

The Causes and Consequences of Individual Over-Wintering Strategies in Northern Gannets

Submitted by

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Summary

Within populations, individual behavioural variation is determined by intrinsic factors such as morphological sex differences, or extrinsic environmental factors. However, accounting for these differences, individual variation often persists as a result of individual niche specialisation. Variation in the foraging behaviour of avian marine predators has received particular attention, owing to the strong association between these species and fishing vessels. While the foraging strategies of seabirds have been investigated in the breeding season, non-breeding strategies and their carry-over effects (COEs), remain poorly understood. Furthermore, behaviour in one season should be considered in the context of previous and subsequent processes, as there are likely downstream impacts between seasons.

In this thesis I address this gap in our understanding by investigating individual variation in the over-winter behaviour of Northern gannets (*Morus bassanus*) from a number of UK breeding colonies. Two types of foraging behaviour have been described for diving seabirds: natural plunge-diving and discard foraging, the prevalence of which suggests population and individual flexibility in foraging strategy. Furthermore, with changes in discard availability likely to occur with future fisheries management, it is important to understand the predictors of this foraging behaviour and COEs on subsequent breeding success. I combine sequential tissue sampling for stable isotope analysis with geolocation to quantify individual repeatability in diet and hence foraging strategy, and parameters of migration. My findings reveal, firstly, that the UK gannet population is flexible in its foraging behaviour, as individuals exhibit one of three foraging strategies differing in trophic level and foraging habitat specialisation (Chapter 2). One of these strategies suggests a high level of discard foraging. Secondly, I explore previous individual state as a predictor of foraging behaviour and the destination of winter migration. Here I find that while migration strategy appears to be limited by state, foraging strategy is a result of individual niche specialisation independent of state. However, individuals of poor state foraged from a high trophic level, suggestive of discard foraging. Finally, in Chapter 3, I quantify the consequences of over-wintering behaviour on individual arrival at the breeding colony and subsequent onset of breeding. Perhaps surprisingly, early arrival does not correspond to earlier breeding. However, I find the telling result that individuals foraging, on what is suggested as discards, hatch their chicks later in the season, which may be attributable to the low nutritional value of such a diet.

I conclude firstly that migration appears to be limited by previous state. And secondly, that foraging from a high-trophic level may enable individuals of low state to survive, but with this strategy comes a cost for subsequent breeding. The level of detail achieved in following this large set of individuals over multiple years, reveals the interaction between individual niche specialisation and carry-over effects, and highlights the continuous impacts of discard foraging in a population so closely associated with anthropogenic fishing practices.

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Chapter 4: General Discussion

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Abbreviations

SIA	Stable Isotope Analysis
GLS	Global Location Sensing
COE	Carry-over effect
TNW	Total niche width
WIC	Within-individual component
BIC	Between-individual component
SUREC	Scottish Universities Environmental Research Centre
BAS	British Antarctic Survey
GLMM	Generalised linear mixed model
AIC	Akaike's information criterion
Cent.con	Centralised pre-winter condition
Cent.lat	Centralised mean December latitude
Cent.arr	Centralised arrival day at colony (Julian day)
Strat	Foraging strategy
Chick	Chick age standardised to the June 1 st
CL	Confidence limit
SE	Standard error
\bar{x}	Mean
IQR	Interquartile range

Author's Declarations

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HJW prepared most feather samples for Stable Isotope Analysis (SIA), though some preparation was made by TB prior to HJW starting this degree. SIA was conducted at the Scottish Universities Environmental Research Centre (SUERC) by HJW with the help and guidance of Jason Newton.

Great Saltee logger data was downloaded by TB and Bass Rock by Ewan Wakefield (EW) at the University of Leeds. HJW processed the logger data with BAS software and analysed the position data. An R-script for converting logger activity data to proportion wet/dry per night for the identification of first dry-night on land and hence arrival day at the colony, was created and provided by EW. R-script for calculation of Naglekerke R^2 was created by Richard Inger and Xavier Harrison at the University of Exeter. Finally, the world map shape-file used for ArcGIS is property of Lucy Hawks and Matthew Witt at the University of Exeter.

Chapter 1

General Introduction

1.1. Individual niche specialisation

Populations of animals have traditionally been considered as ecologically equivalent individuals, homogenous in their niche space, diet, competition pressure and predator prey-dynamics, yet individual niche specialisation, within a natural population, is a widespread phenomenon (Jaeger et al 2010; Bolnick et al 2003). It is often the case that within the population ecologically heterogenous individuals exploit different subsets of the resources available to them (Araújo et al 2007; Svanbäck & Bolnick 2005).

The theory of individual niche specialisation, originally designed by Roughgarden (1972, 1974), states that the total niche width (TNW) of the population is the sum of two variable components: the within-individual component (WIC), the average diet variation within individuals; and the between individual component (BIC), the variation between individuals within the population (Bolnick et al 2003). A population that appears somewhat generalist, with a broad ecological niche, may in fact be made up of specialist individuals with discrete behavioural strategies. In this case the total niche width is largely a product of BIC and the proportion explained by WIC is a small (Bolnick et al 2003).

This theory of niche specialisation can refer to individual foraging variation in a population of consumers. Variation may result from resource availability and ecological opportunity (e.g. Tinker et al 2008; Pierotti and Annett 1991), or sex differences in social rank or physiological performance (e.g. Bearhop et al 2006). However individual niche specialisation partitions the niche occupied by individuals via mechanisms independent of such factors. Little is known about these mechanisms, but assessing the cause and consequence of behavioural strategies is essential to our understanding of the implications of individual variation for community ecology and conservation (Bolnick et al 2003).

The implications of individual variation are likely to be more complex for migratory species. These species often make energetically expensive journeys to distant locations that differ in environmental conditions and the locations of resources. Furthermore, different processes govern behaviour across seasons. For example, among birds, individual behaviour in the

breeding season may be constrained by having to return and feed offspring as central placed foragers, unlike the winter non-breeding period when adults are no-longer constrained, but where the potential for competition may still be high and resources limited (Phillips et al 2009). The dynamics of migration are likely to promote flexibility among populations and individuals with respect to their behavioural strategies.

1.2. Carry-over effects

It has been recognised for some time that access to resources in one season is likely to have downstream impacts on individual state and subsequent processes, via a mechanism of Carry-over effects (COE) (Norris & Taylor 2006), influencing subsequent performance, fitness and possibly population dynamics (Harrison et al 2010; Gunnarsson et al 2006). For migratory species such seasonal asymmetries may be much more pronounced because of the range of environments experienced through the annual cycle and the energetic costs of fuelling a migratory life style. Carry-over effects may therefore be responsible for a large proportion of the variance in individual reproductive success (Harrison et al 2010). An example is seen in Black-Tailed Godwits (*Limosa limosa islandica*). For individuals that winter in higher-quality habitats there is a Carry-over effect onto transition into the next season as they are able to reach their Icelandic breeding grounds earlier, and as a consequence, their breeding success is greater than those that winter in habitats of poorer-quality (Gunnarsson et al 2005).

The combined ecological impacts of individual variation in foraging niche and COEs shape the effectiveness of management and conservation practices. The occurrence, proportions and density of generalists and specialists, differing in their exploitation of resources will determine the ecological impact of the species (Furness et al 2007; Svanbäck and Bolnick 2005). Additionally individuals of differing foraging strategy may be more or less susceptible to environmental change (Kernaléguen et al 2012). Consequently anthropogenic exploitation of resources may also have implications directed towards certain subsets of the population. For example, Bearhop et al (2001) recognised the impact of commercial fisheries on discard foraging individuals in the Great Skua (*Stercorarius skua*), as foraging from the discards of these vessels led to long term drops in their territorial attendance when the ships were in port.

1.3. Quantifying over-wintering behaviour

For migrating species it is the habitat quality and foraging behaviour that will likely have most influence on future events. To quantify the variation in behaviour during the non-breeding season of migrants, data collection techniques need to collate information on individuals throughout the over-wintering period. However, observation of foraging behaviour with spatial and temporal coverage during the migration period is particularly difficult as individuals range over vast distances (Phillips et al 2009), and are no-longer central-placed foragers, often spending the night at sea.

1.3.1. Stable Isotope Analysis

Traditional methods of dietary analyses include the analysis of gut contents and faecal samples. Both of these methods only provide a snapshot of foraging behaviour and are highly suspect to sampling error; often with the underlying assumption that samples represent long-term resource use (Araújo et al 2007). Whereas Stable Isotope Analysis (SIA) allows individual variation to be quantified and defined within total niche space, or “isospace”, over various time periods (Araújo et al 2007; Bearhop et al 2004a; Bolnick et al 2003).

This technique works on the basis that as prey proteins are assimilated into body tissues, these tissues will reflect the diet at the time of synthesis. Stable isotopes are forms of elements that vary in mass and relative abundance; the presence of which is expressed as the ratio (δ) of the most common heavy to light isotope forms in parts per thousand (‰), (Inger and Bearhop 2008). Assuming that prey species differ isotopically and that the isotopic signatures of these prey types are temporally invariant, this approach can be used to quantify individual foraging variation and hence niche width (Bearhop 2004) (see Araújo et al 2007 for further comparison of techniques).

In terms of foraging studies, nitrogen and carbon isotopes are most commonly used. The light isotope of nitrogen, ^{14}N is lost in nitrogenous waste to a greater extent than the heavy isotope ^{15}N , as the heavy isotope is preferentially assimilated in tissue synthesis (Kelly 2000). This results in the enrichment of the $^{15}\text{N}/^{14}\text{N}$ ratio ($\delta^{15}\text{N}$) by $\sim 3\text{-}5\text{‰}$ with each trophic level (Post 2002; Kelly 2000; Hobson et al 1994) and can be used to determine the trophic

position of a consumer. Carbon on the other hand, has very little enrichment between trophic levels and a mean trophic fractionation of 0.4‰ ($\pm 1.3SD$; Post 2002), though this varies with consumers. The ratio of carbon's heavy isotope ^{13}C to the lighter ^{12}C ($\delta^{13}C$) varies between producers at the base of the food web with the different photosynthetic pathways (Inger and Bearhop 2008; Kelly 2000; Deniro and Epstein 1978; Smith and Epstein 1971). Consequently $\delta^{13}C$ differs between C_4 , C_3 and marine producers, but also between producers of different habitat types e.g. inshore/offshore, pelagic/benthic and latitudinal gradient (Inger and Bearhop 2008; Kelly 2000). Hobson et al (1994) found that pigeon guillemots had high $\delta^{13}C$ enrichment consistent with inshore benthic foraging, likely due to consumption of detrital carbon. Though enrichment decreases with pelagic feeding, it is still greater in inshore than offshore for pelagic feeders (Hobson et al 1994). Basal nitrogen-isotope ratios will also vary between habitats, but to a lesser extent. This may result from geochemical, biosynthetic and/or discrimination processes or anthropogenic nitrification (Inger and Bearhop 2008; Michener and Kaufman 2007). The isotopic ratios of the producers are maintained within the tissues of primary consumers and persist up the foodweb (Kelly 2000; Inger and Bearhop 2008).

The tissue selected for stable isotope analysis must correspond to the expression period of the foraging behaviour or niche width of interest (Bearhop et al 2004a). Isotopic information is integrated into different tissues over different temporal scales, depending on the turn-over rate of that tissue (Ramos et al 2009). Bone stores an inert record of isotopic information over the lifetime of the animal, whereas muscle tissue can reflect the previous 3-4 weeks, red blood cells 6-8 weeks and plasma just 2-5 days (Hobson 2005; Hobson and Clark 1992). The most reliable tissues are metabolically inactive and retain a record of isotopic ratios following a short and fixed period of growth (Hobson 2005). For example, vibrissae have been used in pinniped (Hobson et al 1996) and California sea otter (*Enhydra lutris nereis*) studies (Newsome et al 2009) and feathers in studies of seabird foraging specialisation (Ramos et al 2009; Hobson et al 1994).

In seabirds, feathers can be used to investigate long term foraging specialisation, provided that the growth rate and specific moult patterns are known (Hobson 2005). Feathers collected in the breeding season at colonies to which individuals have high fidelity, can

therefore provide isotopic information for foraging specialisations during the previous winter migration at the time of feather growth. In sequentially sampling down the length of these feathers, it is possible to identify long-term variation in foraging behaviour (e.g. Votier et al 2010). This can also be achieved by sampling from tissues with different turn-over rates at one point in time (e.g. Bearhop et al 2006). However tissue types may be synthesised from different dietary components and have varying trophic enrichment factors (TEFs) due to metabolic routing, making such comparisons difficult (Inger and Bearhop 2008).

1.3.2. Geolocation

To investigate individual specialisations in long-distance migrants and from season-to-season, stable isotope analysis can be combined with remote tracking methods. Together they provide a powerful tool for identifying ecologically important habitats and can reliably differentiate between individual specialisation due to geographic separation and individual foraging preferences.

Recent advances in tracking technology have facilitated the deployment of large numbers of tracking devices on small animals, for long periods of time and over great distances (González-Solis et al 2007). By tracking migration routes we can identify habitats of ecological importance, staging areas and biodiversity hotspots, to increase our understanding of species interactions with anthropogenic processes e.g. renewable energy installations or fisheries (Montevecchi et al 2012; Votier et al 2010; Croxall et al 2005; Bearhop et al 2001). Where breeding site fidelity is high in marine vertebrates, but the wintering destination is unknown or of high plasticity (Dias et al 2011), data-logging tags can be attached in the breeding season and collected the following year upon their return. Light level loggers are an ideal tool for tracking large-scale movements and migratory pathways with marine vertebrates and have been used successfully in migration studies of marine turtles (e.g. Fuller et al 2008), marine mammals (e.g. Bradshaw et al 2004) and a range of seabird species (e.g. Phillips et al 2006, 2007).

1.4. Carry-over effects of over-wintering individual specialisation in seabirds

Tracking devices and SIA have been successfully applied in studies of seabird foraging behaviour, and have quantified the association that has been long known between avian

marine predators and fishing vessels. Such studies have tended to focus on the breeding season (e.g. Votier et al 2010; Bartumeus et al 2010; Garthe and Hüppop 1994) and have found the prevalence of discard foraging to be related to prey-availability and density-dependent processes (Garthe et al 2007; Svanbäck & Persson 2004) and has implications for individual condition (Votier et al 2010). Additionally, in many species individuals exhibit flexible foraging strategies as they alter their diet during self- and chick-provisioning within the same season (Davoren and Burger 1999; Granaderio et al 1998) or alter foraging strategies in relation to prey abundance (Garthe et al 2011; Montevecchi et al 2009).

