grey bars), and in the Seabird 2000 census (black bars). This includes 7 colonies that established or grew to greater than 1000 AOS since the analysis by Furness and Birkhead (1984) (The Nev to Kame, NW Yell, SW Unst, Boddam to Collieston, Melvich, Saxavord-Norwick Herda and Scarfi Taing to Noup of Noss). The percentage difference between counts is shown above each bar.

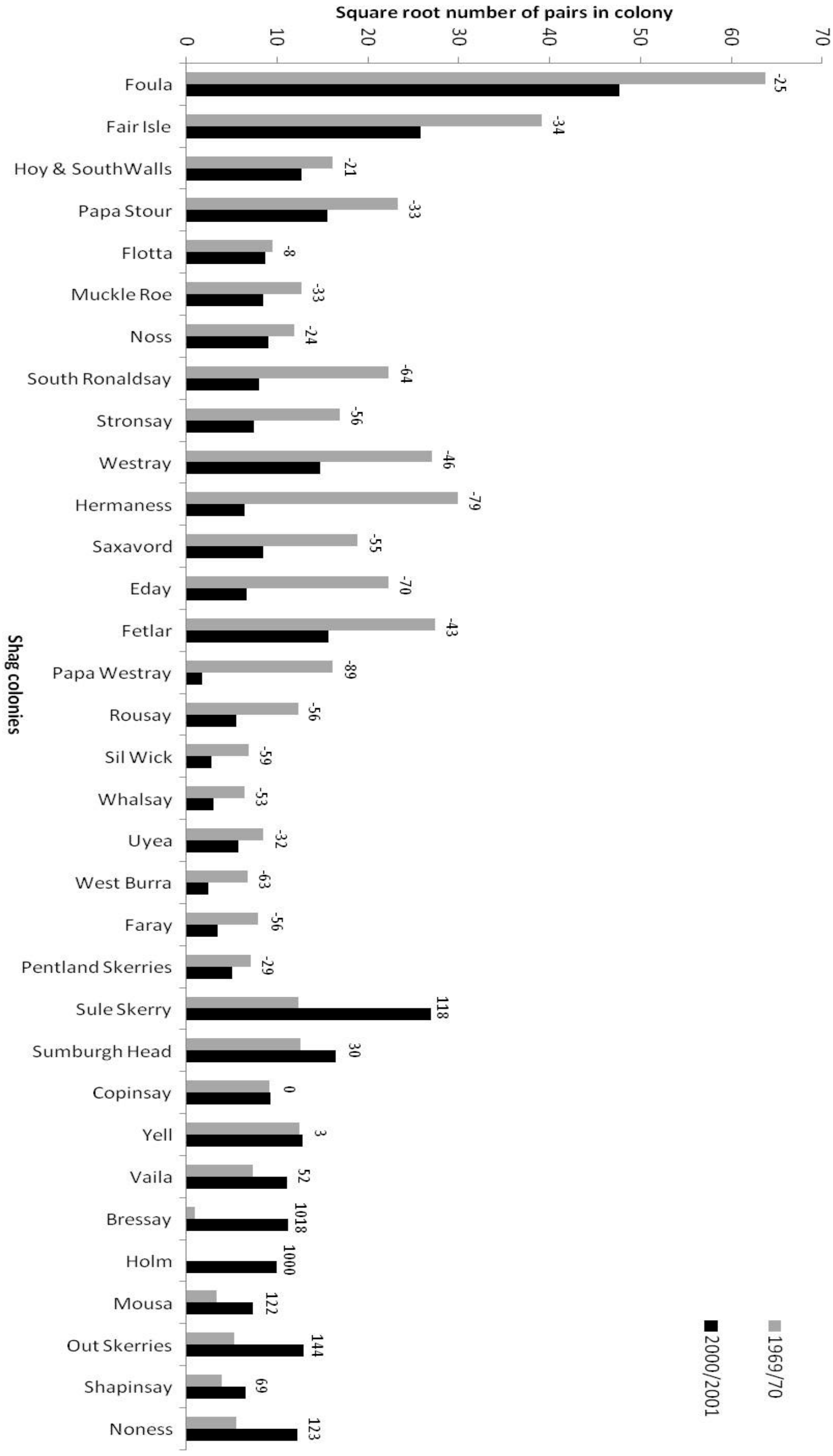

Figure 3.5. Size of shag colonies (square-root number of pairs) in Shetland and Orkney in 1969/70 (grey bars), and in the Seabird 2000 census (black bars). This includes 6 colonies that were established or grew to greater than 40 pairs since 1969/70 (Bressay, Holm, Mousa, Out Skerries, Shapinsay and Noness). The percentage difference between counts is shown above each bar.

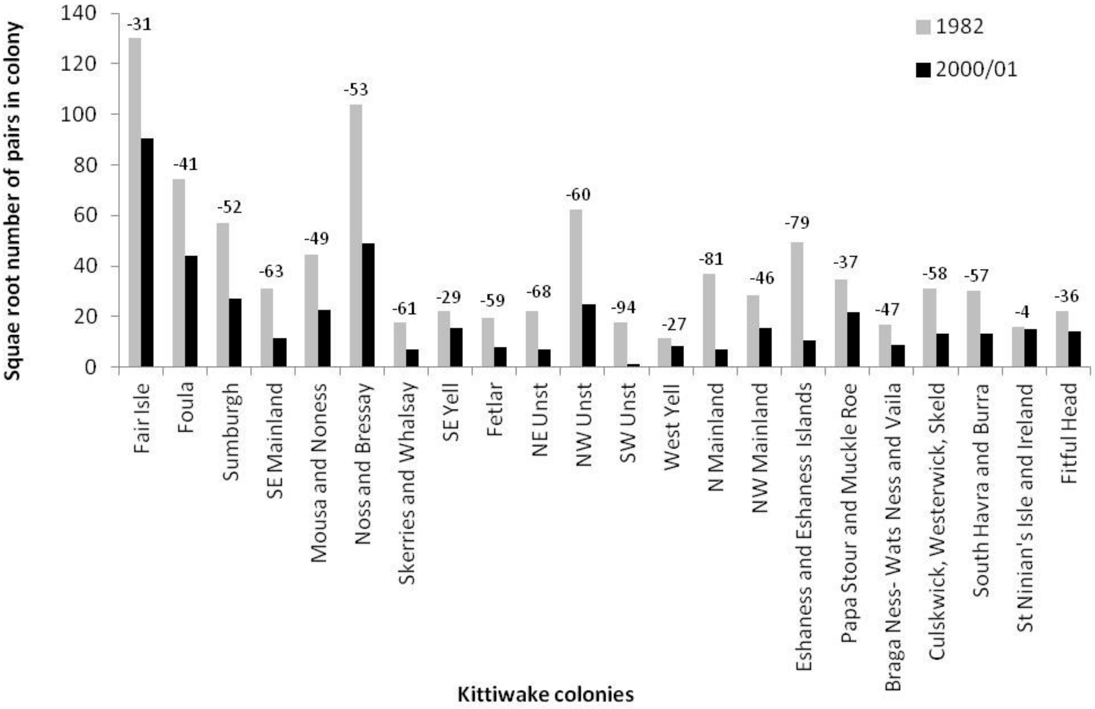

Figure 3.6. Size of kittiwake colonies (square-root number of pairs) in Shetland in 1982 (grey bars), and the Seabird 2000 census (black bars). The percentage difference between these counts is shown above each bar.

Semi-variograms generally showed evidence for negative spatial autocorrelation in population size over short distances and positive autocorrelation at larger distances (see figures B.1. – B.4. in Appendix B).

The distance at which population size best predicted neighbouring conspecific density has changed with time (Table 3.1, Fig. 3.7). Randomisation tests showed that, with one exception, these results were unlikely to have occurred by chance (Wilcoxon assigned rank test, $p < 0.05$, Table 3.1, Fig 3.8). For gannets, the relationship was no longer significant within a range of ≤ 150 km, but became significant over greater ranges (200 km; b = - 0.5491, $P<0.01$: 300 km; b = -0.6454, $P<0.001$). For puffins, while the smallest range gave a similar result to the original study, there was no longer a significant association between population size and number of neighbouring conspecifics at the two largest ranges. The correlation within the 150 km range was less significant than previously found (Table 3.1). For shags, there was no longer a significant relationship at distances between 30 and 60 km. Only the relationship at the smallest distance considered (20 km) was significant (Table 3.1). Finally, for kittiwakes there was still no significant relationship between population size and the number of neighbouring conspecifics within the three largest distances. Although population size correlated with neighbouring conspecific density at 40 km, the permutation test showed that this result may have arisen by chance (Table 3.1). However, the relationship remained significant at the 20 km and 30 km ranges.

Table 3.1. Correlation between square-root population size and square-root number of conspecifics breeding at other colonies within putative foraging range for four species of seabird breeding in the UK, with varying population trends. Correlations are shown for population sizes estimated in the 1970s and the 2000s. For each species and time period, the spatial scale(s) with the strongest relationship is highlighted in bold.

Time period		**1970s**			**2000s**		
Species (*trend*)	**Range (km)**	**Mean no. colonies**	**Correlation**	***P***	**Mean no. colonies**	**Correlation**	***P***
Gannet *Increased*	100	0.8	**-0.92**	**<0.001**	1.0	-0.36	NS
	150	0.8	**-0.92**	**<0.001**	1.3	-0.44	NS
	200	1.0	-0.47	NS	2.3	-0.55	<0.01
	300	1.8	-0.51	NS	3.8	**-0.76**	**<0.001**
Puffin *Unchanged*	50	0.7	-0.56	<0.05	2.3	-0.46	<0.05
	100	2.5	-0.81	<0.001	4.1	-0.43	NS
	150	4.9	**-0.88**	**<0.001**	6.6	**-0.56**	**<0.05**
	200	6.6	-0.74	<0.001	7.8	-0.2	NS
	250	9.0	-0.58	<0.05	9.7	-0.04	NS
Shag *Declined*	20	2.0	-0.45	<0.05	1.8	**-0.55**	**<0.01**
	30	3.5	-0.54	<0.01	2.7	-0.13	NS
	40	4.9	-0.48	<0.05	3.7	-0.11	NS
	50	6.4	-0.58	<0.01	4.5	-0.10	NS
	60	7.2	**-0.66**	**<0.001**	5.6	-0.07	NS
	70	8.1	-0.32	NS	6.1	-0.08	NS
	80	9.3	-0.24	NS	7.9	0.08	NS
Kittiwake *Declined*	20	1.5	-0.55	<0.01	1.5	**-0.49**	**<0.01**
	30	3.3	-0.49	<0.05	3.3	-0.47	<0.05
	40	4.9	**-0.67**	**<0.001**	5.3	-0.49	<0.05^{+}
	60	8.8	-0.36	NS	9.2	-0.13	NS
	80	11.7	-0.32	NS	12.6	0.10	NS
	100	14.5	-0.08	NS	15.6	0.10	NS

$^{+}$ indicates randomisation test showed correlation not significant at α = 0.05 level

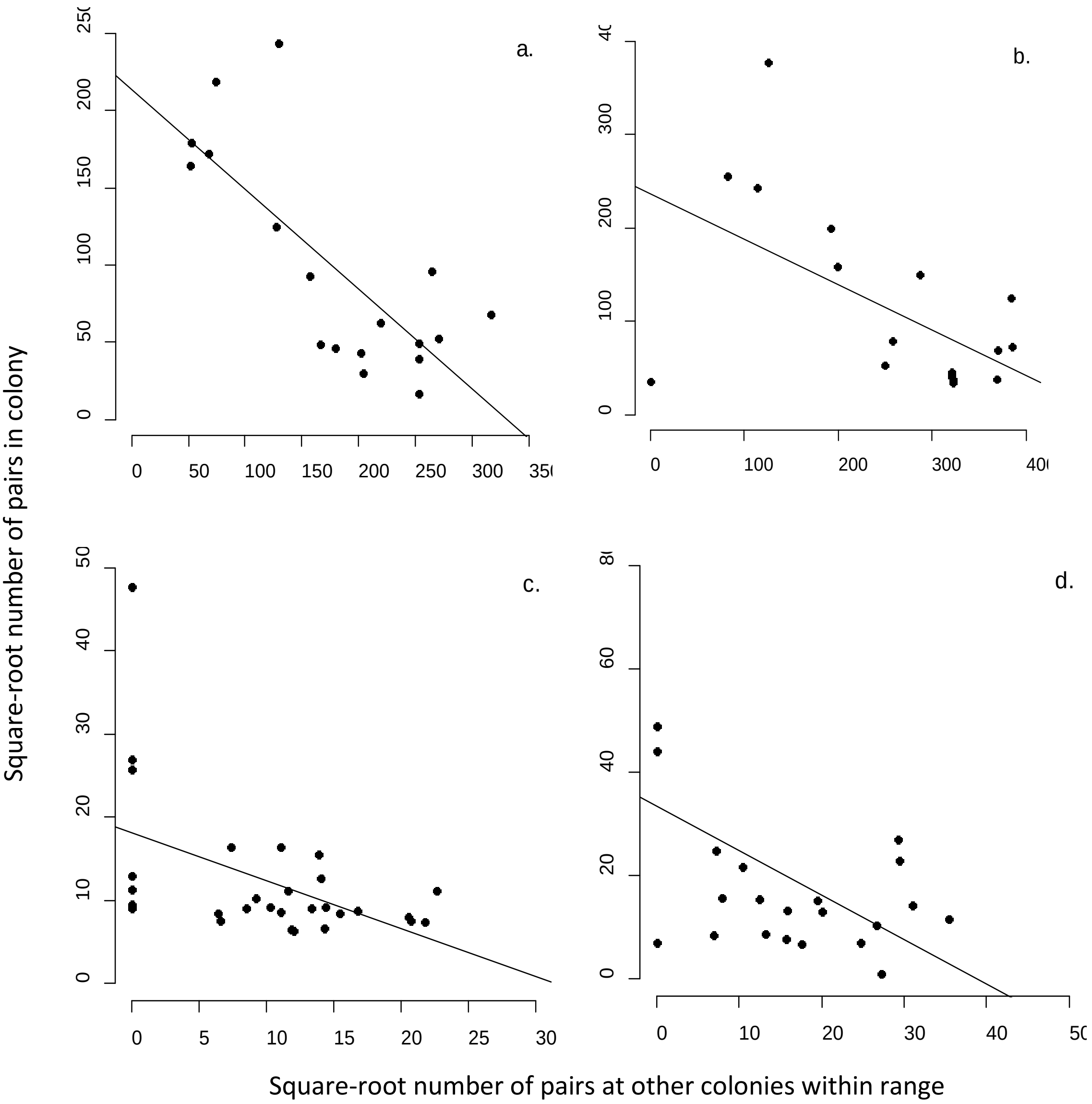

Figure 3.7. Strongest significant relationships between population size of and number of conspecifics breeding at neighbouring colonies within putative foraging range for **a.** gannets, (range = 300 km); **b.** puffins (range = 150 km); **c.** shags (range = 20 km); and **d.** kittiwakes (range = 20 km).

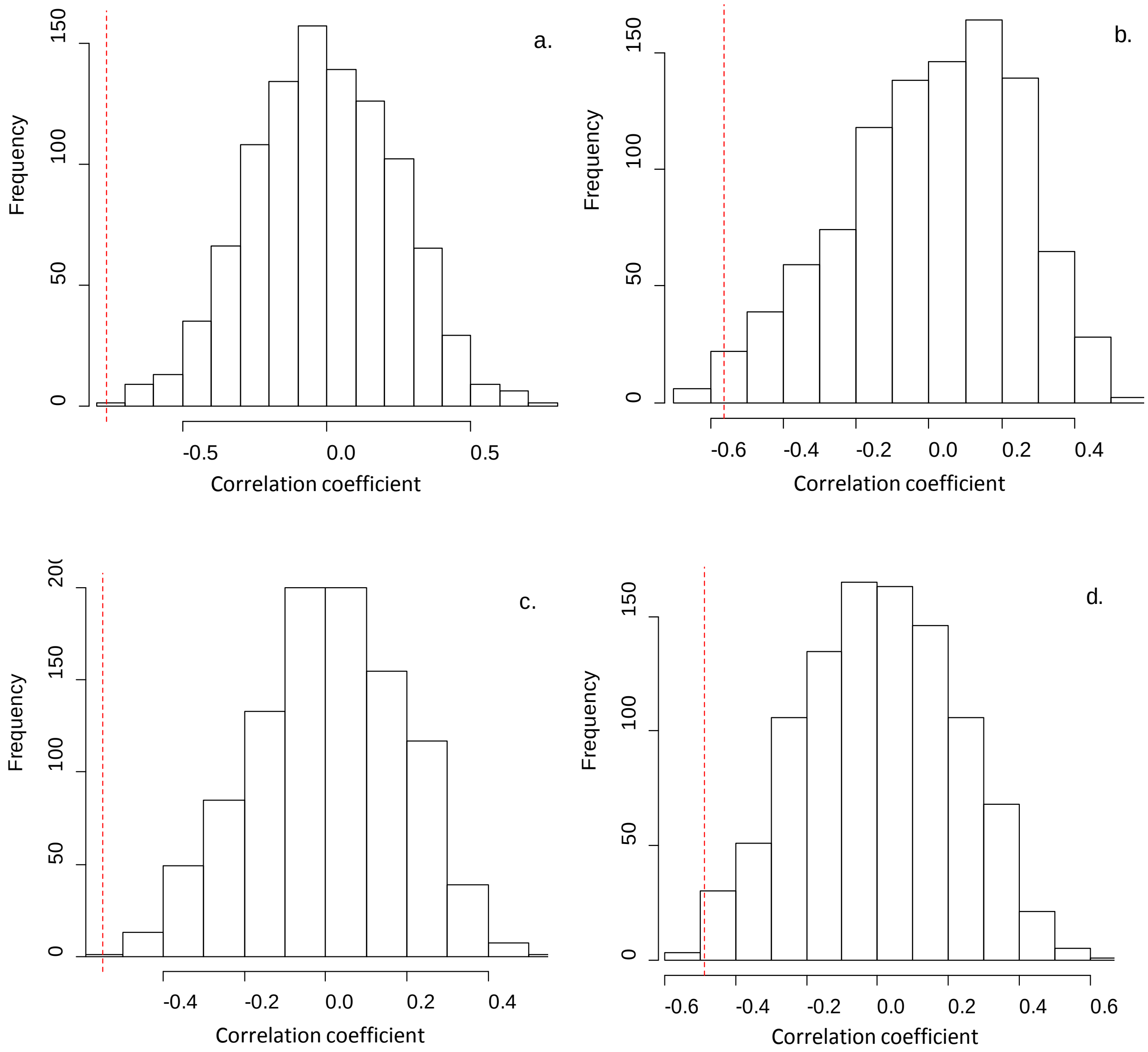

Figure 3.8. Observed Pearson's correlation coefficient (red dotted line) in relation to the null distribution generated by carrying out 1000 permutations of population sizes, for the ranges within which the strongest significant relationships were found between population size and number of conspecifics breeding at neighbouring colonies for **a.** gannets, (range = 300 km); **b.** puffins (range = 150 km); **c.** shags (range = 20 km); and **d.** kittiwakes (range = 20 km).

For gannets, analysis of intermediate population counts (from 1984/85 and 1994/95) showed that the range over which a significant relationship occurred became progressively larger as the population grew (Table 3.2, Fig 3.9). These relationships also became stronger for the greater range size, whereas the significant negative correlations between population size and neighbouring conspecific density became weaker in the smaller range groups until they were eventually non-significant in the most recent count (Table 3.2, Fig 3.9). Again, randomisation tests showed that these results were unlikely to have occurred by chance (Wilcoxon assigned rank test, p <0.05), apart from the correlation within the 300 km distance range using the 1984/85 population counts and within the 200 km distance range using the 1994/95 population counts. These were not significantly different from the null distribution of coefficients generated by permutation (Table 3.2).

Table 3.2. Correlations between square-root gannet population size and square-root number of conspecifics breeding at other colonies within specific putative foraging ranges, in 4 separate census counts; including 1970's, used by Furness and Birkhead (1984); 1984/5; 1994/5 and 2004.

Count	**n**	**Range (km)**	**Mean no. of colonies**	**Correlation**	***P***
1970s (Furness and Birkhead, 1984)	12	100	0.8	-0.92	<0.001
		150	0.8	-0.92	<0.001
		200	1	-0.47	NS
		300	1.8	-0.51	NS
1984/5 (Murray and Wanless, 1986, Lloyd et al., 1991)	14	100	0.9	-0.75	<0.01
		150	1	-0.72	<0.01
		200	1.3	-0.39	NS
		300	2.1	-0.48	<0.05$^+$
1994/5 (Murray and Wanless, 1997, Mitchell et al., 2004)	16	100	1.1	-0.66	<0.01
		150	1.4	-0.65	<0.01
		200	2.0	-0.46	<0.05$^+$
		300	3.0	-0.56	<0.01
2003/4 (Wanless et al., 2005)	18	100	1	-0.36	NS
		150	1.3	-0.44	NS
		200	2.3	-0.55	<0.01
		300	3.8	-0.76	<0.001

$^+$ indicates randomisation test showed correlation not significant at $\alpha = 0.05$ level

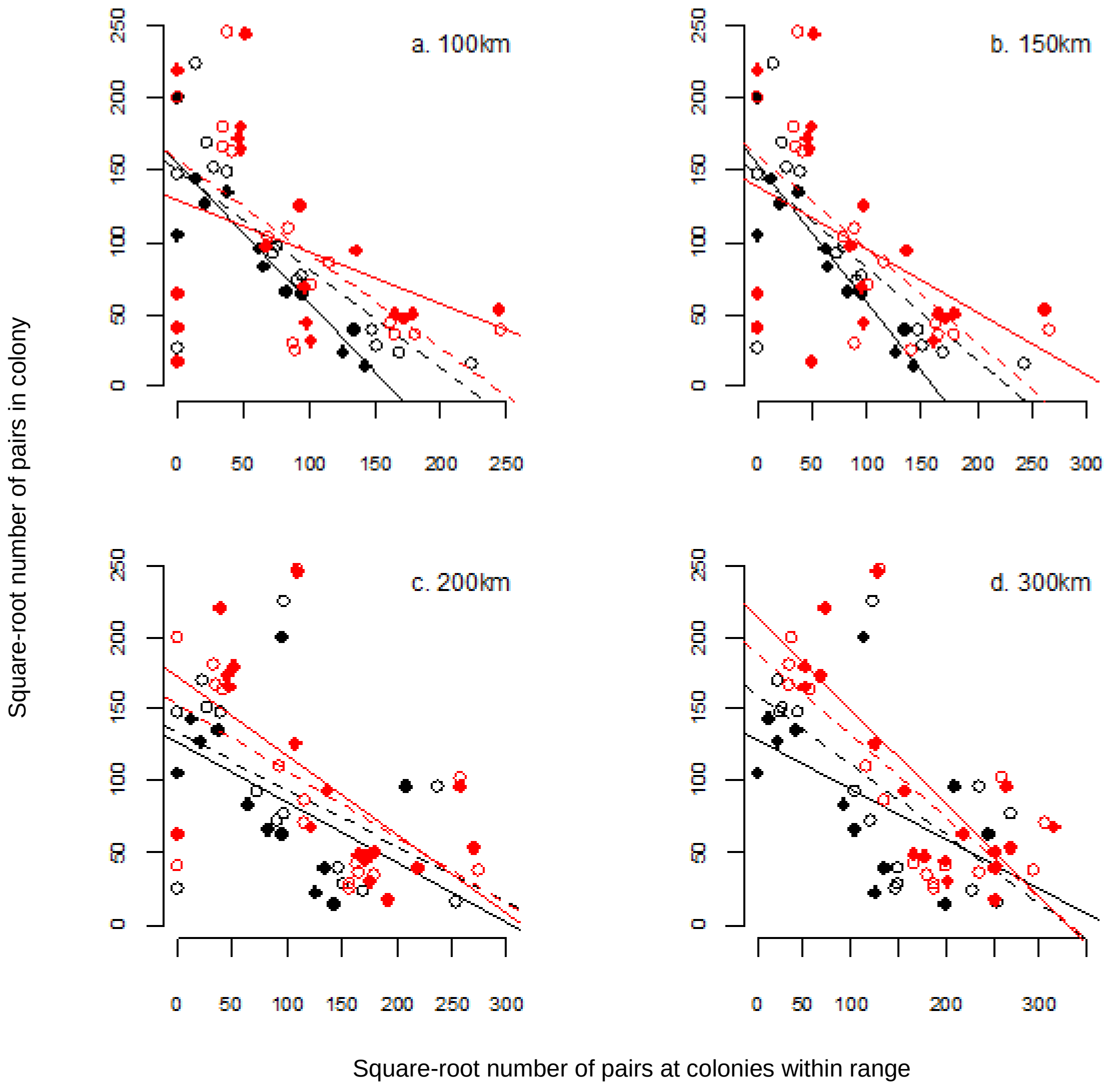

Figure 3.9. Changes over three decades in the relationship between square-root gannet population size and square-root number of pairs at neighbouring colonies within specified distances: a.100 km; b. 150 km; c. 200 km; and d. 300 km. Relationships for 1970s (solid black symbol, solid black line), 1980s (open black symbol, dashed black line), 1990s (open red symbol, dashed red line) and 2000s (solid red symbol, solid red line).

Semi-variograms of linear model residuals showed that the models accounted for most negative autocorrelation in the data but unexplained positive autocorrelation remained unaccounted for in some species (see figures B.5. – B.14. in Appendix B).

3.4. Discussion

My results support the hypothesis that seabird population sizes are regulated in part by competition for food with conspecifics breeding at adjacent colonies. Assuming that competition is proportional to population size and thus that there is a positive relationship between foraging range and population size (Storer, 1952, Ashmole, 1963, Lewis et al., 2001, Elliott et al., 2009), I predicted that as population sizes change so do the foraging ranges of colony members, thereby altering the scale of dependency between population size and competition with neighbouring conspecifics. My results support this prediction such that the distance at which the negative relationships between population size and number of neighbouring conspecifics were strongest shifted in line with population change. This was the case for all four species considered, which had experienced contrasting population trends over the study period. The study species also use a range of different foraging strategies e.g. foot-propelled and wing-propelled pursuit-divers (shags and puffins respectively), plunge and surface divers (gannets) and surface feeders (kittiwakes). They also variously exploit near shore (shags), offshore (puffins and kittiwakes) and pelagic (gannets) habitats. The importance of neighbouring conspecific competition appears to be a general feature of many colonially breeding seabirds.

For puffin colonies, which were relatively unchanged over the study period, I found the strongest negative relationship between population size and neighbouring conspecific density within the same range (150 km) in both the 1970s and 2000/01. Information on foraging ranges from bio-logging for this species is extremely limited but suggests that the maximum for this species is 100 to 200 km, although most birds probably forage closer to the breeding colony (Harris et al., 2012, Thaxter et al., 2012). For shags and kittiwakes, where populations decreased in size substantially, I found shifts towards stronger relationships at shorter putative foraging ranges. For example in shags, only the 20 km range gave a significant correlation for the 2000/01 counts, in-keeping with recent information on the foraging ranges of this species, maximum generally < 20 km (Thaxter et al., 2012). The negative correlations at larger ranges in count data for the 1970s were likely due to the larger populations at that time inferring more intense intra-specific competition and likely greater foraging ranges, although there are no independent direct data on foraging range to check this.

Over the 30 years covered by the study there was almost a twofold population increase in the UK gannet population. For this species large amounts of direct data on foraging ranges are available and there is increasing evidence of competition at the colony level resulting in density-dependent foraging behaviour (Lewis et al., 2001 and chapter 4). Such positive relationships between foraging range and population numbers have been found to hold across seasons, even under varying feeding conditions (chapter 2). My results imply that this has increased the scale over which intra-specific competition with neighbours limits population growth. Whereas Furness and Birkhead (1984) found significant correlations between population size and neighbouring conspecific density within the smaller ranges tested (100 km and 150 km), this is no longer the case. More recent population counts show strong correlations between population size and the number of neighbouring conspecific pairs within larger ranges (200 and 300 km). These accord well with distances recorded using tracking technology in the late 1990s and 2000s, i.e. mean and mean maximum foraging range of individuals estimated at 93 km and 229 km respectively (Hamer et al., 2007, Thaxter et al., 2012).

The positive autocorrelation remaining in the models for some species is likely a result of similar foraging and breeding conditions experienced by certain clusters of colonies, however this would not have an effect on these results. It is also likely that there is regional variation in population trends. For three of the species studied here (puffins, shags and kittiwakes), only limited parts of the overall breeding range were considered. It is therefore possible that more complex patterns of change and regulation may be apparent at larger spatial scales. Further work is now required to explore such spatial patterns and relationships. The possibility of negative correlations occurring by chance if all colonies were included within the maximum range tested could also be considered a limitation of this study. However, this was countered by the use of permutation tests, which found that these results were highly unlikely to have occurred by chance, apart from very few instances. Taken together, my findings provide little support for the hypothesis that population size is limited by availability of breeding habitat alone.

Although the locations of seabird colonies have changed very little over the last 30 years, there is evidence of shifting distributions of ocean productivity (Richardson and Schoeman, 2004, Behrenfeld et al., 2006). It is thus possible that the usage of marine areas by breeding seabirds may also have changed. Lags between changes in foraging conditions and seabird population dynamics also potentially mean that these results are likely to have been affected by changes occurring several years previously. However, I show here that neighbouring seabird colonies are non-independent. Along with other factors contributing to population size and distribution, such as nest site availability (Kildaw et al., 2005), local prey availability (Kitaysky et al., 2010) and winter mortality (Lack, 1968), competition between neighbouring conspecifics has been found sufficient to limit population size, and is therefore likely to be intense. Indeed, if one colony is lost due to either anthropogenic or natural processes, neighbouring colonies would be expected to grow. This competition between neighbouring colonies may also be sufficient to mediate spatial segregation of feeding grounds during the breeding season, in order to reduce such competition between neighbouring colonies (Cairns, 1989, Grémillet et al., 2004, Wakefield et al., 2011). As such, processes occurring during the breeding season play a role in the limitation of seabird populations. This has conservation implications, whereby foraging areas as well as colonies require protection, potentially in the form of Marine Protected Areas (Lascelles et al., 2012, Grecian et al., 2012).

While this study focuses on seabird colonies, all of these factors are also likely to be of relevance to the population regulation of other colonial central-place foragers, including other colonial birds (Lack, 1968, Butler, 1994, Soutullo et al., 2006), mammals (Robson et al., 2004, Zahn et al., 2006), reptiles (Trillmich and Trillmich, 1984, Doody et al., 2009) and invertebrates (Adams and Tschinkel, 2001, Billick, 2001).

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Chapter 4: Annual variation in foraging ranges and fine-scale foraging behaviour of northern gannets

Abstract

Marine ecosystems are changing in response to natural and anthropogenic pressures. The distribution of primary productivity, which influences higher trophic level production, including the distribution of demersal fish, is thought to be altering in response to climate change. Hence, climatic effects can impact on marine top predators, such as seabirds. In this chapter, I use northern gannets *Morus bassanus* as a model species to investigate the extent to which wide-ranging seabirds can respond to changes in prey availability by altering their diet, foraging range and fine scale foraging behaviour.

I combine published data on the foraging movements and diet of northern gannets breeding on Bass Rock in 1998, 2002 and 2003, with diet and GPS tracking data I collected in 2010 and 2011, to determine the flexibility in the foraging behaviour of gannets during this period. Prey captured by chick-rearing adults varied between years, with mackerel replacing sandeels as the predominant species in the latter two seasons. Foraging trips in 2010 and 2011 were significantly shorter, both in distance and time, compared to those in the late 1990s and early 2000s. In addition, in 2011, birds made a higher proportion of V-shaped dives as distances from the colony increased. Together, these findings support models of foraging based on prey depletion around seabird colonies, implying that gannets can avoid competition in response to prey scarcity by foraging further from the colony. Birds also expressed flexibility in the frequency of Area Restricted Search (ARS) behaviour and dive rates outside ARS zones. Hence, flexibility in diet, habitat use and aspects of finer scale foraging behaviours may buffer this species against environmental change.

4.1. Introduction

Marine ecosystems are changing as a result of multiple environmental pressures (Richardson and Schoeman, 2004, Behrenfeld et al., 2006, Worm et al., 2006). For example, increases in sea surface temperature, as a result of climate change, have been shown to be associated with marked changes in the abundance and distribution of phytoplankton and zooplankton (Richardson and Schoeman, 2004, Kirby et al., 2008). Due to tight trophic coupling, changing sea-surface temperatures influence the spatial distribution and abundance of higher trophic level pelagic production (Lenoir et al., 2010). For example, the latitudinal or depth distribution of demersal fish in the North Sea has altered in response to temperature increases over recent decades (Perry et al., 2005). Such changes may occur gradually over long periods of time, i.e. decades, or over much shorter periods, even annually between years (Beaugrand et al., 2003, Rindorf and Lewy, 2006). These effects, along with the impacts of industrial and commercial fishing (Hjermann et al., 2004, Camphuysen, 2005, Österblom et al., 2006), which may act synergistically, can therefore be propagated along food chains and impact on the breeding success of top predators such as seabirds (Furness and Tasker, 2000, Rindorf et al., 2000, Furness, 2002, Davis et al., 2005, Furness, 2007).

