INTRA- AND INTER-COLONY DIFFERENCES IN NON-BREEDING STRATEGIES IN THE NORTHERN FULMAR, *FULMARUS GLACIALIS*

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Photo: L.Quinn

*'The hero of the story which I have to tell…appears to observers in different guise; to some it is a ghost, to some the conqueror of the sea, to others foul, or a fool, or food…**Its name is fulmar**'*

James Fisher, 1952.

THESIS CONTENTS

AUTHOR'S DECLARATION

I declare that the work presented in this thesis has been composed and undertaken by myself. No part of this work has been accepted in any previous application for a degree. All sources of information have been specifically acknowledged and all quotations have been distinguished by quotation marks. All assistance from others has been specifically acknowledged.

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Summary

Both natural and anthropogenic changes in marine resources potentially influence foraging in many species. It is therefore imperative to understand space use in indicator species such as seabirds, and identify differences in key areas of usage between and within populations. This thesis used GLS tracking and multi-elemental analyses to investigate individual and colony differences in northern fulmar non-breeding strategies, and their potential influence on population dynamics. Seasonal variation in colony attendance was noted – fulmars spent most time at sea during September and October. Individual differences in winter distribution existed within a single North Sea colony, with a higher proportion of females than males utilizing the West Atlantic region, compared to local North Sea waters. Older individuals were more likely to remain within North Sea waters than travel further from the colony. A comparison of winter foraging across five North-east Atlantic colonies revealed a consistent sex difference in winter diet, with females feeding on prey items with lower $\delta^{15}N$ values than males. Consistency in both winter distribution and diet was detected in the majority of individuals. Irish fulmars spent significantly more time in waters surrounding the colony than Scottish fulmars. Irish fulmars also demonstrated substantially higher $\delta^{15}N$ values, indicative of foraging at a higher trophic level, and $\delta^{13}C$ signatures more related to near-shore signatures. Variation in the usage of fishery discards may exist between these colonies. Winter strategy affected average reproductive success at a single colony. In the most successful pairs, males wintered closer to their breeding colony and females wintered outwith the North Sea. This thesis demonstrates that differential non-breeding strategies exist in a wide-spread marine top predator and that these differences can influence reproductive success. To predict how changes in marine resources could influence a species' population dynamics, non-breeding areas should be included as a factor.

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CHAPTER 1

GENERAL INTRODUCTION

Photo: H.Dombrowe. “Incoming”

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Understanding the underlying causes of population change, be they density-dependent (such as competition for food) or density-independent (such as climate) is a key concept in ecology, particularly if we wish to predict changes in population dynamics (Levin 1992). The two most important aspects of any animal's life are to survive and to reproduce (Townsend *et al.* 2008). Life history theory predicts that there will be a trade-off in the allocation of resources given to both survival and reproduction as both require energy (Martin 1987). The effective intake of this energy, i.e. through foraging, is therefore key (Lecomte *et al.* 2010).

Despite its importance as a factor affecting population dynamics, knowledge remains limited of how foraging can act as a proximate influence on demography (Davis *et al.* 2005; Furness *et al.* 2006; Lewis *et al.* 2006). There is a large body of literature on a wide range of taxa with strong evidence to support temporal (Lima & Magnusson 1998; Guillemain & Duncan 2002; Torres & Puig 2010), spatial (Agosta & Morton 2003; Codron *et al.* 2006; Hasui *et al.* 2009) and individual (Knudsen *et al.* 2007; Brzezinski 2008) variation in diet within a species. In the marine environment, studying the foraging ecology of a species can be problematic due to the difficulties in collecting data from such an extensive system, particularly during the non-breeding period when individuals from a breeding population may be more dispersed (Egevang *et al.* 2010; Dietz *et al*. 2013). The current thesis explores the non-breeding foraging ecology of an iteroparous breeder, the northern fulmar *Fulmarus glacialis*, and investigates both individual and colony-wide differences in non-breeding distributions and diet. Finally, it assesses the potential carry-over effects of non-breeding habitat choice on subsequent population dynamics, as measured by breeding success.