During the non-breeding period individuals must replenish any reserves lost during the previous breeding season. The “choice” of overwintering location is a further dimension for individual variation for migratory species. Whereas it would be beneficial for individuals to locate and exploit regions of high resource availability, individuals may be limited in their ability to locate or travel to such areas. Variation in non-breeding site is therefore a consequence of extrinsic environmental effects, intrinsic limitations and COE from the previous season.

Global Location Sensing (GLS) has furthered our knowledge of migration routes and destination from traditional observation and ringing studies for avian migrants. Seabirds migrate long distances to temperate regions, spatiotemporally congregating with hetero- and con-specifics. Such areas are often upwelling zones running along continental shelf edges (Montevecchi et al 2009; Garthe et al 2007; González-Solis et al 2007; Phillips et al 2006). These zones provide an abundance of forage fish (Camphuysen and Van Der Meer 2005) and are hence an optimal region for individuals to replenish energy lost in the previous breeding season. Consequently popular regions for marine predator over-wintering are also hotspots for fisheries, providing discards as a further resource for migrants (Grémillet et al 2008).

Alongside discard foraging, suilid species, the gannets and boobies, commonly forage on small forage fish caught naturally using plunge-diving behaviour e.g. Capelin, *Mallotus villosus* (Garthe et al 2000; Nelson 1978). Plunge-diving involves stereotypical U- or V-shaped dives. Both behaviours can involve some energetically expensive underwater pursuit, but it is likely that plunge-diving U-shaped dives are the most expensive. U-shaped

dives are often long and flat bottomed dives that involve more underwater wing-propulsion than the rapid and shallow V-shaped dives (Garthe et al 2000). Energy income depends on the encounter rate and energetic content of the prey as-well-as the effectiveness of individual detection, capture, handling and digestion (Svanbäck and Bolnick 2005). The occurrence of these foraging behaviours has been related to prey-availability, density dependent processes (Garthe et al 2007; Tavecchia et al 2007; Svanbäck & Persson 2004) and Individual foraging condition (Votier et al 2010).

Whitefish and benthic discards are often low in calorific and nutrient value (Stauss et al 2012) compared to small forage fish (Garthe et al 2000). In the breeding season a diet predominantly of discards negatively impacts chick growth rate in Cape gannets, *Morus capensis* (Grémillet et al 2008). Grémillet et al (2008) termed this effect the 'Junk Food Hypothesis' and suggest that a diet containing discards is beneficial to individuals self-provisioning, but harmful for their chicks. The prevalence of discard foraging and its impact on adults in the non-breeding season remains relatively unexplored, yet our understanding of this process is critical to effective fisheries management and marine conservation.

1.5. Thesis Objectives

This thesis aims to combine the concepts of individual niche specialisation and COEs to investigate the cause and consequence of over-wintering foraging behaviour in a top marine predator, the Northern gannet (*Morus bassanus*). This species is an important bioindicator of the marine ecosystem (Furness and Camphysen 1997) whose numbers in recent years have been increasing at UK breeding colonies (Nelson 2002). It has been postulated that the close association between this species and fishing vessels (Furness et al 2007) has led to this population increase. Using SIA, studies in the breeding season have highlighted the frequency of interaction between gannets and fishing vessels (Votier et al 2013; Garthe and Hüppop 1994), however, the strength of this association does not appear homogenous between individuals. Though most if not all individuals regularly encounter fishing vessels, not all forage from their discards, as observed using animal borne video cameras (Votier et al 2010).

Recognising the importance of the behaviour of this species, recent studies have quantified individual specialisation of foraging behaviour in the breeding season and to some extent

individual migration strategies to and from their breeding colonies, using SIA and GLS. However, typically, seasonal events have been looked at independently, and individual specialisation in the winter has been explored very little. This thesis investigates the sequential effects of behaviour and individual condition throughout the year, to quantify the cause and consequences of individual specific over-wintering strategies.

1.6. Thesis Structure

In **Chapter 1**, I investigate the occurrence of individual foraging specialisation in the non-breeding season of adult Northern gannets having provisioned chicks in the previous breeding period. For these gannets over-wintering is a period to replenish energy and prepare for breeding in the next season. This chapter quantifies the possible carry-over effect of pre-winter condition on individual foraging strategy.

In **chapter 2**, I quantify the impact of the over-wintering strategy of the same individuals on condition and events in the following breeding season. In addition to individual foraging specialisation this chapter quantifies variation in over-wintering location. The consequence of this behaviour on arrival date back at the colony; the onset of hatching; and change in the condition between the years is predicted in an investigation of the possible carry-over effects of individual variation.

Chapter 2

The Causes of Individual Foraging Strategies in Over-Wintering Northern Gannets (*Morus bassanus*)

2.1. Abstract

The foraging behaviour of seabirds has been well studied in the breeding season. Central-placed foraging from the nest allows sequential data collection for dietary analysis in the investigation of behavioural strategies. However, with the difficulties associated with data collection, foraging behaviour in the non-breeding has received far less attention and individual variation in over-wintering strategy remains unknown. Here I use Stable Isotope Analysis (SIA) and geolocation to quantify individual variation in the over-wintering behaviour of Northern gannets (*Morus bassanus*). I analyse sequential feather samples for SIA and analyse individual repeatability in foraging behaviour to identify three distinct foraging strategies: a specialist offshore high-trophic strategy; a specialist inshore low-trophic strategy; and a generalist strategy of individuals switching their foraging habitat and/or the trophic level of their prey. I demonstrate that: 1) though individual foraging strategy appears to be a product of individual niche specialisation, alongside this partitioning, a carry-over effect (COE) of pre-winter condition predicts a large amount of variation in the trophic level of prey. This effect is stronger for males, where males of poor previous condition feed from a higher-trophic level, suggestive of discard foraging. 2) A further COE acts on the repeatability of foraging habitat, increasing the range in foraging habitat for individuals of poor previous condition. I suggest that this may indicate either decreased foraging success or decreased ability to defend a productive site. Using AIC average modelling I quantify the carry-over effect of previous state (pre-winter condition) on subsequent processes in the following season. This work suggests a persistent association between an avian marine top-predator and anthropogenic fishing practices, but highlights individual condition as a predictor of the strength of this association. Furthermore, the existence of three discrete strategies indicates behavioural variation within the population, and for generalist foragers, an individual flexibility in foraging behaviour.

2.2 Introduction

Annual cycles in biological systems are sequential in nature and seasonal events are linked by cause and consequence (Harrison et al 2010; Gunnarsson et al 2006). 'Decisions' made by animals in one season are therefore likely to have downstream consequences that 'carry-over' into the next season. Following on from Norris and Marra's (2007) definition, Harrison et al (2010) defined carry-over effects (COE) as events and processes in one season, that affect the transitional state into, and individual performance in, the subsequent season. For migrating species, COEs are likely to be a prominent feature and complex in nature, as individuals make the often energetically demanding migration between habitats for breeding and over-wintering. Moreover, migrants will experience spatial and temporal state changes with relation to seasonal events. Owing to the difficulties of monitoring individuals across seasons, individual behavioural specialisations have typically been investigated within seasons, independent of previous and subsequent events. Hence we have built up our knowledge of proximal causes and consequence, but to fully understand individual specialisation we must not treat different events within the annual cycle independently (Harrison et al 2010).

Likewise, within natural populations of animals individuals are ecologically heterogeneous occupying different niche space. This concept of 'individual niche specialisation' should be considered alongside COEs as downstream consequences will vary among individuals of different behavioural strategies. Roughgarden's (1972; 1974) theory of Individual niche specialisation states that within a generalist population, individuals may specialise on the exploitation of certain resources. Hence, within the total niche width (TNW) the within-individual component (WIC) of individual niche space is separated by the between-individual component (BIC) (Bolnick et al 2003).

We are beginning to explore individual specialisation in seabird foraging as central placed foragers from their breeding colonies, and the effects of these diets on breeding behaviour. COEs of winter diet quality have also been identified affecting subsequent breeding success (e.g. Sorensen et al 2009; Furness et al 2006). However, only a handful of studies have investigated the consequence of summer breeding on over-wintering behaviour (e.g. Inger

et al 2010). The causes of variation seen in migration strategy and over-wintering behaviour are still poorly understood.

Top-marine predators exploit upwelling regions (Camphuysen and Van Der Meer 2005) during over-wintering including Cory's shearwater (González-Solis et al 2007), the Pomarine skua (*Stercorarius pomarinus*), grey phalaropes (*Phalaropus fulicarius*) and lesser black-backed gull (*Larus fuscus graellsii*) (Camphuysen and Van Der Meer 2005; Grecian 2011). Since these productive upwelling regions are also exploited by fisheries, it is likely that the strong association between seabirds and fishing vessels is also seen in the non-breeding season. Flexibility in individual foraging behaviour (Montevecchi et al 2009; Davoren and Burger 1999) may give rise to specific over-wintering strategies for individuals to replenish any decrease in state following breeding.

Pelagic and demersal fisheries discard fish caught above their quota, bycatch and offal providing a prey source for marine predators. A substantial amount of commercial discards are benthic whitefish such as plaice (*Pleuronectes platessa*) and red gunard (*Aspitrigla cuculus*) caught from a depth beyond the diving depth of most seabirds, including gannets (0.9-3.7m in Cape gannets *Morus capensis*; Ropert-Coudert et al 2004). For some individuals discards make up a significant proportion of their diet. However, though most individuals encounter fishing vessels on foraging trips, not all forage from their discards (Votier et al 2010). In one study male gannets consumed a higher proportion of discards in their diet than females, and Votier (2004a) identified a relationship between the proportion of whitefish in the diet of Great Skuas (*Stercorarius skua*) and Body Mass Index, finding that those with a low BMI had a higher proportion of whitefish in their diet. With central-placed foraging from the colony some individuals will adjust their search behaviour to actively pursue fishing vessels (Votier et al 2010).

Here we investigate whether seabirds exhibit parallel foraging behaviours in the non-breeding season, and whether individual variation in this behaviour is the result of niche partitioning or caused by COEs from the previous breeding event. Only then can we fully understand the interaction and possible reliance on fishing practices throughout the annual cycle of a migrating seabird.

Stable isotope analysis has emerged as a powerful technique in providing dietary information through migration, a period that is difficult to observe using traditional methods such as observation and analysis of regurgitate or faecal samples (Kernaléguen et al 2012; Inger and Bearhop 2008; Newsome et al 2007). A consumer's inert keratinous tissues store a dietary record of the prey consumed and assimilated during tissue synthesis (Deniro and Epstein 1978; Hobson et al 1994; Hobson 2005). Sequential samples of keratinous tissues reveal the repeatability of diet in isotopic space; integrating temporal, spatial and trophic information of foraging strategies (Araújo et al 2011; Kernaléguen et al 2012; Hedd & Montevecchi 2006), without the need to obtain absolute isotopic values of the prey consumed (Hobson et al 1994).

Typically in SIA studies of foraging behaviour, the common isotopes of nitrogen and carbon are used to identify the trophic level and foraging habitat (respectively) of the consumer during tissue synthesis. The ratio of heavy to light nitrogen isotopes ($^{15}\text{N}/^{14}\text{N}$) given as $\delta^{15}\text{N}$, relates to the trophic level of prey consumed, with the enrichment of ^{15}N by ~3-5‰ with each trophic level (Post 2002; Kelly 2000; Hobson et al 1994). The ratio of carbon stable isotopes ($^{13}\text{C}/^{12}\text{C}$) $\delta^{13}\text{C}$ differs with foraging habitat in the marine environment, along a gradient of offshore-inshore and benthic-pelagic feeding (Inger and Bearhop 2008; Kelly 2000; Deniro and Epstein 1978; Smith and Epstein 1971). This is due to differences in the photosynthetic pathway of producers.

For moulting species we can use knowledge of moulting patterns to collect samples from tissues grown during the winter period (Furness et al 2006; Phillips et al 2009), and using SIA collate a large amount information to model individual variation and COEs between seasons. This technique has been successfully applied to avian species. For example, Marra et al (1998) and Bearhop et al (2004) employed carbon SIA to identify the consequences of wintering in good quality mesic habitats on migration schedules compared to xeric habitats, in American redstarts (*Setophaga ruticilla*) and black-throated blue warblers (*Dendroica caerulescens*) respectively . Both studies concluded that wintering in habitats of good condition allowed individuals to return to the breeding site early.

SIA has been used in combination with animal borne tracking devices to build up an extensive body of quantitative evidence for the observed association between fishing

vessels and avian marine predators feeding from their discards. This work, however, has focused on the breeding season (e.g. Votier et al 2010; Bartumeus et al 2010; Garthe and Hüppop 1994). The occurrence of discard foraging in the summer months of colonial central place foragers, has been related to prey-availability, density dependant processes (Garthe et al 2007; Tavecchia et al 2007; Svanbäck & Persson 2004) and individual condition (Votier et al 2010). Individuals modify their foraging strategy and the intake of different prey types whether foraging for self- or chick-provisioning (Montevecchi et al 2009; Davoren and Burger 1999; Granadeiro et al 1998), suggesting a degree of individual flexibility. But in addition to these factors, individual niche specialisation may partition the niche space of individuals (Araújo et al 2011; Bolnick et al 2003; Roughgarden 1972; 1974).

We looked at gannets as important bioindicators (Furness and Camphysen 1997) whose numbers in recent years have been increasing at UK breeding colonies (Nelson 2002). It is known that they have a strong interaction with fisheries around their colonies (Furness et al 2007) and studies in the breeding season have made us aware of the frequency of interaction between gannets and fishing vessels (Votier et al 2013; Garthe and Hüppop 1994). However, though all individuals appear to encounter them, not forage from their discards (Votier et al 2010). Whitefish, and other discarded species, tend to be of a higher trophic level and more benthic than the small forage fish preyed upon by gannets in plunge diving. Hence SIA can be applied to quantify the presence of prey types and foraging behaviours in the diet. Specifically we questioned whether gannets differ in their winter diet and therefore foraging strategy, and secondly whether carry-over effects from the previous breeding season influence individual strategy in the winter.