In periods of poor prey availability, wide-ranging higher predators may respond by shifting their foraging distributions. For example, seabirds may forage further away from their colonies (Pinaud et al., 2005b, Weimerskirch and Lecorre, 2006, Cresswell et al., 2008). Generalist predators may also respond by altering their diets (Barrett and Krasnov, 1996, Montevecchi and Myers, 1996, Votier et al., 2004). This flexibility potentially buffers against environmental variability (Hamer et al., 2006b, Hamer et al., 2007). In addition to mesoscale shifts (ca. 10^2 km; Haury et al. 1977) in foraging ranges of wide-ranging species (Fritz et al., 2003, Hamer et al., 2007, Burke and Montevecchi, 2009, Garthe et al., 2011), relationships can also be found at finer or coarse scales, of ca. 10 m - 100 km (Haury et al., 1977), between the movements of marine predators and areas of higher marine productivity (Pinaud and Weimerskirch, 2007, Bost et al., 2009, Raymond et al., 2010). Many species have been found to adopt area-restricted search (ARS) behaviour at finer spatial scales, often associated with zones of higher productivity, such as mixing fronts and upwellings (Pinaud et al., 2005a, Hamer et al., 2009, Scheffer et al., 2010). For example, gannets tracked from the Bass Rock colony in 2003 were found to exhibit ARS in the vicinity of a small scale, shelf-sea mixing front (Hamer et al., 2009). Examination of such fine-scale foraging behaviour as ARS, whereby predators adjust movement in response to environmental cues or prey density, can therefore indicate key foraging locations (Fauchald and Tveraa, 2006, Pinaud and Weimerskirch, 2007). Patterns of ARS have been considered to be possible characteristics of the species studied or the habitat in which they subsist (Pinaud and Weimerskirch, 2007), and thought unlikely to be greatly affected by the conditions experienced on feeding grounds. However, as predators have been found to adjust their movements, reflecting the scale of the habitat patches they exploit (Fauchald and Tveraa, 2006), more investigation is required to examine finer scale search strategies under varied conditions.

The ongoing development of global positioning systems (GPS) technology has made it increasingly possible to track species' spatial responses to environmental change (Markones et al., 2010, Garthe et al., 2011, Schwemmer and Garthe, 2011). The northern gannet provides a good model species for this type of study. It is large and therefore capable of carrying devices. It is also a generalist and wide-ranging species (Hamer et al., 2007). There are also synoptic environmental data available, which aid the estimation of foraging conditions experienced by these birds, such as sea-surface temperatures and chlorophyll-α concentrations, as well as information on prey stocks (ICES, 2012). Published data on the foraging movements and diet of northern gannets breeding on Bass Rock during the 1998, 2002 and 2003 breeding seasons indicate that chick-provisioning adults forage over a large area of the North Sea, with mean foraging ranges of ca. 230 km, and exploit a wide variety of prey species (Hamer et al., 2000, Hamer et al., 2007, Hamer et al., 2009). In this chapter, I combine these data with data I collected in 2010 and 2011 to describe how gannets adjust their foraging behaviour, including both larger and finer scale movements, in response to environmental change over a fourteen year period. I assume that variation in prey availability is approximated in part by variation in winter sea-surface temperature and summer chlorophyll-α concentrations (Beaugrand et al., 2003, Wegner et al., 2003, Behrenfeld et al., 2006, Jansen and Gislason, 2011).

By comparing trip durations, feeding locations and fine-scale foraging patterns between years, I describe how the foraging behaviour of a flexible, generalist predator responds to prey abundance and distribution. I predicted shorter foraging trips in years when conditions were more favourable. I also aimed to use the dive activity data from the latest season to test the theory of greater competition for food closer to the colony, resulting in an annulus of prey forming around the colony. I predicted that dive profiles would alter as distance from the colony increases, with more U-shaped dives (see materials and methods) closer to the colony, indicative of underwater pursuit and thus greater competition closer to the colony (Davoren et al., 2003b, Elliott et al., 2009). Finally, I hypothesised that fine-scale foraging behaviour between the two years for which both high resolution GPS data and dive activity data were available, would vary under differing foraging conditions. If aspects of search behaviour were similar between years, they may be considered as characteristic of the species, or the environment they exploit. However, if this species shows flexibility in their finer scale behaviour, I would predict a higher occurrence of ARS behaviour during the year with apparently improved conditions, owing to more encounters with prey or environmental cues.

4.2. Materials and methods:

4.2.1. Field site

Fieldwork was carried out on Bass Rock, southeast Scotland (56°4.6’N, 2°38.3’W, Fig. 4.1), during the 2010 and 2011 breeding seasons (June – August). At the most recent count, this colony was estimated to contain 52,292 apparently occupied sites (AOS) in 2009 (Murray, 2011). Both the Tay estuary and the sandeel (*Ammodytes marinus*) fishing grounds of St Andrew’s Bay lay within ~50km north of the colony, while to the east lays Wee Bankie and to the south east the fishing grounds of the Farnes Deep (Fig. 4.1.).

Zooplankton and phytoplankton biomass and recruitment of some fish species are known to have a negative relationship with sea-surface temperature (SST) in the preceding winter (O'Brien et al., 2000, Beaugrand et al., 2003, Wegner et al., 2003, Jansen and Gislason, 2011). Hence, a proxy for prey availability was developed based on the SST for each study season in the preceding winter (December-February). SST data over a 6 x 6° area containing Bass Rock were obtained from ICES (http://www.ices.dk/ocean/data/surface/surface.htm), together with chlorophyll-α concentrations in this area during the summer (June-August inclusive) each year (http://www.ices.dk/Ocean/data.asp). Summary stocks biomass assessment data for key prey species known to be consumed by Bass Rock gannets (North Sea mackerel *Scomber scomber*, Norwegian spring-spawning herring *Clupea harengus* and sandeels *Ammodytes marinus* in the three regions for which data were available, Dogger Bank, central North Sea and southern North Sea) were obtained from the ICES stocks summary database (http://www.ices.dk/datacentre/StdGraphDB.asp).

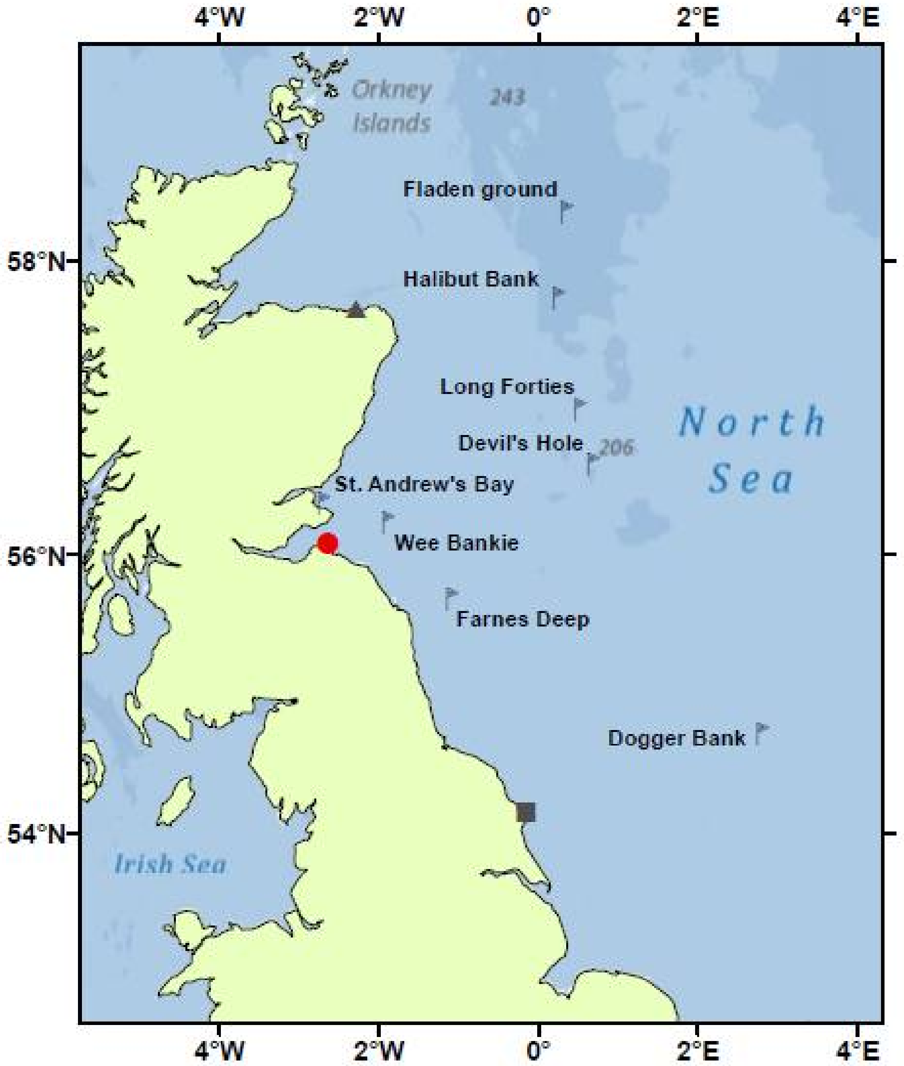


Figure 4.1. Location of Bass Rock in the UK (red circle) and other gannetries within 300 km (Troup Head: grey triangle; Bempton: grey square). Also shown are bathymetric features and fishing grounds mentioned in the text (blue flags).

4.2.2. Diet

Regurgitated prey items were collected opportunistically each year, either from chick-rearing adults during routine handling or from non-breeding birds disturbed in the colony. The proportion of species in these regurgitates did not differ between breeders and non-breeders. Samples from breeding birds were collected before chicks reached 10-11 weeks of age. Prey items were stored separately, frozen and returned to the laboratory, where I identified and weighed all samples (to the nearest

1g). Identification was based either on external morphology or sagittal otoliths and vertebrae (Härkönen, 1986, Watt and Boyle, 1997). Where possible, body lengths of prey items were measured to the nearest 1cm (1mm for sandeels).

4.2.3. Satellite tracking

The foraging movements of forty-nine chick-rearing adults were recorded in 2010. Of these, 22 were tracked for a second time in 2011, together with an additional 6 birds (total sample size 28). Birds were caught at the nest using a pole fitted with a brass noose or hook. Only adults with chicks $\geq$ 2.5 weeks were caught.

In 2010, birds were fitted with either an IgotU GT-120 (mass 20 g) or an IgotU GT-200e GPS logger (37 g) (n = 13 and 45 respectively, 9 individuals being fitted with both consecutively). In 2011, birds were fitted with an IgotU GT-200e or an IgotU GT-600e GPS (37 g) logger (n = 22 and 6 respectively). Additionally, in 2011, 22 birds were also fitted with a CEFAS G5 (2.7 g) or Modular Signal Recorder (MSR) 145 (18 g) time-depth recorder (TDR). Devices were attached with Tesa tape to the three central tail feathers, close to the base of the tail in order to minimise drag and prevent the tags being dislodged during plunge diving (Hamer et al., 2000). Birds were weighed (± 25 g) at capture to ensure that instrument mass did not exceed 2% of body mass (2010 mean = 2.95 kg, SD = 0.3; 2011 mean = 2.97 kg, SD = 0.21).

GPS devices were set to record locations at either 2 or 10 minute intervals. G5 TDRs recorded pressure every hour until they came into contact with water, when they began recording at 10 Hz (0.1 sec). As gannets spend time sitting on the water surface without diving, G5 TDRs were programmed to log only 4 data points if the logger became wet but its depth did not exceed 1.5 m. Due to this set up and because the loggers being deployed on the tail rather than leg, landings involving only very shallow dives were not consistently registered. Therefore dives with just 4 data points were removed from further analyses. MRS145 TDR loggers recorded pressure continuously at 1 Hz (1 sec). Devices were deployed for 1-2 weeks. Previous studies have found no discernible effect on the foraging or provisioning behaviour of gannets equipped with such devices (Hamer et al., 2000, Hamer et al., 2007). Each individual was also fitted with a metal BTO ring and plastic Darvic colour ring. Handling time to complete instrument deployment and recovery was < 15 minutes.

The utilisation distribution of birds at sea was estimated by calculating fixed kernel density (FKD) (Beisiegel and Mantovani, 2006), using Geospatial Modelling Environment (GME) in ArcGIS 10. The contours encompassing the 95% and 50% FKD estimates were considered to represent the area of active use, along with the core foraging area respectively. The farthest location recorded from the colony during each trip was defined as the trip destination, separating the outward and return legs. Trip durations were calculated as the period between the first recorded location after leaving the colony, and the first recorded location back at the colony (Hamer et al., 2000, Hamer et al., 2007). The total distance travelled on each trip was calculated as the sum of the distances between each consecutive position location. For birds for which 3 or more consecutive trips were recorded, the percentage time spent foraging was calculated by dividing mean trip duration by mean trip duration plus the mean time spent at the colony between trips (Hamer et al., 2007).

With gannets, there are strong linear relationships between trip duration, distance to trip destination and total distance travelled (Hamer et al., 2001, Hamer et al., 2007). Average speed over complete foraging trips was estimated as twice the slope of the linear regression of maximum distance against trip duration (speed^{b}), and also the slope of the linear regression of total distance against trip duration (speed^{c}, Hamer et al., 2007). Both measures of speed were calculated as these can vary depending on the sinuosity of tracks. For example, speed calculated using time taken to reach trip destination may appear slow if the route taken was highly sinuous, despite actual speeds over the total distance travelled being high. Using platform terminal transmitter (PTT) and GPS tracking data recorded previously (Hamer et al., 2007), comparisons were made between the trips recorded in 1998, 2002 and 2003 and those recorded in 2010 and 2011.

4.2.4. Fine scale foraging behaviour

Foraging tracks where concurrent dive data were collected in 2011 (22 birds, 95 complete tracks), were compared with data collected in 2003 (13 birds, 15 tracks, Hamer et al., 2009), to investigate fine-scale foraging behaviour. These were the only two years in which both high resolution GPS and concurrent dive data were recorded.

First passage time (FPT) is defined as the time taken for an animal to cross a circle of a given radius, and is thus a measure of how much time an animal spends within a certain area (Fauchald and Tveraa, 2003). A highly sinuous path will have a high FPT, which is assumed indicative of Area Restricted Search (ARS) (Fauchald and Tveraa, 2003). To identify zones of ARS, I used the R packages ‘adehabitat’ and ‘ade4’ to estimate FPT following Fauchald &Tveraa (2003). Prior to analyses, the data were made regular in space by spatially interpolating locations at 1 km intervals following Hamer et al. (2009), using the ‘ltraj’ and ‘redisltraj’ functions, to ensure all points along foraging tracks were equally spaced in distance rather than time (Fauchald and Tveraa, 2003, Pinaud, 2008). As gannets do not fly at night, but rather sit on the water when away from the colony (Hamer et al., 2000, Lewis et al., 2002b), data points recorded during darkness hours were removed from this analysis, restricting it to hours of daylight (4:00-23:00 BST), to avoid artificially inflating the variance in FPT at small spatial scales (Weimerskirch et al., 2007).

Following Hamer et al. (2009), FPT was calculated every 1 km for circles of radius *r* varying from 1 to 100 km. Variance in log(FPT) was then plotted against *r*. Log-transformation was used in order to ensure that the variance in FPT was independent of the magnitude of the mean (Fauchald and Tveraa, 2003). A peak in the variance (S(r)) indicates the presence of ARS behaviour in a foraging trip and identifies the scale *r* at which the bird increases its search effort (Fauchald and Tveraa, 2003). I then identified when and where birds increased their search efforts, entering and leaving zones of ARS, by plotting FPT values at the scale at which peak variance occurred as a function of time elapsed since departure from the colony (Hamer et al., 2009). The area of each ARS zone was estimated by measuring the maximum distance between any two points within the zone as a measure of diameter (Hamer et al., 2009). Once these larger scale search areas were defined, FPT analysis was repeated at a finer scale with *r* varying from 100 m to 10 km every 100 m, to identify nested zones of ARS within the previously defined zones.

The timing, duration and depths of dives were calculated using custom scripts written in R. Dives were then classified into one of three types, V-shaped dives, U1 and U2 dives. These classifications were made using the following rules; if the bottom phase of the dive exceeded 2.7 seconds the dive was regarded as a U type. Otherwise, the dive was classified as a V-shaped dive. The U type dives were then further divided into U1 dives (those where the overall descent gradient > 1.5 m/s), or U2 dives (overall descent gradient < 1.5 m/s), with an appreciable further wing-propelled descent following the initial steep dive (Ropert-Coudert et al., 2009). As there was a strong correlation between the durations and depths of dives ($R^2 = 0.64$, $n = 6287$, $P < 0.001$), only results for depths are presented.

4.2.5. Data analyses

All statistical analyses were carried out in R (R-Development-Core-Team, 2011). To examine annual and individual variation in foraging behaviour while taking account of potential pseudoreplication of data, linear or generalised linear mixed effects models (LMEs or GLMMs) were used for analyses using the packages ‘nlme’ and lme4’ respectively. Behavioural characteristics, including trip duration and distance to trip destination, were modelled as a function of single covariates - ‘year’, and ‘sample size’, to compensate for difference in sample sizes, when testing for annual variation. ‘Bird identity’ was treated as a random effect, as multiple trips were recorded for a number of birds. Models were compared to a null, intercept only model, using likelihood ratio tests (Crawley, 2007), and the AIC value of each model attempted was retrieved to assess the model fit (Zuur et al., 2009) .

Similarly, to investigate finer-scale foraging behaviour, GLMMs were run in order to determine whether there was a significant association between ARS scale (tested for normality and log-transformed before statistical tests) and the foraging trip characteristics: square-root trip duration, square-root maximum foraging range and square-root total distance travelled on trips. These were modelled as a function of a single covariate – ‘Julian day’, and ‘bird identity’ was included as a random effect. These models were also compared to a null model, using likelihood ratio tests (Crawley, 2007) and the AIC values retrieved to assess the fit of each model (Zuur et al., 2009). I also compare the frequency, locations and sizes of these zones of ARS, between those recorded in 2003 and 2011, using GLMMs including ‘year’ and ‘sample size’ as fixed effects and ‘bird identity’ as a random effect.

4.3. Results

4.3.1 Environmental conditions

Average winter sea-surface temperatures around Bass Rock prior to each breeding season, between 1998 and 2011 varied annually, with the highest temperature recorded prior to the 2002 season and coldest prior to the 2011 season (Fig. 4.2). Summer chlorophyll-*a* concentrations in the region also varied among seasons, with the lowest concentrations recorded in 2002 and the highest recorded in 2003 (Fig. 4.3).

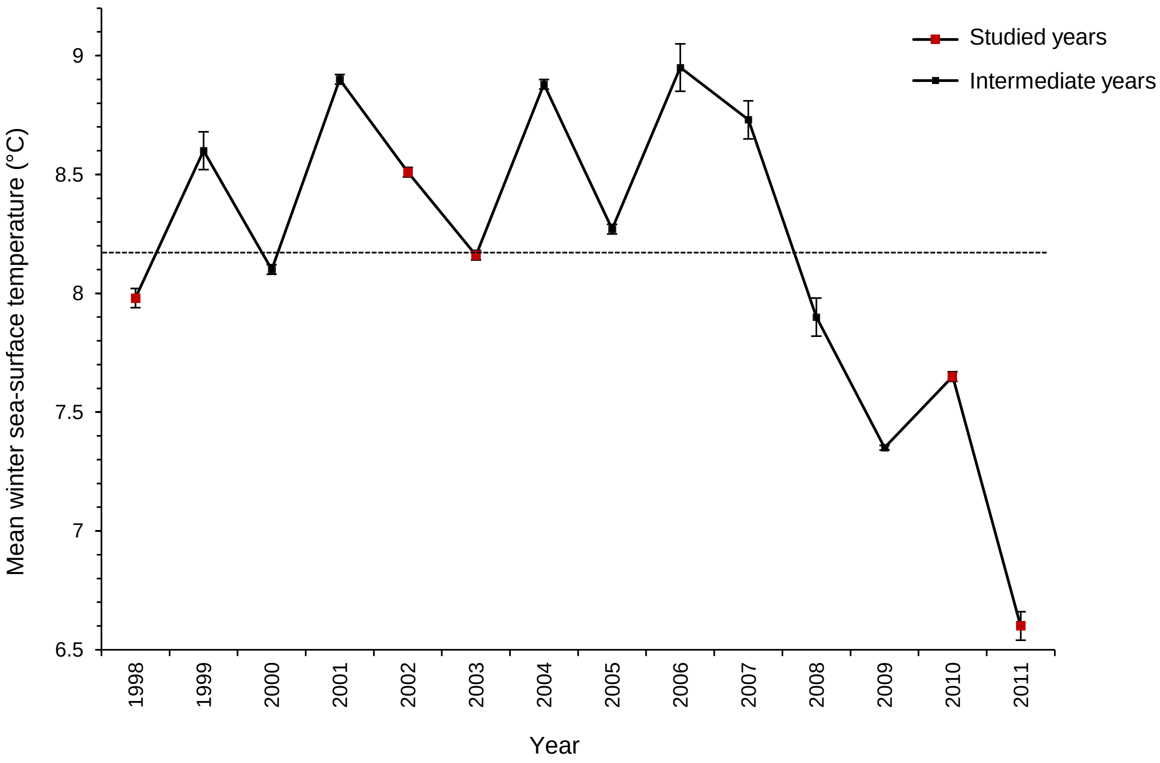


Figure 4.2. Mean sea-surface temperatures (°C) with associated standard errors, recorded in the 6° x 6° cell of the North Sea containing Bass Rock, during the winter (Dec-Feb) preceding each breeding season since 1998. Red markers indicate years during which tracking data were recorded and comparisons made; black markers indicate intermediate years. The horizontal dotted line indicates the mean winter sea-surface temperature in this region across the fourteen year period.

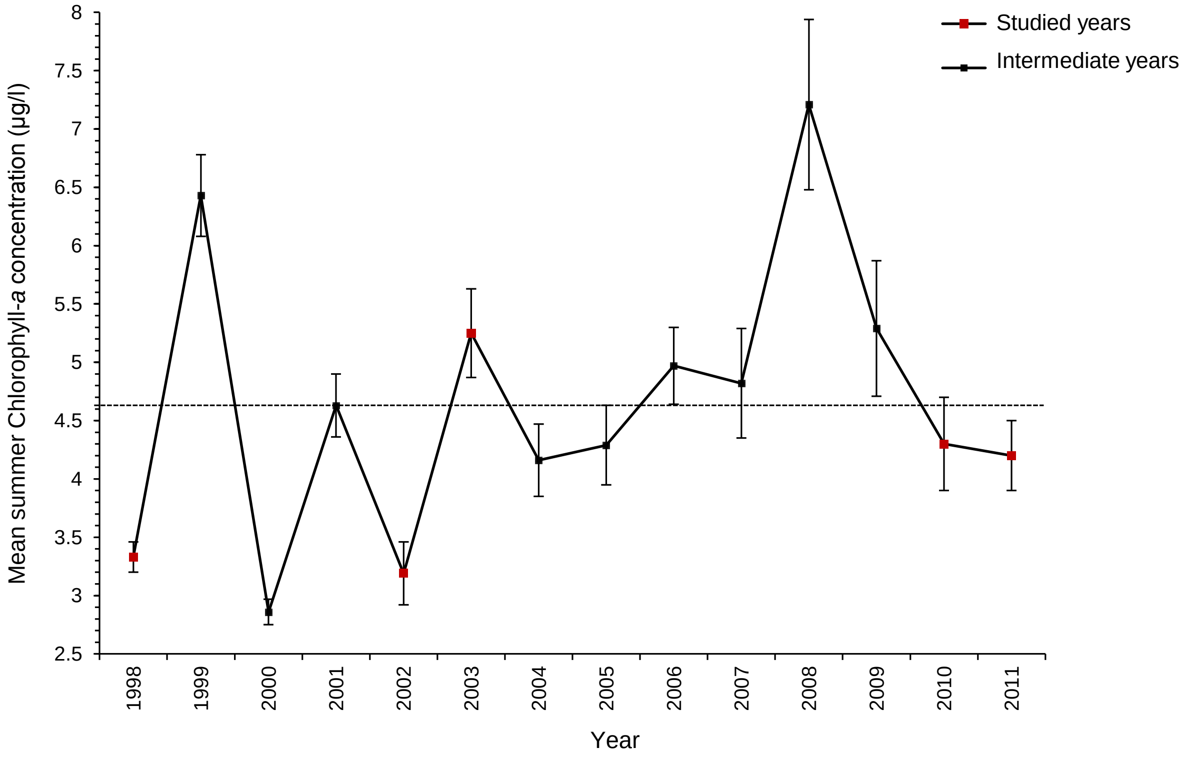


Figure 4.3. Mean summer Chlorophyll-*a* (µg/l) concentrations with associated standard errors, recorded in the 6° x 6° cell of the North Sea containing Bass Rock, during chick-rearing (Jun-Aug) since 1998. Red markers indicate years during which tracking data were recorded and comparisons made; black markers indicate intermediate years. The horizontal dotted line indicates the mean summer Chlorophyll-*a* concentrations in this region across the fourteen year period.

Abundance of fish stocks in the North Sea also fluctuated markedly among years (ICES, 2012, Table 4.1). The overall total biomass of sandeels in 2010 was 36% and 19% greater than in 1998 and 2002 respectively, and over four times greater than in 2003 (Fig. 4.4). The total biomass of mackerel was highest in 2011 (35%, 63%, 51% and 5% higher compared to 1998, 2002, 2003 and 2010 respectively, Fig. 4.5), and the biomass of Norwegian spring spawning herring was greatest in 2003 (Table 4.1, Fig. 4.6).

Table 4.1. Total biomass (tonnes) of three key prey species for northern gannets breeding in the UK, 1998 – 2010 (ICES, 2012).

		Total biomass (tonnes)				
Species	**Region**	**1998**	**2002**	**2003**	**2010**	**2011**
Sandeel	Dogger Bank	896,145	1,357,150	258,154	1,8054,150	693,689
	Central Eastern North sea	351,199	314,730	157,418	357,087	220,037
	SE North sea	601,971	305,851	133,060	561,655	267,917
Mackerel	Combined S, W and N North Sea	3,065,937	2,534,243	2,737,811	3,936,896	4,131,457
Herring	NE North Sea (Norwegian spring spawning)	8,186,000	7,862,000	9,554,000	9,551,000	7,788,000

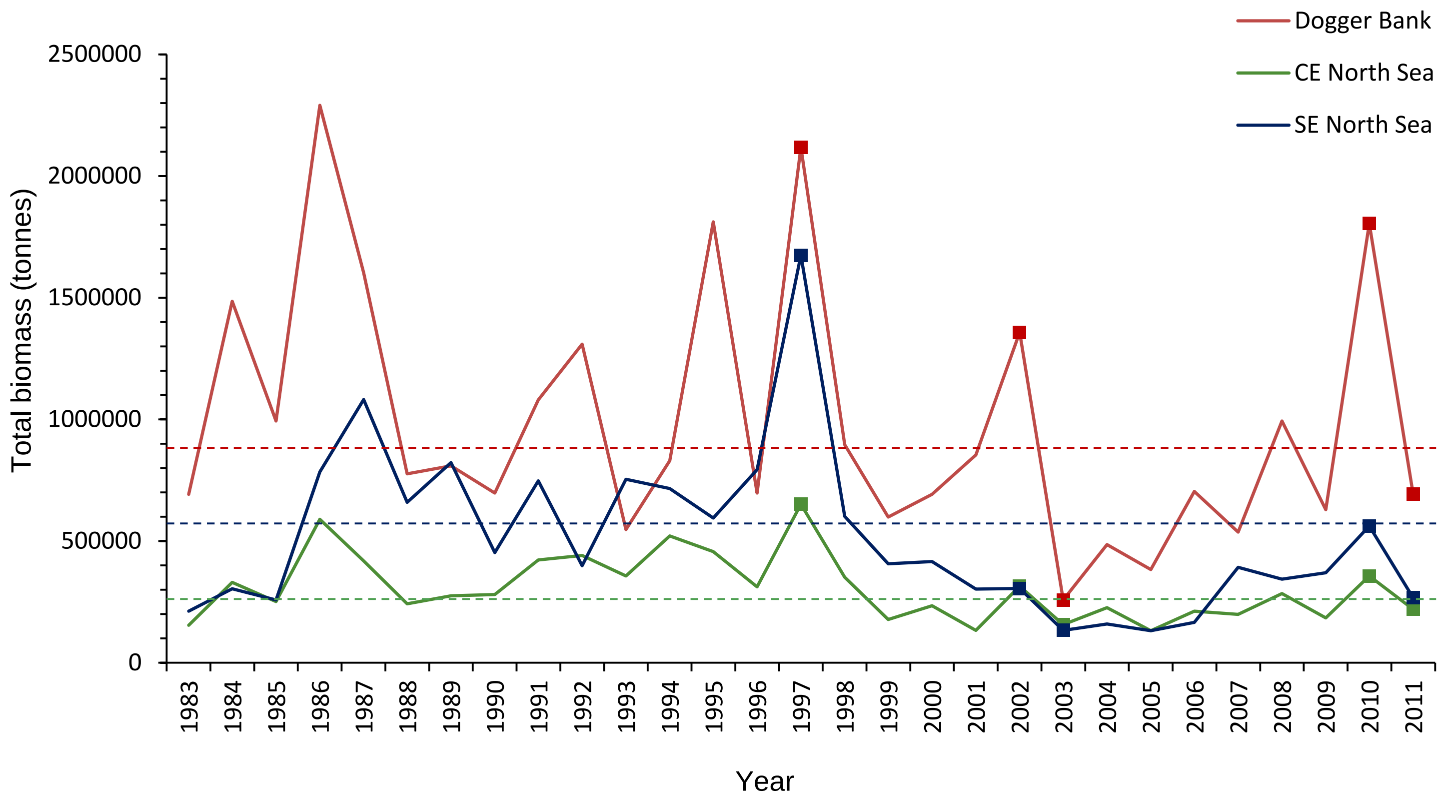


Figure 4.4. Annual total biomass (tonnes) of sandeels *Ammodytes marinus*, recorded in the Dogger Bank region (red), central eastern (green) and southern eastern (blue) North Sea from 1983 to 2011 (ICES, 2012). Years for which I present gannet foraging data are marked on the graph (square markers) and the horizontal dotted lines indicate the mean total biomass in each region across the 28 year period, for which data are available.

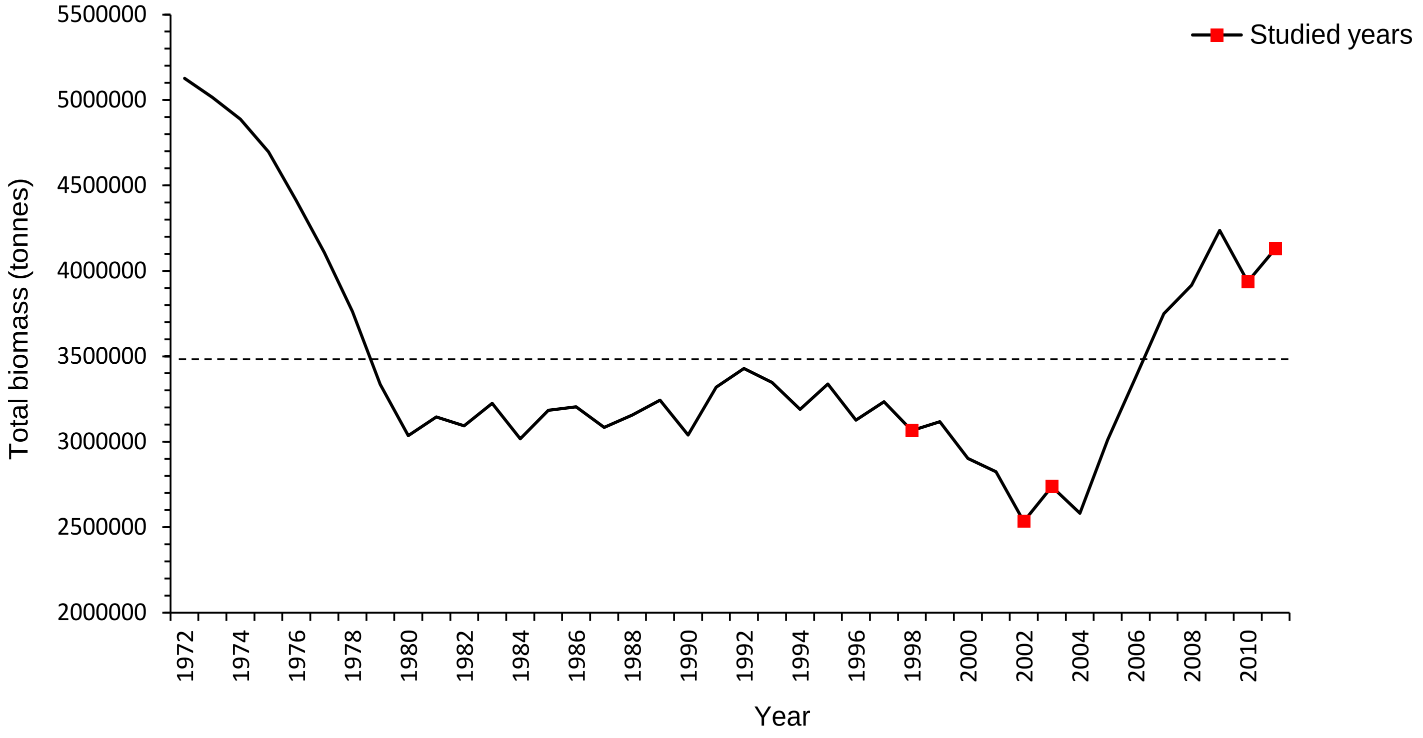


Figure 4.5. Annual total biomass (tonnes) of mackerel *Scomber scomber*, recorded in the southern, western and northern North Sea from 1979 to 2011 (ICES, 2012). Years for which I present gannet foraging data are marked on the graph (red squares) and the horizontal dotted line indicates the mean total biomass across the 39 year period, for which data are available.