2.3 Methods:

2.3.1 Study Population and Feather sample collection

Adult Northern gannets (*Morus bassanus*, hereafter gannet) occupy their breeding colonies in the Northeast Atlantic from May to July, returning to the same sites each year following migration (Nelson 2002). 69 % of the population occurs around the British Isles (60-70% of the global total; Nelson 2002). Samples and measurements were taken from breeding adults at five UK colonies: Bass Rock, Scotland (56.08, -2.64), Bull Rock (53.37, -6.15), Great Saltee (52.12, -6.60) and Little Skellig (51.77, -10.53), all Republic of Ireland, and Grassholm, Wales (51.73, -5.48). Feather samples were taken in the summer breeding periods of 2011 and 2012 from gannets at Bass Rock and Great Saltee, corresponding to the non-breeding periods of 2010-11 and 2011-12 respectively. At Grassholm, Bull Rock and Little Skellig samples were only collected in 2011.

Breeding adults, nesting away from the colony edge, were selected at random and caught at nest changeover with a brass noose (Votier et al 2010). Only pairs with chicks older than two weeks of age were caught for data collection. Small cuttings were taken from the base, mid and tip sections of the eighth primary feather of all captured individuals. Flight feathers are moulted and grown during the winter months and are inert after tissue synthesis. Thus samples capture dietary information from three sequential time periods, with the base sample being most recently synthesised. Following initial analyses tip sample were removed as $\delta^{13}\text{C}$ was much greater than expected, compared to base and mid sections. The increase in $\delta^{13}\text{C}$ was suggestive of an effect of feather synthesis during the first stages of feather growth, possibly related to the dark colour and increased melanin in the tip section (Michalik et al 2010).

2.3.2 Stable Isotope Analysis

Feather samples were thoroughly washed with distilled water and placed in a drying oven at $\sim 40^{\circ}\text{C}$ until dry. Between 0.6 and 0.8mg of each sample was weighed out and finely cut into tin cups for stable isotope analysis in Isotope Ratio Mass Spectrometers (IRMSs). Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios were measured using a ThermoElectron Delta Plus XP with Flash HT elemental analyser and a Thermo Fisher Scientific Delta V Plus with a Gas

Bench II configured for simultaneous $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ isotope analysis. SIA was conducted at the Life Sciences Mass Spectrometry Facility, Scottish Universities Environmental Research Centre (SUERC). Ratios are reported in parts per thousand (‰) with reference to international standards following the equation $\delta X = 1000[(R_{\text{sample}}/R_{\text{standard}}) - 1]$. At set intervals standards of GEL, ^{14}N ALA, glycine and tryptophan were analysed between feather samples in the IRMSs.

2.3.3 Biometrics and Body Condition

Biometrics were taken from all individuals on capture as birds departed for a foraging trip, ensuring individuals had an empty stomach. These included body mass (kg) to the nearest 50g, and wing, tarsus and mandible length, measured from bill tip to first feather growth. Each of these measures of skeletal size were analysed in regression analyses against body mass. The strongest of these regressions existed between mandible length and body mass ($r=0.32$, $t=2.32$, $df=42$, $p=0.025$). Using the equation of Peig and Green (2009), the scaled mass of each individual was calculated relative to that of the population by year, using mandible length as a measure of size. Outliers with mass $<3.5\text{kg}$ were removed to calculate SMA regression values and the mean mandible length of the population. The resultant equation used to calculate the scaled-mass of all individuals:

$$SM = \hat{M}_i \left[\frac{L_0}{L_i} \right]^{SMA}$$

$$2010: \hat{M}_i \left[\frac{98.028}{L_i} \right]^{3.1062} \quad 2011: \hat{M}_i \left[\frac{98.178}{L_i} \right]^{2.9906} \quad 2012: \hat{M}_i \left[\frac{97.3378}{L_i} \right]^{2.1989}$$

where M_i and L_i are the body mass and the linear body measurement of the individual (respectively); SMA is the regression exponent of M on L; and L_0 the mean of the linear measurement for the population. Scaled body mass was used as a measure of body condition in the breeding season. As feather samples were taken in 2011 and 2012, pre-winter condition was measured in the summer prior to feather growth (2010 and 2011 respectively) and post-winter condition in the summer of feather collection (2011 and 2012 respectively).

2.3.4 Foraging strategy

Following preliminary analyses, stable isotope analysis of all feather samples over the two years of data indicated two dietary clusters during winter migration. The two clusters were defined by k-means cluster analysis (Figure 1a). Three foraging strategies were identified (Figure 1b). Strategies 1 and 2 were specialist strategies as both the individual's base and mid feather samples were found in the same cluster, indicating a diet of similar prey in terms of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ during the two periods of tissue growth. Strategy 3 individuals foraged across clusters and are hereafter termed mixed foragers. This mixing was not directional.

2.3.5 Foraging specialisation

The foraging specialisation in terms of trophic level and foraging habitat specialisation was calculated as the difference in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between the two feather samples respectively. This measure reflected individual variation in foraging behaviour and is referred to in analyses as isotope distance.

2.3.6 Over-wintering latitude

BAS light-level loggers were attached to gannets and Bass Rock and Great Saltee. On retrieval the data was downloaded and processed, and the complete winter migration of these individuals tracked. As latitude was the major axis of movement for all individuals and all gannets settled in a certain region during the month of December, the mean December latitude for each individual defined their winter location in the non-breeding season (See Chapter 2 for detailed methods). Consequently where latitude is present in the analyses, the number of individuals is reduced to 61.

2.3.7 Statistical Analyses

A series of generalised linear mixed models (GLMMs) were fitted to response variables of diet ($\delta^{15}\text{N}/\delta^{13}\text{C}$) and foraging specialisation ($\delta^{15}\text{N}$ distance/ $\delta^{13}\text{C}$ distance).

Two GLMMs were designed to investigate potential causes of diet, where the response variables $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were analysed separately. Models included the fixed effects of sex

with pre-winter condition and December latitude in interaction, and the random factors of individual ID nested within colony, and year, again as a random factor.

A second set of models analysed the potential predictors of foraging specialisation. In these two models, the response variables of $\delta^{15}\text{N}$ distance and $\delta^{13}\text{C}$ distance quantified foraging specialisation in terms of trophic level and foraging habitat respectively. These models included the fixed effects of sex, pre-winter condition and the three level factor of strategy, again in interaction. December latitude was removed from these models due to convergence with strategy. Both models included ID nested within colony as a random factor, but year was removed due to insignificance.

For each of these four GLMMs a set of top models within 2 Akaike's information criterion (AIC) of the topmost model was identified. These top model sets were averaged using the MuMIn package (Bartoń 2013), averaging the terms and their estimates by the weighting of candidate models. The significance of model terms was assessed using relative importance and 95% confidence intervals for these two tailed tests. The resulting average model was compared to a null model (including only random terms) to calculate Nagelkerke pseudo R^2 , over dispersion and model residuals to assess model fit. All statistical analyses were carried out using R 3.0.0.

2.4. Results

A total of 198 feathers were sampled from the five colonies. Isotope ratios ranged from 11.42 to 19.12 for $\delta^{15}\text{N}$ and -17.22 to 12.99 for $\delta^{13}\text{C}$ across all colonies. Using individuals caught in consecutive years at Bass Rock ($n = 26$), there is a significant difference in the diet of this population between these two years (Mann-Whitney test, $\delta^{13}\text{C}$: $W=19234.5$, $p<0.001$; $\delta^{15}\text{N}$: $W=9592.5$, $p<0.001$). $\delta^{15}\text{N}$ increased from a median of 14.08 (± 2.53 interquartile range, herein IQR) in 2011 to 15.24 (2.34 IQR) in 2012, and $\delta^{13}\text{C}$ decreased slightly from -15.12 (2.43) to -15.835 (1.59).

Cluster analysis identified two discrete clusters in isotopic space centred on the cluster means (Figure 2.1.a): Cluster 1 comprise a higher nitrogen isotope ratio ($15.64 \pm 0.07 \delta^{15}\text{N}$) and more negative carbon ratio ($-15.943 \pm 0.036 \delta^{13}\text{C}$) and Cluster 2 forms from samples with a low nitrogen ratio ($13.089 \pm 0.048 \delta^{15}\text{N}$) and less negative carbon ratio ($-13.807 \pm 0.050 \delta^{13}\text{C}$).

Three foraging strategies were identified with the assignment of individual base and mid feather sections to clusters (Figure 2.1.b). Strategy 1, where gannets specialised in cluster 1 enriched $\delta^{15}\text{N}$ and more negative $\delta^{13}\text{C}$, comprised 49.0% of individuals ($n= 97$); strategy 2, where gannets specialised on a diet in cluster 2 of low $\delta^{15}\text{N}$ and less negative $\delta^{13}\text{C}$, comprised 36.4% of individuals ($n=72$), with the remainder (14.6 %, $n=29$) exhibiting a mixed strategy where base and mid sections of the same feather were not found in the same cluster.

The dietary mixing of strategy 3 individuals was not directional, with 58.6% ($n=17$) showing a decrease in $\delta^{15}\text{N}$ and increase in $\delta^{13}\text{C}$, shifting from cluster 1 to 2 over the course of feather growth (Figure 2.1.b, individuals 3a); while the remaining 41.4% ($n=12$) shifted diet from cluster 2 to 1 (Figure 2.1.b, individuals 3b). These strategies were seen in individuals of all colonies, in males and females and in both 2010-11 and 2011-12.

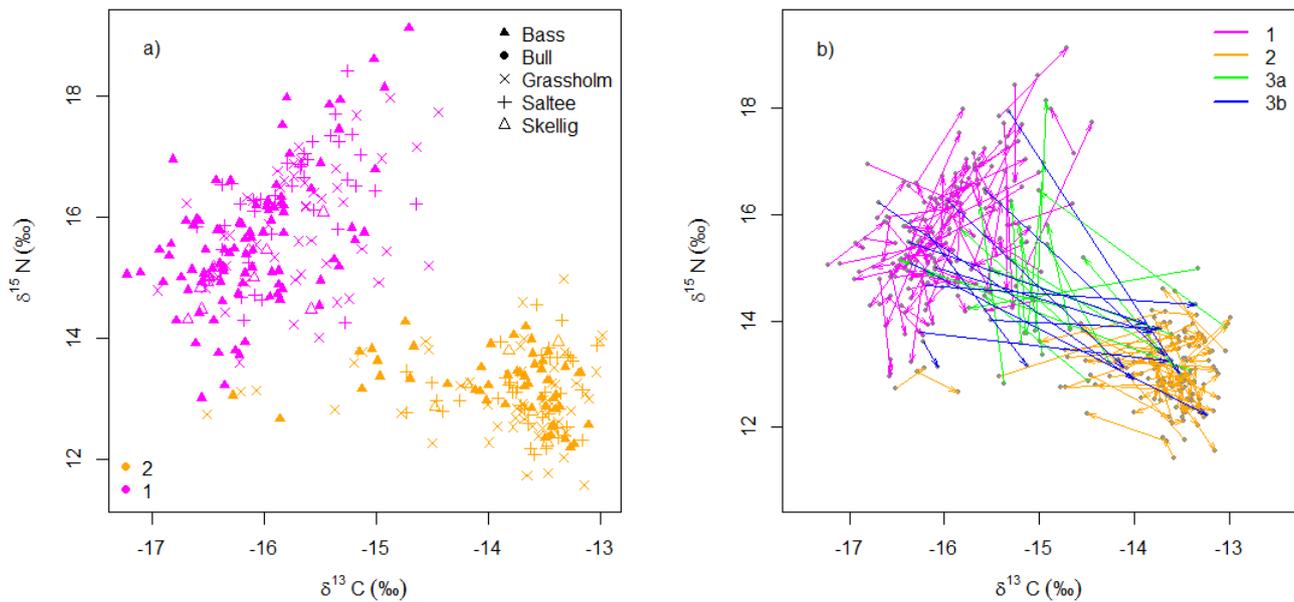


Figure 2.1. Foraging clusters and foraging strategy in isotopic space. a) K-means cluster analysis defined two discrete dietary clusters, b) Three foraging strategies identified: strategy 1 seen in magenta and 2 in orange. Individuals shifting from cluster 2 to 1 in green and from 1 to 2 in blue. Each arrow joins the mid to base feather samples.

Though there was no significant relationship between mean December latitude and pre-winter condition ($r=-0.17$, $t=-1.35$, $df=59$, $p=0.181$). All individuals of good condition relative to the population wintered at the low latitudes of the southern region ($<40^{\circ}\text{M}$), whereas the northern region was dominated by individuals of poor previous condition (Figure 2.2.). For these individuals in the northern region 94% ($n=16$) specialised on an offshore-high-trophic diet in foraging strategy 1.

From top model sets (Table 2.1.a) the effect of latitude was of high importance in predicting both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, but this was of only of significance for $\delta^{15}\text{N}$ where confidence intervals did not cross zero (Table 2.1.b). The importance is confounded by the fact that 94% of individuals wintering in the northern region close to breeding colonies were of high nitrogen isotope ratio strategy 1. The interaction between pre-winter condition and sex is of equal importance to latitude for $\delta^{15}\text{N}$, occurring in all top models with a relative importance of 1 in the average model (Table 2.1.b). Females $\delta^{15}\text{N}$ tend to be of good pre-winter condition, whereas were of poor pre-winter condition (Figure 2.2.b). Whereas individual condition

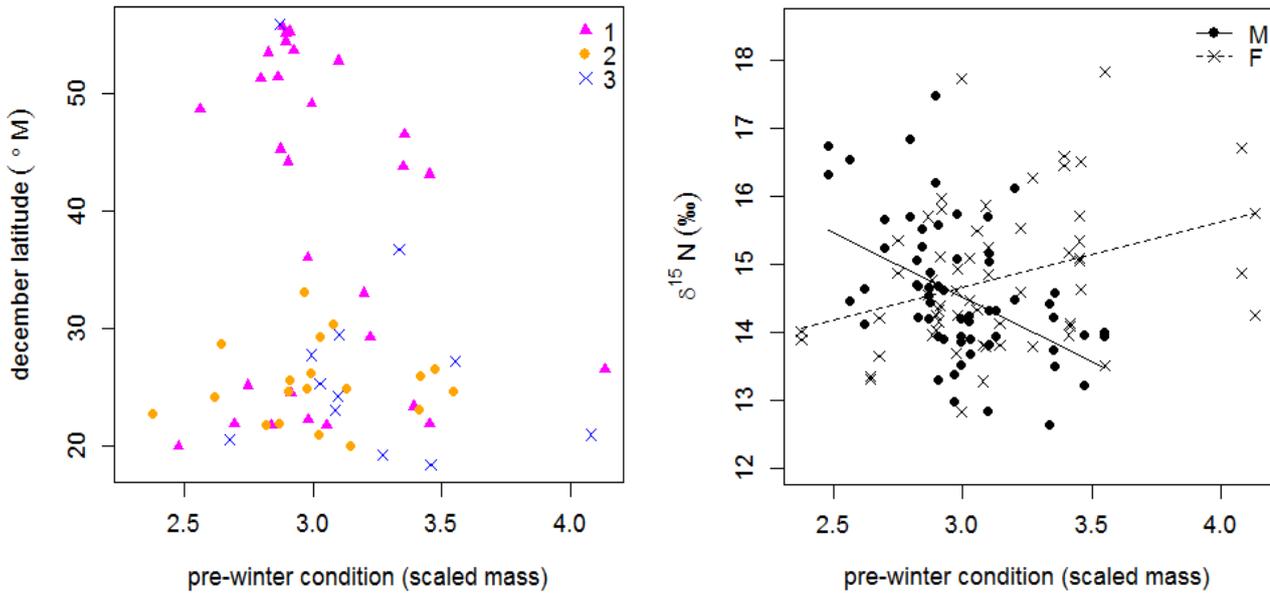


Figure 2.2. a) The mean latitude of all location points in December for each individual with a geolocator ($r=-0.17$, $t=-1.35$, $df=59$, $p=0.181$). Individuals were from Bass Rock or Great Saltee and points have been coloured by foraging strategy. b) The predicted effect of pre-winter condition in interaction with sex on $\delta^{15}\text{N}$, Males: dots and solid line; Females: crosses and dotted line. Lines are the average model predictions and points the residuals.

alone and in interaction separately with sex and latitude, is of little importance and affect in predicting $\delta^{13}\text{C}$.

Model selection for the predictors of foraging specialisation, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ distance, selected 3 and 5 top models respectively (Table 2.2.a). All top models included strategy: individuals of mixed strategy 3 had a greater $\delta^{13}\text{C}$ (1.51 ± 1.05) and/or $\delta^{15}\text{N}$ (2.23 ± 1.21) than specialist strategies 1 (0.35 ± 0.25 ; 0.73 ± 0.58 respectively) and 2 (0.46 ± 0.41 ; 0.41 ± 0.32 respectively). An interaction between the pre-winter condition and foraging strategy strongly predicted $\delta^{13}\text{C}$ distance (Table 2.2.b), this is created by an increasingly negative relationship between condition and $\delta^{13}\text{C}$ distance from strategy 2 to 3, where individuals in poor pre-winter condition have a greater $\delta^{13}\text{C}$ distance between feather samples (strategy 2: estimate=-0.29, CI=-0.62,0.03; strategy 3: estimate=-1.04, CI=-1.47,-0.60). Individuals in poor condition with low-trophic specialist strategy 2 and mixed foraging strategy 3 have a greater distance between feather samples (Figure 2.3).

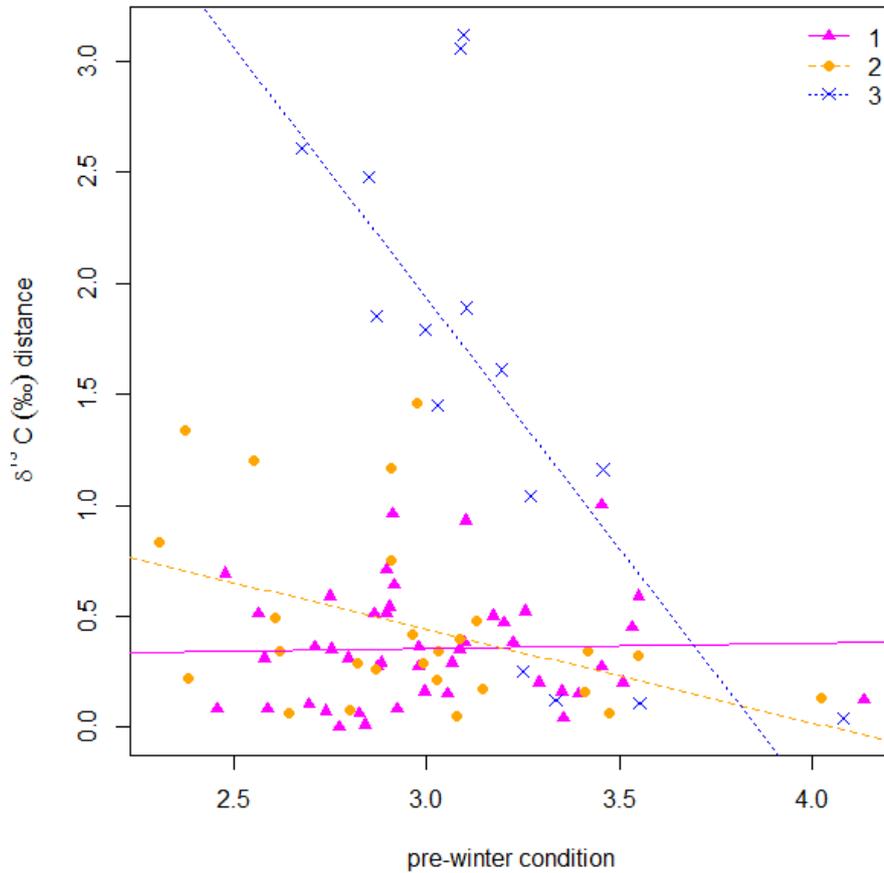


Figure 2.3. The interacting effect of pre-winter condition and foraging strategy on the distance between base and mid feather sections in carbon isotope space. Individuals with a greater foraging habitat range were of poor pre-winter condition compared to specialists, for strategies 2 and 3. Individuals specialised on a high-trophic diet (strategy 1) are also highly specialised in their foraging habitat, independent of their pre-winter condition.

2.5 Discussion

In combining stable isotope analysis and geolocation I have found that within this population of Northern gannets certain individuals are flexible in their over-wintering foraging strategy. Furthermore I have revealed that decreased pre-winter condition may be linked to shorter migration and an increase in the trophic level of prey consumed and the range of foraging habitats.

2.5.1. Dietary Clusters

Two dietary clusters were identified from SIA, discrete in isotopic space (Figure 2.1.a). The first of these clusters was defined by an enriched $\delta^{15}\text{N}$ and depleted $\delta^{13}\text{C}$ relative to the second. This is consistent with a high trophic level ($\delta^{15}\text{N}$), offshore ($\delta^{13}\text{C}$) diet, (Inger and Bearhop 2008; Post 2002; Kelly 2000; Hobson et al 1994). Two types of foraging behaviour are commonly found in suilid pelagic predators. The first is a plunge-diving behaviour (Nelson 1978) in pursuit of small forage fish (Garthe et al 2000). And the second involves foraging for discards on pelagic and demersal prey that is usually of higher trophic level than the small forage prey caught via plunge-diving. It is likely that the dietary cluster of high-trophic level (high $\delta^{15}\text{N}$) is formed primarily from discard prey, whereas the inshore low-trophic cluster suggests more natural foraging behaviour. Interestingly within the high-trophic cluster there is a positive relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ which may reflect the target catch of fisheries encountered during winter migration.

2.5.2. Foraging Strategy

From the two dietary clusters three over-wintering foraging strategies were identified (Figure 2.1.b), two of which are as specialised strategies and the third a mixed strategy. Unlike traditional methods, SIA does not just look at a snapshot of diet but combines the isotope signature of all prey consumed during synthesis, which in this case is likely to be days to weeks (Inger & Bearhop 2008). Therefore where both feather samples lay within the same cluster the individual will be foraging mostly if not exclusively from either high-trophic level-offshore prey (high-trophic specialists) or low-trophic level-inshore prey (low trophic specialists), over lengthy periods.

Around the Cap Blanc of Mauritania the convergence of currents, including the Canary Current, along the continental shelf creates a year round offshore upwelling region (Camphuysen and Van Der Meer 2005; Grecian 2011). Pelagic fisheries exploit this region for the horse mackerel, sardine and anchovy that congregate on the shelf edge (Camphuysen and Van Der Meer 2005). In combination, the high density of foraging seabirds and pelagic shoaling fish, spatially and temporally predictable along the shelf break (Davoren et al 2006; Garthe et al 2007; Montevecchi et al 2009) creates a high propensity for competition (Lewis et al 2001). The three strategies only overlapped spatially at the lower overwintering latitudes. The majority of tracked individuals (67%) travelled beyond the Straits of Gibraltar (36° meridian) down to Northwest Africa. As this was a random selection of breeding individuals, it is likely that a high proportion of the population also travel to this region. It is therefore probable that individuals travelling to Africa face a greater level of competition leading to the divergence of behavioural strategies via a density-dependent mechanism, as seen in the breeding season at larger colonies (Garthe et al 2007).

2.5.3. Interaction of Individual niche specialisation and carry-over effects

Seabirds show flexibility in their foraging strategies in a pattern that aligns with the theory of individual niche specialisation, proposed by Bolnick et al (2003). Individuals differed in their foraging behaviour and the repeatability of this behaviour. Though gannets have traditionally be thought of as opportunistic predators, it appears as though only a proportion of individuals are truly opportunistic; mixing their foraging behaviour to forage at different trophic levels and foraging habitats. Many individuals were more repeatable in isotopic space, indicative of specialisation rather than opportunism.

Condition, or state, in the previous season appears to have a carry-over effect on the winter habitat specialisation in interaction with strategy (Figure 2.3). Individuals that specialised on a particular foraging behaviour consistently foraged in the same habitat type, unlike individuals with a mixed strategy, where their previous condition influenced the range in their foraging habitat. Within this strategy there was a negative correlation between pre-winter condition and the range of their foraging habitat. Individuals in poor condition may be limited in the ability to learn and memorise successful foraging locations, whereas those in good condition may locate productive locations, but be opportunistic in how they catch

their prey resulting in a diet of prey varying in trophic level. Good condition individuals are also likely to have a greater rate of foraging success and a greater range in foraging habitats could suggest that gannets of poor condition are less successful, having to increase their foraging attempts across different habitats.

Individuals in poor condition within a year tended to winter at higher latitudes, in the northern region. Interestingly all 4 of the individuals that showed a decrease in their pre-winter condition between the two years decreased their migration distance, wintering at higher latitudes in the latter year. Though, with such a small sample size the significance of this could not be tested.

Males that were in good pre-winter condition, had a low trophic level diet, suggesting that they were more likely to have foraged naturally on shoaling pelagic prey by plunge-diving. This negative relationship is also seen within the breeding season where BMI is negatively correlated to the amount of whitefish in the diet, made available by fisheries (Votier et al 2010). Natural plunge-diving will involve some amount of underwater swimming (Garthe et al 2000). U-shaped dives are an expensive method of foraging as the long, flat-bottomed dives involve underwater propulsion; a more expensive method of foraging than the shallow V-shaped dives (Ropert-Coudert et al 2004; Garthe et al 2000) often associated with discard foraging (Grémillet et al 2008). Males of poor-previous condition may therefore be more successful in exploiting discards rather than small forage fish if dives are too expensive. Additionally individuals in poor condition may be less able to capture and handle more complex prey, and resort to easy to catch and readily available discards.

The act of foraging can disrupt shoals dispersing fish and increasing competition (Lewis et al 2001). This may increase the difficulty of natural diving for males in poor condition. It may also be more risky for individuals to target more variable natural resources compared to discard foraging. Males in better previous condition may be better able to capitalise on the high reward of natural prey, despite the potential of high cost if unsuccessful (Caraco 1981). Males feeding from discards may be better able to compete for position around fishing vessels than females explaining why only females of good prior condition foraged from a high trophic level.

The findings of this chapter demonstrate firstly that individual niche specialisation is acting on the population, leading to discrete foraging strategies that differ in their degree of specialisation and flexibility. And secondly, that COEs are also acting on individual foraging behaviour, in interaction with the phenomenon of niche specialisation.

2.6. Appendix of tables

Table 2.1.b. Top model sets, within 2 AIC, predicting the variance in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively. The Nagelkerke R^2 has been calculated for each model and presented with the model weight.

Original model: $\text{Isotope} \sim \text{cent.con} * \text{dec_lat} * \text{sex} + (1 | \text{colony/id}) + (1 | \text{year})$

Isotope	intercept	Cent.con	Cent.lat	sex	Cent.con : cent.lat	Cent.con :sex	Cent. lat:sex	df	ΔAIC	weight	R^2
Carbon	+		+	+			+	8	0.00	0.153	0.107
	+	+	+					7	0.08	0.147	0.091
	+		+					6	0.61	0.131	0.072
	+	+	+	+			+	9	0.92	0.097	0.116
	+	+	+	+				8	1.61	0.069	0.094
	+		+	+				7	1.62	0.068	0.078
	+	+	+	+		+	+	10	1.74	0.064	0.125
	+	+	+		+			8	1.80	0.062	0.093
Nitrogen	+	+	+	+		+		9	0.00	0.330	0.248
	+	+	+	+		+	+	10	1.00	0.199	0.255
	+	+	+	+	+	+		10	1.62	0.147	0.251

Table 2.1.b. Average models and their estimates for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, presented with the 95% confidence intervals and the relative importance of each term. The Naglekerke R^2 of the average model was for $\delta^{13}\text{C} = 0.13$ and $\delta^{15}\text{N} = 0.26$.