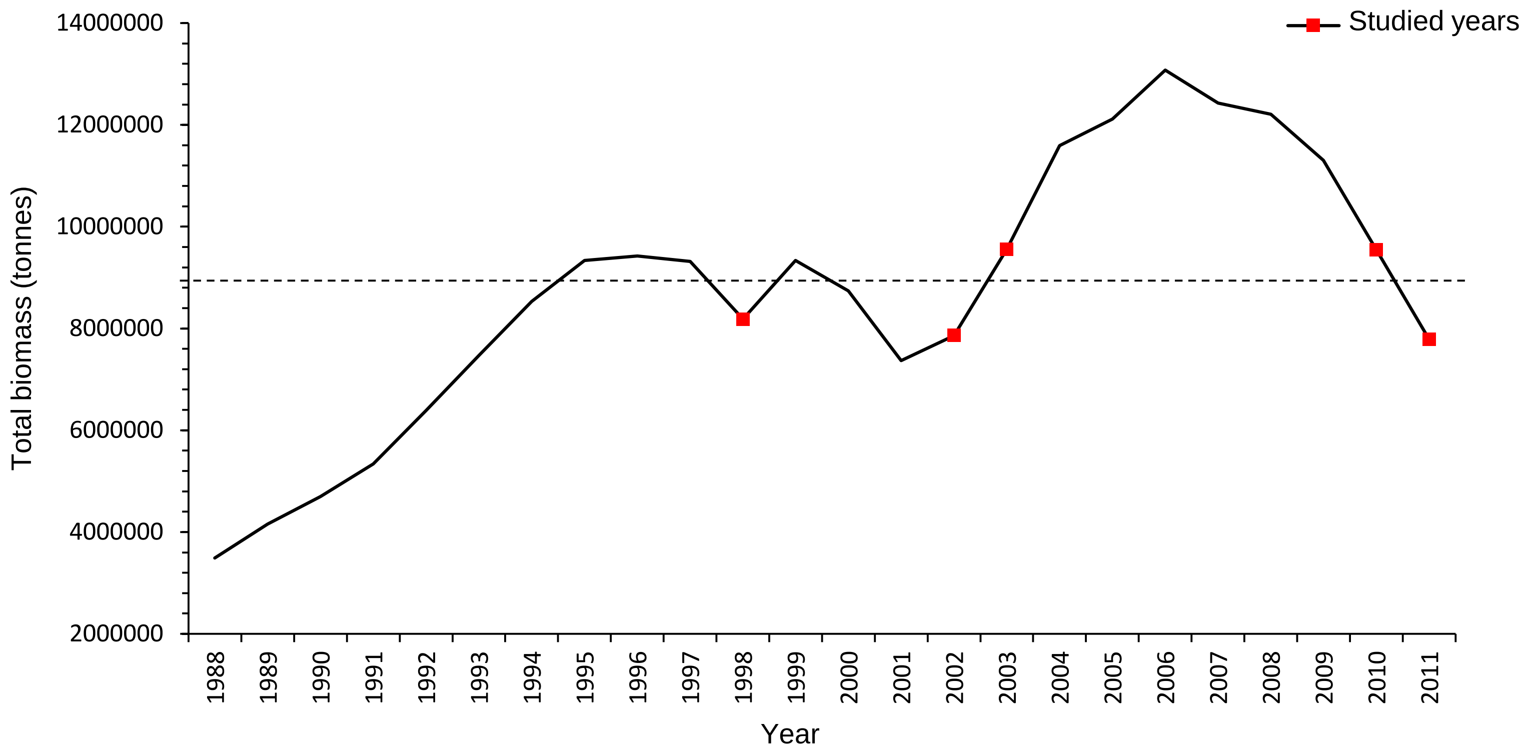


Figure 4.6. Annual total biomass (tonnes) of Norwegian spring spawning herring *Clupea harengus*, recorded from 1998 to 2011 (ICES, 2012). Years for which I present gannet foraging data are marked on the graph (red squares) and the horizontal dotted line indicates the mean total biomass across the 23 year period, for which data are available.

4.3.2. Diet

Data from all years in which diet samples were previously recovered on Bass Rock were obtained from Hamer et al. (2007); these included 1998, 2002 and 2003, when 226, 114 and 92 fish samples were collected respectively (Table 4.2). While mackerel made up the highest proportion of the diet samples in 1998 (30.8% of biomass), sandeel was the predominant species, both by frequency and biomass, in 2002 and 2003 (55.1 and 51.5% of biomass respectively), constituting over half of all samples in each of these years (Table 4.2).

In 2010, 77 individual fish from 42 regurgitate samples were identified. Mackerel was the predominant species, in terms of both biomass and by frequency of samples in which it was recorded. Furthermore, mackerel made up a higher proportion of the diet in 2010 than in any other year (Table 4.2). In contrast to other years, sandeels were entirely absent from the diet in 2010 (Table 4.2). Fewer regurgitate samples were obtained in 2011 (n = 19), with 31 individual fish identifiable. Of these, 13% were sandeels and 79% mackerel. A small number of sprat were also present (Table 4.2). The lengths of mackerel in the diet were significantly longer in 2010 than 2011 (2010: mean: 24.2 cm, SD = 5.9; 2011: 18.4 cm, SD = 5.3; GLM: $F_{1,42} = 9.8$, $P = 0.003$).

Table 4.2. Frequency (% of regurgitates containing each species) and biomass (% of total estimated biomass) of various species of fish in the diet of northern gannets at Bass Rock in 5 seasons studied. Data from 1998, 2002 and 2003 adapted from Hamer et al. (2007).

Species	------ 1998 ------ n = 266 (27.3 kg)		------ 2002 ------ n = 114 (13.6 kg)		------ 2003 ------ n = 92 (10.2 kg)		------ 2010 ------ n = 42 (3.54 kg)		------ 2011 ------ n = 31 (2.3 kg)	
	Frequency	Biomass	Frequency	Biomass	Frequency	Biomass	Frequency	Biomass	Frequency	Biomass
Mackerel	31.6	30.8	21.9	23.6	17.2	14.6	85.7	93.9	45.2	78.7
Herring	21.5	20.3	7.7	5.4	22.2	12.2	-	-	3.2	3.1
Sprat	23.0	12.6	6.7	2.3	19.0	6.6	19.0	6.1	12.9	3.4
Sandeels[a]	29.3	17.9	69.3	55.1	73.9	51.5	-	-	32.3	12.8
O-group	27.0	12.5	68.4	55.0	68.5	51.4	-	-	29.0	11.6
Older	2.3	5.4	0.9	0.1	5.4	0.1	-	-	3.2	1.3
Gadidae[b]	15.0	16.4	15.6	10.7	11.9	10.4	-	-	-	-
Others[c]	3.7	2.1	4.5	2.9	6.5	4.8	-	-	6.5	1.9

[a] All lesser sandeel *Ammodytes marinus*, except for 3 greater sandeel *Hyperoplus lanceolatus* (all older than O-group in 2003)

[b] Mainly haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus* and cod *Gadus morhua*.

[c] Plaice *Pleuronectes platessa*, Atlantic salmon, *Salmo salar*, sea trout *S.trutta*, grey gurnard *Eutrigla gurnardus*, red gurnard *Aspitrigla cuclus*, garfish *Belone belone*, common dragonet *Callionymus lyra*, scad *Trachurus trachurus* and greater forkbeard *Phycis blenoides*.

4.3.3. Time spent at sea:

In 2010 and 2011, 342 complete foraging trips (2010: n =199, 2011: n =143 were recorded by 55 individual birds (49 birds in 2010, 28 birds in 2011). The median number of trips recorded per bird was 3 (range: 1-12) in 2010 and 5 (range 1-14) in 2011.

Previous GPS tracking of gannets from Bass Rock showed marked annual variation in trip duration, with mean durations of 31.5, 40 and 25.9 hours recorded in 1998, 2002 and 2003 respectively (Hamer et al. 2007, Table 4.3, Fig. 4.7). Mean trip durations for both 2010 and 2011 were shorter than all those recorded during any previously studied season (2010: mean = 23.9 h, SD = 12.5; 2011: mean = 20.7 h, SD = 10.8, Table 4.3, Fig. 4.7). There was a significant difference trip durations among years (GLMM: $F_{1,421} = 57.7$, $p<0.001$). Trip durations in 2010 and 2011 were shorter than those recorded in 2003 (average 25.9 h) by an average of 8% and 20% respectively (Fig. 4.7). Though trip durations in 2003 were not significantly longer than those recorded in 2010 (GLMM: $F_{1,68} = 0.74$, $P > 0.05$), they were significantly longer than trips recorded in 2011 (GLMM: $F_{1,47} = 6.9$, $P <0.05$, Fig. 4.7). Further detailed comparisons between seasons for which dive data were also recorded are made below (2003 and 2011, section 4.3.6). Similar to Hamer et al. (2007), I found no significant difference in trip durations among individual birds within these latter studied seasons (GLM: $F_{22,400} = 0.65$, $p = 0.88$). Trip duration was significantly shorter in 2011 (20.7 ± 0.5 h) than in 2010 (23.9 ± 0.8 h; LME: $F_{1,282} = 4.45$, $P = 0.036$).

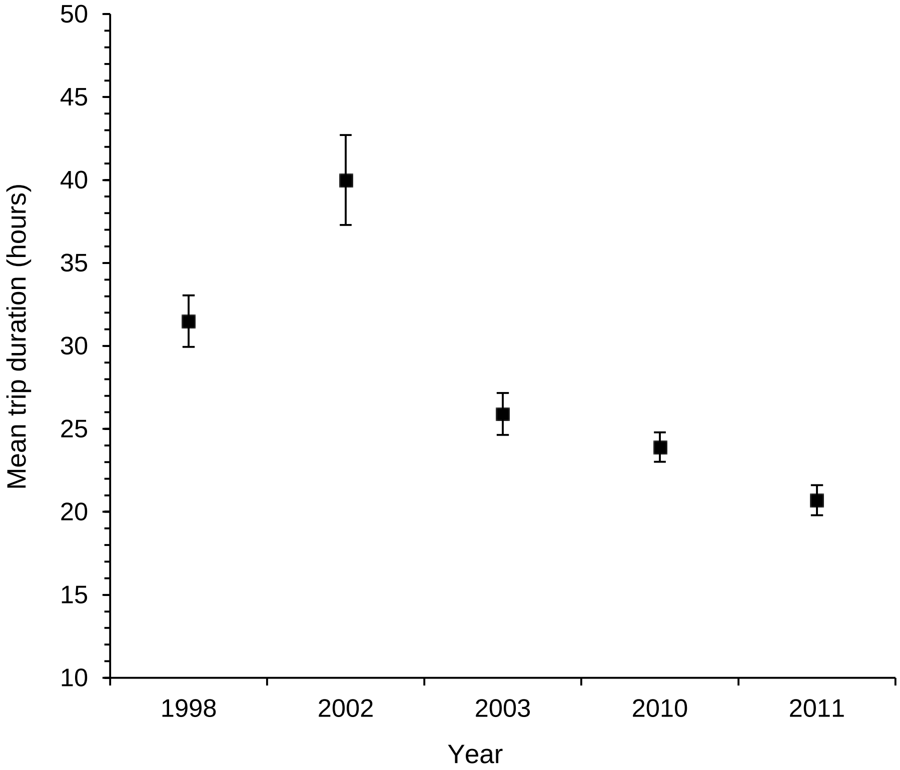


Figure 4.7. Annual mean foraging trip durations (hours), with associated standard errors, recorded by gannets tracked from Bass Rock in 1998 (n = 14), 2002 (n = 13), 2003 (n = 21), 2010 (n = 49) and 2011 (n = 28).

Table 4.3. Characteristics of foraging trips made by chick-rearing northern gannets at Bass Rock during 5 breeding seasons. Data for 1998, 2002 and 2003 were adapted from Hamer et al., 2007. 199 trips recorded in 2010 and 143 recorded trips in 2011. FKD: fixed kernel density estimate.

	1998 (70 trips by 14 birds)		2002 (42 trips by 13 birds)		2003 (58 trips by 21 birds)		**2010** (199 trips by 49 birds)		**2011** (143 trips by 28 birds)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Proportion of time foraging (%)[a]	60.3	5.5	57.4	4.0	52.5	7.5	53.5	6.0	51.5	8.1
Trip duration (h)	31.5	13.0	40.0	17.6	25.9	9.6	23.9	12.5	20.7	10.8
95% FKD (km^2)	96,300		211,100		45,900		60,200		53,600	
50% FKD (km^2)	10,800		30,600		4,200		29,400		9,100	
Max. distance (km)	224.3	96.8	319.7	132.9	170.5	94.2	198.7	101.1	134	84.1
Total distance (km)	588.2	245.5	786.0	344.3	417.6	231.3	517.3	271.8	388.1	236.8
Trips to north of colony:										
Max. distance (km)	203.0	85.2	363.7	93.9	181.7	93.9	224.9	106.5	140	91.9
Total distance (km)	546.8	216.1	902.9	331.0	444.4	230.0	578.4	290.0	403.8	256.4
Trips to south of colony:										
Max. distance (km)	233.4	100.8	261.0	112.0	152.2	93.8	163.8	80.1	130	55.7
Total distance (km)	606.0	257.0	630.2	304.5	373.7	231.8	435.7	215.3	386	168.6
Speed[b] ($km\ h^{-1}$)	14.4	3.2	16.3	3.7	14.1	3.9	11.8	3.2	11.9	4.2
Speed[c] ($km\ h^{-1}$)	18.9	3.8	19.5	4.3	18.3	4.2	22.1	6.4	19.6	5.8

[a] Calculated for birds with data for ≥ 3 consecutive foraging trips

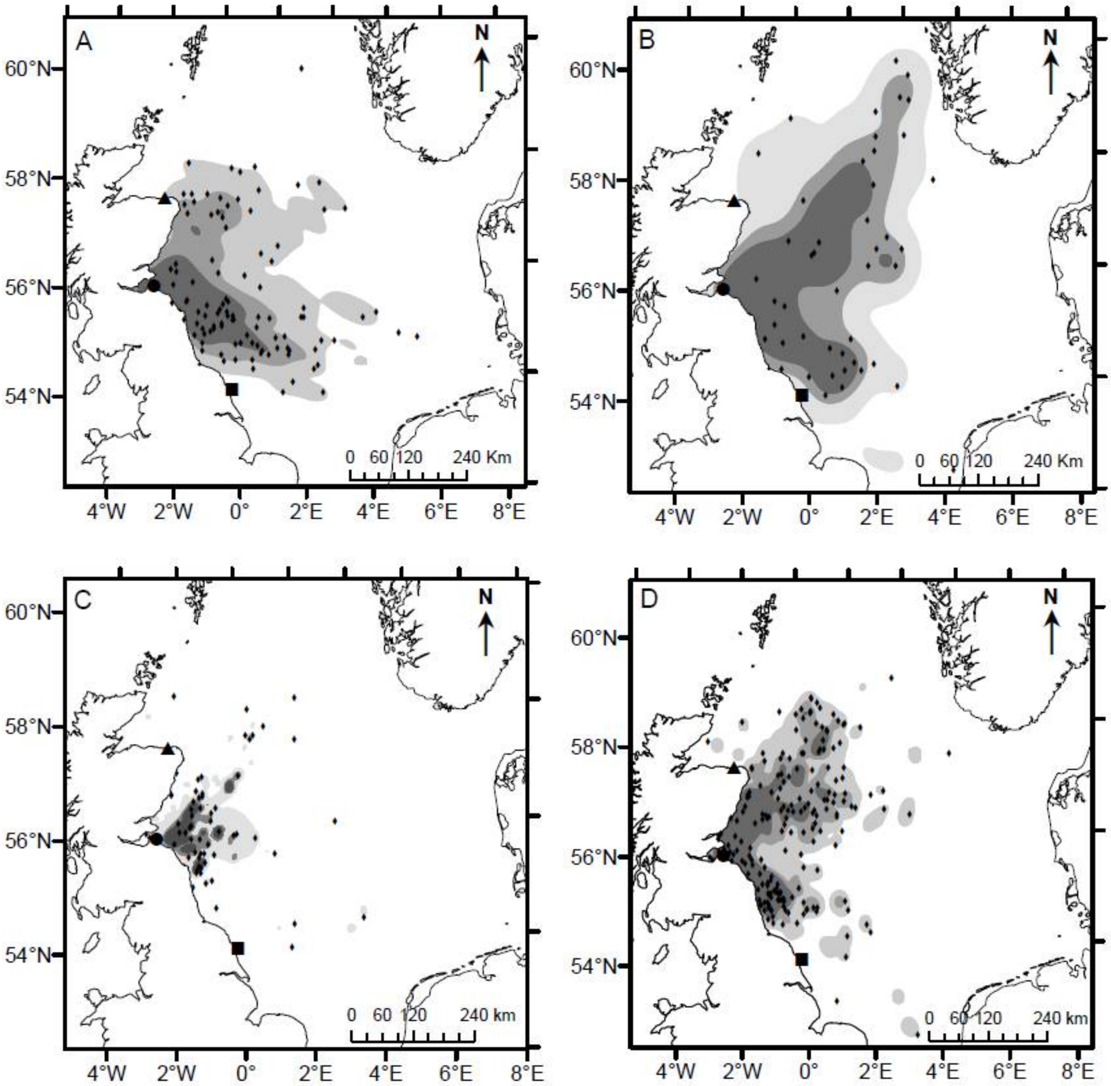
[b] Calculated using maximum distance reached from the colony for trips < 62 hours

[c] Calculated using total distance travelled for trips < 64 hours

4.3.4. *Foraging ranges and distances travelled*

Similar to previous seasons, birds tracked in 2010 and 2011 ranged widely in the north-western North Sea. During both years, many trips were to deep water areas on Fladen Ground and the Farnes Deep, to the northeast and southeast of Bass Rock respectively. Shallower areas on the northern Halibut Bank and Wee Bankie were also used (Fig. 4.1**)**. Trips in 2011 were more coastal (Fig. 4.8).

The 95% utilisation distribution of birds in 2010 (60,200 km^2) and 2011 (53,600 km^2) were 38% and 44% smaller than those in 1998 and 72% and 75% smaller than those in 2002 respectively (Table 4.3; Fig. 4.8). Despite shorter average trip durations in 2010 and 2011, the overall foraging ranges were larger than in 2003 (by 31% and 17% respectively), possibly due to the faster travel speeds on average recorded during 2010 and 2011 (see section 4.3.5 below). The core foraging area (50% FKD) formed a much higher proportion of the home range in 2010 (0.49) compared to other years (1998: 0.11, 2002: 0.15, 2003: 0.09, 2011: 0.17, Fig. 4.8).



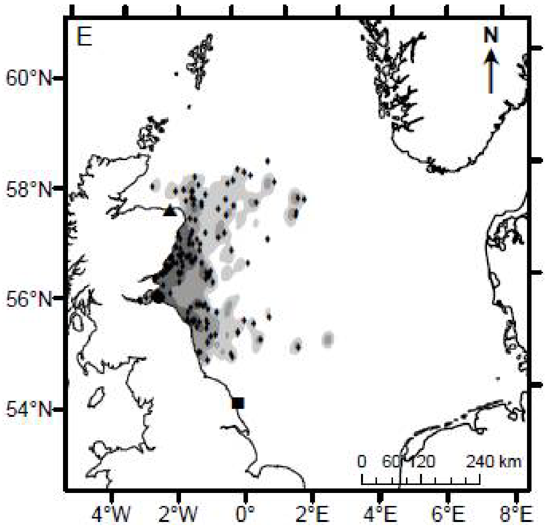


Figure 4.8. Utilisation distributions of chick-rearing gannets tracked in; A: 1998, B: 2002, C: 2003, D: 2010, E: 2011; including all foraging trip destinations each year marked by black diamonds. Grey scales indicate the extent of the isopleths encompassing 50% (dark grey), 75% (medium grey) and 95% (light grey) of recorded locations. Black circle: Bass Rock, Black square: Bempton Cliffs, Black triangle: Troup Head

The mean maximum distance reached on foraging trips was 198 km in 2010 and 134 km in 2011, compared to 170.5 km in 2003. Similarly, the mean total distance travelled on foraging trips in 2010 (517 km) was longer than in 2003, but the mean total distance travelled in 2011 (388 km) was shorter than in either 2003 or 2010 (Table 4.3). Both the maximum and total distances travelled on foraging trips were significantly shorter in 2011 than in 2010 (Max: 2010: 198.1 ± 7.3 km, 2011: 134.0 ± 11.2 km, GLMM: $F_{1,283} = 18.45$, $P < 0.001$; and Total: 2010: 524.5 ± 21.2 km, 2011: 388.1 ± 19.8 km, GLMM: $F_{1,283} = 11.57$, $P < 0.001$, respectively).

Considering data from all previous studied seasons, I found that the distances to trip destinations differed significantly between years (GLMM: $F_{4,393}= 12.6$, $p < 0.01$, Table 4.3), as did the total distance travelled on trips (LME: $F_{4,393}= 11.2$, $p < 0.001$, Table 4.3). However, I found no significant variation among birds within each year in either the distances travelled to trip destinations or total distances travelled (GLM: $F_{21,375} = 1.19$, $P > 0.05$ and GLM: $F_{21,375} = 1.24$, $P > 0.05$ respectively).

4.3.5. Speed of travel

Foraging trip data from the 5 study seasons combined showed a significant linear relationship between maximum distance reached from the colony (trip destination) and trip duration (Eq. 1: Max dist (km) = 6.01 (SE ± 0.26) x trip duration (h): $F_{1,509} = 537.8$, $P < 0.0001$, $R^2 = 0.51$). There was also a positive linear relationship between the total distance travelled on a trip and trip duration (Eq. 2: Total dist (km) = 16.97 (SE ± 0.65) x trip duration (h): $F_{1,509} = 691.01$, $P < 0.0001$, $R^2 = 0.58$).

Average speed during a trip was 12.02 (SE ± 0.5) km h^{-1} (twice the slope of Eq. 1), estimated using maximum distance from the colony (speed^b), and 16.97 (SE ± 0.7) km h^{-1} (the slope of Eq. 2), estimated using the total distances travelled (speed^c). There was no difference between years in the slopes of the relationship between maximum distance and trip duration (GLM: $F_{1,404} = 1.92$, $p = 0.17$). However, unlike the study by Hamer et al. (2007), there was a difference in the slope of the relationship between total distance travelled and trip duration (GLM: $F_{1,404} = 4.72$, $p = 0.03$). In 2010 and 2011, adults were recorded travelling faster on average over the total distance travelled, encompassing all data fixes on a complete trip (speed^c), compared to previous years (Table 4.3). Conversely, birds were found to have the lowest average travel speed when estimated using the distance from the colony to the trip destination (speed^b), suggesting less direct flight paths were taken in these latter years, i.e. paths were more sinuous before the flight destination was reached.

4.3.6. Area-restricted search behaviour

Area restricted search behaviour was identified along foraging tracks recorded in 2011, when concurrent dive activity data were also recorded. Of the 96 foraging trips that year, with accompanying dive data, 95 were found to include identifiable periods of ARS behaviour, comprising a total of 175 zones of ARS (Fig. 4.9.A). As indicated by the variation in FPT during each track, birds used between 1 and 4 zones of ARS per trip (mean = 1.9, Fig. 4.9.A).

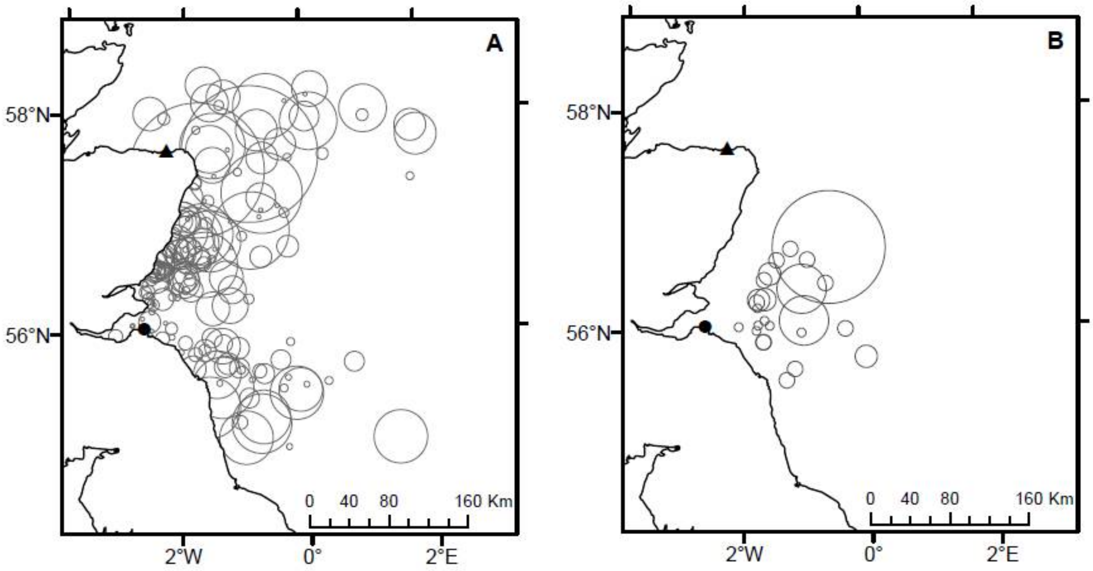


Figure 4.9. A. 175 zones of ARS (1-100 km) initiated on 95 foraging tracks in 2011, **B.** 25 zones of ARS (1-100 km), recorded by 13 birds in 2003, as indicated by open grey circles. The area of each circle indicates the area of each intensively searched zone. Black circle indicates the position of Bass Rock, black triangle indicates the position of Troup Head colony.

In 2011, the mean spatial scale at which ARS behaviour was adopted was 11.6 ± 0.81 km (range 2 - 69 km). The mean estimated area of ARS zones was therefore 422.7 ± 2.06 km^2 (range 12.6 – 14,957.1 km^2), and this differed significantly among individuals (GLM: $F_{94,90}$ = 16. 2, $P < 0.001$). There was a significant positive relationship between log transformed ARS scale and trip durations that season (GLMM: $P < 0.03$, Table 4.4). Log transformed ARS scale also increased significantly with maximum foraging range (GLMM: $P < 0.02$, Table 4.5), but there was no relationship between ARS scale and the total distance travelled throughout trips (GLMM: $P > 0.05$).

Table 4.4. Summary table of the most parsimonious model describing the significant positive relationships between log-transformed ARS scale and trip duration (h) in 2011, with bird identity as a random effect.

Fixed effects:	Estimate	SE	DF	z-value	p-value
Intercept (Bird)	0.4708	0.1535	83	3.068	0.0022 *
Trip duration (h)	0.0135	0.0058	83	2.308	0.0210 *

Table 4.5. Summary table of the most parsimonious model describing the significant positive relationships between log transformed ARS scale and maximum foraging range (km) in 2011, with bird identity as a random effect.

Fixed effects:	Estimate	SE	DF	z-value	p-value
Intercept (Bird)	0.4784	0.1414	83	3.383	0.00072**
Max. range (km)	0.0019	0.0008	83	2.523	0.01164 *

All 25 ARS zones recorded in 2003 were on the outward phase of foraging trips, before reaching the trip destination. In contrast, in 2011, 25 (14.2%) zones of ARS occurred on the inward phase of the foraging trip, when the bird was returning to the colony. There was no difference found in the scales of ARS zones between the two years (GLMM: $P > 0.05$). Zones of ARS were initiated significantly further from the colony in 2011 (GLMM: $F_{1,32} = 0.52$, $P < 0.03$). However, the distance between ARS zones and the coast was significantly shorter in 2011 compared to 2003 (2003: 53.9 ± 5.4 km, 2011: 41.3 ± 3.4 km, GLMM: $P < 0.001$, Table 4.6), with a higher proportion of zones initiated within 50 km of the coast in 2011 (70%) compared to 2003 (48%).

Table 4.6. Summary table of the most parsimonious model describing the significant difference in distance of ARS zones from the coast (km) between years (2003 and 2011), with maximum foraging range of trip (km) included as a fixed effect and bird identity as a random effect.

Fixed effects:	Estimate	SE	DF	z-value	p-value
Intercept (Bird)	1.25e+02	2.80e+01	200	4.459	8.23e-06 ***
Foraging range (km)	3.46e-03	3.76e-04	200	9.200	< 2e-16 ***
Year	-6.16e-02	1.40e-02	200	-4.412	1.02e-05 ***

4.3.7. Nested zones of ARS

Only 18 of the 95 tracks during which ARS behaviour was initiated in 2011 included smaller areas of nested ARS (Fig. 4.10). These indicate where birds concentrate their search effort further, within the intensively searched areas. The 18 tracks during which nested ARS was recorded were made by just 9 birds, suggesting that some birds show a greater tendency to adopt nested ARS behaviour than others, or perhaps these birds encountered multiple adjacent concentrations of shoaling prey. Of the birds that exhibited nested ARS, an average of 3.4 smaller scale zones were recorded in larger scale zones. Altogether, 31 zones of nested search behaviour were recorded within 25 of the larger scale zones (14.2%). This is a substantially smaller proportion of larger zones found to include nested zones than in 2003 (60%).

The mean spatial scale of the nested ARS zones in 2011 was 4.4 ± 0.43 km (range 0.2-8.1 km), and the vast majority lay to the northeast of the Bass Rock (87% within 100 km and 74% within 50 km of the coast). I found a significant positive relationship between the scale of the nested ARS zone and trip duration (GLMM: $P < 0.001$, Table 4.7). However, there was no relationship between the nested ARS scale and either the maximum foraging range or total distance travelled (GLMM: $P > 0.05$). Neither was there a significant relationship between the scale of the larger ARS zones and the nested ARS zones within them (GLMM: $P > 0.05$).

Table 4.7. Summary table of the most parsimonious model describing the significant positive relationships between nested ARS scale and trip duration (h) in 2011, with bird identity included as a random effect.

Fixed effects:	Estimate	SE	DF	z-value	p-value
Intercept (Bird)	0.5764	0.2877	18	2.003	0.045152 *
Year	0.0394	0.0112	18	3.537	0.000405 ***

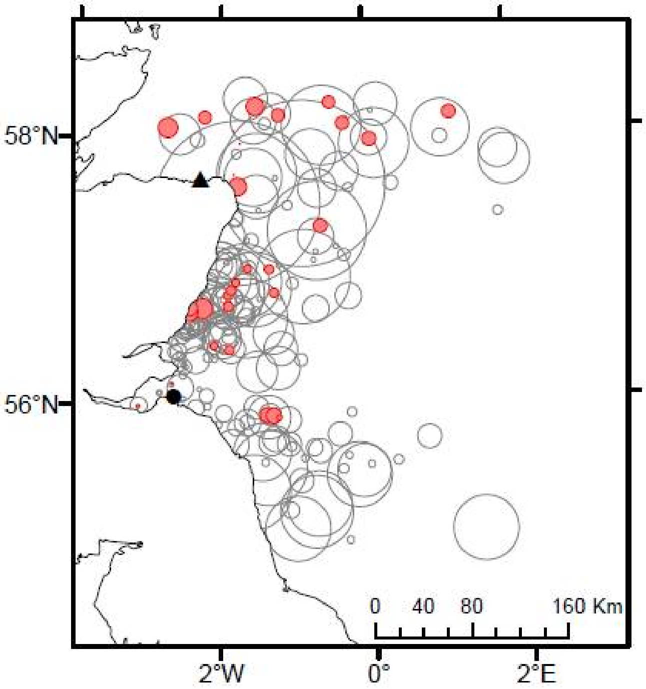


Figure 4.10. 31 zones of nested ARS behaviour (100 m – 10 km) found during 18 of the 95 foraging tracks (red circles), superimposed over all 175 zones of ARS (1-100 km) initiated on 95 foraging tracks recorded in 2011 (open grey circles). The area of each circle indicates the area of each intensively searched zone. Black circle: Bass Rock, black triangle: Troup Head.