$\delta^{13}\text{C} \sim \text{cent.con} + \text{cent.lat} + \text{sex} + \text{con:lat.} + \text{con:sex.} + \text{lat:sex.} + (1 | \text{colony/id}) + (1 | \text{year})$

$\delta^{15}\text{N} \sim \text{cent.con} + \text{cent.lat} + \text{sex} + \text{con:lat.} + \text{con:sex.} + \text{lat:sex.} + (1 | \text{colony/id}) + (1 | \text{year})$

Isotope	Parameter	estimate	2.5%	97.5%	Relative importance
carbon	(Intercept)	-15.177	-15.636	-14.718	
	Cent.lat	-0.390	-0.817	0.036	1
	sexM	0.243	-0.367	0.852	0.57
	Cent.lat: sexM	-0.517	-1.097	0.062	0.40
	Cent.con	-0.145	-0.371	0.081	0.55
	Cent.con :sex M	0.265	-0.205	0.736	0.08
	Cent.con: cent.lat	0.071	-0.188	0.331	0.08
nitrogen	(Intercept)	14.713	14.205	15.221	
	Con	0.320	-0.017	0.658	1
	Lat	0.880	0.519	1.242	1
	Sex M	-0.314	-0.870	0.243	1
	Con:sexM	-0.937	-1.510	-0.365	1
	Lat:sexM	0.285	-0.255	0.825	0.30
	Cent.con:cent.lat	0.123	-0.263	0.510	0.22

Table 2.2.a. Top model sets, within 2 AIC, predicting the variance in $\delta^{13}\text{C}$ distance between the two feather samples and $\delta^{15}\text{N}$ distance respectively (values were box cox transformed). The Nagelkerke R^2 has been calculated for each model and presented with the model weight.

*Isotope distance ~ cent.con*strat *sex +(1|colony/id)*

Isotope distance	(l)	Cent.con	sex	strat	Cent.con: sex	Cent.Con : strat	Sex: strat	Df	ΔAIC	weight	R^2
Carbon	+	+	+	+		+		10	0.00	0.419	0.489
	+	+		+		+		9	0.62	0.308	0.470
	+	+	+	+	+	+		11	1.99	0.155	0.489
Nitrogen	+			+				6	0.00	0.243	0.407
	+	+		+				7	0.09	0.232	0.422
	+	+	+	+				8	1.43	0.119	0.427
	+		+	+				7	1.76	0.101	0.409
	+	+	+	+			+	10	1.82	0.098	0.454

Table 2.2.b. Average models and their estimates for $\delta^{13}\text{C}$ distance and $\delta^{15}\text{N}$ distance between the two feather samples of each individual, presented with the 95% confidence intervals and the relative importance of each term. The Naglekerke R^2 of the average model was for $\delta^{13}\text{C} = 0.49$ and $\delta^{15}\text{N} = 0.45$.

*$\delta^{13}\text{C}$ distance ~ pre-winter condition * strat + sex + condition:sex + (1|colony/id)*
 *$\delta^{15}\text{N}$ distance ~ strat * sex + pre-winter condition+(1|colony/id)*

Isotope	Parameter	estimate	2.5%	97.5%	Relative importance
carbon	(Intercept)	-1.028	-1.282	-0.774	
	Cent.con	0.033	-0.196	0.262	1
	Sex M	-0.247	-0.545	0.054	0.65
	Strat 2	0.128	-0.200	0.456	1
	Strat 3	1.602	1.174	2.030	1
	Cent.con:strat 2	-0.293	-0.620	0.034	1
	Cent.con:strat3	-1.039	-1.473	-0.604	1
	Cent.con:sexM	0.016	-0.323	0.354	0.18
nitrogen	(Intercept)	-0.582	-0.851	-0.313	
	Strat2	-0.462	-0.904	-0.020	1
	Strat3	1.267	0.812	1.722	1
	Cent.con	0.126	-0.038	0.291	0.57
	sexM	0.193	-0.246	0.632	0.40
	sexM:strat2	-0.687	-1.391	0.018	0.12
	sexM:strat3	-0.167	-1.050	0.715	0.12

Chapter 3

Consequences of Individual-Specific Over-Wintering Strategies in Northern Gannets (*Morus bassanus*)

3.1 Abstract

Our understanding of the impacts of individual variation in foraging behaviour comes primarily from studies in the breeding season of proximal effects on breeding success. However, for migrants especially, such behaviour should not be considered independently of processes in previous and subsequent seasons. Here I use Stable Isotope Analysis (SIA) and geolocation to quantify individual variation in the over-wintering strategies of Northern gannets (*Morus Bassanus*) exhibited in the non-breeding season. I document the spatial occurrence of three distinct foraging strategies along a continuous latitudinal gradient of over-wintering destinations and identify a southern wintering region off the coast of West Africa as a productive region. Competition in the area may promote individual niche partitioning.

As expected, females over-wintering at lower latitudes are delayed in their return to the breeding colony. However, males return before the females and their timing of arrival was found to be independent of their distance from the colony. I suggest that distant migration to the southern region is highly rewarding for males despite an extended return journey that may potentially delay their arrival at the colony. Individual over-wintering foraging strategy explained a large proportion of the variation in the timing of hatching. For individuals specialising on a diet suggestive of discard foraging, breeding onset was delayed, which may be attributable to the low nutritional value of discards. I conclude that for individuals wintering at high latitudes, this is not a strategy 'chosen' to improve condition between years. And though the 'decision' to feed at a high-trophic level cannot yet be identified as cause or effect, I suggest that individuals specialising on this diet suffer a breeding cost via a COE.

3.2. Introduction

In migrating species the interaction between individual variation and the downstream effects of seasonal events is likely to be complex. Different processes dominate the breeding and non-breeding seasons, which alongside environmental variation increases the scope for variation in individual 'decisions' and the consequences of these decisions. As such individuals may be flexible in their behavioural strategies between seasons and locations. Flexibility at the population level for the adoption of such strategies can influence future behaviour and success via a mechanism of Carry-over effects (COEs) (Harrison et al 2010; Gunnarsson et al 2006).

Different strategies may arise with ecological opportunity and seasonal resource availability (e.g. Pierotti and Annet 1991), with sex differences and physiological performance (e.g. Kernaléguen et al 2012; Bearhop et al 2006; Phillips et al 2011, 2009, 2004), or age and skill acquisition. However, individual specialisation may occur independently of these factors (Araújo et al 2011; Bolnick et al 2003). Roughgarden's (1972; 1974) theory of individual niche specialisation, developed by Bolnick et al (2003), states that the total niche width (TNW) of the population is the sum of the within- and between-individual components (WIC; BIC). This theory of niche specialisation refers to differences in behavioural strategies between individuals within the population, including variance in the exploitation of resources.

Variation in individual strategy within the TNW has subsequent consequences. With the occurrence of specialists and generalists with various foraging strategies, the impact of the consumer species on the ecosystem will not be homogeneous (e.g. Furness et al 2007). Additionally these individuals may be more or less susceptible to environmental variability and change (Kernaléguen et al 2012). Hence, exploitation of anthropogenic resources may have implications directed towards certain subsets of the population (e.g. Bearhop et al 2011; Plummer et al 2013).

There is ample evidence to suggest a strong association between fishing vessels and seabirds feeding from their discards (Furness et al 2007; Arcos & Oro 2002; Blaber et al 1995). This association has been quantified during the breeding period (e.g. Votier et al 2010; 2004b), and the effects considered independently of behaviour in the non-breeding

period. However it is highly likely that migration routes and/or wintering sites also overlap with fisheries as they congregate at the most productive regions of the sea. Fishing practices provide access to increased resources and to prey types of a high trophic level that are normally out of reach, beyond the diving capabilities of these birds. In the breeding season males tend to exploit this resource more than females and individuals using fisheries waste tend to have lower Body Mass Indices (BMI) (Stauss et al 2012; Votier 2004a). I have also found that this relationship is continued between seasons in the Northern gannet (*Morus bassanus*); following breeding in the summer, individuals poor condition foraged at a high trophic level during the non-breeding season (Chapter 2). It is likely that in light of the sequential nature of seasonal and migratory systems, events in the non-breeding season will have impacts on future processes and subsequent breeding. Moreover, Individuals of differing foraging strategy may be more or less susceptible to environmental change (Kernaléguen et al 2012). Hence, the combined ecological impacts of individual variation in foraging niche and COEs shape the effectiveness of management and conservation practices. With this in mind it is important to investigate the potential downstream impact of environmental variation and/or anthropogenic processes, in the context of COEs.

For migrating species it has been hypothesised that migration distance, quality of non-breeding habitat and quality of diet will have COE on the transition into the following breeding season, subsequent state and breeding success (e.g.Sorensen et al 2009; Furness et al 2006; Gunnarson et al 2005; Bearhop et al 2004b; Marra et al 1998). Bearhop et al (2004) documented that winter habitat quality in migrating black-throated blue warblers (*Dendroica caerulescens*), acted on subsequent arrival at the breeding colony via a COE. Additionally in a study of Cape gannet (*Morus capensis*) foraging behaviour, Grémillet et al (2008) identified the negative effect of a poor quality winter diet in discard foraging on chick growth in the following season. But ultimately, very little is understood regarding the possible downstream impacts of individual decisions made in the non-breeding season. This is especially so for seabirds, as their vast migration and at sea foraging behaviour, makes it difficult to follow individuals through seasons.

Though there is a paucity of long-term studies that have followed individuals through multiple seasons, one such study quantified the COE of winter habitat quality onto the transition into the next season, which consequently influenced breeding success.

Gunnarsson et al (2005) identified this COE in Black-Tailed Godwits (*Limosa limosa islandica*), where individuals that wintered in higher-quality habitats returned to their Icelandic breeding grounds earlier in the season. Subsequently their breeding success was greater than those wintering in poor-quality habitats.

Studies that have used Stable Isotope Analysis (SIA) (e.g. Cherel et al 2006; Hobson et al 2002) have identified discrete foraging strategies among individuals within populations. For migratory species SIA has been of great importance. By sampling keratinous tissues of specific turnover/growth rates foraging behaviour and individual strategies can be investigated across seasons, with large sample sizes to examine variation within the population (Kernaléguen et al 2012; Jaeger et al 2010; Hedd and Montevecchi 2006). This technique has been successfully used in seabird species, sampling feathers of known moulting patterns and growth rates.

For avian migrants ringing effort has highlighted individual and population level variation in over-wintering destination (e.g. Nelson 2002). The use of global location sensing (GLS) and tracking devices has furthered our knowledge of migration routes and destinations in a range of migrants. Seabirds have been found to migrate long distances to temperate regions, spatiotemporally congregating with hetero- and con-specifics. Areas of great importance for overwintering are often in upwelling zones that run along continental shelf edges (Davoren et al 2006; Garthe et al 2007; Montevecchi et al 2009; Phillips et al 2006). These regions provide a high abundance of forage prey (Camphuysen and Van Der Meer 2005) for individuals to replenish energy lost in the previous breeding season and prepare for breeding in the next.

Here I investigated population and individual variation in the overwintering behaviour of Northern gannets (hereafter gannet). There has been increased study effort investigating the strong association between fishing vessels and northern gannets around the UK. These studies have developed an understanding of the proximate influences in individual foraging strategy. However, to fully understand the sequential nature of cause and consequence in individual variation this association and related processes should be considered between seasons. The relationship between individual condition and non-breeding foraging behaviour can shed light on the impacts and importance of foraging strategies and

interactions with human fisheries, revealing some of the causes and consequences of individual variation. Here we focus on four questions 1) what is the individual variation in migration schedule? 2) Do the overwintering strategies of migration and foraging affect arrival date at the colony following spring migration? 3) Does the migration and foraging strategy influence the chick hatch date in the following season? 4) If these are COEs on arrival and hatch date, what are their consequences for change in condition between consecutive years?

3.3 Methods

3.3.1 Geolocation

In July of 2010 and 2011, Mk19 and Mk5 British Antarctic Survey (BAS) light-level geolocators (global location sensing; GLS) were deployed on adult breeding gannets at Bass Rock, Northwest Scotland (56.08⁰N, 2.64⁰W) and Great Saltee, Southwest Ireland (52.12⁰N, 6.60⁰W). Breeding adults, nesting away from the colony edge, were selected at random and caught at nest changeover with a brass noose (Votier et al 2010). Only pairs with chicks older than two weeks of age were caught for data collection. Chick age was estimated into weekly categories by thickness of down, plumage patterns and size relative to chicks of known age (Nelson 2002) and standardised to July 1st of that year.

Geolocators potted in hard epoxy were fitted to the tarsus attached to a tarsus plastic ring using cable ties (Fox & Phillips 2010). At less than 10g the device was less than 0.35% of the average adult body mass. Geolocators were collected in the following breeding seasons in July 2011 or 2012, providing data from a single winter migration or two consecutive winters.

Mk 19, 15 and 5 loggers were used, these models recorded ambient light-level intensity with reference to time every minute and the maximum light intensity every 10/5/2 minutes. Data was downloaded and converted into daily light curves using BASTrak TransEdit2 (Fox & Phillips 2010). Using a light-intensity threshold of 16 sunrise and sunset transitions were identified. A minimum dark period of 4 hours was set to remove any light-dark transitions created by shading, or cloud cover. Daily position was calculated from day length providing latitude and the absolute time of midday and midnight providing longitude. All positions four weeks either side of the spring and autumn equinoxes were removed as it is during this period that day length cannot provide an accurate estimate of latitude. Individual tracks were projected using ArcGIS10.0.

3.3.2 Identifying Winter Location

Individual tracks of migration showed that all gannets moved along a major latitudinal flyway from the UK running parallel to the coast of West Europe and North West Africa. For each individual, displacement from the colony indicated that it was during the month of December that all individuals were settled at a non-breeding location following post-

breeding migration. Geolocators are only accurate to ± 100 miles due to the light-logger sampling rate (Fox & Phillips 2012). All latitude coordinates in December were therefore averaged and the December mean taken as the 'winter location'. This provided a continuous variable for analyses.

3.3.3 Arrival Day

Loggers also measured conductivity providing wet/dry information. With the Mk 5 logger this is sampled every 3 seconds and for every 10 minutes the total number of wet samples recorded ranging from 0 (always dry) to 200 (always wet) (Fox & Phillips 2012). Mk19 loggers record the exact time of wet-dry state change, but only where the new state is sensed for more than 6 seconds (Fox & Phillips 2012). During migration gannets spend much of their time on the sea, as opposed to the breeding season where the need to care for the egg or chick means long periods are spent on land at the colony. The first night following migration where all activity recordings were dry was therefore taken as the arrival day at the colony, recorded as Julian day.

3.3.4 Biometrics and Condition

Measurements were taken from individuals as they were leaving the colony for local foraging trips, this removed any influence of recent catch on the over-estimation of body measurements. Biometrics recorded included wing, tarsus and mandible length (measured from the tip of the bill to first feather growth) and body mass (kg) to the nearest 50g. The strongest correlation between size and body mass was seen with mandible length ($r=0.32$, $t=2.32$, $df=42$, $p=0.025$). Individual scaled mass was therefore calculated using the SMA regression values and mean mandible length of the population for individuals by year, following Peig and Green's (2009) equation:

$$SM = \hat{M}_i \left[\frac{L_0}{L_i} \right]^{SMA}$$

where M_i and L_i are the body mass and the linear body measurement of the individual (respectively); SMA is the regression exponent of M on L; and L_0 the mean of the linear measurement for the population. Scaled body mass was used as a measure of body condition in the breeding season. As feather samples were taken in 2011 and 2012, pre-

winter condition was measured in the summer prior to feather growth (2010 and 2011 respectively) and post-winter condition in the summer of feather collection (2011 and 2012 respectively).

Condition, was highly positively correlated between consecutive breeding seasons ($r=0.452$, $t=3.511$, $df=48$, $p < 0.001$). Investigating post-winter condition alone may therefore only highlight the intrinsic effects of body condition; hence the change in condition was investigated between years to examine possible carry-over effects.

3.3.5 Feather sample collection

3 samples were taken from the feather with biometrics post breeding from the Primary 8 wing feather: base, middle and tip. The moult pattern indicates that feather growth of P8 occurs during overwintering, therefore SIA of these samples gave dietary information of prey consumed and assimilated during these three periods of growth, where the base sample was synthesised most recently. Tip samples were later removed from analysis as the $\delta^{13}\text{C}$ ratio was greatly enriched compared to base and mid samples. It is probable that this may be due to the dark brown colour of the feather tip due to high melanin (Michalik et al 2010).

3.3.6 Stable Isotope Analysis

Feather samples were thoroughly washed with distilled water and dried at $\sim 40^{\circ}\text{C}$ in a drying cupboard for at least 36 hours over 3 days. Between 0.6 and 0.8mg of each sample was weighed out and finely cut into tin cups for stable isotope analysis in Isotope Ratio Mass Spectrometers (IRMSs). Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios were measured using a ThermoElectron Delta Plus XP with Flash HT elemental analyser and a Thermo Fisher Scientific Delta V Plus with a Gas Bench II configured for simultaneous $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ isotope analysis. SIA was conducted at the Life Sciences Mass Spectrometry Facility, Scottish Universities Environmental Research Centre (SUERC). Ratios are reported in parts per thousand (‰) with reference to international standards following the equation $\delta X = 1000[(R_{\text{sample}}/R_{\text{standard}}) - 1]$. At set intervals standards of GEL, ^{14}N ALA, glycine and tryptophan were analysed between feather samples in the IRMSs.

3.3.7 Foraging strategy

Stable isotope analysis of all feather samples over the two years of data indicated two dietary clusters during winter migration. The two clusters were defined by k-means cluster analysis. Three foraging strategies were identified: strategies 1 and 2 as specialist strategies where both the individual's base and mid feather samples were found in the same cluster. For individuals of the third strategy, a mixed strategy, base and mid sections were found in opposing dietary clusters.

3.3.8 Foraging specialisation

The absolute difference in $\delta^{15}\text{N}$ between the two feather sections indicates trophic level foraging specialisation or repeatability, and that of $\delta^{13}\text{C}$ the foraging habitat specialisation. This is reported as isotope distance in analyses

3.3.9 Statistical Analyses

A series of generalised linear mixed models (GLMMs) were fitted to investigate predictors of arrival day, standardised chick age and change in condition between breeding seasons. The continuous variables of arrival day, December latitude and pre-winter condition were centralised for modelling by the following equation: $(x - \bar{x})/sd$. As arrival day is present in all models only Bass Rock data was analysed in GLMMs. Great Saltee individuals were removed from analysis due to their significantly earlier arrival day at the colony ($\chi^2=44.55_{1,4}$, $p<0.001$). Even with colony as a random effect the inclusion of these individuals greatly affected model estimates. A separate model for this colony could not be analysed due to the small sample size of individuals with successfully downloaded geolocation data.

The first model was fitted to centralised arrival day as the response variable. This model included the fixed effects of foraging strategy, sex and centralised pre-winter condition and December latitude, all in interaction. Random factors included year and individual ID.

The second model was fitted to standardised chick age as a continuous variable. This model included the fixed effects of foraging strategy, sex and centralised pre-winter condition. Only ID was present as a random effect as year was insignificant. Though centralised December latitude did not converge with any of the variables included, it could not be run in

this model due to too small a sample size. Latitude was therefore removed from analysis in favour of foraging strategy.

Finally, two GLMMs were run to investigate the change in condition between years. The first included fixed effects of sex, centralised arrival day, foraging strategy and centralised December latitude. The second included fixed effects of sex, centralised arrival day and standardised chick age. All fixed models could not be included in the same model due to too small a sample size. Both models only included ID as a random factor. Year was removed due to insignificance.

For each of these four GLMMs a set of top candidate models within 2 Akaike's information criterion (AIC) of the topmost model was identified for each model analysis. These top model sets were averaged using the MuMIn package (Bartoń 2013), averaging the terms and their estimates by the weighting of candidate models. The significance of model terms was assessed using relative importance and 95% confidence intervals for these two tailed tests. The resulting average model was compared to a null model (including only random terms) to calculate Nagelkerke pseudo R^2 , over dispersion and model residuals to assess model fit. All statistical analyses were carried out using R 3.0.0.

3.4. Results

3.4.1 Individual variation in migration

Having had feather samples collected for SIA, geolocators were attached and the data successfully 43 geolocators were deployed across the two study years at the Bass Rock (27 geolocators deployed in 2010; 16 in 2011), with 13 birds tagged in both years, and data were successfully downloaded from 30 individuals. 8 geolocators were successfully retrieved from Great Saltee having been deployed in 2010. One of these individuals was removed from analyses as they did not leave the vicinity of the colony, and spent periods on dry land from the 1st January.

All individuals travelled along a latitudinal gradients south of the UK to the Bay of Biscay, Portugal and Northwest Africa, with very little longitudinal movement. Following breeding at the colony individuals made a large scale movement over a short time period before settling in one area for the winter. Though there was no staging apparent during autumn migration, after over-wintering many of the gannets staged during spring migration when returning to their colony. Some even travelled beyond their colony further north before returning to the colony (Figure 3.1.b).

Gannets wintered in two regions: the Northern region ($>40^{\circ}\text{M}$) around the UK and Bay of Biscay and the Southern region ($<40^{\circ}\text{M}$) from Gibraltar down to Mauritania (Figure 3.2). The majority of individuals wintered in the southern region; 72.2% ($n=26$) in December 2010 and 70.8% ($n=17$) in 2011. All but one of the 13 Bass gannets tracked over both years wintered in the same region in 2010 and 2011. This lone individual switched to the northern region in the winter of 2011 to 2012 and decreased in pre-winter condition from 4.13 to 3.18 between the two years, a change of 0.680 compared to the average change of 0.308 (± 0.114) for all individuals that decreased in condition between the two years.

In the non-breeding period when gannets are at their winter location, on all nights where activity was recorded individuals spent a high proportion of their time on the water. This behaviour dramatically changes in the breeding period when individuals spent many nights on dry land at the colony (Figure 3.1.b). The first night spent completely dry was significantly

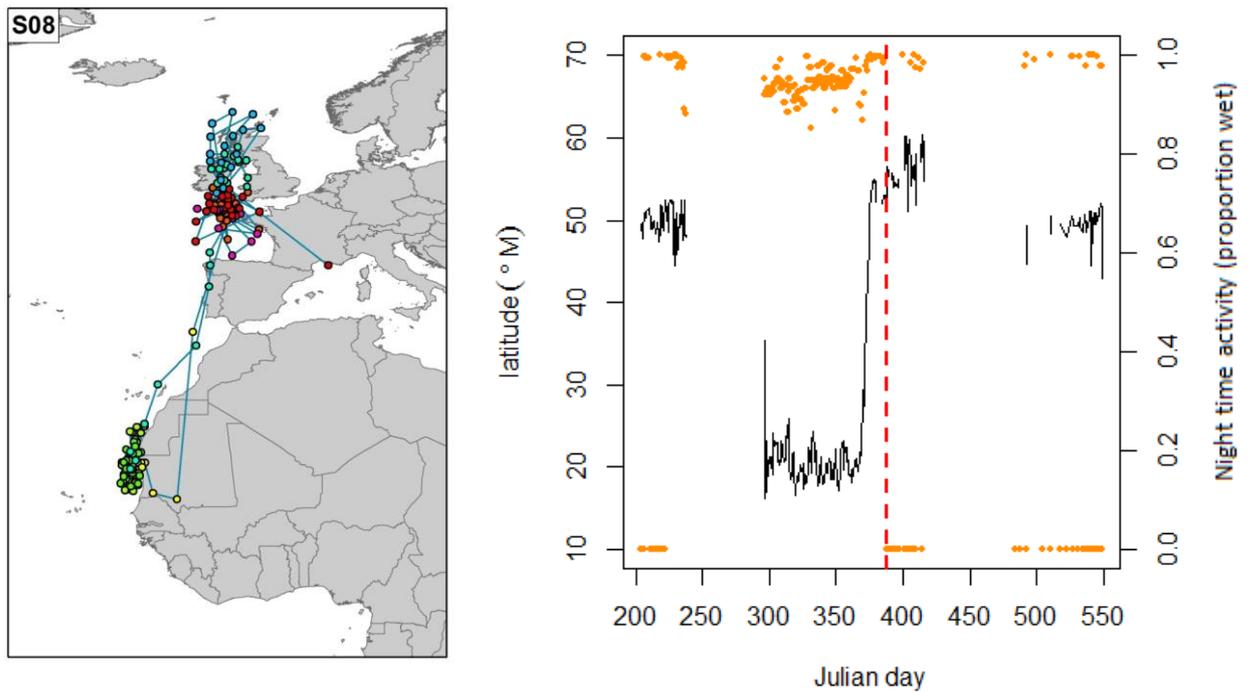


Figure 3.1. a) Migration track of individual S08 tagged at Saltee in 2010, a colour gradient from red through yellow and green to blue follows time from July 2010 to June 2011, b) noon and midnight latitude estimated from logger light-level curves (accurate to 200km) and proportion of night-time wet geolocation readings. The first dry night is taken as the return date to the colony highlighted with the red dashed line. Data were removed four weeks either side of the spring and autumn equinoxes.

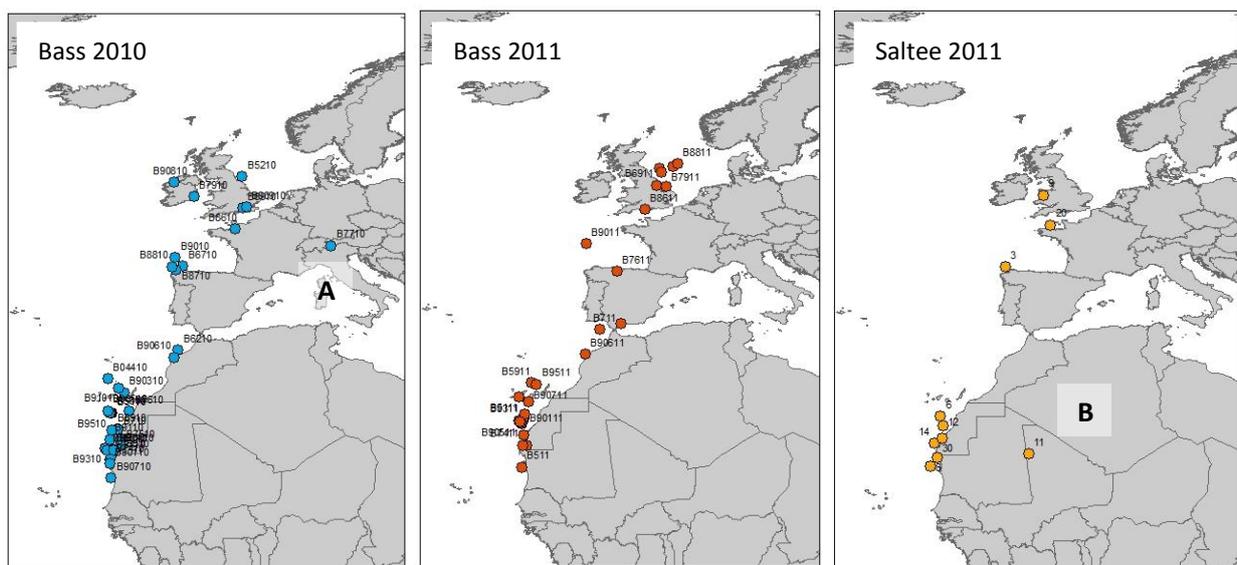


Figure 3.2. The over-wintering location for all tracked individuals taken as the mean December latitude. Individuals A and B were removed from analyses due to GLS data download errors.

earlier for gannets arriving at Great Saltee (median Julian day 23) compared to those arriving at Bass rock (median 70) ($\chi^2=44.55_{1,4}$, $p<0.001$).

3.4.2. Arrival day predicted by over-wintering foraging and migration strategy

The day of arrival was affected very little by the foraging specialisation in terms of $\delta^{13}\text{C}$ distance with an average model of R^2 0.032. Since nitrogen correlated strongly with latitude ($r=0.638$, $t=7.598$, $df=84$, $p<0.001$) the effects of foraging behaviour in terms of trophic level were investigated using the three category variable of foraging strategy.