4.3.8. Dive activity and zones of ARS

In 2011, 6287 dive events by gannets foraging from Bass Rock were recorded (25 birds, mean = 251 dives per bird). These were made up of 4213 V-shaped dives, 1312 U1 dives and 762 U2 dives; 4457 were recorded with accompanying GPS locations, constituting 96 complete foraging tracks by 22 birds (mean = 203 dives per bird, mean = 46 dives per foraging trip). There was considerable variation in the dive duration and depth and also with respect to distance from the colony. For all dives, the mean dive duration was 7.8 s (SD = 6.3, range: 0.8 - 48.8 s), and the mean depth was 6 m (SD = 3.2, range: 1.5 - 27.8). Dive type was significantly related to the distance from the colony (LME: $F_{2,4275} = 76.57$, $p < 0.001$), with U2 dives tending to occur closest to, V-shaped dives furthest away from and U1 dives at intermediate distances from the colony(Table 4.8).

Table 4.8. Summary characteristics of the three dive types made by 22 northern gannets on 96 foraging trips from the Bass Rock during the 2011 breeding season.

Dive type	V (n = 4213)		U1 (n = 1312)		U2 (n = 762)	
	Mean	SD	Mean	SD	Mean	SD
Proportion of all dives (%)	67.0		20.9		12.1	
Duration (s)	5.1	2.3	9.1	4.2	20.2	8.2
Max. Depth (m)	5.3	2.3	5.4	2.0	11.3	4.2
Distance from colony (km)	109.6	77.8	83.9	62.5	67.6	48.0

The first dive of each trip was recorded on average, 35.8 ± 3.8 km from the colony, markedly closer in 2011 than in 2003 (53.9 ± 45.7 km). 40% of dives per trip were not in ARS zones, a greater percentage than in 2003 (27%, Hamer et al., 2009). All but 20 of the larger scale ARS zones (86%) included dives (2003: 92%). The majority of dives (76.7%) were on the outward phase of the foraging trip.

Average dive frequency was twice as high within zones of ARS (4.2 ± 0.46 h^{-1}) as outside these zones (2.1 ± 0.2 h^{-1}) in 2011 (GLMM: $P< 0.0001$, Table 4.9). However, open dive frequency (dives initiated outside zones of ARS) was higher during 2011 than in 2003, when dive frequencies in ARS zones were 4 times higher than those outside in 2011 (2 times higher in 2003; Hamer et al., 2009).

Table 4.9. Summary table of the most parsimonious model describing the significant difference in dive rates inside zones of area restricted search (closed) compared to those outside these zones (open dives) in 2011, with maximum foraging range (km) included as a fixed effect and bird identity as a random effect.

Fixed effects:	Estimate	SE	DF	z-value	p-value
Intercept (Bird)	1.6959	0.1121	444	15.125	< 2e-16 ***
Max. Range (km)	-0.0027	0.0004	444	-7.084	1.4e-12 ***
Zone (open)	-0.6914	0.0558	444	-12. 383	< 2e-16 **

4.4. Discussion

Marine environments are dynamic and continuously altering in response to natural and anthropogenic pressures (Behrenfeld et al., 2006, Worm et al., 2006), and it is increasingly important to understand how the effects of these changes propagate along food chains to higher trophic level marine organisms. I have found that foraging characteristics of a top predator can act as an indicator of broad scale changes in environmental conditions and prey stocks, building on the evidence of past studies (Hamer et al., 2006b, Einoder, 2009, Pichegru et al., 2009). On average, foraging trips of gannets from Bass Rock in 2010 and 2011 were significantly shorter, both in distance and time, compared to trips recorded in the late 1990s and early 2000s. In spite of an overall increase in sea-surface temperature over the past decade (ICES, 2011), both the 2010 and 2011 breeding seasons followed winters of relatively low sea-surface temperatures and during both seasons, high concentrations of chlorophyll-α were recorded in the region. These conditions appear to have benefitted fish stocks in the wider region in the latter two seasons, particularly considering mackerel. In many cases, there are indirect links between top predators and climatic conditions which operate via the food chain. Thus it is also important to consider that there may be spatial and temporal lags in the trophic and mechanistic links between prey and climate (Wakefield et al., 2009), along with other drivers of prey densities such as commercial fisheries exploitation. Temperature may affect spawning and recruitment of key fish species that are important for predators in subsequent seasons. Future studies may therefore benefit from using stock assessments from previous years, or information on cohort strength based on age structures of key fish species.

Annual variation in gannet diet during the chick rearing period was also apparent. Prior to 2010, sandeels made up a large proportion of diet samples retrieved (Hamer et al., 2007). In contrast, sandeels were entirely absent from gannet diet in 2010 and formed only 12.8% of the biomass taken in 2011. The diet data indicated that mackerel became the predominant prey species in 2010 and 2011, coinciding with recent increases in North Sea stocks (ICES, 2012). Pelagic landings by the Scottish fishing fleet were dominated by mackerel in 2011, according to the Scottish Sea Fisheries Statistics 2011 (http://www.scotland.gov.uk/Resource/0040/

00401747.pdf). Although more local data on mackerel abundances in the Firth of Forth during the latter seasons is as yet unavailable, a large number of this species were caught by anglers in this area from June onwards in both 2010 and 2011 (*pers obs*.). Thus, not only were stocks higher but also some shoals appeared to be close to the Bass Rock. Compared to most of the other prey items taken by gannets, mackerel are both large and have a high lipid content, making them a high quality source of food (Montevecchi et al., 1984). One reason for the success of gannets over recent years may be their ability to switch to larger prey items, namely mackerel, which are too large to be taken by most other seabirds in this region, such as kittiwakes and auks (Furness, 2002, Frederiksen et al., 2007, Langoy et al., 2012).

Improved feeding conditions in the latter two seasons are indicated by the foraging characteristics of the tracked gannets, with shorter trips in 2010 and 2011. I also found that the types of dives made by gannets from the Bass Rock in 2011 were significantly related to the distance of the dive from the colony, with a higher proportion of V-shaped dives at greater distances. This effect could be indicative of greater competition for prey nearer the colony where U-shaped dives were recorded. With more prey disturbance occurring closer to the colony, fish will be more commonly pursued by individuals propelling themselves underwater, before being caught (Garthe et al., 2000). Conversely, V-shaped dives, which are of short duration and relatively shallow, allow gannets to surprise their prey (Garthe et al., 2000). These may therefore be adopted at greater distances from the colony, where prey are less likely to be disturbed by the activity of foraging competitors. Together, my findings of shorter foraging trips in the latter two seasons and variation in dive types with distance from the colony lend further support for Ashmole’s model of prey depletion around seabird colonies, through passive interference or removal (Lewis et al., 2001, Davoren et al., 2003b, Elliott et al., 2009).

I found that distances travelled by gannets were significantly and linearly related to trip duration, in accordance with previous studies (Hamer et al., 2001, Grémillet et al., 2006, Hamer et al., 2007, Votier et al., 2010). Moreover, I found no difference in the relationship between maximum foraging range and date during the study period. However, the higher travel speeds in 2010 and 2011, estimated using total distance travelled throughout entire trips compared to travel speeds to the maximum distance reached on trips, suggest paths to the trip destinations were less direct. More sinuous paths can result from the initiation of search behaviour along the track (Fauchald and Tveraa, 2003). A higher proportion of trips were found to include ARS behaviour in 2011, with all but one trip including such a zone. More frequent occurrence of ARS is assumed to be associated with more favourable feeding areas, likely to be characterised by more frequent encounters with prey or environmental cues (Fauchald and Tveraa, 2006, Pinaud and Weimerskirch, 2007), or mediated by information transfer when other birds are seen feeding (Silverman et al., 2004, Davoren et al., 2003b). Conversely, when prey is scarce, individuals are likely to encounter fewer such cues as they fly out from the colony. Travelling further and spending more time at sea may also limit an individual's capacity to initiate ARS at numerous locations due to energetic and time constraints (Shaffer et al., 2003, Pinaud et al., 2005a, Hamer et al., 2007). Under such conditions, individuals may spend more time searching less intensively over larger areas, or just initiate fewer zones of ARS further from the colony (Wiedenmann and O'Neil, 1991, Veit, 1999, Pinaud et al., 2005a). While analyses of the different scales of ARS zones suggest no significant difference in the average scale of these zones between each season, the variation in zone sizes during both seasons was tremendous, implying a great deal of plasticity in search behaviour, even within the same season (2003: 4 – 57 km; 2011: 2- 69 km). This illustrates the flexibility of this species to adjust foraging behaviour in response to environmental cues. Along with finding more frequent initiation of ARS in 2011, I also found that ARS behaviour occurred on the inward phase of a number of foraging trips, when birds were returning to the colony. This was never recorded in 2003 (Hamer et al. 2009), however the smaller sample size of the 2003 study must be considered. Coupled with the higher dive rates recorded outside zones of ARS and a higher proportion of dives recorded outside these zones, this suggests more opportunistic foraging in 2011 compared to 2003. It appears that gannet search strategies are flexible and vary in relation to changing distributions of prey. In particular, the marked reduction in nested search behaviour in 2011 compared to 2003, suggests a lower incidence of increased search effort by adopting nested search behaviour in seasons with more favourable feeding conditions. The apparent improved feeding conditions in 2011 appear to have enabled gannets on Bass Rock to feed more opportunistically, diving or initiating zones of ARS when they encountered prey, certain environmental cues or flocks of conspecifics. The almost linear orientation of the mixing front along the coast of eastern Scotland in 2011 (Miller et al. unpublished data, and see chapter 6), may also have influenced gannets' foraging behaviour, with the majority of trips following the coast, parallel with the front, so that birds encountered it as they left and entered the Firth of Forth. This may also have contributed to the higher occurrence of feeding bouts on return phases of trips.

Marked shifts in both foraging behaviour of northern gannets breeding on the Bass Rock and the locations of key feeding areas as a result of shifting hydro-biological features in the north-western North Sea, are apparent in recent years. These results add to the growing number of studies of a variety of marine top predators, which have recorded adjustments of search and dive strategies in response to altered hierarchal distribution of prey exploited and environmental conditions encountered (Paiva et al., 2010, Scheffer et al., 2010, Anderwald et al., 2012). The great variation in the scale of ARS and the altered frequency at which they are adopted, as well as the different use of nested search behaviour reflects great flexibility in this species, along with the initiation of dive behaviour within and outside these zones. In the case of gannets, this ability to adjust foraging strategies and habitat use appears important to buffer environmental variation. The ability to increase foraging effort and initiate finer scale, more concentrated searches enables this species to respond to dynamic, shifting environments. However, as the two seasons during which ARS behaviour were recorded in this study were both seasons with relatively favourable conditions, it is possible that gannets have not yet been observed in conditions which would make further adjustments necessary. Therefore further study is required to investigate how search strategies alter during more difficult conditions, when prey are scarce. Such information as can be retrieved on the more intensive feeding locations can also help to identify areas of high importance to marine predators breeding in the North Sea. These should be considered when regarding conservation management measures, such as the implementation of Marine Protected Areas (Hyrenbach et al., 2006, Grecian et al., 2012).

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Chapter 5: Temporal variation in northern gannet foraging effort and parental care: Consequences of varying environmental conditions

Abstract

Within-season variation in the foraging behaviour of chick-rearing seabirds may be attributed to the changing energy requirements of chicks, or shifts in prey availability as the season progresses. As provisioning rates limit chick growth and survival, adults must balance the costs of foraging with the needs of their growing chicks, as well as their own needs and energetic limits. I use a combination of GPS tracking and detailed observational methods to investigate within-season variation in foraging behaviour and parental investment in northern gannets *Morus bassanus* during two study seasons (2010 and 2011) on Bass Rock.

In line with recent evidence of inter-annual variability in foraging behaviour of gannets in response to changing environmental conditions, I find differences in the patterns of parental care and foraging between years. During the season when foraging trips were longer (2010), trip durations and foraging ranges showed a humped quadratic response to chick age, with shorter trips taken when chicks were very young and again when pre-fledging. This was not the case in 2011, when foraging trips were shorter on average than 2010. However, a humped quadratic relationship was found between chick age and travel speed during that latter season, but not in 2010. Speed increased when chicks were ca. 6 weeks, the same age at which trip durations were longest in 2010. I also find annual variation in parental attendance at the nest, with chick neglect more frequent and longer in duration during the season with longer foraging trips. Flexibility in foraging behaviour may buffer potential negative impacts of variable environments on parental care. These differences were found between two relatively good seasons. This highlights the need for further study into temporal variation during seasons with substantially worse conditions, when adults may reach their energetic limits, thereby reducing their ability to maintain feeding rates during key stages of chick development.

5.1. Introduction

Within-season variation in foraging effort and movements of chick-rearing seabirds, suggest birds may adopt a number of strategies. Trip durations or proportion of time spent foraging may change either in response to chick age and nutritional requirements, or to the intensity of chicks' begging behaviour, which itself may vary with chick age (Salamolard and Weimerskirch, 1993, Weimerskirch et al., 1993, Shaffer et al., 2003). In addition, parents may vary distances travelled (Weimerskirch et al., 1993, Kato et al., 2003), key foraging locations visited (Ito et al., 2010, Lyver et al., 2011) and prey type exploited (Montevecchi et al., 1984, Elliott et al., 2009) during the breeding season. In some cases, adults may even adjust their own body condition to cope with varying feeding conditions (Williams et al., 2007, Ballard et al., 2010). Studies of chick energy requirements have found switching of prey types, with older chicks optimally being delivered higher energy, lipid-rich species by adults (Montevecchi and Porter, 1980, Montevecchi et al., 1984). If such switching of prey occurs, this is likely to reflect altered foraging and feeding behaviour. However, altered prey type or feeding locations could also occur in response to reduced prey availability either as a result of prey disturbance (Lewis et al., 2001, Litzow et al., 2004), prey depletion (Birt et al., 1987), or due to the strong seasonal patterns of certain prey species distributions (Macer, 1965, Jensen et al., 2003, Bils et al., 2012). There therefore arises a trade-off between travel costs and prey availability, such that net energy gain may be increased by visiting more distant foraging locations (Cuthill and Kacelnik, 1990, Wanless et al., 1993, Waite and Ydenberg, 1996), unless meal mass is no greater following such long trips. Such adjustments in time budgets of pelagic species has been recorded (Burger and Piatt, 1990). Foraging seabirds need to balance the requirements of growing chicks with their own needs and energetic limits, and are ultimately limited by their potential flight durations and speeds (Hamer et al., 2007). Whether foraging efforts are adjusted in response to the altering demands of the chick or as a result of changing prey availability, provisioning rate limits both chick growth and survival (Harris and Wanless, 1997, Gray et al., 2005, Enstipp et al., 2006). Such temporal shifts in foraging behaviour and impacts on parental investment are likely to vary between seasons with differing prey availability, which has already been seen to result in annual variation in foraging characteristics (Shaffer et al., 2001, Hamer et al., 2007, Garthe et al., 2011).

Many pelagic seabirds are altricial. That is, their offspring hatch in a relatively undeveloped state and rely heavily on parental care (Nelson, 1978). For example, gannet chicks are vulnerable to hypothermia up to the age of 3 weeks, being only sparsely covered with neossoptiles and therefore unable to fully regulate their own body temperature (Nelson, 1966, Montevecchi et al., 1984). Young chicks are also vulnerable to displacement from the nest by heavy rain and attacks from both adult gannets and older chicks (Nelson, 1978). Successful breeding therefore requires the chick to be constantly guarded by one or other of the parents for at least the first 4 weeks after hatching. Incidences of simultaneous non-attendance by parents can sometimes occur and are often referred to as periods of brood neglect. Such incidences commonly occur following extended periods of chick guarding by the remaining parent, that eventually also needs to leave the nest in order to feed (Lewis et al., 2004). Such periods of non-attendance can leave the chicks vulnerable to the elements and unguarded from conspecifics and predation (Nelson, 2002) and have been recorded in a number of species (Harris and Wanless, 1997, Tveraa et al., 1998, Ashbrook et al., 2008).

Although foraging decisions of adults are in part governed by their own energetic requirements (McNamara and Houston, 1996), trip durations are also probably influenced by parental duties. Gannet chicks grow most rapidly between the ages of 4 and 8 weeks (Poulin, 1968, Nelson, 1978, Montevecchi et al., 1984), with body mass increasing 40 fold within their first 2 months of life and lipid eventually accounting for the majority of energy in tissues (Montevecchi et al., 1984). This age group thus demands regular provisioning to maintain such rapid growth (Nelson, 1978). This supposition is supported by Lewis et al., (2004), who found that trip durations of parents decreased as chicks aged. Studies of other seabirds have also revealed significant effects of chick age on parental trip duration, although the direction of the response has varied. For example, while trip duration increases with chick age in northern fulmars *Fulmaris glacialis* (Ojowski et al., 2001) and African penguins *Spheniscus demersus* (Petersen et al., 2006), whereas trips became shorter in the Antarctic petrel *Thalassoica Antarctica* (Varpe et al., 2004), thick-billed murre *Uria omvia* (Hipfner et al., 2006) and Cape gannets *Morus capensis* (Mullers, 2009).

Recent evidence indicates that northern gannets respond to inter-annual environmental variability by adjusting their foraging behaviour (Hamer et al, 2007, also chapters 2 and 4). Adults forage further away from the colony and spend more time away from the nest during seasons when conditions are poorer, as indicated by local stock sizes and inferred from changes in local physical conditions i.e. winter sea-surface temperatures and summer chlorophyll-a concentrations (chapter 4). Although there are a number of studies that document foraging behaviour in northern gannets in different seasons, few combine data on foraging behaviour and parental care throughout the chick-rearing period and across multiple seasons. My aim was to use data from Bass Rock, where annual variation in foraging behaviour has been recorded using GPS devices (Chapter 4), and detailed observations on parental behaviour were made in two seasons (2010 and 2011). Conditions appeared better during the latter season (2011), indicated by significantly smaller foraging ranges and less time spent away from the colony (Chapter 4). I also compare frequency and duration of unattendance with previously published data from the same colony during a different season (2002: Lewis et al., 2004), when conditions were poorer still, previously attributed to markedly smaller sandeel stocks in the region, and foraging effort was substantially greater (Hamer et al., 2007, Chapter 4).

As a result of flexible foraging behaviour and time budgets, leading to increased foraging effort and therefore more time spent away from the nest during poorer seasons, I predict: 1) more frequent and/or earlier occurrences of simultaneous non-attendance by parents; 2) longer periods of parental non-attendance of older, less vulnerable chicks; 3) less flexibility in parents’ foraging strategies, trip durations and speeds, in response to chick requirements under poorer conditions.

5.2. Materials and Methods

Fieldwork was carried out on Bass Rock, Firth of Forth, Scotland (56°4.6’N, 2°38.3’W) throughout a 10 week period during the 2010 breeding season (20th June - 24th August), and a 10 week period in 2011 (31st May - 3rd August). Fieldwork on Bass Rock was alternated with time using the web-camera each season (see below). This covered the main chick rearing period on Bass Rock, and the timing of the breeding season was similar each year, as observed during pre-season and incubation site watches. Chick survival at all known nests, including both those on the observation plot and the plot where adults were captured to track, were also recorded during the last visit to colony in August each season (2010: n = 101, 2011: n = 52) as a measure of breeding success.

5.2.1. Nest attendance:

Nest observations were carried out as described in chapter 2, using images from a digital stills Mobotix© surveillance camera with a fixed view, mounted in the colony with the aid of the Scottish Seabird Centre and monitored by remote radio link (Fig. 5.1.). The early installation of this camera, during the March prior to each study season, prevented disturbance to the nests during incubation and chick rearing, and also enabled regular information on copulation and egg-laying, as well as the ability to estimate directly hatch dates for the study nests to aid aging of chicks. Estimated chick ages were checked and supported using plumage characteristics (Nelson, 2002). By observing this group of breeding pairs, the arrival and departure times of parent gannets and the time they spent together at the nest were recorded, along with any incidences of brood neglect. Due to technical problems with the web-camera, it was not possible to carry out site observations between 23rd June and 4th July in 2011.

As continuous watches were not always possible in 2010, observation shifts of 4 hours were carried out. Therefore, during this season, average trip duration at each nest calculated by dividing the time available per day for undertaking foraging trips (24 hours minus the mean time adults spent together at the nest) by the recorded changeover rate (Hamer et al., 1993, Lewis et al., 2001). In 2011, continuous observations over three day periods were carried out by multiple observers and full trips were recorded. Trip durations recorded at each nest that season were not significantly different from those estimated using the calculation described above. Trip durations recorded at the observation site were also not significantly different from those recorded directly using GPS loggers each year. This suggests that any potential bias against long trips during that season, as to only full trips were used is unlikely to have affected my results.

Chick ages within the observation plot varied between 0.5 and 3 weeks at the start and 7.5 and 11 at the end of fieldwork in 2010; and between 0 and 2 at the start, and 6.5 and 10 weeks at the end of fieldwork in 2011. Due to the early start of observations in 2011, it was also possible to observe nest attendance during incubation at a sample of these nests.

Figure 5.1. View from the Mobotix© web camera on Bass Rock, taken on 28th June 2010. Red asterisks indicate the nests that were included in the sample used to monitor attendance. Time and date are indicated in the top right-hand corner.

5.2.2. GPS tracking of foraging trips:

Detailed information on foraging tracks was obtained using GPS loggers. Deployments were carried out in a study plot ca. 30 m from the observational sites. In 2010, adults with chicks were fitted with Igtou GT-120 and Igotu GT-200e GPS loggers (21 and 53 individuals respectively; 14 individuals were fitted with both, one after the other); in 2011, 28 individuals were fitted with Igotu GT-200e or Igotu GT-650e GPS satellite transmitters (see Materials and Methods, Chapter 4 for details). Devices were not deployed on adults with chicks less than 2 weeks old. So chicks of tracked birds and those in the attendance watches were aged between 2 and 9 weeks.

Capturing birds with older chicks was difficult as they were more likely to leave the chick unattended.

The percentage of time each adult spent at sea was calculated by dividing the mean trip duration by the mean trip duration plus the mean time spent at the nest between foraging trips (Hamer et al., 2007). This was limited to birds for which 3 or more consecutive trips were recorded.

5.2.3. Statistical analyses:

All statistical analyses were carried out using the program R, version 2.12.1 (R-Development-Core-Team, 2010). In order to test for variation in: trip duration (hrs), time adult pairs spent together at the nest (mins), feeding frequency (defined as parental visits per day) and occurrence of unattendance as chicks on the observation plot aged each year, generalized linear mixed-effects models (GLMMs) were run, using the R package “lme4” (Bates et al., 2011). Trip duration, time together, feeding frequency and proportion of trips that left a chick unattended were modeled as a function of Julian day as a single covariate. Nest identity was treated as a random effect. As feeding frequency was not normally distributed with unequal variance, a Poisson error structure was specified in this model (Bolker et al., 2009, Thaxter et al., 2009). When investigating effect of chick age on the proportion of trips whereby the chick was left unattended (unattended trip vs. attended trip), a binomial error distribution was used due to the presence/absence data (Crawley, 2007). These models were compared to a null, intercept only model, using likelihood ratio tests (Crawley, 2007) and AIC values for each model were also retrieved, to indicate the best fitted model in each case (Zuur et al., 2009). Analyses of covariance were used to test for annual differences in these foraging characteristics between the two study seasons (2010 and 2011), by including year as a covariate in the model.

The same approach was used for data recorded by GPS devices, whereby temporal variation in trip duration, maximum distance travelled from the colony and total distance travelled, were again tested using GLMMs with ‘bird identity’ included as a random effect. Included in each model were chick age, Julian date and whether the bird travelled to the north or south of the colony (defined as trips with trip destinations north or south of 56°4.6’N) as fixed effects. Likelihood ratio tests were used to find the most parsimonious model in each case, along with assessing AIC values for each model tested (Zuur et al., 2009). When investigating foraging characteristics, the I^2 term was tested in each model in order to look for a quadratic, ‘humped’ relationship (Crawley, 2007), after initial exploration and visualisation of the data appeared to demonstrate this pattern. I also tested for variation in flight speed during both breeding seasons. Speed^b (speed on outward leg of the trip) is calculated using distance to trip destination, and Speed^c (overall travel speed during a foraging trip) is calculated as the average speed of travel over the complete foraging trip (as described in Chapter 4).

5.2.4. Previous parental care data and annual variation:

To increase the number of years for which paired data on foraging trips and parental care were available, I also included data collected during the 2001 and 2002 breeding seasons (Lewis et al., 2004). This study differed from my own, with the adults from the observed nests radio-tracked from the mainland using VHF radio transmitters. The radio frequencies of all tags were scanned every 15 min, and arrival and departure times were recorded for each bird. Similar to my study, trips were classified as either attended (commencing after the return of the foraging partner, leaving the chick attended by one adult) or unattended (commencing prior to the partner’s return, resulting in the chick being left unguarded). There was no significant effect of year on any of the foraging behaviours, and thus data were pooled (Lewis et al., 2004). I therefore compare results for 2001 and 2002 combined, with the data collected in 2010 and 2011 when environmental conditions for the foraging birds appeared to have improved (Chapter 4).

5.3. Results

The number of nests observed each day using the web-cam ranged from 20 to 28 pairs (mean: 26) in 2010, and from 17 to 20 pairs (mean: 19) in 2011. These observations were carried out for a minimum of one full day each week (2010 mean: 41 hrs; range 18 - 60 hrs, 2011 mean: 58 hrs; range 34 - 60 hrs per week). Of all known nests on the observation site plus those with tracked adults in 2010 (n = 101) and 2011 (n = 52), 84 and 47 chicks survived respectively, an estimated breeding success of 83% in 2010 and 90% in 2011. There was no significant difference in the breeding success between these years (GLMM with binomial error structure: $F_{1, 151}$ = 0.78, $P > 0.05$, with nest included as a random effect).

A total of 636 trips were recorded in 2010 using the web-cam (overall mean trip duration 23.45h (SD = 14.4, range: 5 – 70 h). In 2011, 399 trips were recorded (mean duration 16.73h; SD = 10.7, range: 0.8 – 58.4 h). The 2011 data included some trips made during incubation. These were significantly longer (n = 32, mean = 23.6 h, SD = 16.2) than those made during chick-rearing (n = 367, mean = 16.13 h, SD = 9.9; GLMM: $F_{1, 397}$ = 13.2, $P < 0.01$, with nest included as a random effect). Hence, incubation trips were excluded from subsequent analyses. Including both nest observations and tracking data, trip durations were significantly shorter in 2011 (16.1 ± 0.5 h) than in 2010 (19.3 ± 0.8 h; GLMM: $P < 0.001$, Table 5.1).

Table 5.1. Summary table of the minimum adequate model testing for annual variation in square-root trip duration between 2010 and 2011 (Year), with chick age included as a fixed effect and bird ID included as a random effect.

Fixed effects:	Estimate	Std. Error	z value	P value
Intercept (bird)	1.60949	0.04610	34.91	< 2e-16 ***
Chick age	-0.01152	0.00718	-1.61	0.108
Year	-0.18123	0.03209	-5.65	1.63e-08 ***

5.3.1. Annual variation in parental care:

In 2010, 12% of all trips observed (n = 636) resulted in a chick being left unattended. In contrast, only 3% of all trips in 2011 (n = 399) resulted in brood neglect, a significantly lower occurrence of neglect in the latter season (GLMM: $x^2 = 13.6$ $P < 0.001$, including nest as a random effect). Both these values were lower than the average value for 2001/2002 (Lewis et al. 2004; 17% GLMM: $P < 0.001$). The youngest chicks left unattended in 2010 and 2011 were 4.5 and 5 weeks old respectively, although there was no significant difference in the mean age at which chicks were first left unattended between these years. The age at which the first chick was left unattended was 4 weeks during the 2001/2002 breeding seasons.

As in 2001 and 2002 (Lewis et al., 2004), foraging trips during which chicks were left unattended were significantly shorter than those where an adult remained with the chick (2010 attended trips: 21.94 ± 0.9 h, unattended trips 1.7 ± 0.3 h, GLMM: $x^2 = 13.7$ $p < 0.001$; 2011 attended trips: 16.51 ± 0.5 h, unattended trips 4.04 ± 1.5 h, GLMM: $x^2 = 14.1$, df = 1, $p < 0.001$, Fig. 5.2). Although chick neglect was less frequent in 2011, the length of neglect periods was significantly longer than in 2010 (GLMM: $x^2 = 4.05$, $P < 0.05$). Compared to unattended periods reported in 2001/2002 (5.61 ± 0.83 h), durations of chick neglect in 2010 and 2011 appear shorter.

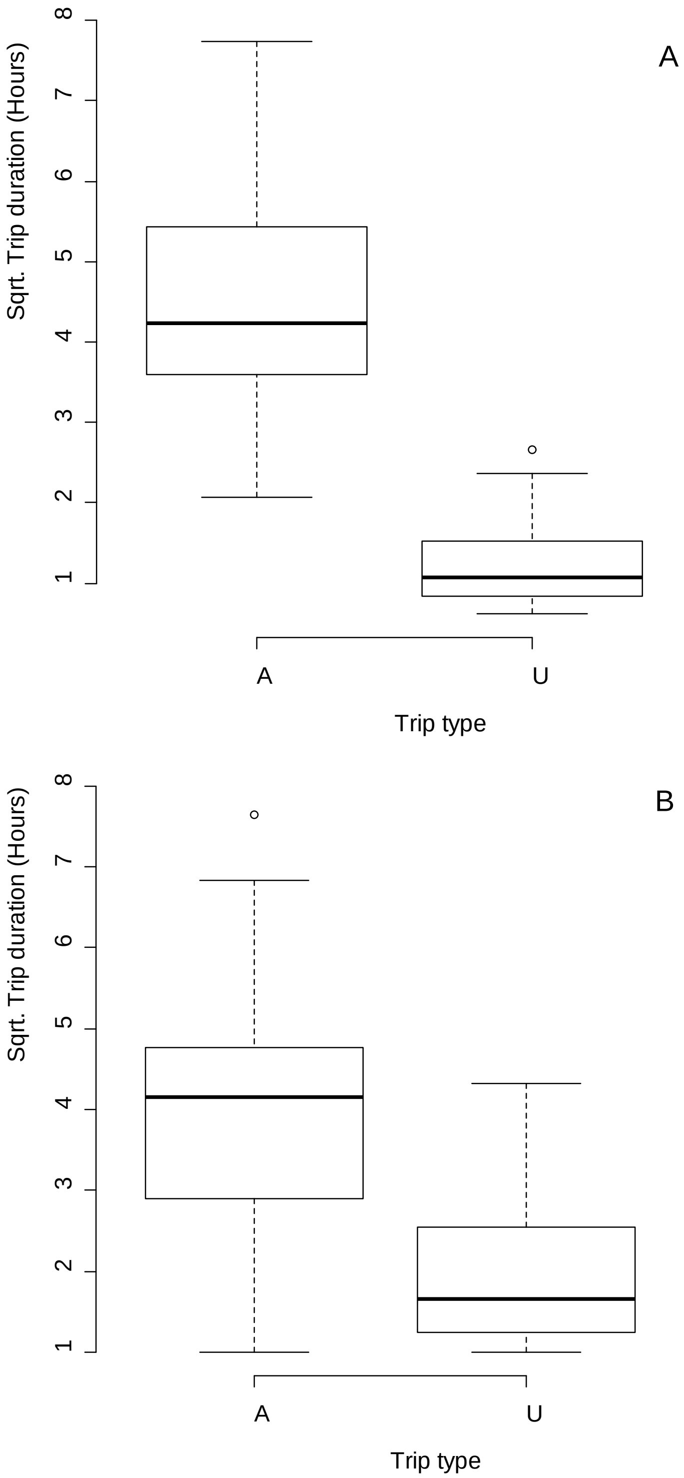


Figure 5.2. Square-root trip duration (hours) of attended (A) and unattended (U) foraging trips recorded on Bass Rock in **A:** 2010 and **B:** 2011

5.3.2. Within season variation in parental care:

As in 2001 and 2002, the proportion of trips whereby a chick was left unattended increased significantly as chicks aged in both 2010 and 2011 (2010: GLMM with binomial distribution, $P < 0.001$, 2011: GLMM with binomial distribution, $P < 0.01$, Fig. 5.3). However, proportions were consistently lower in 2010 and 2011 compared to 2001 and 2002. In 2010, the proportion of trips where birds left chicks unattended increased from 0 for chicks aged < 4.5 weeks, to 0.27 for 10 week old chicks, with a peak of 0.35 for chicks aged between 8 and 9 weeks old (Fig. 5.3). The majority (93%) of unattended trips occurred when chicks were ≥ 8 weeks, with only 7% of all trips by adults with chicks under 8 weeks resulting in brood neglect. In 2011, the proportion of trips where the chick was left unattended increased from 0 for chicks < 5 weeks to 0.08 by the time chicks were 9 weeks, with a peak of 0.11 for chicks of 7 – 8 weeks. Thus, brood neglect occurred when chicks were older and the overall proportion of trips where the chick was left unattended was much lower in 2011 compared to 2010 (Fig. 5.3.).

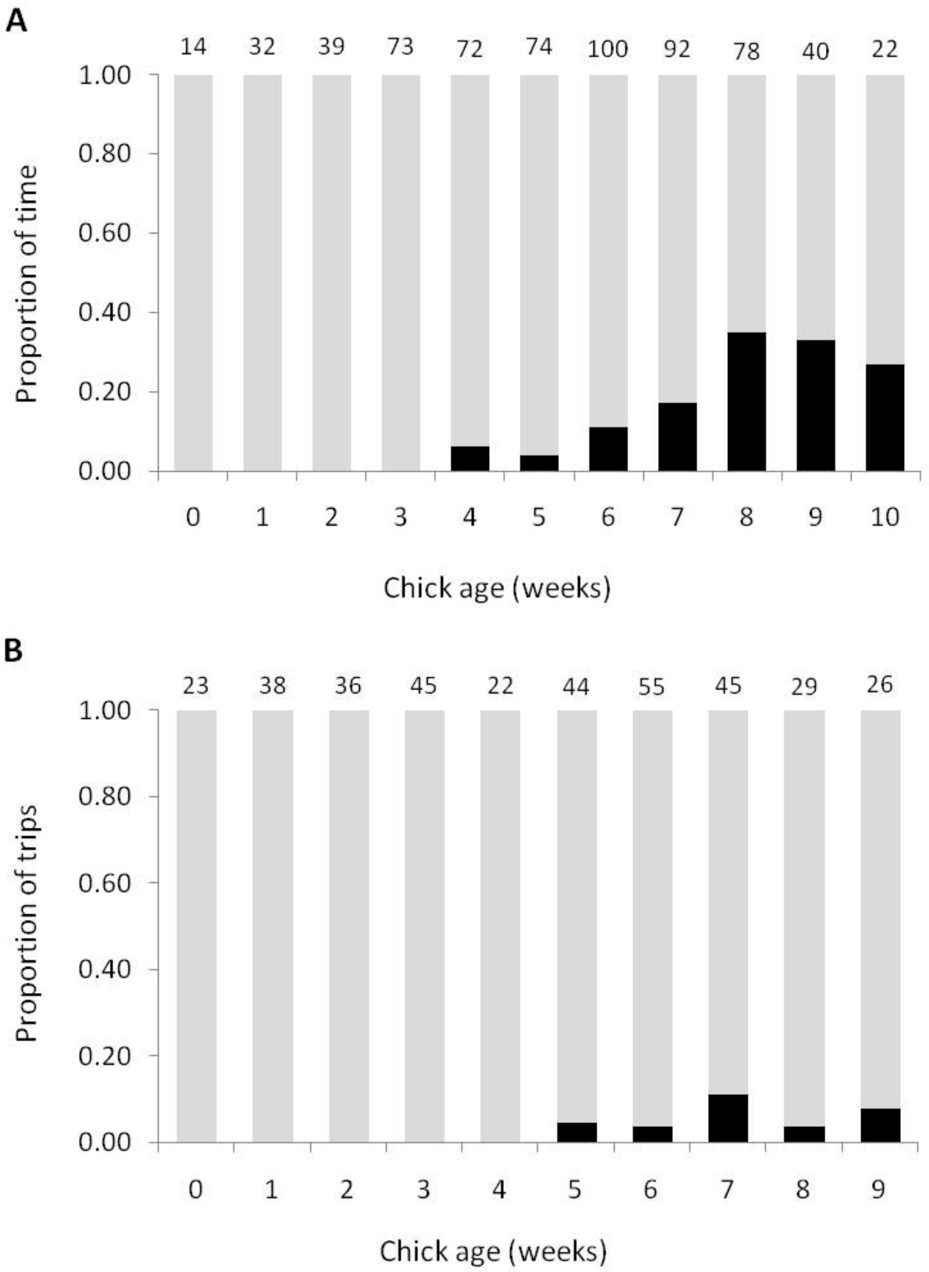


Figure 5.3. The proportion of foraging trips where a chick was attended by one adult (*grey bars*), and was left unattended before the foraging adult returned (*black bars*), with increasing chick age (weeks), for northern gannets on Bass Rock in **A:** 2010 (n = 34 birds) and **B:** 2011 (n= 20 nests). The total numbers of trips recorded are shown above each bar.

5.3.3. Time together at the nest

In 2010, adult pairs spent on average 32.4 minutes together at the nest during change-overs (n = 232, SD = 42.03, range 0 – 348 mins), compared to an average of 22.1 minutes in 2011 (n = 519, SD= 48.46, range 0 – 641 mins). The square-root transformed amount of time (minutes) adult pairs spent together at the nest during change-overs was significantly shorter during the 2011 breeding season compared to 2010 (GLMM: P < 0.0001, Table 5.2).

Table 5.2. Summary table of the most parsimonious model describing the significant difference between square-root time pairs spent together at the nest (mins) between the 2010 and 2011 breeding seasons. Pairs spent less time together at the nest in 2011 than 2010. Nest identity was included as a random effect, and chick age was found to have a significant effect on the model.

Fixed effects:	Estimate	Std. Error	z value	P value
Intercept (nest)	557.620540	98.964312	5.635	1.76e-08 ***
Chick age	-0.038562	0.007314	-5.272	1.35e-07 ***
Year	-0.276558	0.049222	-5.619	1.93e-08 ***

The length of time adults spent together at the nest was also found to be linearly related to chick age during both seasons, with change-over periods becoming shorter as chicks aged (2010, GLMM: P = 0.003, Table 5.3; 2011, GLMM: P = 0.02, Table 5.4). While the duration of these change-over periods were also found to be significantly related to the Julian date in 2010 (GLMM: P < 000.1), there was no relationship between length of time adults spent together and date in 2011 (GLMM: P > 0.05).

Table 5.3. Summary table of the most parsimonious model describing the significant relationship between time pairs spent together at the nest (mins) and chick age in 2010, with number of hours of observation and Julian day included as fixed effects. Nest identity is included as a random effect.

Fixed effects:	Estimate	Std. Error	z value	P value
Intercept (nest)	4.3846	0.8452	5.187	2.13e-07 ***
No. Hours of obs	0.020234	0.002391	8.462	< 2e-16 ***
Julian day	-0.0213	0.0051	-4.207	2.59e-05 ***
Chick age	0.1124	0.0379	2.966	0.00301 **

Table 5.4. Summary table of the most parsimonious model describing the significant relationship between time pairs spent together at the nest (mins) and chick age in 2011, with Julian day included as a fixed effect. Nest identity was included as a random effect.

Fixed effects:	Estimate	Std. Error	z value	P value
Intercept (nest)	0.050043	0.838120	0.060	0.9524
Julian day	0.008743	0.005359	1.632	0.1028
Chick age	-0.088111	0.037494	-2.350	0.0188 *

5.3.4. Foraging activity and parental care

The mean percentage of their time adults spent away from the nest on foraging trips was 54% (n = 37, SD = 7) and 52% (n = 28, SD = 8) in 2010 and 2011 respectively, with no significant difference between the two seasons (GLMM: $F_{1, 18} = 1.3$, $P > 0.05$, bird identity included as a random effect). Trip durations estimated from web-cam observations did not differ significantly from those recorded by GPS loggers in either year. Both the maximum and total distances travelled during foraging trips recorded using GPS loggers were significantly shorter in 2011 than in 2010 (2010: 198.1 ± 7.3 km, 2011: 134.0 ± 11.2 km using 95% confidence intervals, LME: $_{F1,282}$

= 26.6, P < 0.0001, Table 5.5; and 2010: 524.5 ± 21.2 km, 2011: 388.1 ± 19.8 km, LME: $_{F1,282}$ = 17.2, P < 0.0001, Table 5.6, respectively).

Table 5.5. Summary table of the most parsimonious model testing for annual variation in maximum distance reached from the colony between 2010 and 2011 (Year), with Julian day included as a fixed effect and bird identity included as random effect.

Fixed effects:	Value	SE	DF	t-value	F-value	P value
Intercept (bird)	1909.1	370.447	282	5.1536	17323.8	<0.0001***
Julian day	-0.0124	0.0069	282	-1.8146	131.4	0.0706 *
Year	-0.9478	0.1838	282	-5.15586	26.6	<0.0001***

Table 5.6. Summary table of the most parsimonious model testing for annual variation in total distance travelled on trips between 2010 and 2011 (Year), with Julian day included as a fixed effect. Bird identity was included as a random effect.

Fixed effects:	Value	SE	DF	t-value	F-value	P value
Intercept (bird)	-2576.2	621.472	282	-4.14525	24010.4	<0.0001***
Julian day	0.0253	0.0109	282	2.32581	101.9	0.0207*
Year	1.2793	0.3084	282	4.14755	17.2	<0.0001***

Although there was no significant difference in the overall feeding frequencies between the two study seasons (2010: n = 232, mean = 1.34, SD = 0.89; 2011: n = 147, mean = 1.35, SD = 0.61, GLMM: $P > 0.05$), there was a significant positive relationship between chick age and feeding frequency in 2010. Adults provisioned their chicks more frequently as chicks aged in that season (GLMM: $F_{1,234} = 5.1$, $P = 0.03$, Table 5.7). Feeding rates increased by 20% from first hatching (1.1 feeds per day, SD = 0.5) to 4 weeks old (1.33 feeds per day, SD = 0.9), and by 57% between hatching and 8 weeks old (1.75 feeds per day, SD = 0.9).

However, this was not the case in 2011, when there was no significant relationship between feeding frequency and chick age (GLMM: $F_{1,146} = 1.3$, $P > 0.05$). Feeding frequency was also found to significantly increase with date in 2010 (GLMM: $F_{1,234} = 5.44$, $P = 0.02$), but there was no association found between Julian day and feeding frequency in 2011.

Table 5.7. Summary table of the most parsimonious model describing a significant positive relationship between feeding frequency (arrivals per day) and chick age in 2010. Nest identity was included as a random effect.

Fixed effects:	Estimate	SE	DF	t-value	P value
Intercept (nest)	1.067	0.142	234	7.492	< 0.0001***
Chick age	0.052	0.023	234	2.248	0.0255*

5.3.5. Within-season variation in foraging behaviour:

Comparing these observational data to foraging behaviour recorded directly using GPS devices indicated that, in 2010, there was a significant, hump-shaped, quadratic relationship between trip duration and chick age (GLMM: df = 191, $P < 0.05$, Table 5.8, Fig. 5.4a), such that trip durations were shorter when chicks were younger. This increased to a peak when chicks were 6-7 weeks of age and then decreased in older chicks (Fig. 5.4a). A relationship was also found between trip duration and Julian day, though this positive relationship was found to be linear rather than quadratic (GLMM: df = 191, $P = 0.001$, Table 5.8).

Table 5.8. Summary table of the minimum adequate model describing a significant relationship between GPS recorded trip durations and I(chick age^2) in 2010, with orientation (trip destination north or south of the colony) and Julian day included as fixed effects, and bird identity as a random effect.

Fixed effects:	Estimate	SE	DF	z-value	P value
Intercept (Bird)	-0.5006	0.9724	191	-0.515	0.6067
Orientation (N)	0.76391	0.2548	191	2.998	0.0027 **
Orientation (S)	0.2155	0.2608	191	0.826	0.4087
Julian day	0.0156	0.0049	191	3.211	0.0013 **
I(Chick age^2)	-0.0071	0.0033	191	-2.138	0.0325 *

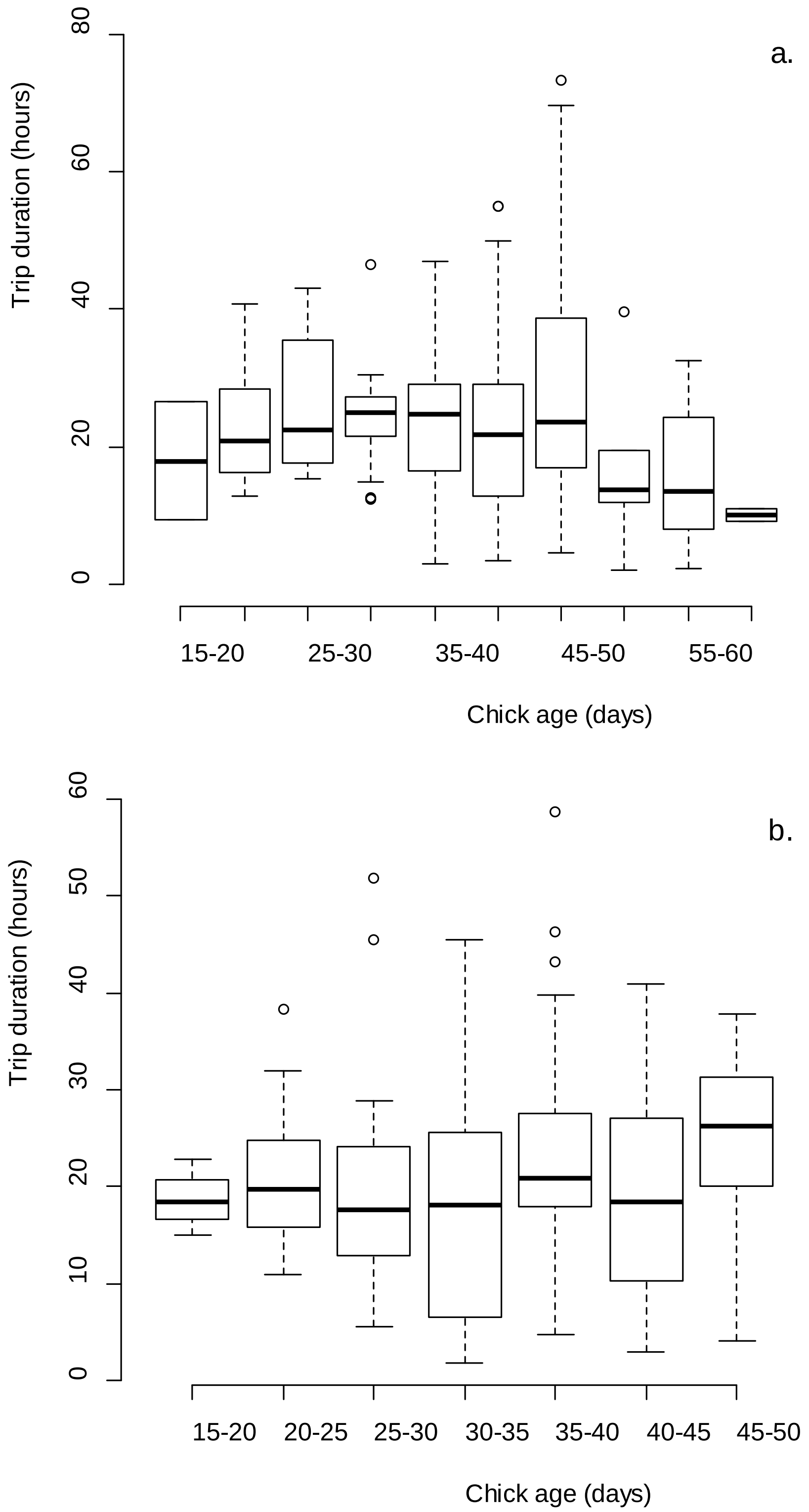


Figure 5.4. Foraging trip durations (hours) of tracked birds with chick age (days) in **a**. 2010, when a quadratic relationship was found between duration and chick age and **b.** 2011, when no relationship was found. Thick lines indicate the median values, while the boxes show the upper and lower quartiles. The whiskers extend to the smallest and largest values recorded.

In 2010, this pattern was also apparent when comparing maximum distances travelled from the colony on foraging trips and chick age (GLMM: df = 191, P = 0.004, Table 5.9, Fig. 5.5a). Birds travelled shorter distances from the colony when chicks were very young; distances increased as chicks aged to ca. 6-7 weeks, before declining in older age groups. A relationship was also found between maximum distance travelled from the colony and Julian day, although this relationship was linear rather than quadratic (GLMM: df = 191, P < 0.0001, Table 5.9). A significant quadratic relationship was also found between total distance travelled on foraging trips and chick age in 2010 (GLMM: df = 191, P < 0.0001, Table 5.10, Fig. 5.6a). Total distance travelled was also significantly related to Julian day in 2010; again the relationship was linear rather than quadratic (GLMM: df = 191, P < 0.0001).

Table 5.9. Summary table of the minimum adequate model describing the significant relationship between GPS recorded maximum distances reached from the colony and I(chick age^2) in 2010, with orientation (destination was north or south of the colony) and Julian day included as fixed effects, and bird identity as the random effect.

Fixed effects:	Estimate	SE	DF	z-value	P value
Intercept (Bird)	1.0799	0.5000	191	2.160	0.0308 *
Orientation (N)	0.4952	0.0816	191	6.069	1.29e-09 ***
Orientation (S)	-0.0735	0.0849	191	-0.866	0.3866
Julian day	0.0189	0.0025	191	7.477	7.58e-14 ***
I(Chick age^2)	-0.0043	0.0015	191	-2.856	0.0043 **

Table 5.10. Summary table of the minimum adequate model describing the significant relationship between GPS recorded total distances travelled on round foraging trips and I(chick age^2) in 2010, with orientation (destination was north or south of the colony) and Julian day included as fixed effects. Bird identity was included as a random effect.

Fixed effects:	Estimate	SE	DF	z-value	P value
Intercept (Bird)	1.0335	0.3463	191	2.984	0.0028 **
Orientation (N)	0.5594	0.0521	191	10.739	< 2e-16 ***
Orientation (S)	-0.0060	0.0540	191	-0.111	0.9115
Julian day	0.0235	0.0017	191	13.462	< 2e-16 ***
I(Chick age^2)	-0.0047	0.0010	191	-4.572	4.83e-06 ***

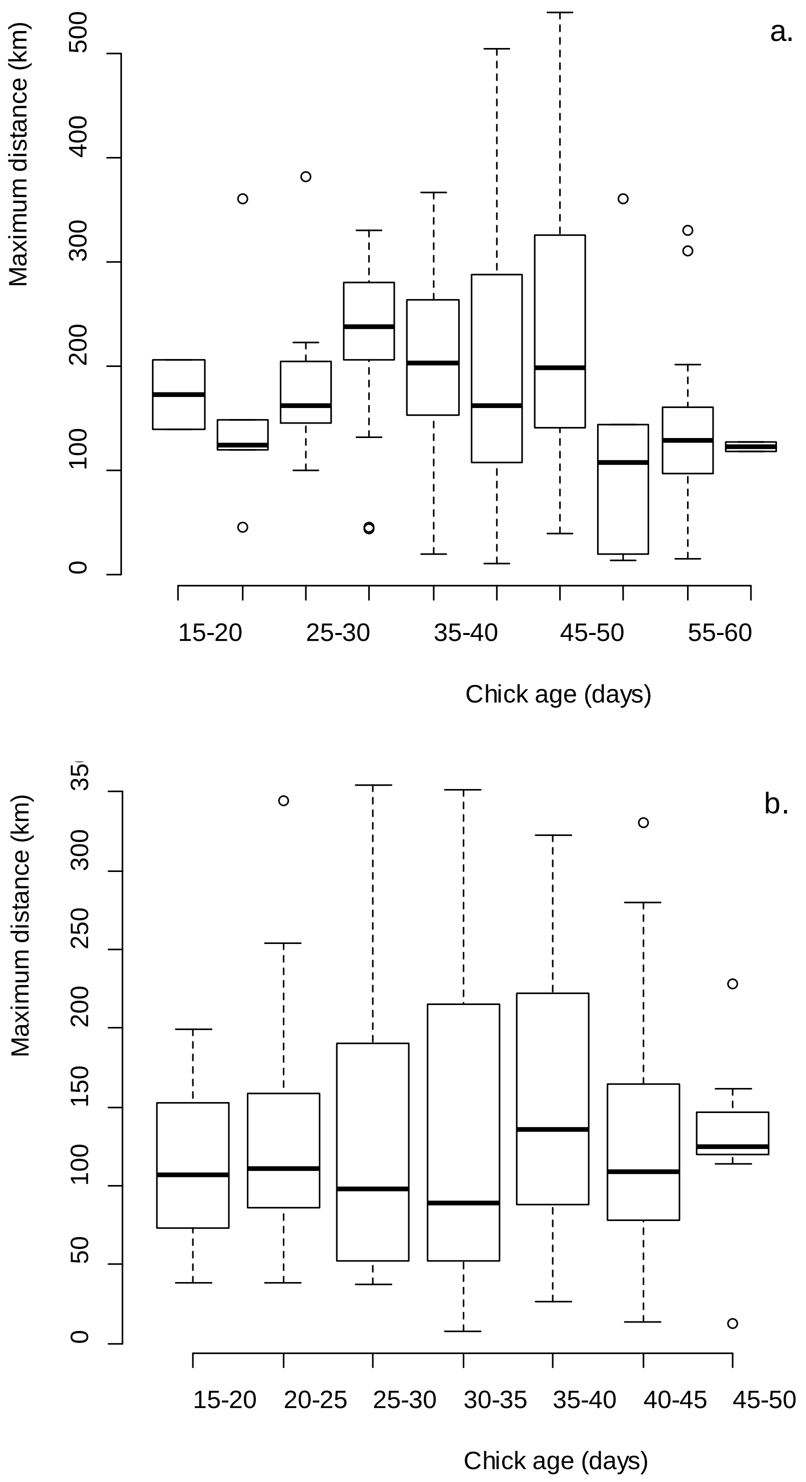
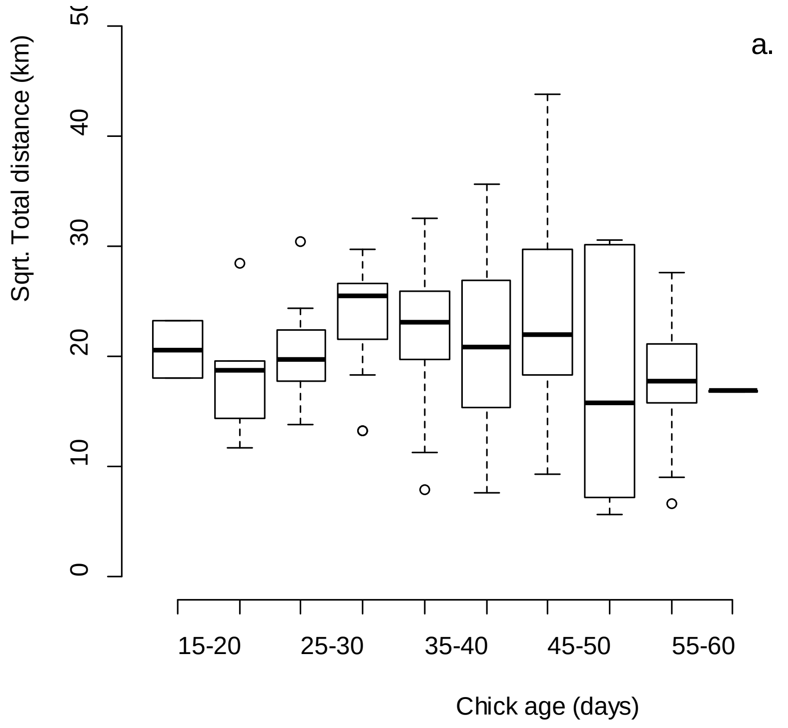


Figure 5.5. Maximum distance travelled from the colony (km) by tracked birds with chick age (days) in **a**. 2010, when a quadratic relationship was found between maximum distance and chick age, and **b.** 2011, when no relationship was found. Thick lines indicate the median values, while boxes show the upper and lower quartiles. The whiskers extend to the smallest and largest values recorded.



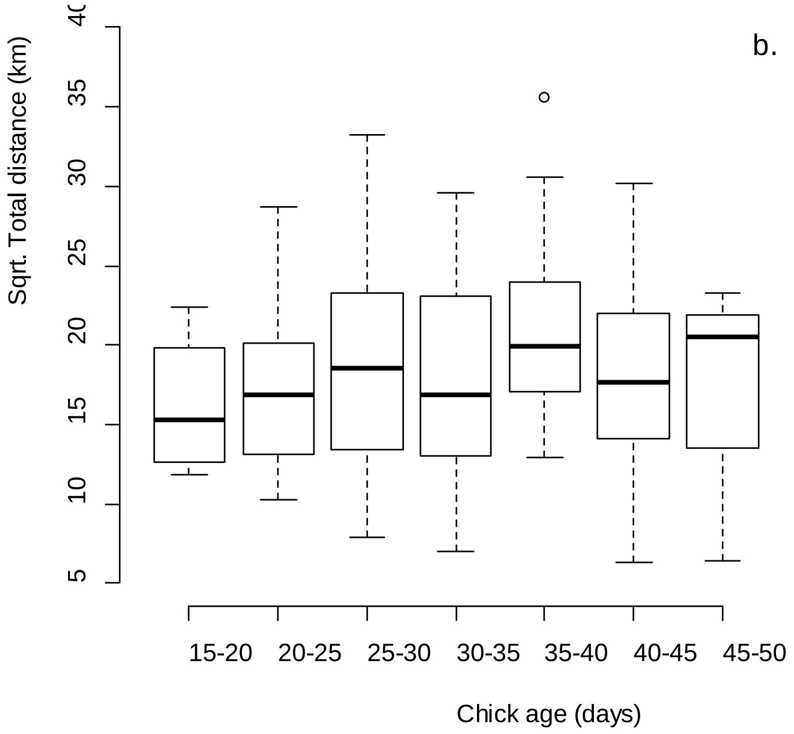


Figure 5.6. Total distance travelled on foraging trips (km), by tracked birds with chick age (days) in **a**. 2010, when a quadratic relationship was found between total distance and chick age, and **b.** 2011, when no relationship was found. Thick lines indicate the median values, while boxes show the upper and lower quartiles. The whiskers extend to the smallest and largest values recorded.

In contrast, in 2011 I found no significant relationships between trip duration and either chick age or Julian day (GLMM: df = 141, z = 2.0, P > 0.05, and GLMM: df = 141, z = 1.6, P > 0.05 respectively). Neither was there any relationship between maximum or total distance travelled and chick age (GLMM: $F_{1,141}$ = 0.02, P > 0.05 and GLMM: $F_{1,141}$ = 0.54, P > 0.05 respectively), or with Julian date (GLMM: $F_{1,141}$ = 0.01, P > 0.05 and GLMM: $F_{1,141}$ = 0.35, P > 0.05 respectively). Therefore, unlike the tracks recorded in 2010, I found no temporal variation in these behavioural characteristics during this latter season.

5.3.6. Within-season variation in travel speeds:

Travel speeds were, on average, faster in 2010 compared to 2011 when considering both speed on outward leg (speed^b 2010: n = 195, Mean = 17.49 km/hr, SD = 6.65; 2011: n = 143, Mean = 13.4 km/hr, SD = 6.01; LME: $F_{1,284}$ = 32.9, P < 0.001) and overall travel speed (speed^c 2010: n = 195, Mean = 22.66 km/hr, SD = 7.73; 2011: n = 143, Mean = 18.92 km/hr, SD = 5.75; LME: $F_{1,284}$ = 20.04, P < 0.001). During 2010 there was no association between flight speed (either speed^b or speed^c) and chick age (speed^b GLMM: P > 0.05, Fig 5.7a; speed^c GLMM: P > 0.05, Fig 5.8a), nor any significant relationships with date (GLMM: P > 0.05).

In contrast, in 2011 both speed^b and speed^c showed a significant quadratic effect of chick age (GLMM: df= 141, P = 0.01, Table 5.11, Fig 5.7b and GLMM: df = 141, P = 0.02, Table 5.12, Fig. 5.8b respectively). There was also a borderline significant positive linear, but not quadratic, relationship between speed^b and date in 2011 (GLMM: $F_{1,141}$=3.5, P = 0.05). However, there was no significant effect of date on speed^c during the whole foraging trip (GLMM, df = 141, P > 0.05).

Table 5.11. Summary table of the most parsimonious model describing the significant quadratic relationship between speed^b, calculated using maximum distance reached from the colony and I(chick age^2) in 2010, with maximum distance reached and trip duration (TD) included as fixed effects. Bird identity was included as a random effect.

Fixed effects:	Estimate	SE	DF	z-value	P value
Intercept (Bird)	2.5000	0.0786	141	31.81	<0.0001***
Max. Dist	0.0071	0.0004	141	17.01	<0.0001***
TD (hrs)	-0.0509	0.0036	141	-14.24	<0.0001***
I(Chick age^2)	0.0045	0.0023	141	1.94	0.0118*

Table 5.12. Summary table of the most parsimonious model describing the significant relationship between speed^c, calculated using total distance travelled on a round trip and I(chick age^2) in 2010, with total distance travelled and trip duration (TD) included as fixed effects. Bird identity was included as a random effect.

Fixed effects:	Estimate	SE	DF	z-value	P value
Intercept (Bird)	18.9079	0.7263	141	45.55	<0.0001***
Tot. Dist	0.0469	0.0021	141	13.81	<0.0001***
TD (hrs)	-0.9468	0.0464	141	-12.33	<0.0001***
I(Chick age^2)	0.0529	0.0223	141	1.45	0.0191*

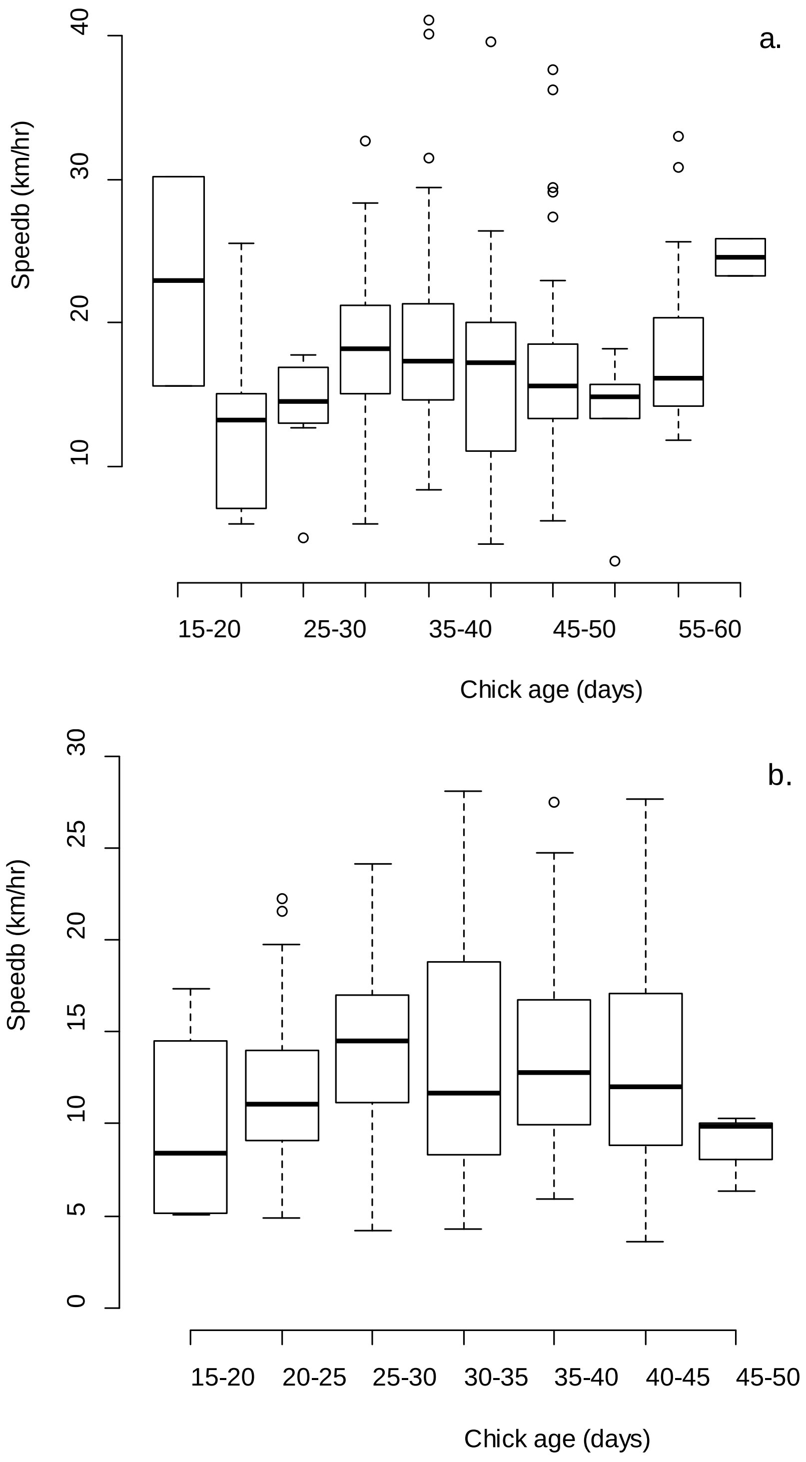
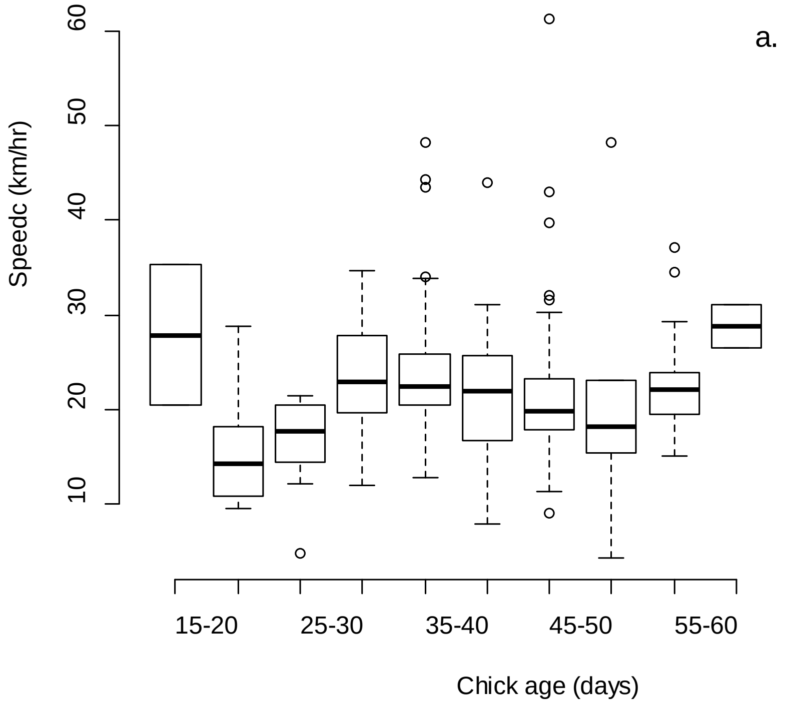


Figure 5.7. Variation in Speed^b (km/hr), calculated using maximum distance reached from the colony by tracked birds, with chick age (days) in **a.** 2010, when no relationship was found and **b.** 2011, when a quadratic relationship was found between Speed^b and chick age. Thick lines indicate the median values, while boxes show the upper and lower quartiles. The whiskers extend to the smallest and largest values recorded.