Arrival day was best explained by a model set of eight models (Table 3.1.a.) with an average model that explained 26.7% of the variance in arrival day. An interaction between pre-winter condition and winter latitude was both significant with confidence intervals not crossing zero and highly important (relative importance 0.51; Table 3.1.b.). Both latitude and pre-winter condition separately interacted with sex (0.32 and 0.10 relative importance respectively), with relatively strong effects (Table 3.1.b.). Males returned to the colony within a short window around a median Julian day of 68 (± 9.5 IQR), independent of winter latitude and hence distance from the colony (Figure 3.3.a). In contrast, females that wintered further from the colony returned later and over a greater time period (74 ± 16.5) with a negative relationship between December latitude and arrival day (Figure 3.3.a). Though most males returned within a short time period, those that did arrive slightly later were of higher pre-winter condition relative to population than those that arrived slightly later (0.439 parameter estimate; Table 3.1.b.). Whereas, in females, individuals in good pre-winter condition returned to the colony earlier than those of poor pre-winter condition (Figure 3.3.b.).

Foraging strategy also explained some of the variance in arrival day, where individuals of mixed strategy 3 returned later than those of high trophic-level strategy 1 (Figure 3.4). Though this effect had a relatively low importance of 0.13, it was significant and of a strong predicted effect (parameter estimate of 0.634). The high proportion of individuals wintering around the UK with foraging strategy 1 did not influence this effect as it was independent of December latitude.

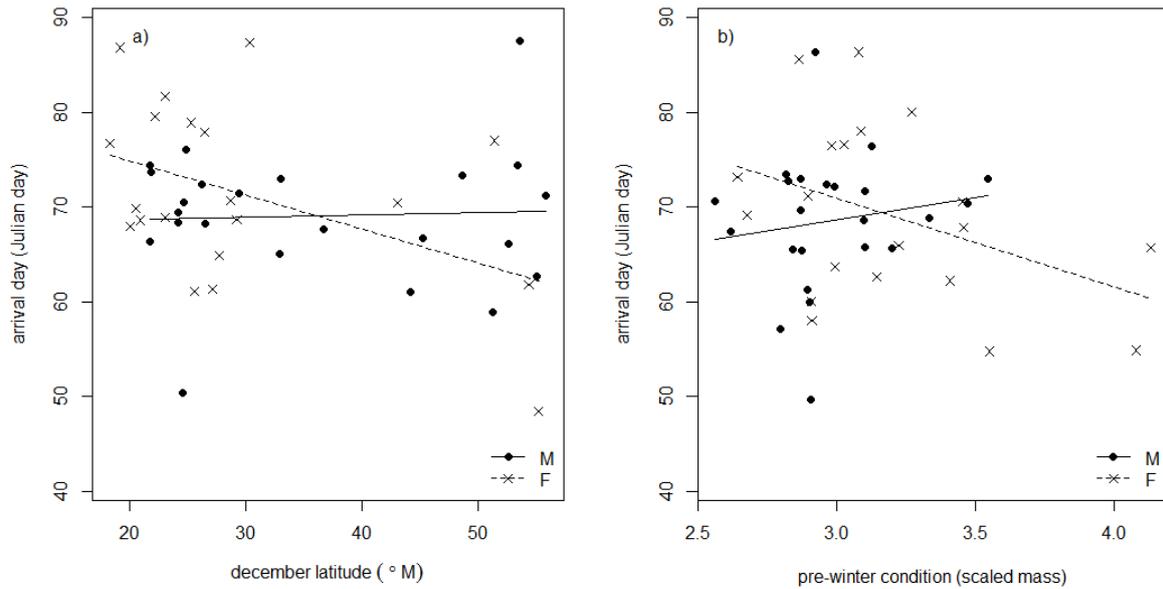


Figure 3.3. a) The effect of winter latitude on individual arrival day at the colony **b)** The effect of pre-winter condition on arrival day (males: solid circles, solid line, females: crosses, dotted line). Lines are the predicted effects and points the residuals of the average model.

3.4.3 Predictors of subsequent chick hatch date

Variation in standardised chick age was best explained by a top model set of five models (Table 3.2.a). Foraging strategy in interaction with pre-winter condition was of relatively high importance (0.30) in a robust average model ($R^2=0.37$). The interaction highlighted that for individuals in poor pre-winter condition, those that foraged in mixed strategy 2 hatched their chicks much earlier than those of strategies 1 or 3 (Figure 3.5.a).

3.4.4 Change in Condition

The change in condition between breeding seasons was largely explained by winter latitude and the interaction between arrival day and sex in an average model of $R^2=0.393$. Lone terms were of high importance (winter latitude=0.35; arrival day=0.67; sex=0.42), but of no significance and of little effect (Table 2.3.b). The interaction between sex and arrival day was of relatively little importance (0.08), however for both sexes individuals that returned relatively early decreased in condition between years (Figure 3.5.c). This model also included foraging strategy though this had very little relative importance (0.07).

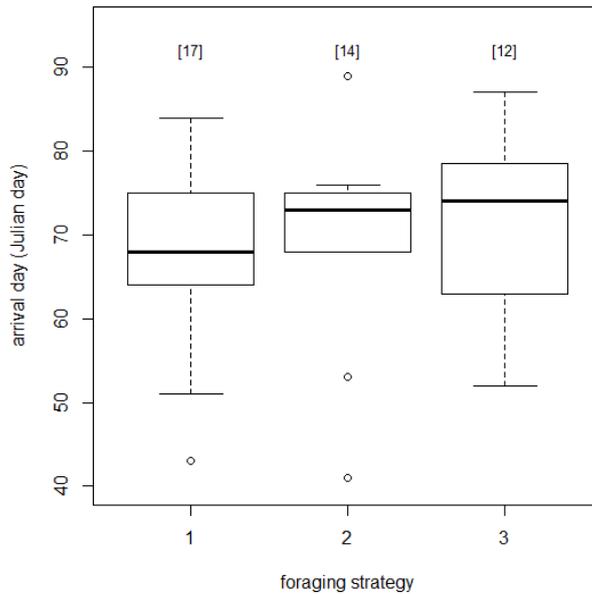


Figure 3.4. The arrival date of the three winter foraging strategies: 1) high trophic-level specialist 2) low trophic-level specialist 3) mixed foraging strategy. Numbers in parentheses are sample sizes. The effect is independent of winter latitude.

The second model investigated the variance in change in condition predicted by chick age, accounting for the variation predicted by sex and arrival at the colony. The average model highlighted the importance of chick age on the change in condition in interaction with sex (relative importance 0.56; Table 3.4.b), with a relatively strong effect (parameter estimate 0.209). Males that commenced breeding earlier with chicks of an older standardised age improved their condition between consecutive breeding seasons, whereas those that commenced breeding later showed a decrease in condition (Figure 3.5.d). The opposite was seen in females; as the chick increased in age, females had an increasingly negative change in condition. This average model explained a large proportion of the variation recorded in change in condition with a Nagelkerke R^2 of 0.524.

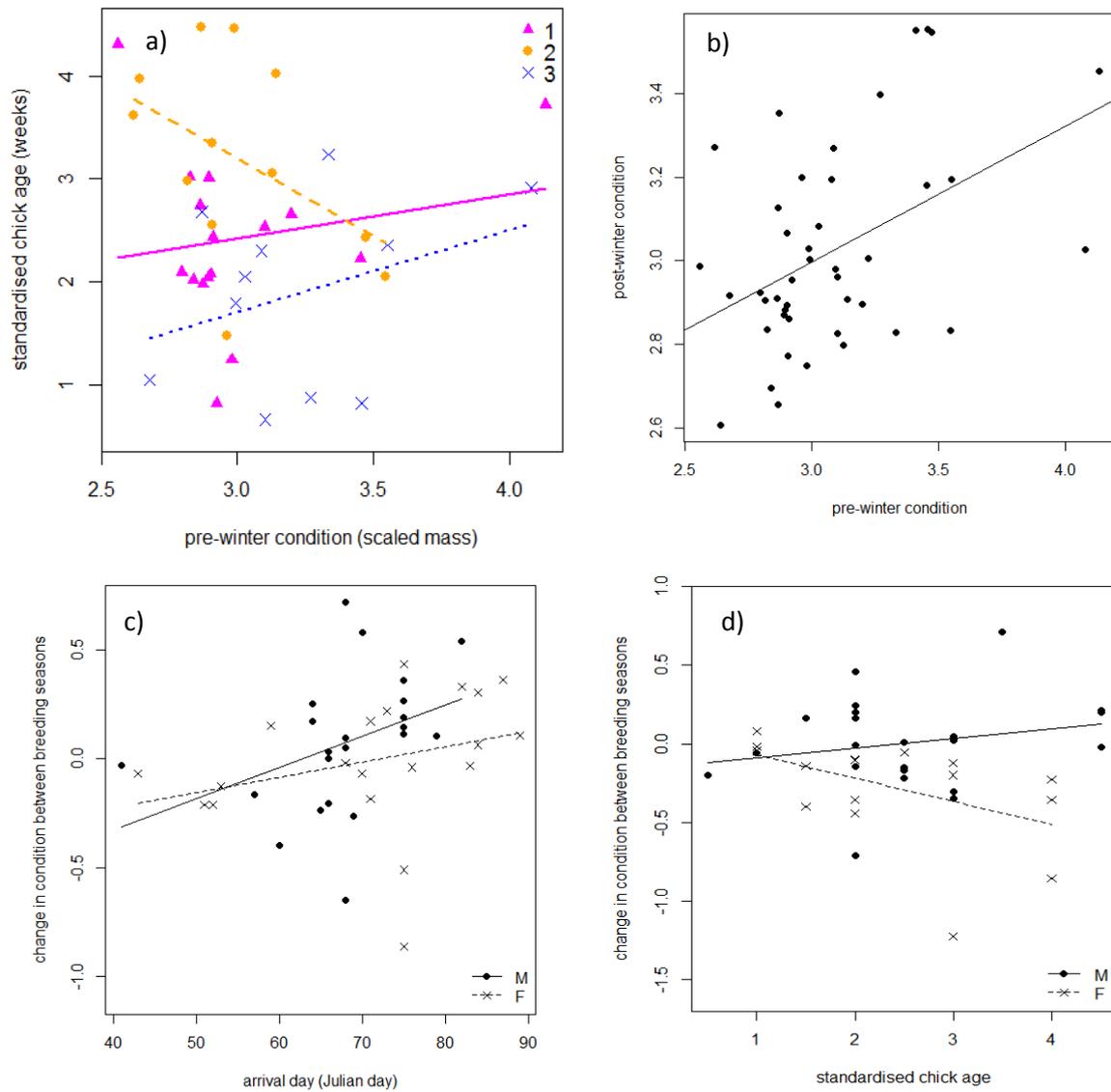


Figure 3.5. a) standardised chick age influenced by pre-winter condition in interaction with overwintering foraging strategy, b) relationship between pre- and post-winter condition for Great Saltee and Bass Rock gannets ($r=0.452$, $t=3.511$, $df=48$, $p=0.00098$), c) interaction between arrival day and sex (parameter estimate 0.079) affecting change in condition between consecutive breeding seasons for Bass Rock gannets, d) the effect of standardised chick age, hence breeding commencement on this change in condition. Figures a), c) and d) are derived from parameter estimates of average models, the lines are the predictions of these models and points the residuals.

3.5. Discussion

This study has revealed the carry-over effects of individual-niche specialisation in the non-breeding season, having detailed information on condition, or 'state', before and after over-wintering. I have identified clear sex differences in the parameters of winter migration, again influenced by the interaction of COE and INS phenomena. I have for the first time found evidence for the downstream impact of foraging strategy on subsequent breeding events in the Northern gannet, highlighting the continued effects of their strong association with fisheries.

3.4.1 Consequences of migration strategy on arrival day at the breeding colony

The strong interaction between winter latitude and sex was an important predictor of arrival date at the breeding colony, in a highly robust model. In females, latitude explained a large proportion of the variance that existed in the arrival date (Figure 3.3.a); with those migrating to low latitudes in the southern region returning later in the season than those that wintered at higher latitudes in the northern region. Phillips et al (2011, 2009) have identified further differences in winter distribution between the sexes in albatross and petrel species. Northern gannets migrate uniformly southward along a major latitudinal flyway (Fort et al 2012) and so it may be expected that those that travel further take longer to return the colony. This pattern was observed by Grecian (2011) in both sexes, however in contrast to this result we found no such pattern in males (Figure 3.3.a). Most males returned within a tight three week window and earlier than the median return date for females. This result suggests that firstly it is beneficial for males to arrive before females to prepare for breeding and defend the nest site, and secondly that it must be highly beneficial for males to make the long migration south to Africa despite the potential cost of a rapid return migration or delayed arrival at the colony.

Gannets breeding at Great Saltee returned an average of 47 days earlier than those returning to Bass Rock. This is a much greater difference than would be expected if it was solely due to distance between colonies, or the extrinsic environmental factors encountered along the way (Alves et al 2013; Gunnarsson et al 2006); though a gradual latitudinal gradient in the temporal pattern of breeding schedule have been noted by Wanless et al (2008).

Interestingly the average return date of males and females at Great Saltee was within two days of each other, whereas males at Bass Rock returned an average of 6 days earlier than the females of this colony. This may be a density-dependent effect as with increased density at Bass there is greater potential for local competition for breeding sites and resources (Gunnarsson et al 2006; Lewis et al 2001). This hypothesis is supported by the fact that within the variation of male return date those of good prior condition returned slightly later (Figure 3.3.b), suggesting they are at less risk of losing access to resources when they return.

In light of these results, it is probable that the migration distance is less costly than the timing of arrival at the colony for this species, owing to the relative homogeneity of marine migration routes compared to the migration routes of terrestrial avian species.

3.4.2 Consequences of foraging strategy on subsequent breeding

In the breeding season prey-switching has been recorded as individuals alter their foraging behaviour between trips for self-provisioning and chick-provisioning (Montevecchi et al 2009; Davoren and Burger 1999; Granadeiro et al 1998). Female northern gannets alter their diet feeding on oily forage fish when providing for a chick rather than discards that are low in fat (Strauss et al 2012). These findings suggest that while fishing practices may benefit individual survival, there is a cost for future breeding. However for individuals are prepared to make the costly journey to Africa and forage only on high quality low-trophic prey they can return to the colony later and still hatch their chicks early in the breeding season. This affect is analogous to the findings of Plummer et al (2013) and Robb et al (2008), who recorded strong negative downstream effects of food supplementation on the breeding success of garden birds.