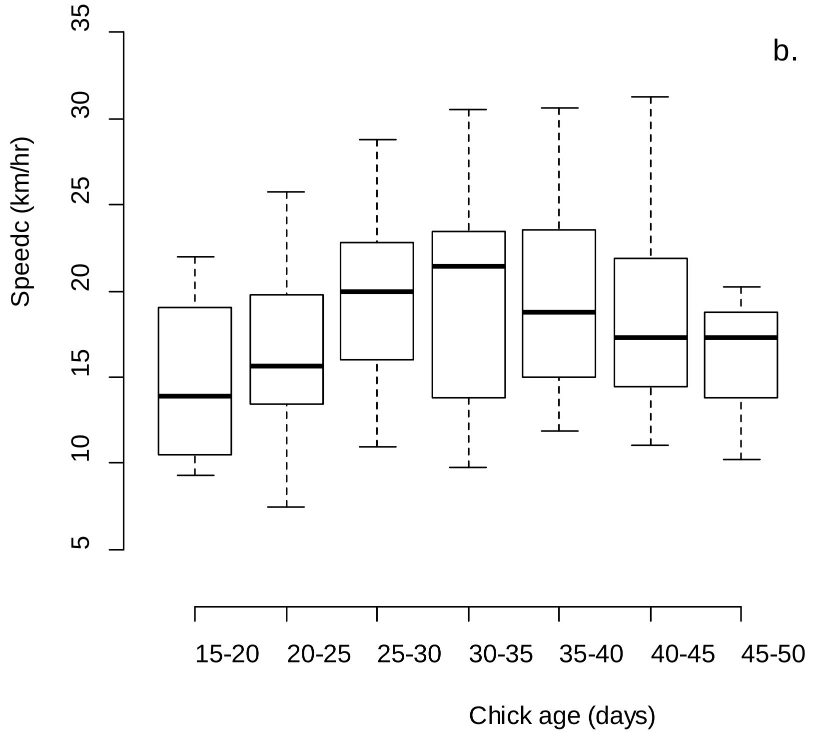


Figure 5.8. Variation in Speed^c (km/hr), calculated using total distance travelled on a round trip by tracked birds, with chick age (days) in **a.** 2010, when no relationship was found and **b.** 2011, when a quadratic relationship was found between Speed^c and chick age. Thick lines indicate the median value, while boxes show the upper and lower quartiles. The whiskers extend to the smallest and largest values recorded.

5.4. Discussion

Flexibility in foraging behaviour can buffer the potential negative impacts of variable environments on reproductive success (Burger and Piatt, 1990, Pinaud et al., 2005a, Hipfner et al., 2006). For such species such as gannets, natural selection favours the re-direction of resources towards self-maintenance during adverse environmental conditions, due to high residual reproductive value (Drent and Daan, 1980, Reznick, 1985). However, this chapter provides evidence of both annual variation in parental investment, and temporal variation in foraging characteristics and parental care throughout breeding seasons. Both of these can buffer breeders from environmental variation and maintain productivity (Cairns, 1987).

In this region of the North Sea, breeding success of several seabird species has declined since the mid 1980s (Burthe et al., 2012), but was higher since 2009 than for a number of previous years (JNCC, 2012), possibly due to greater availability of key prey species during these latter years (ICES, 2012); also see chapter 4. Indeed productivity of most species on the nearby Isle of May in 2010, such as European shags, common guillemots and Atlantic puffins, saw a continued marked improvement (CEH, 2011), and conditions appear to have again improved in 2011. As predicted, the frequency of brood neglect was greater during years with longer foraging trips, thereby providing further evidence of increased incidence of chick neglect due to poorer conditions, forcing both parents to forage simultaneously (Caldow and Furness, 2000, Ashbrook et al., 2008). The proportion of trips where the chick was left unattended was higher in 2010 than in 2011, and the proportion was higher still in 2001/2002 (Lewis et al., 2004), when foraging conditions were considered to be even worse because of low prey stocks (Hamer et al., 2007). Periods of unattendance were also shorter when conditions appeared better, rarely lasting longer than 3 hours in either 2010 or 2011. This was shorter than the durations of brood neglect in 2002, which often exceeded 6 hours (Lewis et al., 2004). Conditions during my two study years were thus relatively favourable in terms of chick feeding frequency and also the incidence of chicks being left unattended, which was relatively low. This was even the case in the poorer of my study seasons (2010), and therefore risks of attack from conspecifics or hypothermia were both lower in these years. Accordingly, the breeding success recorded during these seasons were relatively high compared to previous data available for the region (Mavor, 2008).

Temporal variation in provisioning and foraging behaviour during the 2010 breeding season, as well as the time adults spent at the nest, may reflect the feeding requirements of the chicks, either instigated through altered begging behaviour (Kitaysky et al., 2001, Quillfeldt, 2002), or as a strategy by the adults to maintain provisioning rates and minimise occurrence of brood neglect, whereby chicks are left vulnerable to prevailing weather and attacks from conspecifics (Hipfner et al., 2006, Mullers and Tinbergen, 2009). In 2010 there was a significant increase in feeding frequency, similar to that recorded in 2002 (Lewis et al., 2004), but at a more rapid rate, with feeding rates increasing by 20 - 57% between 4 and 8 weeks post-hatching, coinciding with the period of rapid growth (Montevecchi et al., 1984). Lewis et al. (2004) found that there was no relationship between adult weight and provisioning rate; it is therefore more likely that feeding frequency increased to maintain high energy requirements of the chicks. In addition, the time adults spent together at the nest became shorter as chicks aged, during both seasons. Again, this may be to maintain increased feeding frequency as chicks age, by spending more time at sea foraging (Burger and Piatt, 1990). Though frequent intake of energy rich food is key to chick development during the first 8 weeks post-hatching, when the majority of body mass is accumulated, the increased size, development of juvenile plumage and increased energy expenditure of older chicks are also associated with high energy requirements (Nelson, 1978, Montevecchi et al., 1984). It is not uncommon among marine birds without post-fledging care, such as gannets, for chicks to accumulate mass in excess of their parents followed by decreases pre-fledging (Harris, 1966, Ricklefs, 1968, Montevecchi et al., 1984). Phillips and Hamer (1999) found that for northern fulmars, it was declining total body water rather than fat that resulted in mass recession. Gannet chicks typically fledge with large fat stores, and thus at considerably higher masses than adult birds (Nelson, 1978). These reserves may play a crucial role in the post-fledging period, while juveniles learn to obtain food for themselves (Nelson, 1978, Phillips and Hamer, 1999). Thus, although changes in feeding frequency in the latter stages of chick development may not have a great impact on reproductive success, high feeding rates late in development may enable chicks to maintain a larger fat store, which could play a key role in survival post-fledging. This is difficult to measure however, because of the difficulties and cost of tracking chicks once fledged.

The quadratic relationship found between chick age and both trip duration and distances travelled also appears to reflect the needs of chicks at different stages of development. Short trips with smaller foraging ranges while the chicks are very young reduces the likelihood of brood neglect, while also maintaining frequent provisioning. As the non-attendance of chicks was infrequent and of short duration in the latter study years, the shorter foraging trips prior to fledging were also consistent with the suggestion that the initial increases in provisioning with chick age were not a result of increased occurrence of brood neglect, i.e. both adults foraging at the same time. The relationships between these foraging characteristics and the date differed from those with chick age, as they were found to be linear rather than quadratic response patterns. This suggests that both chick age and nutritional requirements, as well as environmental conditions and prey distributions, influence the foraging decisions of the adults. Indeed, chick condition and begging behaviour have been found to influence provisioning and meal masses in a number of species (Bolton, 1995, Granadeiro et al., 2000, Phillips and Croxall, 2003, Varpe et al., 2004), but changes in prey distributions and availability throughout the season are also likely to affect foraging characteristics.

Foraging trip durations and ranges were significantly shorter in 2011 than 2010, despite both being relatively good years, as indicated by parental foraging effort and the percentage of time adults spent away from the nest. However, even between these two years there were marked differences in the variation in foraging behaviour recorded across the seasons. In 2010, the season was characterised by longer and more distant foraging trips, and higher travel speeds, therefore greater foraging effort, quadratic relationships were apparent with duration and distance, but not speed. In contrast, in 2011, when trips were on average shorter and closer and travel speeds were on average slower, the quadratic relationship found was between speed and chick age. But no relationship was found between chick age and the other variables. This suggests that, due to the lower average travel speeds that year, birds in 2011 could adjust feeding frequency and parental effort by increasing travel speeds to a certain extent, or more likely adjusting time budgets by altering the number of landings and time spent resting, to avoid increased trip durations during the period when overall daily chick requirements are greatest. There can be variation in flight speeds between different seasons (Chapter 4), and these results suggest that when birds are not flying to their energetic capacity, they may have more leeway to adjust time spent in flight slightly in response to the needs of their growing chicks. We may also consider however, that higher flight speeds in seasons with long foraging trip durations may, in part, be an artefact of a longer commute to foraging locations. This is because flight speeds are likely to be faster during straighter, more direct phases of foraging trips.

Foraging adults in 2010 appeared to adjust foraging characteristics to attain high feeding rates when chicks were young, growing rapidly and vulnerable to being left unattended; and prior to fledging when chicks were more active and building fat reserves. This suggests that these are two stages of chick development sensitive to environmental conditions and potentially increased foraging effort, for both reproductive and fledging success respectively. It appears the shorter foraging trips and ranges in 2011 allowed adults to maintain high chick feeding frequencies throughout the season. Although trips were shorter in 2011, the difference found between 2010 and 2011 is comparatively small compared to long term variation at this colony (Hamer et al. 2007, Chapter 4). Despite this, differences in foraging behaviour were still apparent. In order to fully understand the seasonal dynamics of interactions between food availability, parental foraging behaviour and the nutritional requirements of chicks, further study is required during a season with substantially poorer feeding conditions. Under more extreme conditions we may see a greater impact of date on foraging trip characteristics due to seasonal changes in prey availability and increased likelihood of local prey depletion throughout the season (Litzow et al., 2004, Elliott et al., 2009). Further study is also required into the possibility of shifting distributions of mobile prey throughout the season contributing to temporal variation in foraging characteristics such as flight speed and trip durations.

5. 5. Literature cited

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Chapter 6: General discussion

Changing environmental conditions are known to be impacting on the population dynamics of many organisms (Walther et al., 2002, Bradshaw and Holzapfel, 2006). This situation can be particularly acute in colonial species, where breeders frequently share a common feeding area around the colony and intra-specific competition for resources can be intense (Lewis et al., 2001, Ballance et al., 2009, Elliott et al., 2009). Seabirds are a major component of the predator community in many marine ecosystems, and most seabirds breed in colonies, often containing many thousands of individuals (Coulson, 2002). Thus, this is an ideal group to investigate how various aspects of the colonial breeding habit impact on parental foraging behaviour under changing environmental conditions. In this thesis I first consider inter-decadal, population-level effects on four seabird species, over a period in which colony size and environmental conditions changed markedly. I then examine finer-scale, individual-level, effects on foraging behaviour and parental effort of gannets from a single colony, where population size changed little but feeding conditions varied markedly.

Varying trends in the populations of seabirds are evident worldwide (Schreiber and Burger, 2001, Butchart et al., 2004). Within the British Isles, many species have been exhibiting large annual variation in breeding success (Mavor, 2008). As with numerous terrestrial species (Devictor et al., 2008, Møller et al., 2008, Jiguet et al., 2010), seabirds have been faced with climatic changes (Walther et al., 2002, Parry et al., 2007). In the case of pelagic species, this has affected the spatial distribution and abundance of primary production (Lenoir et al., 2010) and therefore prey stocks (Perry et al., 2005, Sundby and Nakken, 2008, Ter Hofstede et al., 2010). Differences in population trends among UK species may reflect the greater resilience to environmental change of generalist species because of their capacity to alter their diet and foraging behaviour (Furness and Tasker, 2000). However, few studies have considered the role density-dependent competition, within or between colonies, plays in seabirds' responses to environmental change.

Northern gannets are a relatively flexible species, with a generalist piscivorous diet, an ability to travel over great distances in order to locate prey and a variety of prey capture techniques (Hamer et al., 2007). On the numerical scale devised by Furness & Tasker (2000), the criteria for which include species size, cost of foraging, foraging range, ability to dive, daily budget and ability to switch diet, they are considered to be the species in the UK least sensitive to changes in sandeel abundance. They have been found to maintain consistently high levels of productivity in recent decades, whereas in other species, breeding success has fluctuated markedly (JNCC, 2012). In contrast to many seabirds where numbers have been declining since 2000, most gannet colonies in the UK have continued to grow (Wanless et al., 2005), but with the rate of growth strongly associated with colony size (chapter 2). Nevertheless there is evidence that in very recent years, birds have approached the energetic and time limits to their foraging efforts and parental investment, with recorded incidences of parents leaving chicks unattended, which was not recorded previously in this species (Nelson, 1966). There is also recent evidence of the energetic limits to the foraging ranges of gannets for trips lasting longer than 60 hours, beyond which they are likely to spend a greater proportion of their time spent on a trip, resting on the water surface (Lewis et al., 2004, Hamer et al., 2007). Such findings probably reflect changing conditions in the seas around the UK in recent years, as a result of large-scale environmental changes (Edwards et al., 2002, Reid et al., 2003, Beaugrand, 2004). Foraging conditions are also likely to have been affected by human fisheries pressure affecting marine food webs (Frederiksen et al., 2004, Frederiksen et al., 2008). Indeed the combined effects of climate change and overfishing are likely to have posed the greatest threat to fish stocks in the region (Brander, 2007).

In this concluding chapter I summarise the key findings of my research and discuss their relevance to population dynamics and regulation for a wide range of North Atlantic colonial central-place foragers. I provide an overview of the current state of knowledge of the links between spatial and temporal variation in environmental conditions and both foraging effort and parental investment in gannets. I also discuss the implications of my results in the context of management and conservation of seabird populations and the sustainable use of the marine environment, and I identify priorities for further research.

6. 1. The role of population density in tandem with environmental change

Some of the first empirical data to support Ashmole's hypothesis of population regulation mediated by density-dependent intra-specific competition for food was provided by Lewis et al. (2001), who found that during chick-rearing, northern gannets from bigger colonies travelled proportionally further to obtain food for their offspring. Lewis et al. (2001) not only found this key relationship between colony size and trip duration at a cross section of UK gannetries within a single season, but they also suggested this relationship held across years, as the limited historical data available on trip durations also fitted the observed relationship. My re-analysis of both these data and those collected subsequently from the same gannet populations confirms a positive relationship between foraging effort and colony size. However, I also found that for larger colonies i.e. those greater than ca. 3,000 AOS, the effects of changing environmental conditions exceeded those of changes in colony size. Thus there was a weaker influence of population size on parental foraging behaviour when feeding conditions were better. This was presumably because competition for resources was less severe around smaller colonies. In contrast, colony size was the main determinant of trip duration in smaller colonies.

Latterly, the interaction between effects of population size and climatic variation on population dynamics has received increasing attention, both in terrestrial (Coulson et al., 2001, Grotan et al., 2009, Smallegange et al., 2011) and marine species (Lewis et al., 2009, Rotella et al., 2009, Ashbrook et al., 2010). Studies of individual growth rates in harvested populations of fish have provided empirical evidence for density-dependent responses to climate change (Brunel and Dickey-Collas, 2010, Crozier et al., 2010, Xu et al., 2010). Other studies have also found combined effects of climate and density on population growth in terrestrial mammals, as well as on laying dates and clutch sizes in wild birds (Coulson et al., 2001, Mysterud and Østbye, 2006, Ahola et al., 2009, Votier et al., 2009). However, studies in which multiple populations are considered remain rare.

My work suggests that large colonies may be more vulnerable to the adverse effects of reduced prey availability. This finding has conservation and management implications, not just for gannets but also for many other seabird species, which are likely to experience density-dependent intra-specific competition, and changes in local feeding conditions (Ainley et al., 2003, Davoren and Montevecchi, 2003, Dann and Norman, 2006, Ballance et al., 2009). Conservation efforts are often targeted at small and declining populations, particularly of specialist species. However, if these species are threatened by widespread declines in prey availability or nutritional quality, it may be more informative to monitor larger populations, particularly if these hold a high proportion of the regional population. For example, 94% of the British population of gannets breed in just 10 colonies holding > 3,000 AOS (Wanless et al., 2005). Birds from such colonies may have less leeway to increase foraging effort without possible adverse effects on chick survival. My results suggest that changes in feeding conditions will be harder to detect in smaller colonies, where trips durations are more affected by population density. Thus caution is required when using seabird behaviour to monitor marine ecosystems, for example when using foraging trip durations to indicate prey availability (Furness and Camphuysen, 1997b, Hamer et al., 2006b, Einoder, 2009), and the relative size of monitored colonies should be carefully considered.

6. 2. Neighbouring conspecific density

A number of factors combine to regulate colony sizes. As already discussed, these include density-dependent competition between sympatric conspecifics, as well as winter mortality (Lack, 1968), availability of nesting habitat (Thompson and Furness, 1991, Kildaw et al., 2005) and local prey availability (Kitaysky et al., 2000). My results for four species (gannet, Atlantic puffin, European shag and black-legged kittiwake) that have experienced contrasting population trends since the 1980s, provide support for the hypothesis that competition from conspecifics nesting at neighbouring colonies is also limiting (Furness and Birkhead, 1984). As foraging ranges increase with colony size (as discussed in chapter 2), the scale at which this effect operates is also dependent on colony size (chapter 3). My results provided no support for the hypothesis that colony size is limited only by the size of foraging habitat closer to one colony than any other. Moreover, I found that a density-dependent model better explained my data than the Hinterland model proposed by Cairns (1989), whereby colony size is limited by the amount of feeding habitat available to colony members closer to their breeding colony than any other. In addition, competition between conspecific neighbours may also generate spatial segregation between members of different colonies on feeding grounds (Cairns, 1989, Ainley et al., 2003, Grémillet et al., 2004, Wakefield et al., 2011). Indeed, recent evidence has come to light of northern gannets from a number of distinct colonies foraging in separate areas that are essentially non-overlapping, with spatial extents proportional to colony size (Wakefield et al., *in press.*). This pattern is not consistent with segregation occurring along lines of equidistance between colonies (Cairns, 1989), and also suggests there is less overlap between the foraging areas of birds at different colonies than previously assumed (Storer, 1952, Ashmole, 1963, Grecian et al., 2012).

A limiting effect of neighbouring conspecific density on colony size has a number of implications for colony growth and the distribution of foraging birds. My study shows that negative relationships between population sizes and the numbers of neighbouring conspecifics can persist over decades. However, the scale of colony-size interdependence increases with regional population size. Marked changes in the size of one colony will affect the population dynamics of its neighbours. In extreme cases, if one colony expands greatly following conservation efforts (e.g. rat eradication following population depression), there will be more competition for resources with conspecifics at other colonies within foraging range, which may then experience lower or negative growth rates. Conversely, if a colony were extirpated, either by anthropogenic or environmental causes, colonies within its potential home range may increase in size. This may have contributed to the establishment and rapid growth of a puffin colony at Melvich, Scotland, following the marked decline of the population at Clo Mor, less than 70 km away (JNCC Seabird Monitoring Program online database: http://jncc.defra.gov.uk/smp/) . Similarly, repeated culling of herring gulls *Larus argentatus* and lesser black-backed gulls *L. fuscus* on the Isle of May, Scotland led to increases in the sizes of neighbouring colonies (Coulson, 1991). This was attributed mainly to increased recruitment by birds originating from the Isle of May, although there were no data for marked birds to confirm or refute this hypothesis, and it is not known whether or not there was any increase in breeding success at neighbouring colonies. Such interactions between neighbouring conspecific density and population growth rates have also been recorded in very different colonial species, such as soil-feeding termites *Anoplotermes banksi* (Bourguignon et al., 2011) and ants *Aphaenogaster senilis* (Boulay et al., 2010). It is therefore necessary to consider the knock-on effects of single colony events or population conservation and management decisions on neighbouring colonies. While my findings focus on seabird colonies of four different species with differing foraging characteristics, they are also likely to be of relevance to the population regulation of many other colonial central place foragers from diverse taxa including invertebrates (Adams and Tschinkel, 2001, Billick, 2001), reptiles (Trillmich and Trillmich, 1984, Doody et al., 2009) and mammals (Robson et al., 2004, Zahn et al., 2006).

6. 3. Plasticity in response to environmental change

As indicated in chapter 2, the environmental conditions experienced by breeding individuals can modulate the density-dependent relationship between competition and foraging effort, particularly at larger colonies. In chapter 4, I present evidence in support of the view that gannets are flexible in their diet and foraging behaviour, and thus their capacity to respond to environmental change. Along with differing foraging ranges and locations, I also found evidence suggesting prey depletion, and therefore indirect intra-specific competition around the colony (Ashmole, 1963, Birt et al., 1987, Elliott et al., 2009). Gannets make two types of dive: V-shaped dives characterised by a steep dive gradient, short bottom period and almost immediate ascent and U-shaped dives where there is additional propulsion under water that tends to result in increased bottom time, decreased dive gradient and a longer overall dive duration (Ropert-Coudert et al., 2009). The frequency of V-shaped dives increased with distance from the colony. A higher proportion of U-shaped dives closer to the colony could indicate a need for more underwater pursuit due to greater competition for prey, in keeping with other indirect evidence of prey depletion or disturbance closer to the breeding site in other species (Davoren et al., 2003b, Elliott et al., 2009). For example, previous studies have recorded improved quality and size of captured prey (Ainley et al., 1998, Barrette and Giraldeau, 2008, Martin and Vinson, 2008) and shallower dives (Cairns et al., 1990) as distance from the colony increases. Further studies have recorded reduced chick and adult body condition (Kitaysky et al., 2000, Davoren and Montevecchi, 2003, Gaston and Hipfner, 2006a) and increased trip durations (Lewis et al. 2001, chapter 2) with greater colony size. However, a relationship between distance from the colony and foraging effort, considering such characteristics as flight speed and dive rates, are not always observed (Ainley et al., 2004, Petersen et al., 2006), and we must consider that changes in the dive profiles of gannets may also reflect spatial variation in prey species or behaviour rather than effects of competition at feeding sites.

My study also focused on the finer scale search behaviour of gannets during foraging trips. I found that birds breeding at Bass Rock also exhibited plasticity in their finer scale search behaviour. The variation in the scale of ARS zones during both seasons was very large. Also, during 2011, the season with shortest foraging trips, (when prey availability was assumed to be highest), ARS and diving were recorded on the return phase of foraging trips. This contrasted with previous seasons when conditions were thought to be poorer (Hamer et al., 2009), though this may be a product of a smaller sample size during the earlier season. The proportion of dives made outside zones of ARS was also higher in 2011, there were few occurrences of nested ARS (10 m – 10 km) and more foraging trips included larger scale ARS zones (1 – 100km). It therefore appears that gannets have flexibility in their foraging behaviour at different spatial scales and adjust their search and fine scale feeding behaviour in response to altered environmental conditions. When prey are more abundant, adults have greater opportunity to forage opportunistically during the commuting legs of foraging trips. The absence of search behaviour on the return phase of foraging trips in 2003 (Hamer et al., 2009), may reflect the longer foraging trips made that season, resulting in a greater pressure for the adults to return to the nest to provision their chicks and relieve the attending parent (Lewis et al., 2004, Hamer et al., 2007). Similarly, Cape gannets *Morus capensis* foraging off the coast of South Africa, were frequently found to feed on the return leg of journeys when conditions were more favourable and foraging trip durations were shorter (Ropert-Coudert et al., 2004).

Evidence of inter-annual variability in foraging characteristic has been recorded for other marine predators, which has been interpreted as demonstrating plasticity in response to environmental conditions (Bailey and Thompson, 2010, Kappes et al., 2010). Similarly, Antarctic petrels (*Thalassoica antarctica*) have been found to adjust their foraging and search movements to reflect the scale of the habitat patches they exploit at all but the finest scales (Fauchald and Tveraa, 2006). Flexibility in foraging strategies and habitat use is important to buffer the potential negative impacts of environmental variation on productivity (Burger and Piatt, 1990, Uttley et al., 1994, Litzow and Piatt, 2003, Hamer et al., 2007). The ability to increase foraging effort and search at a finer scale enables individuals to respond to dynamic, shifting environments (Fauchald and Erikstad, 2002). Furthermore, the ability to adjust dive profiles and depths at different distances to the colony or when intra-specific competition is more intense, can also improve foraging efficiency and success. However, not all species are so plastic in their responses, and are therefore likely to be more vulnerable to environmental change (Furness and Tasker, 2000, Furness, 2007). Even relatively flexible species such as gannets will have eventual behavioural and energetic limits to this plasticity, when consequences of more time spent at sea or switches to less profitable prey become evident in terms of reduced chick growth and reproductive success. Notwithstanding that colony size influences foraging range, other aspects of behaviour can act as an indication of the abundance and distribution of fish stocks, and the overall conditions experienced by marine predators in different seasons (Furness and Camphuysen, 1997b, Hamer et al., 2006b, Einoder, 2009). Identifying areas that are important feeding locations for a variety of higher predators has important conservation and policy implications, and can help identify potential marine protected areas (Birdlife, 2010, Arcos et al., 2012, Grecian et al., 2012). These may help alleviate threats to seabirds such as climate change, fisheries activities, offshore developments and pollution. Though, the difficulties posed by dynamic nature of the marine environment must not be underestimated in designating such zones.

6. 4. Parental effort and provisioning

Flexibility in foraging behaviour can buffer the potential negative impacts of variable environments on reproductive success (Burger and Piatt, 1990). I found that gannets were flexible both between and within years in the amount of foraging effort expended (chapter 5). Within years, effort was not constant but was high during early and late chick rearing, reflecting variation in the chick's energetic requirements rather than prey availability. Trip durations were shortest during the first few weeks post hatching, when chicks are most vulnerable to chilling and predation (Nelson, 1966, Nelson, 1978, Montevecchi et al., 1984), and again at the latter stages of development when maintaining a lipid store is likely to improve a chicks post-fledging survival, when learning to forage for themselves (Nelson, 1978). Although we may consider that having too much fat could be costly due to high wing loading resulting in lower flight performance. Studies of other seabirds have also recorded relationships between stage of the breeding season and foraging characteristics, including range (Weimerskirch et al., 1993, Kato et al., 2003, Phillips et al., 2004), location (Ito et al., 2010, Lyver et al., 2011) and prey type (Montevecchi et al., 1984, Elliott et al., 2009). My study therefore suggests that the requirements of offspring, as well as environmental conditions, influence the foraging decisions of the adults. Changes in foraging behaviour of adults may not necessarily be tactical decisions by the adults, but result from responses to altered begging behaviour by chicks as they grow and therefore their energetic requirements alter (Kitaysky et al., 2001, Hamer et al., 2006a, Quillfeldt et al., 2006).

In spite of these apparent shifts in behaviour by gannets on Bass Rock, to adjust their effort and investment as the season progresses and their chicks age, both greater occurrence and longer duration of brood neglect was recorded during 2002 when foraging conditions were worse (Lewis et al., 2004). Increased incidence of neglect can impact upon reproductive success in some species (Hochscheid et al., 2002, Nelson, 2002, Ratcliffe and Furness, 2006), although it is not a reliable indicator of the productivity of a population for all (Harris and Wanless, 1997). Further, the inability of adults to maintain provisioning rates will affect chick growth more than pre-fledging survival (Harris and Wanless, 1997, Gray et al., 2005, Enstipp et al., 2006). Optimal foraging theory predicts that adults of many species face a trade-off between the cost of travelling to a more distant location and therefore spending more time at sea, versus the quality of the prey obtained (Cresswell et al., 2001, Litzow et al., 2004, Staniland et al., 2007), even in the absence of prey depletion. This is likely to be influenced by the nutritional status and energy reserves of the adult (McNamara and Houston, 1996, Sherratt, 2003). For adults also foraging for their offspring, there is an additional trade-off between time spent foraging, and time spent incubating or guarding chicks as well as the need to maintain provisioning rates (Lewis et al., 2004, Lormée et al., 2003). Indeed, life history theory predicts a trade-off between the costs of foraging and reproductive investment (Costa, 1991, Roff, 1993). For long-lived species, such as seabirds, natural selection favours the re-direction of resources towards self maintenance during adverse environmental conditions, due to adults' high residual reproductive value (Drent and Daan, 1980, Reznick, 1985).

In many species, individuals have the capacity to adjust foraging behaviour and time budgets to a certain extent, enabling them to buffer the negative impacts of environmental variability on reproductive success, as well as their own survival. However, there is variation in the sensitivity of different species to change (Furness and Tasker, 2000), and while specialist species are more vulnerable to shifts in prey availability, others are more flexible and can maintain breeding success by altering their time budgets or diets, thereby intimating consistently favourable conditions, when in fact feeding conditions are poorer. For species such as gannets, with offspring that are relatively robust during later stages of development, caution is required when estimating conditions from breeding success alone. Also, while adults may be able to provide enough food for survival at the nest, provisioning rates towards the end of development may not be sufficient to facilitate the building up of an energy reserve sufficient to ensure survival after leaving the nest (Nelson, 1978, Montevecchi et al., 1984). It could be beneficial to measure both fledging success and chick condition at fledging, although this would be impractical at most colonies, as it would be likely to cause excessive disturbance. Further, it could be misleading. For instance, Gray et al. (2003) recorded higher body condition of fulmar *Fulmarus glacialis* chicks in a year with low breeding productivity, because of higher mortality among chicks with low body condition. Therefore, in species with flexible fledging ages, the length of the nestling period may be an alternative and informative indicator of conditions throughout the season. However, caution would be required if assessing conditions this way, as chicks in poor conditions may fledge early, or indeed late.

6. 5. Recommendations for further research

My project investigating the foraging behaviour and population dynamics of northern gannets over a period of environmental change has highlighted a number of priorities for further research. Evidently, population density regulates not only colony size but also some aspects of foraging behaviour and parental investment. Notably, it is not only competition *within*, but also *between* colonies that is limiting. However, further research over much broader spatial scales is required to understand population trends and patterns of inter-colony competition across the full breeding ranges of species. More empirical data are also required to understand how the spatial segregation of foraging ranges of individuals from different colonies is related to colony size and the sizes of neighbouring colonies, and to investigate how segregation is mediated. These effects have far reaching implications for colonial breeders from several taxa, for which the distribution and availability of their food resources may be shifting due to anthropogenic effects.

The three breeding seasons during which I collected data on northern gannets could all be considered relatively ‘good’, as indicated by both by oceanographic data and the relatively short foraging trip durations recorded. Therefore, it is unlikely that gannets’ full capacity for flexibility in foraging behaviour was observed. Though this is a common limitation of studying wild populations, continuing these studies at the same breeding colonies but under markedly less favourable conditions would help assess the species’ full capacity to respond to a shifting environment, especially when prey are scarce, and the consequences for reproductive success and ultimately population growth are most acute. This is also true of understanding the interactions between food availability, parental foraging behaviour and the nutritional requirements of chicks within seasons. Further study is required during a season with poor feeding conditions, as we may predict that extreme conditions could result in local prey depletion throughout the season (Litzow et al., 2004, Elliott et al., 2009), therefore hindering adults' ability to sufficiently provision their young during different stages of development.

As my findings include annual variation in finer-scale search behaviour during foraging trips, I also suggest further study is required into the association between fine scale foraging behaviour and shifts in zones of high productivity, such as tidal mixing fronts and eddies, both within and between breeding seasons. Overlaps have been found between such zones of higher productivity and the distribution of marine predators (Pinaud and Weimerskirch, 2007, Bost et al., 2009, Raymond et al., 2010), with some seabird species previously found at elevated densities at fronts, upwellings, etc. (Schneider, 1982, Decker and Hunt Jr, 1996, Begg and Reid, 1997). For example, at fine scales, ARS patterns are associated with these oceanographic zones (Pinaud et al., 2005b, Hamer et al., 2009, Scheffer et al., 2010). In particular, gannets tracked from Bass Rock in 2003 exhibited ARS in the vicinity of small-scale, shelf-sea mixing fronts (Hamer et al., 2009). There was also significant overlap between ARS zones and the tidal mixing front during the 2011 breeding season, with 73% of all zones of ARS initiated within 5 km of the front (Fig. 6.1). I suggest, further study is now required into such fine scale feeding behaviour as frequency of dives and dive profiles in relation to these oceanographic features.

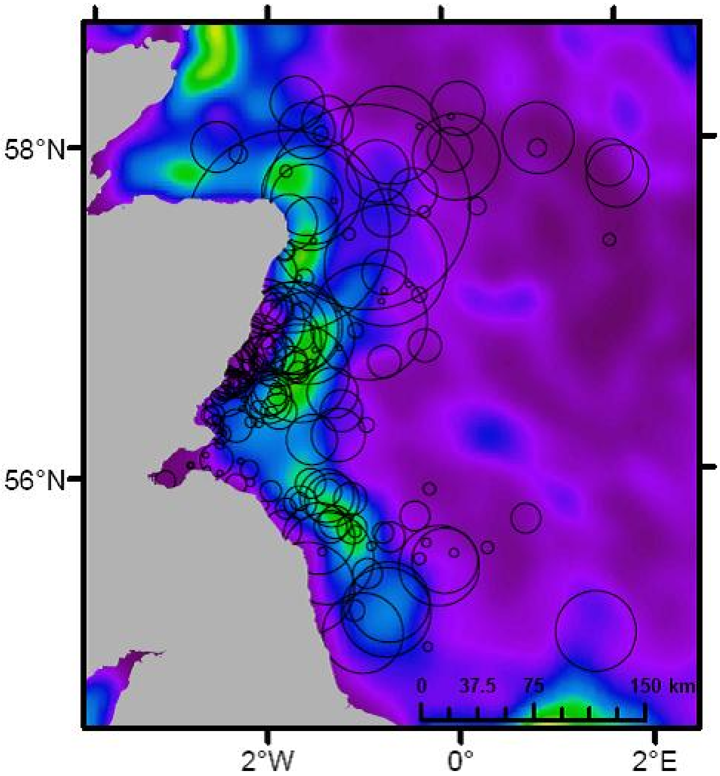

Figure 6.1. Locations of zones of area-restricted search used by gannets from the Bass Rock in 2011, superimposed on the locations of coarse scale and mesoscale frontal waters present during July 2011 (Miller, et al. *unpublished data* reproduced with permission). Fronts were detected using composite sea-surface temperature data during and a recently developed front detection algorithm (Miller, 2009). The composite map combines location, strength and persistence of fronts during the observation period and thus displays density of frontal activity from purple through to yellow were density was greatest. Green indicates high frontal density and purple low.

Because such features are dynamic, shifting under varying environmental conditions, we may predict that predators track their movements. However, few studies have investigated this over long time sales or fine spatial scales. With new methods of mapping fronts at the km scale (Miller, 2009), it is becoming increasingly possible to investigate the importance of these zones to a range of species (Johnston et al., 2005a, Bailey and Thompson, 2010, Raya Rey et al., 2010).

Such studies into small scale feeding hotspots, along with those on foraging movements associated with fishing activities, are urgently needed to help designate and manage marine protected areas and contribute towards wildlife management policies.

6. 6. Conclusions

In light of current projections of climate change and shifting marine environments, the need to better understand the potential impacts of these changes on population dynamics and foraging behaviour of central-place foragers is evident. In summary, my study of British seabird species, namely the northern gannet, found that annual variation in foraging trip durations will be particularly marked at large colonies, making them especially vulnerable to adverse effects of low prey availability at sea. As foraging ranges alter with colony size, the scale of dependency between colony size and neighbouring conspecific competition also alters. My results therefore provide strong support for the limiting effect of competition between conspecifics breeding in adjacent colonies. My findings also support Ashmole's theory of intra-specific competition resulting in prey depletion around seabird colonies (Ashmole, 1963), implying that gannets can reduce the effect of competitive pressure both between and within breeding seasons, in response to prey scarcity by foraging further from the colony.

Gannets also exhibited flexibility in their finer-scale search and dive strategies. This flexibility in habitat use, foraging behaviours and also diet may buffer this species against environmental change, although we may not yet have observed the full range of environments that gannets might experience. There was also annual variation in parental investment at the nest. Furthermore, I found that gannets were flexible within breeding seasons in the amount of foraging and parental effort expended, thereby suggesting that the chick's energetic requirements contribute to adults' foraging behaviour as well as prey availability. Flexibility in foraging and parental behaviour may therefore buffer the potential negative impacts of environmental variation on provisioning rates and productivity, even in long-lived species such as gannets, which are expected to redirect energy towards self maintenance under poor conditions. These findings hold implications for the population dynamics and potential resilience of a wide range of seabird species and central-place foragers, under dynamic and variable conditions. In turn, these have further implications in the context of both the management and conservation of threatened populations, including the identification and monitoring of marine protected areas.

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Appendix A: Northern gannet, Atlantic puffin, European shag and black-legged kittiwake colony codes in reference to those studied in Chapter 3

Table A.1. Abbreviations and full names for A. gannet, B. puffin, C. shag and D. kittiwake colonies in the UK and southern Ireland, illustrated in figures 3.1 and 3.2.

Species	**Abbreviation**	**Colony name**
A. Gannets	A	Ailsa Craig
	B	Bempton Cliffs
	BR	Bass Rock
	Bu	Bull Rock
	F	Foula
	FI	Fair Isle
	FL	Flannan Isles
	G	Grassholm
	GS	Great Saltee
	H	Hermaness
	IE	Ireland’s Eye
	LS	Little Skellig
	N	Noss
	Sc	Scare Rocks
	SK	St. Kilda
	SSg	Sula Sgeir
	SSt	Sule Stack
	T	Troup Head
B. Puffins	BC	Boddam-Collieston
	CM	Clo Mor
	F	Foula
	FaH	Faraid Head
	FI	Fair Isle
	FL	Flannan Isles
	Ft	Fetlar
	H	Hermaness
	L	Landvillas
	M	Melvich
	N	Noss
	NR	North Rhona
	NY	NW Yell
	S	Shiants
	SH	Sumburgh Head
	SSk	Sule Skerry
	SK	St. Kilda
	ST	Scarfi Taing
	SU	SW Unst
	Sx	Saxavord
	TN	The Nev to kame
	U	Uyea
C. Shags	B	Bressay

	C	Copinsay
	E	Eday
	EY	East Yell
	F	Foula
	Fa	Faray
	FI	Fair Isle
	Ft	Fetlar
	H	Hermaness
	Ho	Holm
	HSW	Hoy and South Walls
	Flo	Flotta
	Mo	Mousa
	MR	Muckle Roe
	N	Noss
	Nn	Noness
	O	Outer Skerries
	PeS	Pentland Skerries
	PS	Papa Stour
	PW	Papa Westray
	R	Rousay
	Sh	Shapinsay
	SH	Sumburgh Head
	SR	South Ronaldsay
	St	Stronsay
	SSk	Sule Skerry
	SW	Sil Wick
	Sx	Saxavord-Holm
	U	Uyea
	V	Vaila
	W	Whalsay
	WB	West Burra
	We	Westray
D. Kittiwakes	BV	Braga Ness-Wats Ness and Vaila
	EI	Eshaness and Eshaness Islands
	F	Foula
	FiH	Fitful Head
	FI	Fair Isle
	Ft	Fetlar
	HB	South Havra and West Burra
	MNn	Mousa and Noness
	NB	Noss and Bressay
	NEU	North East Unst
	NI	St. Ninian's Isle and Ireland
	NM	N Mainland
	NWM	NW Mainland
	NWU	NW Unst
	PSM	Papa Stour and Muckle Roe
	RS	Reawick-Skelda Ness and Skelda Ness-Walls
	SEM	SE Mainland
	SEY	SE Yell
	SH	Sumburgh Head
	SWU	SW Unst
	WS	Whalsay and Skerries
	WY	W Yell

Appendix B: Semi-variograms of colony size and model residuals for northern gannets, Atlantic puffins, European shags and black-legged kittiwakes in different years

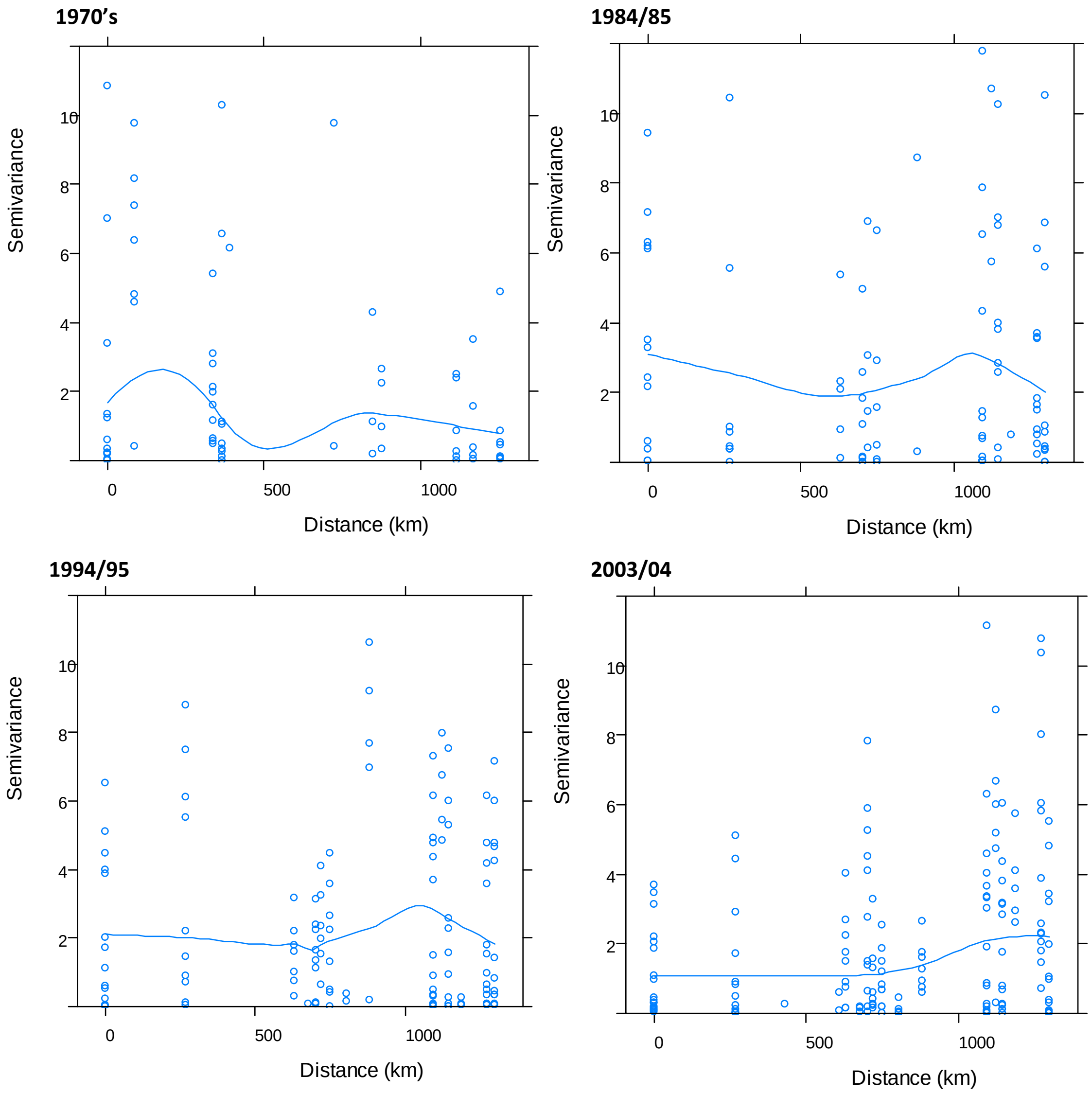


Figure B.1. Semi-variograms of gannet colony counts using matrices of shortest at-sea distance between each pair of colonies during the 1970s, 1984/85, 1994/95 and 2003/04.

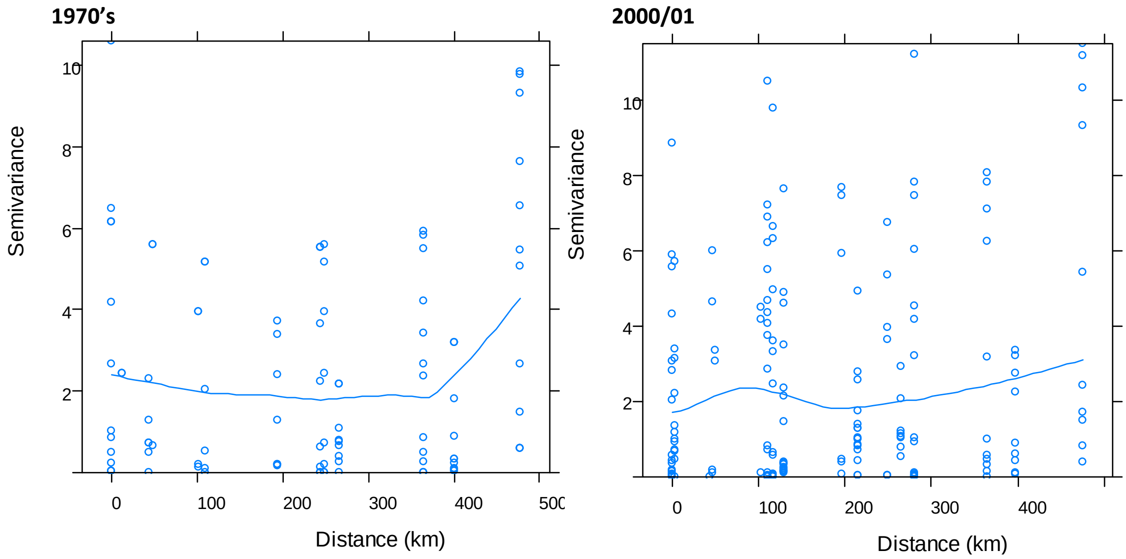


Figure B.2. Semi-variograms of puffin colony counts using matrices of shortest at-sea distance between each pair of colonies during the early 1970s and 2000/01.

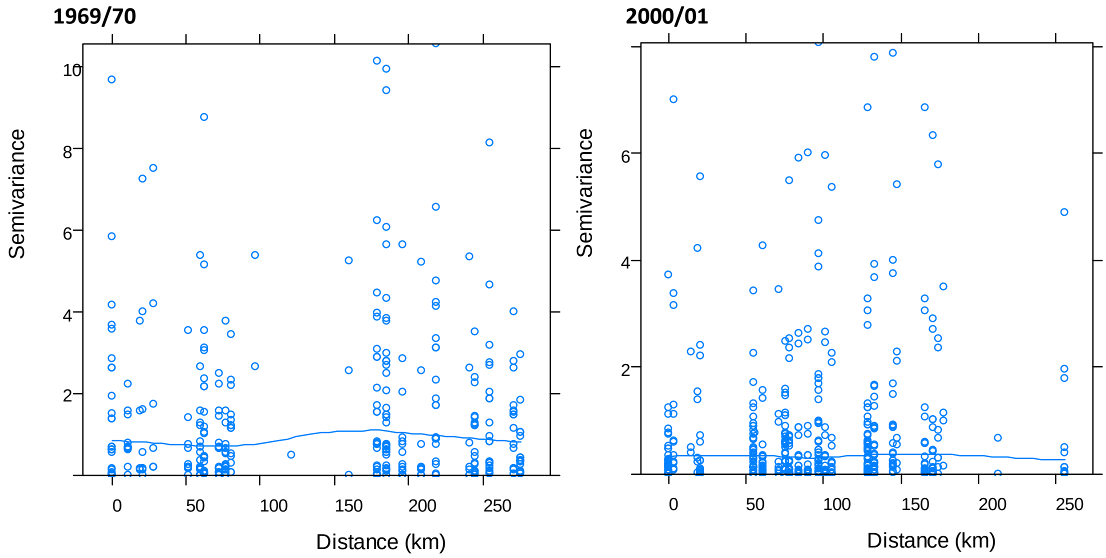


Figure B.3. Semi-variograms of shag colony counts using matrices of shortest at-sea distance between each pair of colonies during 1969/70 and 2000/01.

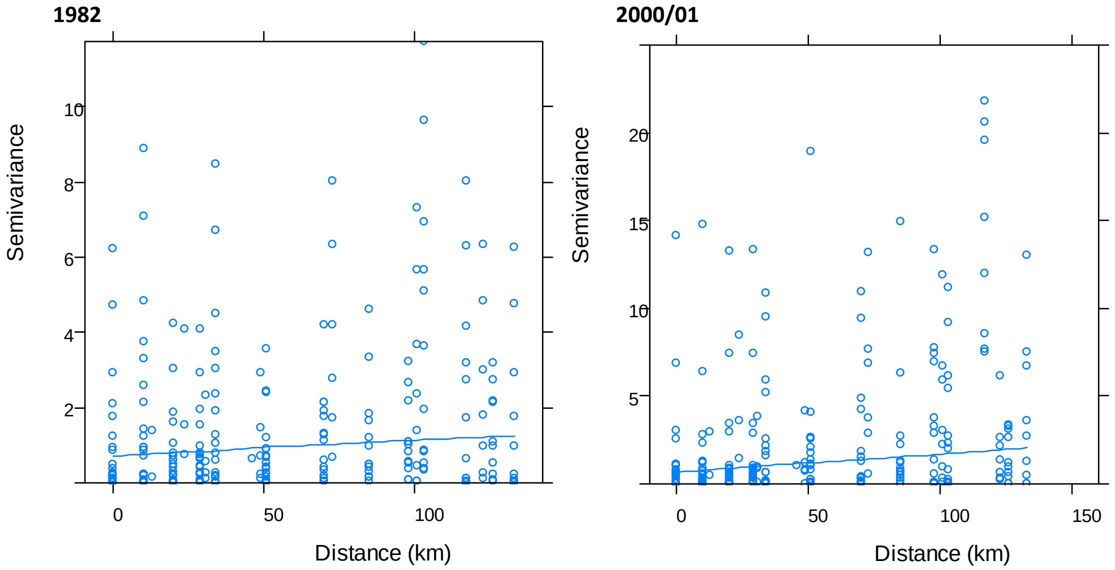


Figure B.4. Semi-variograms of kittiwake colony counts using matrices of shortest at-sea distance between each pair of colonies during 1982 and 2000/01.

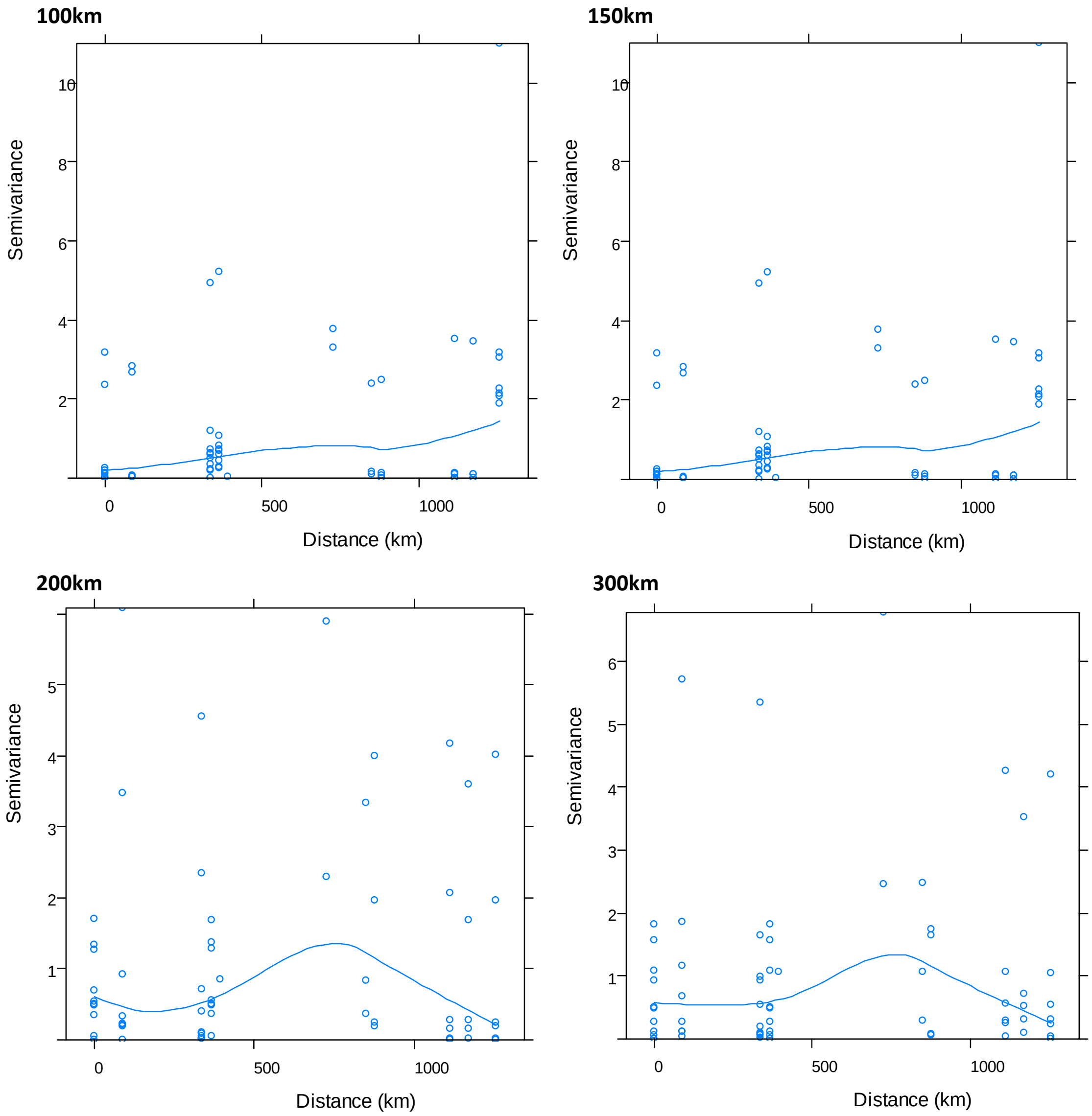


Figure B.5. Semi-variograms of model residuals for gannet colonies within putative foraging ranges of 100km, 150km, 200km and 300km using 1970's colony counts.

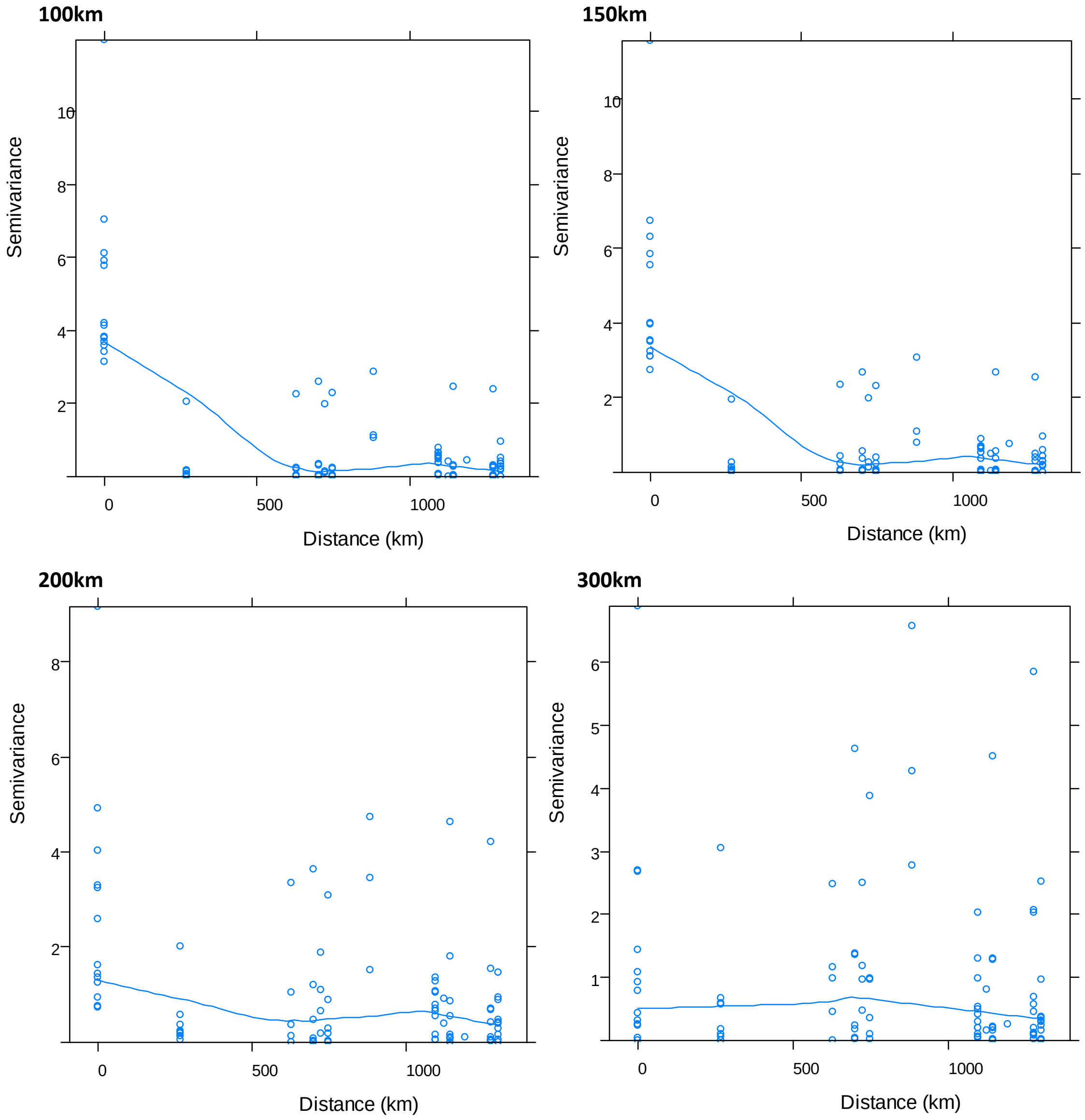


Figure B.6. Semi-variograms of model residuals for gannet colonies within putative foraging ranges of 100km, 150km, 200km and 300km using 1984/85 colony counts.

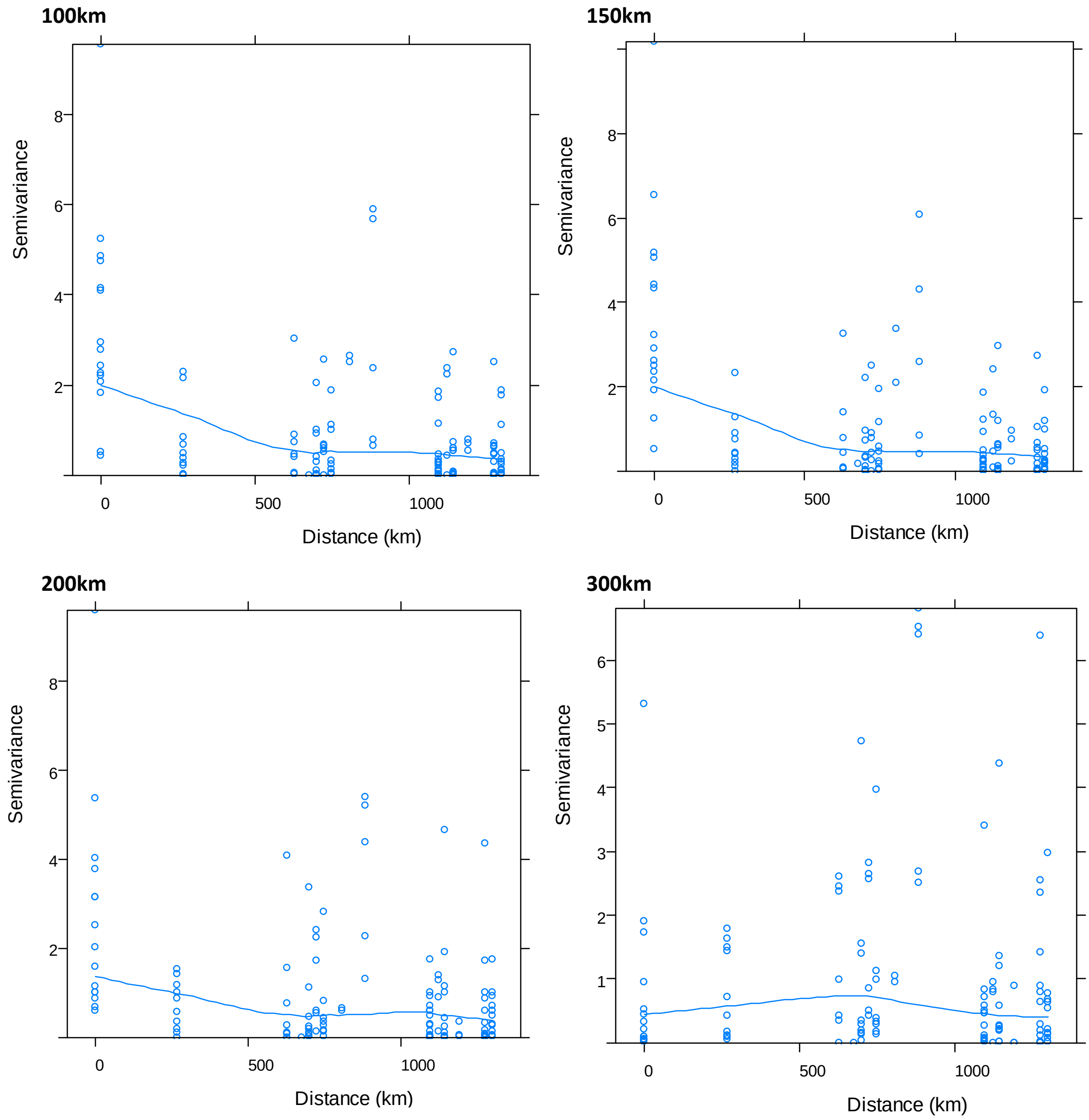


Figure B.7. Semi-variograms of model residuals for gannet colonies within putative foraging ranges of 100km, 150km, 200km and 300km using 1994/95 colony counts.