Individuals specialising on a diet predominantly of high-trophic prey are likely consuming benthic discards that are often low in calorific and nutrient value (Stauss et al 2012). In the breeding season this diet has been found to have a negative impact on the breeding success of seabirds. As an example, this strategy has been found to decrease the chick growth rate in Cape gannets, *Morus capensis* (Grémillet et al 2008). Here I have identified a potential carry-over effect of this strategy between seasons; as individuals that foraged on a high-trophic diet during the non-breeding season arrived earlier at the breeding colony, but hatched their chicks later in the season than low-trophic specialists, or indeed individuals of

a mixed foraging strategy. Hatching late in the season suggests that individuals are in poor condition and are feeding from a low quality diet (Votier et al 2004a), unlike individuals feeding on small forage fish such as capelin, *Mallotus villosus* (Garthe et al 2000). Additionally, gannets feeding on lipid rich discards digest food quickly and inefficiently (Hilton et al 2000; Grémillet et al 2008).

3.4.3 Carry-over effect of over-wintering strategy evident in the change in condition between seasons

Latitude had little direct effect on subsequent state, but in its influence on transition to the next season, the winter location did so via a possible carry-over effect on arrival date (Harrison et al 2010; Gunnarsson et al 2006). Gannets that returned to the colony later from lower latitudes improved their condition between consecutive years. The southern wintering region is highly productive upwelling zone (Camphuysen and Van Der Meer 2005) and the only region where all three foraging strategies occurred spatiotemporally. In this region absolute time spent foraging is lower than that observed in less productive regions, suggestive of favourable foraging conditions with low energetic costs for the avian species that over-winter here (Garthe et al 2012; Hamer al 2007; Montevecchi et al 2009). Exploiting this region for longer may therefore allow individuals to increase energy reserves for rapid spring migration (Gunnarsson et al 2006) and subsequent breeding, reflected their positive change in condition. Furthermore comparing individuals within the region, those that arrive later may prolong their stay to further exploit the region's resources.

Perhaps surprisingly a relationship between arrival date and chick age was not identified, unlike that which has been found in other studies of migrating avian species. Studies across a range of species have identified positive relationships between arrival date and hatching date (e.g. Hotker 2002; Saino et al 2004) improving chick condition (Votier et al 2004a), however there may be a cost of arriving too early. This cost was observed in snow geese where breeding probability decreases with early arrival (Bety et al 2004). The evidence here suggests that arrival date has a strong consequence on change in condition via a pathway not related to chick age.

3.4.4. Conclusions

In line with Harrison et al's (2010) definition of carry-over effects, the latitude of over-wintering location interacts with sex to strongly affect individual return date to the breeding colony. In acting on this transition into the next breeding season, latitude has a downstream effect on post-winter condition. Furthermore, while foraging on a high-trophic diet may support individuals of poor state within the non-breeding season, there appears to be a cost, delaying the onset of breeding. Unlike individuals that forage on a low-trophic diet for a prolonged over-wintering period, that return later in the breeding season, but with the resources to commence breeding earlier.

This study has been the first to collect such detailed information on over-wintering strategies, following individuals through consecutive seasons. In doing so I have identified an interaction between individual niche specialisation and carry-over effects, highlighting the potential negative impact of the continuous association between gannets and fishing vessels.

3.6 Appendix of Tables

Table 3.1.a. Top model set within 2 AIC of the topmost model, explaining the variance in the arrival date as a centralised variable. For each model the degrees of freedom, weighting and calculated Nagelkerke R^2 is given. Terms have been abbreviated from the original model.

*Centralised arrival date ~ foraging strategy*centralised pre-winter condition*sex*centralised latitude +(1|id)+(1|year)*

Intercept	Cent. con	Cent. lat	sex	Strat.	Cent.con :cent.lat	Cent.con :sex	Cent.lat: sex	df	Δ AIC	weight	R^2
+	+	+			+			7	0.00	0.097	0.163
+				+				6	0.98	0.059	0.097
+								4	1.04	0.058	0
+		+	+				+	7	1.20	0.053	0.137
+		+						5	1.29	0.051	0.043
+	+	+	+		+	+	+	10	1.48	0.046	0.255
+	+	+	+		+		+	9	1.69	0.042	0.211
+	+	+	+		+			8	1.72	0.041	0.169

Table 3.1.b. The average model parameter estimates and relative importance of their effects from the average model of the top model set. The parameters highlighted are those with a significant directional effect on the arrival date where confidence intervals do not span zero. Naglekerke $R^2=0.26$.

*Cent.arr ~ lat*con + con:sex + lat:sex + sex + strat +(1|id)+(1|year)*

Parameter	Estimate	2.5%	97.5%	Relative importance
(Intercept)	-0.218	-1.018	0.582	-
Cent.con	-0.290	-0.542	0.062	0.51
Cent.lat	-0.421	-0.849	0.007	0.74
Con:lat	-0.459	-0.864	-0.053	0.51
Strat2	0.175	-0.383	0.734	0.13
Strat3	0.634	0.034	1.234	0.13
sexM	-0.104	-0.589	0.380	0.41
Lat:sexM	0.446	-0.064	0.956	0.32
Con:sexM	0.439	-0.128	1.006	0.10

Table 3.2.a. The variance in standardised chick age predicted by a top model set within 2 AIC of the topmost model. Terms from the original model have been abbreviated.

*Standardised chick age ~ foraging strategy*centralised pre-winter condition * centralised arrival date + (1|id)*

(Intercept)	Cent.arr	Cent.Con	strat	Cent.Con:strat	df	Δ AIC	weight	R ²
+			+		5	0.00	0.207	0.248
+	+		+		6	0.66	0.149	0.276
+		+	+	+	8	1.53	0.097	0.336
+	+	+	+	+	9	1.64	0.091	0.370
+		+	+		6	1.73	0.087	0.254

Table 3.2.b. Average model and parameter estimates with 95% confidence intervals and the relative importance for each included term. The average model Nagelkerke R² was 0.37.

*Chick~cent.arr+cent.con*strat +(1|id)*

	Estimate	2.5%	97.5%	Relative importance
(intercept)	2.454	2.027	2.881	
Strat2	0.648	-0.013	1.309	1
Strat3	-0.693	-1.391	0.004	1
Cent.arr	0.174	-0.100	0.447	0.38
Cent.con	0.149	-0.241	0.539	0.44
Cent.con:strat2	-0.676	-1.402	0.051	0.30
Cent.con:strat3	0.126	-0.498	0.750	0.30

Table 3.3.a. Model set within 2 AIC of the top model explaining the variance in the change in condition between consecutive breeding seasons. Terms have been abbreviated from the original model.

*Change in condition ~ sex*centralised arrival date*foraging strategy*centralised latitude +(1|id)*

(intercept)	Cent.arr	Cent.lat	Sex	Strat	Cent.arr:sex	df	Δ AIC	weight	R ²
+	+					4	0.00	0.080	0.127
+	+		+			5	0.17	0.073	0.229
+						3	0.019	0.073	0
+	+	+				5	0.061	0.059	0.205
+			+			4	0.094	0.050	0.073
+	+	+	+			6	1.36	0.040	0.272
+	+		+		+	6	1.51	0.038	0.265
+		+				4	1.57	0.036	0.037
+	+	+		+		7	1.73	0.034	0.357

Table 3.3.b. The averaged model and parameter estimates given with 95% confidence intervals and the relative importance of each term. The Nagelkerke R² of the average model being 0.393.

*Con_change ~ cent.arr*sex + cent.lat + strat +(1|id)*

	Estimate	2.5%	97.5%	Relative importance
(intercept)	-0.08761	-0.218	0.043	
Cent.arr	0.07585	-0.020	0.171	0.67
sexM	0.11636	-0.065	0.298	0.42
Cent.lat	0.05708	-0.050	0.164	0.35
Cent.arr:sexM	0.07938	-0.112	0.270	0.08
Strat2	0.18749	-0.077	0.452	0.07
Strat3	0.01330	-0.247	0.274	0.07

Table 3.4.a. Model set within 2 AIC of the top model explaining the variance in the change in condition between consecutive breeding seasons including chick age, standardised to age on July 1st of that year. Terms from the original model have been abbreviated.

*Change in condition ~ sex*centralised arrival date*standardised chick age + (1|id)*

(Intercept)	Cent.arr	chick	sex	Cent.Arr:chick	Cent.Arr:sex	Chick:sex	df	ΔAIC	weight	R ²
+		+	+			+	6	0.00	0.134	0.374
+	+	+	+			+	7	0.04	0.131	0.469
+							3	0.89	0.085	0
+	+		+				5	0.99	0.081	0.220
+	+						4	1.12	0.076	0.103
+			+				4	1.24	0.072	0.096
+	+	+	+	+		+	8	1.30	0.07	0.504
+	+	+	+		+	+	8	1.41	0.066	0.499

Table 3.4.b. Average model and parameter estimates with 95% confidence intervals and the relative importance for each included term. The significant parameters where confidence intervals do not span zero have been highlighted. The average model accounted for a high proportion of variance with a Nagelkerke R² of 0.524.

Con_change ~ chick +sex + cent.arr +chick:sex + chick:cent.arr + cent.arr:sex+(1|id)

	Estimate	2.5%	97.5%	Relative importance
(intercept)	0.074	-0.345	0.492	
Chick	-0.147	-0.290	-0.005	0.56
sexM	-0.227	-0.844	0.389	0.77
Chick:sexM	0.209	0.026	0.391	0.56
Cent.arr	0.042	-0.147	0.232	0.59
Cent.arr:chick	0.064	-0.081	0.209	0.10
Cent.arr:sexM	0.080	-0.117	0.277	0.09

Chapter 4

GENERAL DISCUSSION

With the aid of stable isotope analysis (SIA) and tracking devices or global location sensing (GLS) techniques, an extensive body of work has documented the individual variation that exists in the foraging behaviour of seabirds. However, much of this research has focused on the breeding season, quantifying individual variation of central-based foragers and its direct influence on reproductive success (e.g. Grémillet et al 2008). Furthermore the importance of individual specialisation and its feedback loops on population density and community structure remains relatively unstudied (Araújo et al 2011). In the knowledge that seasonal events can have downstream impacts on processes in the next (Harrison et al 2010), it is important to consider individual variation in the non-breeding period and its effect on future condition and breeding.

4.1. Carry-over effects and individual niche specialisation of overwintering behaviour

This thesis has identified individual overwintering variation in the non-breeding period in individual foraging strategy, and over-wintering location and schedule. Within the population, individuals specialised on particular foraging behaviours; foraging either on offshore prey of high trophic level (Strategy 1), or inshore prey of low trophic level (Strategy 2). A third, generalist foraging strategy, comprised of individuals foraging on both prey of these types (Strategy 3). The Northern gannet (*Morus Bassanus*, hereafter gannet) is often described as a generalist opportunistic forager, however within the total niche width (TNW) of the community and the niche space of the generalists individuals, there are clearly discrete foraging strategies, separated by a between individual component (BIC) (Bolnick et al 2003).

Interestingly pre-winter condition following breeding did not, via a carry-over effect (COE), influence the foraging strategy of the individual. This suggested that the spatiotemporal overlap of these strategies was a result of individual niche specialisation. However, the trophic level of prey tended to be higher for individuals of poor previous condition (Figure 4.1). This is a trend that has been documented in avian marine predators in the breeding season (e.g. Votier et al 2004a). Furthermore, for individuals that foraged on prey of a high

individuals in good condition are able to travel the vast distance to benefit from the southern upwelling region, with the trade-off of possible delayed arrival at the colony the following year.

The Canary upwelling region is highly productive and a destination for all individuals of high condition. It has been stipulated that wintering close to the colony is a choice to reduce the cost of migration (Grecian 2011), however for the Northern gannet this appears to be a constraint, as this strategy does not allow individuals to improve their condition, or forward their onset of breeding. The mechanism of this carry-over effect is unknown, but previous studies would suggest that a high trophic diet is indicative of discard foraging on a food of low nutrient quality. Grémillet et al (2008) found a negative effect of extensive discard foraging on the growth pattern of Cape gannet (*Morus capensis*) chicks. They defined the differing effects of discard foraging on adults and their chicks as the “junk food hypothesis”. This work very much supports Grémillet et al’s (2008) hypothesis, as it appears that possible discard foraging supports individual survival between seasons, but has negative downstream impacts on their chicks.

Like the sex differences that have been identified in space use during foraging trips in the breeding season, in a range of seabird species (e.g. Stauss et al 2012; Bearhop et al 2006; Clarke et al 1998), this investigation also highlighted strong sex differences in migration schedules. The median return date of males was earlier in the breeding season than females, suggesting that the males return to prepare for breeding and protect nest sites. Despite the added cost of rapid or delayed return, it still appears to be advantageous for males to winter in the productive upwelling regions of West Africa.

SIA and GLS technology has enhanced our ability to observe, monitor and quantify behaviour spatially and temporally across seasons, however we are still constrained in our ability to accurately measure condition immediately before and after migration. Consequently, though there was a difference in condition between years, we found no direct carry-over effect of over-wintering behaviour on this change in condition. It is likely that foraging behaviour determines resource replenishment and hence the change in condition between years which in turn will, to some degree, influence subsequent onset of breeding.

4.2. Further Comments

The strong correlation in condition between consecutive years questions the use of absolute condition in studies of COEs between seasons. Typically the studies that have investigated the effects of processes between seasons, ignore the feedback loops (Araújo et al 2011) and sequential nature of multiple seasons across years (Harrison et al 2010). However I would suggest that the more subtle 'change in condition' between seasons needs to be measured in order to investigate COEs.

This thesis has identified variation at the individual level within the total niche width (TNW) (Bolnick et al 2003) of a foraging seabird. The population is flexible in its ability to exploit the resources available to it. And additionally, individual foraging strategies differing in their degree of specialisation, suggests that the individuals also differ in their flexibility. The interaction between individual niche specialisation and flexibility will determine the impact of environmental variability on the population. Forthcoming change in fishing management and discard availability will therefore have varied impacts on individuals. Future work should continue to investigate individual dependence on this anthropogenic practice, and question whether discards are supplementing the weaker individuals in the population, or indeed whether it is discard foraging that brings about a negative change in individual condition in marine predators.

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