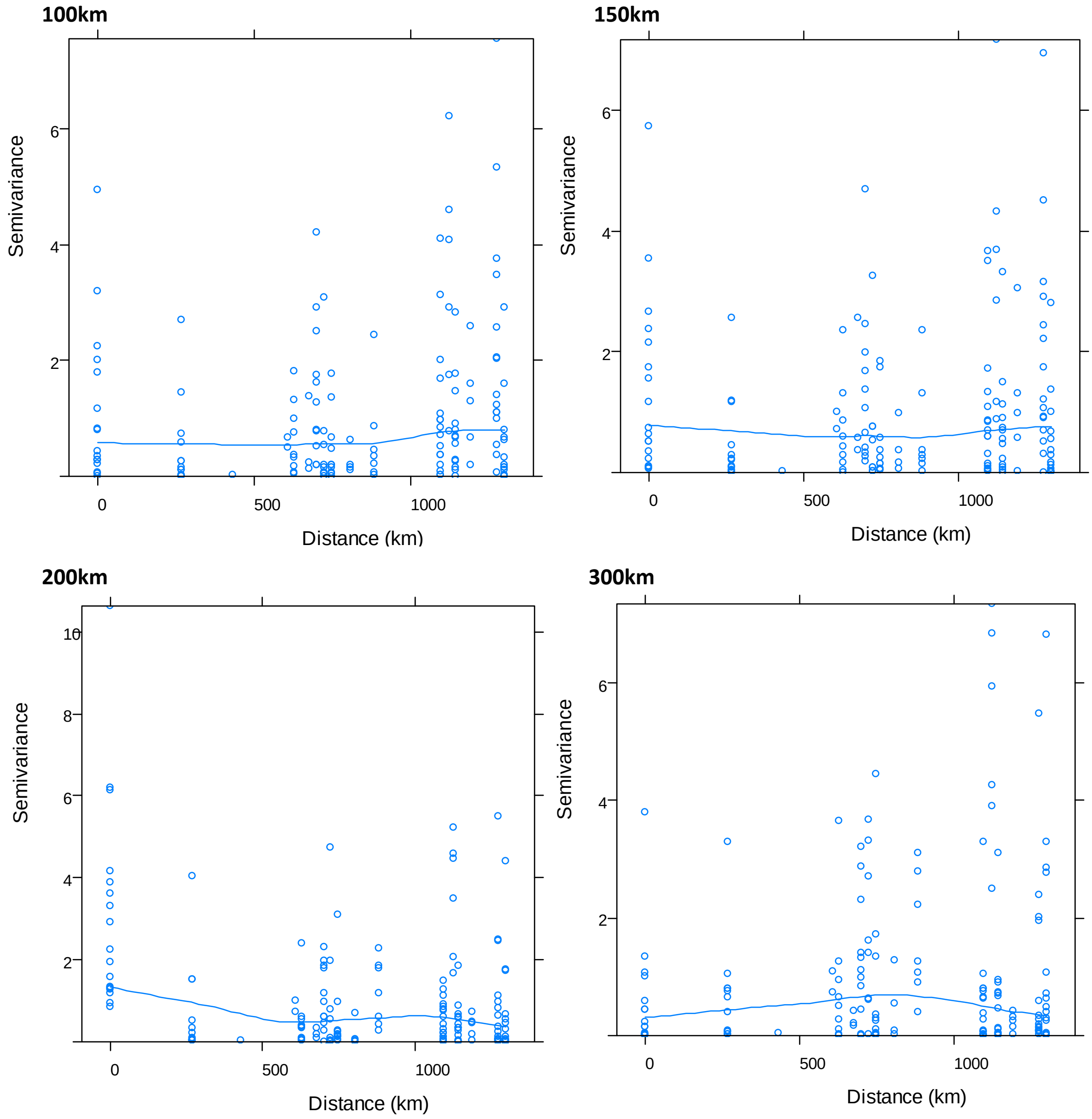


Figure B.8. Semi-variograms of model residuals for gannet colonies within putative foraging ranges of 100km, 150km, 200km and 300km using 2003/04 colony counts.

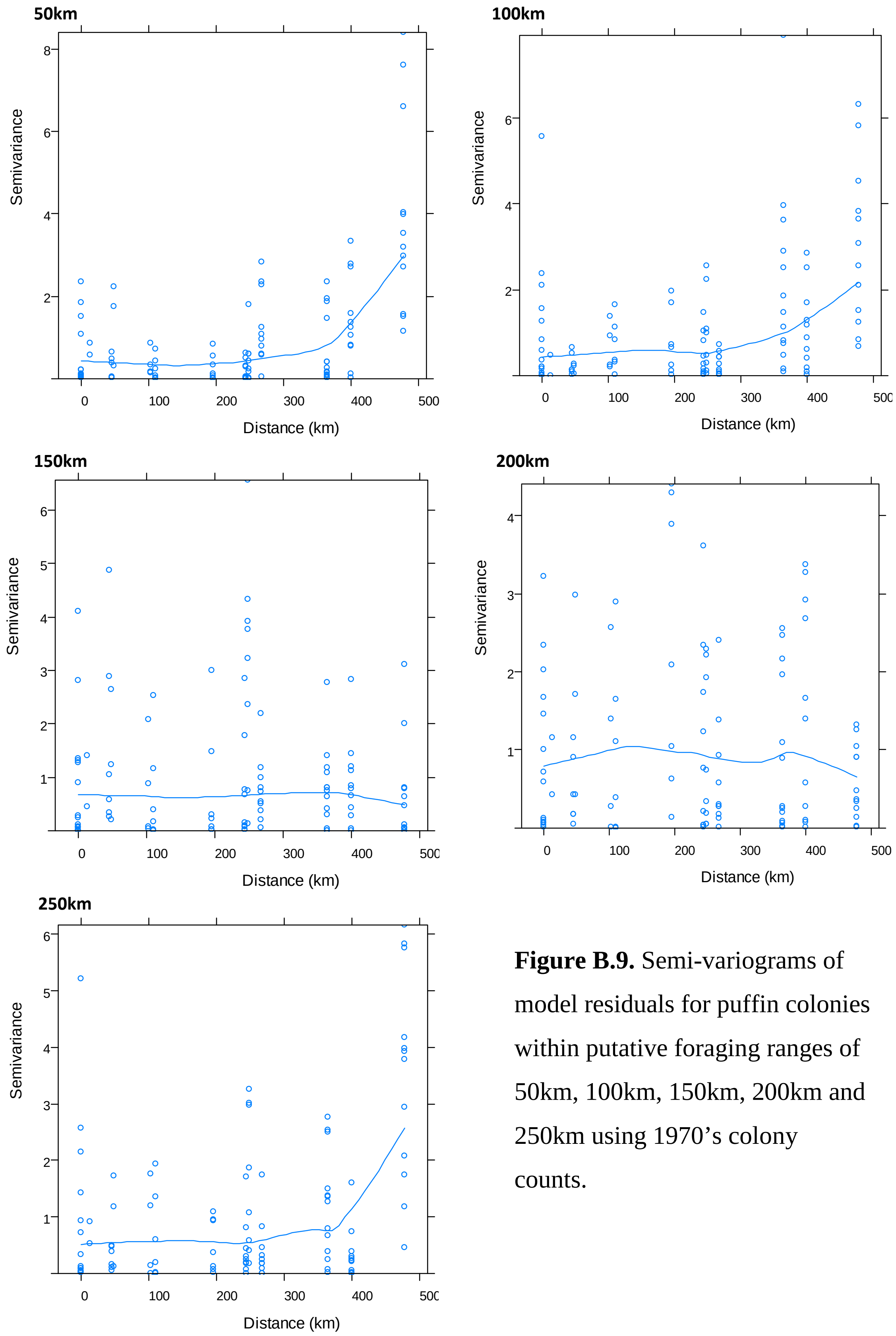


Figure B.9. Semi-variograms of model residuals for puffin colonies within putative foraging ranges of 50km, 100km, 150km, 200km and 250km using 1970's colony counts.

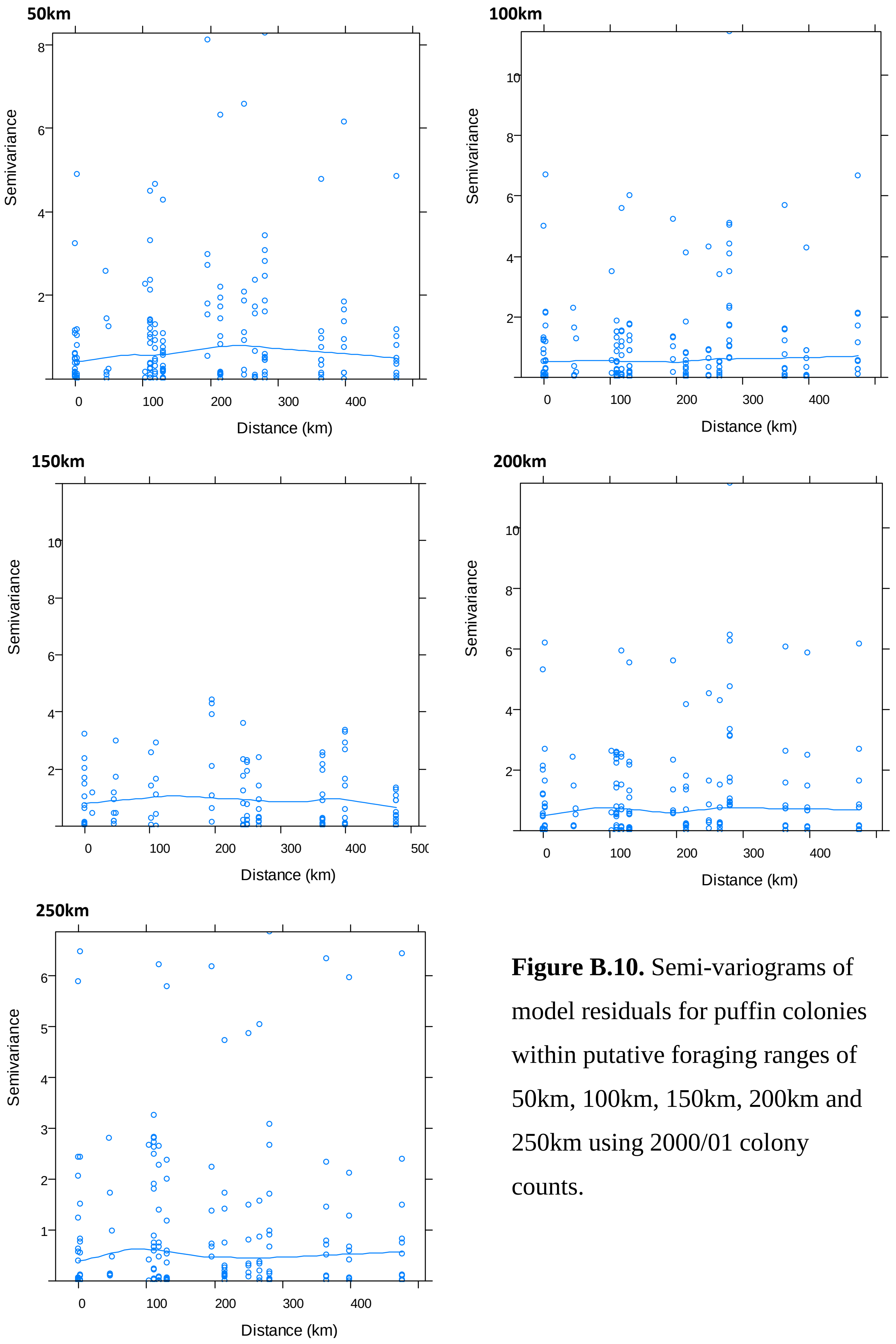
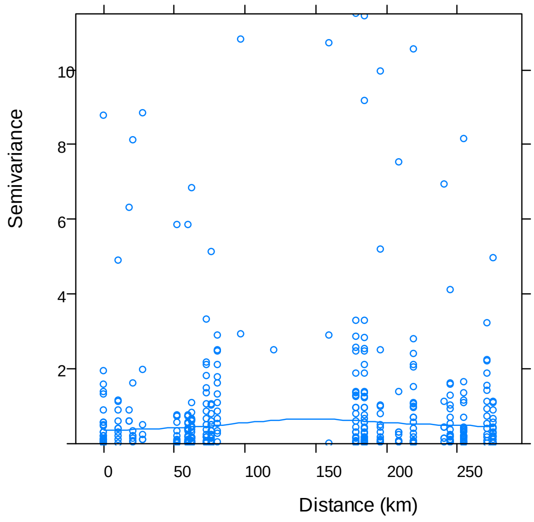
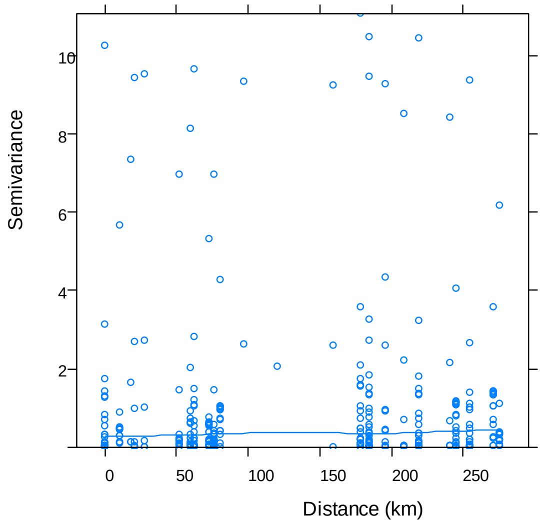


Figure B.10. Semi-variograms of model residuals for puffin colonies within putative foraging ranges of 50km, 100km, 150km, 200km and 250km using 2000/01 colony counts.

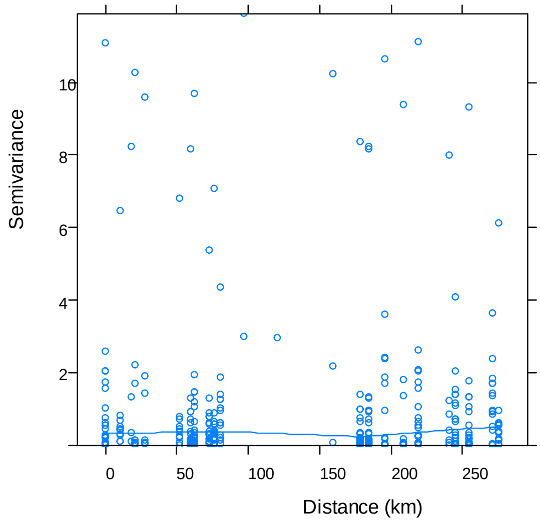
20km



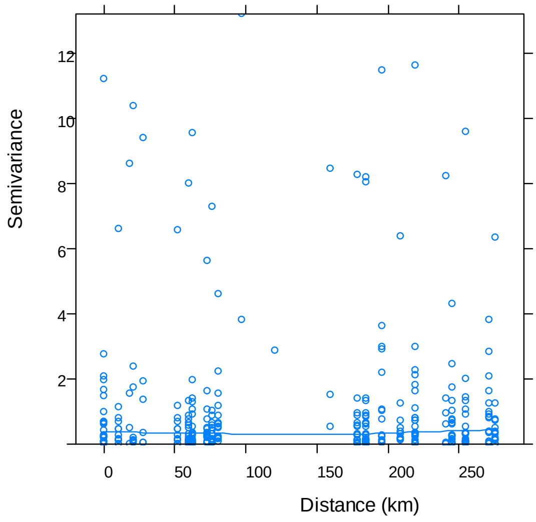
30km



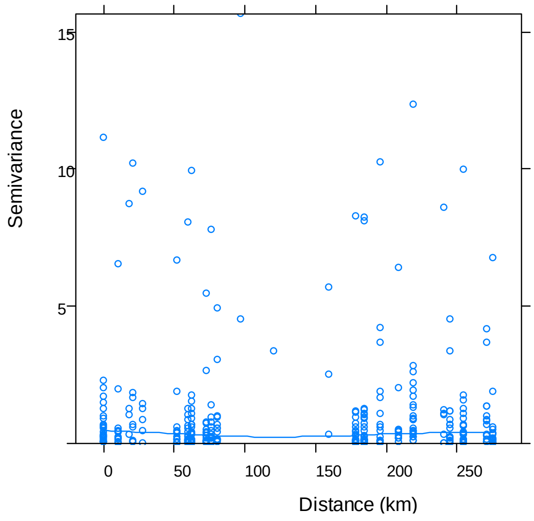
40km



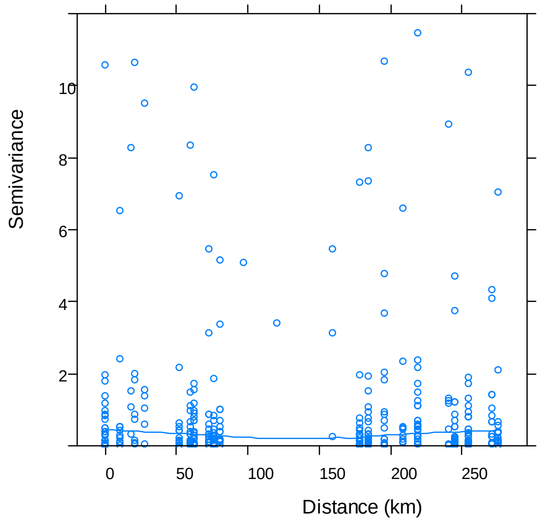
50km



60km



70km



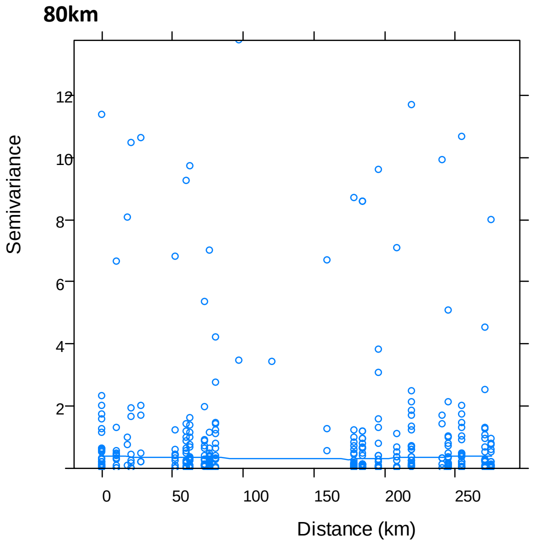
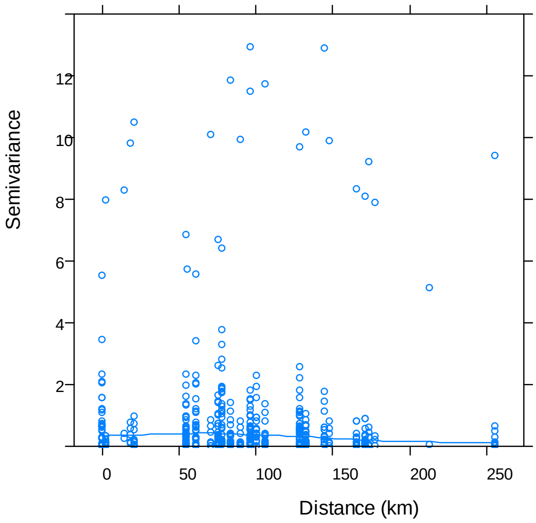
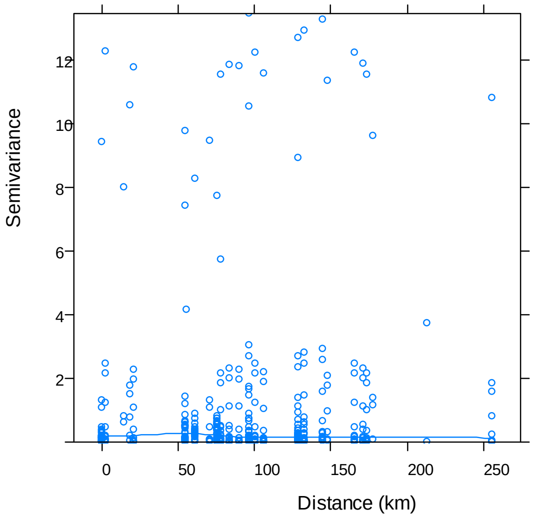


Figure B.11. Semi-variograms of model residuals for shag colonies within putative foraging ranges of 20km, 30km, 40km, 50km, 60km, 70km and 80km using 1969/70 colony counts.

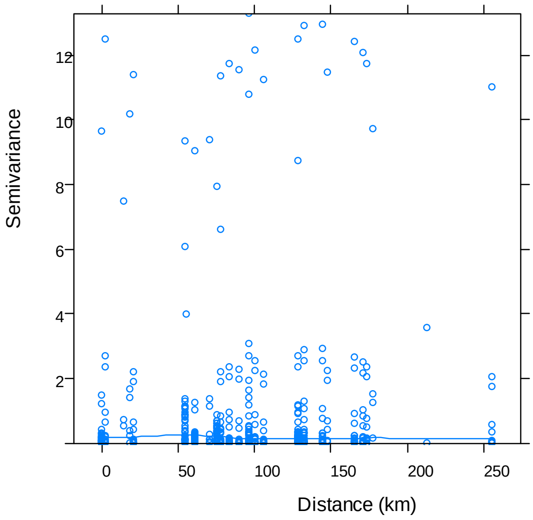
20km



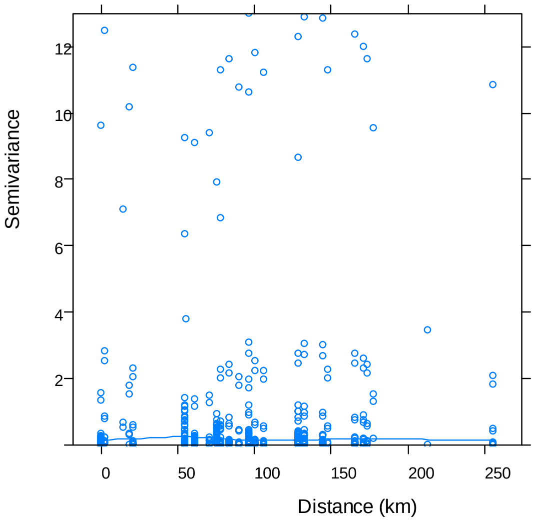
30km



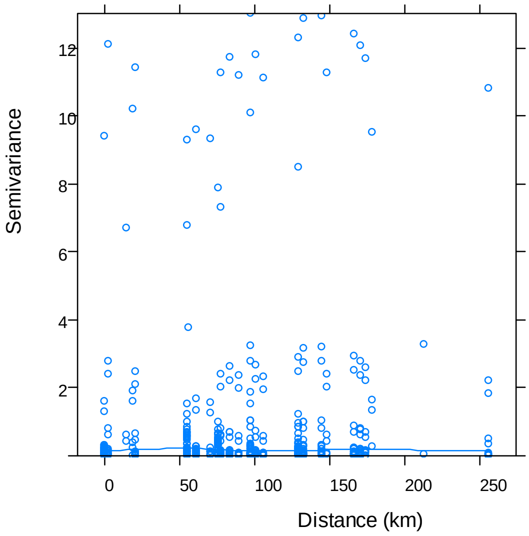
40km



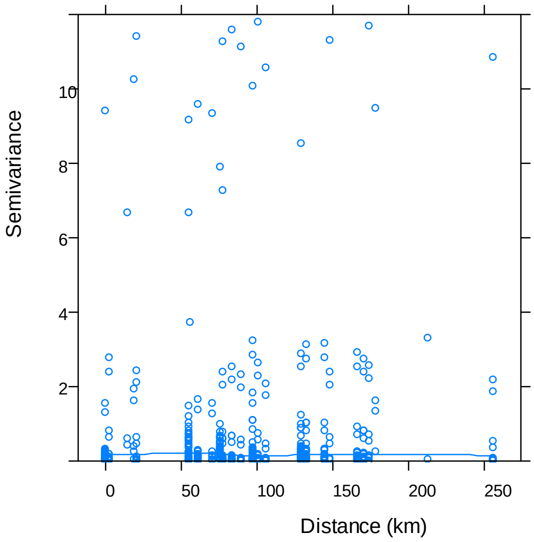
50km



60km



70km



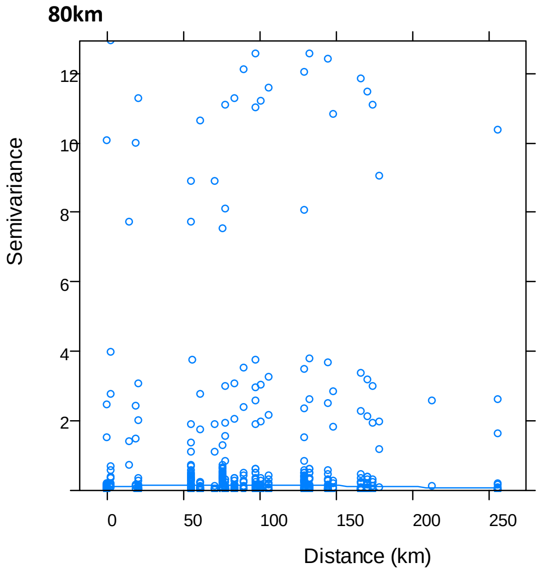


Figure B.12. Semi-variograms of model residuals for shag colonies within putative foraging ranges of 20km, 30km, 40km, 50km, 60km, 70km and 80km using 2000/01 colony counts.

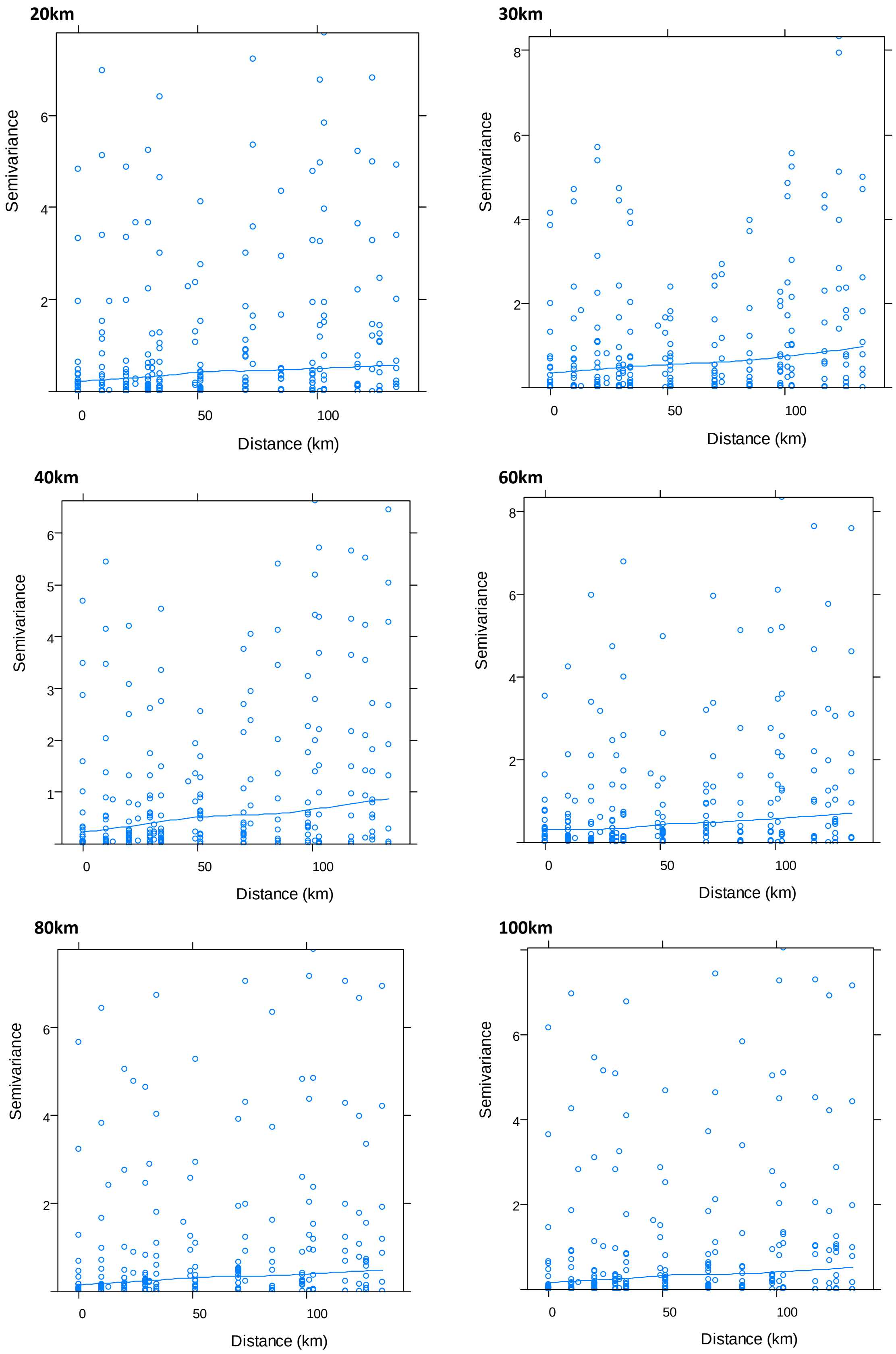


Figure B.13. Semi-variograms of model residuals for kittiwake colonies within putative foraging ranges of 20km, 30km, 40km, 60km, 80km, and 100km using 1982 colony counts.

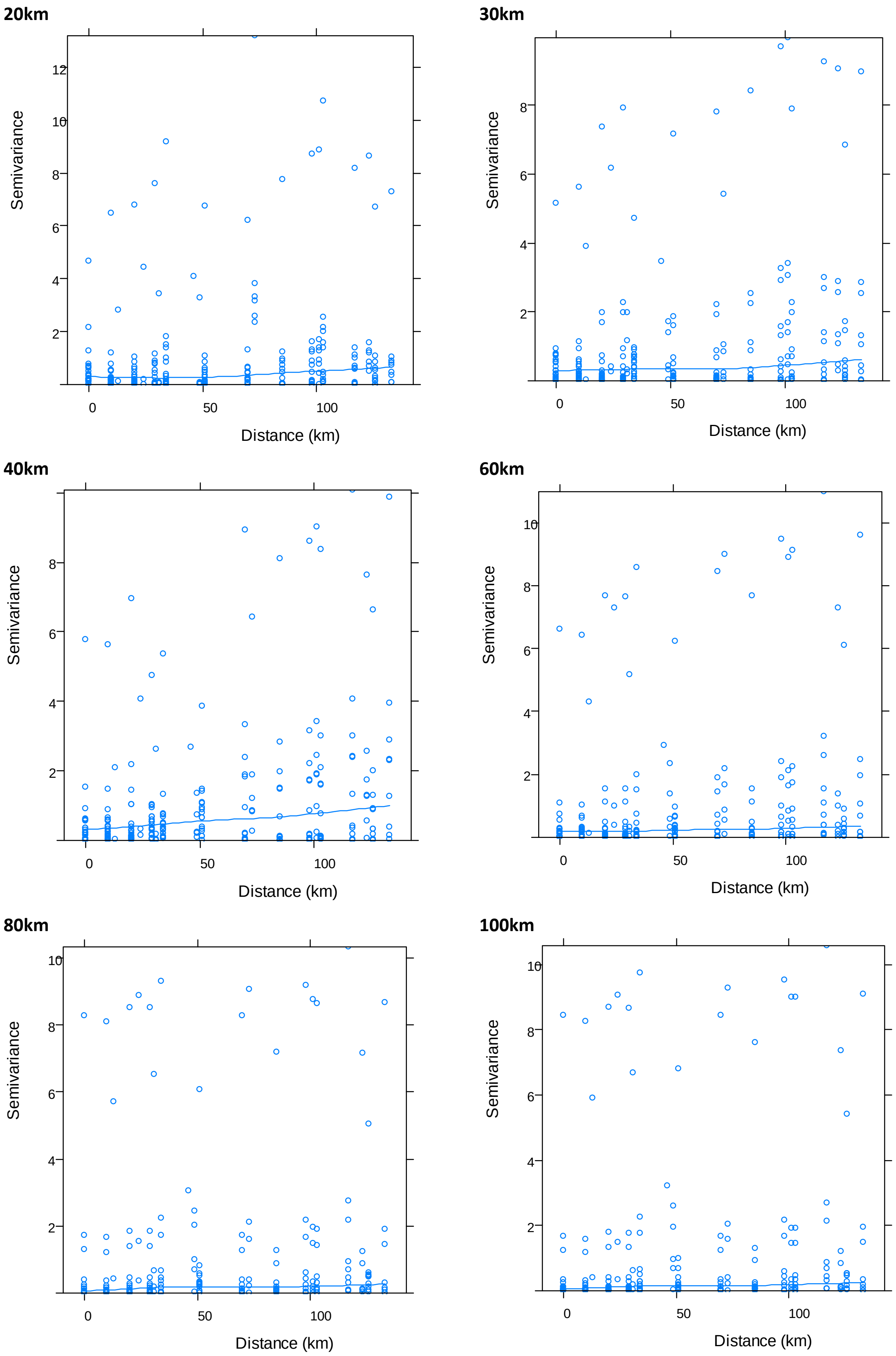


Figure B.14. Semi-variograms of model residuals for kittiwake colonies within putative foraging ranges of 20km, 30km, 40km, 60km, 80km, and 100km using 2000/01 colony counts.