Individual differences in space use in marine systems

The marine environment is a highly heterogeneous and dynamic system (Barry & Dayton 1991). Whilst some food resources are predictable, for example upwellings at oceanic fronts (Kai *et al.* 2009; McKnight *et al.* 2013), or consistent seasonal events (e.g. salmon runs, Hulbert *et al.* 2005), others will be opportunistically gained, for example fishery discards (Furness 2003; Bartumeus *et al.* 2010). Increasing pressure on many oceans from activities such as overfishing (Scheffer, Carpenter & Young 2005), pollution (Votier *et al.* 2005; van Franeker *et al.* 2011) and offshore developments (Inger *et al.* 2009; Vehanen *et al.* 2010) has the potential to impact marine organisms. It is therefore critical to establish how different species' space use varies across their range.

For central place breeders such as seabirds, decisions on where to forage may be limited by having to remain closer to colony waters during the breeding period (Harding *et al.* 2013). Inter-colony foraging variation has been demonstrated in terms of differences in trophic levels at which individual's feed (Forero *et al.* 2005), in the intensity and length of foraging trips (Grémillet *et al.* 2004), and in areas visited (Hatch *et al.* 2010). As overlap in foraging areas and competition between individuals from differing colonies is likely (Grémillet *et al.* 2004), spatial segregation may occur, as seen in a multi-colony study on northern gannets *Morus bassanus* where the degree of overlap between 12 colonies was very low (Wakefield *et al.* 2013). In contrast, during the non-breeding period an individual should be less constrained to their breeding colony (Bearhop *et al.* 2006) and this ability to forage further afield may cause more overlap between colonies. Shared wintering grounds have been shown in a number of species (Gonsález-Solís *et al*. 2007; Gaston *et al.* 2011; Frederiksen *et al.* 2012), though over-wintering segregation, as inferred from stable isoopte analysis, has been demonstrated among some seabird taxa (Cherel *et al.* 2006). It is therefore hypothesised that in this study, the non-breeding foraging distributions of individuals from differing colonies are likely to overlap.

Within a colony, individual variation in foraging ecology has also been demonstrated. Differences in time spent foraging (Weimerskirch *et al.* 2006; Castro *et al.* 2009; Gladbach *et al.* 2009), location of foraging area (Phillips *et al.* 2004b; Pinaud & Weimerskirch 2007; Weimerskirch *et al.* 2009) or in the type or size of prey consumed (Gonsález-Solís *et al.* 2000; Wojczulanis *et al.* 2006; Woo *et al.* 2008) have been identified in individuals from the same colony. Factors affecting an individual's foraging strategy may be intrinsic (such as the age or sex of the individual) or extrinsic (such as climate-induced effects on prey or flight capabilities).

Age-related differences tend to relate to differences in foraging efficiency, whether this is due to foraging skills not yet mastered in the young (Wunderle 1991; Skorka & Wojcik 2008), or due to the utilisation of energy intake changing due to senescence (Lecomte *et al.* 2010). It is also possible that age is linked to competitive ability, such that older individuals may exclude younger individuals from direct consumption of a desirable food resource, such as fishery discards (Bertellotti & Yorio 2000) or refuse tips (Greig, Coulson & Monaghan 1983). Whilst most age-related foraging studies concentrate on differences between life history stages (i.e. juveniles, immatures and adults, e.g. Alonso *et al.* 2012; Peron & Grémillet 2013), far fewer studies compare foraging differences between age groups within breeding adults (see Lecomte *et al.* 2010).

Sex differences may occur within a species through competitive exclusion, niche specialisation, and breeding role differences (see Lewis *et al.* 2002 for review in seabirds). Competitive exclusion may result particularly when sexual dimorphism is present between the sexes (Gonsález-Solís *et al.* 2000). For example, male giant petrels *Macronectes halli*, with a 20% greater mass than females, can outcompete females for energy-rich carcasses close to the colony during incubation, and females are forced to feed primarily on krill and squid further from the colony (Gonsález-Solís *et al.* 2000). Niche specialisation with horizontal segregation within the water column has been demonstrated in Crozet shags *Phalacrocorax melanogenis* with females diving between 15-35m and males preferring to feed either in the shallows or to dive to over 55m (Cook *et al.* 2007). The shags are still largely feeding on the same prey, but in different size groups (Cook *et al.* 2007). It is suggested that morphological differences in beak size, and therefore the ability to handle different prey sizes, may cause the observed niche specialization (Cook *et al.* 2007). Morphological differences between the sexes may also play a role in how far each sex can travel, as has been shown for wandering albatrosses *Diomedea exulans*, where smaller females are able to travel further from the colony in lighter winds (Shaffer, Weimerskirch & Costa 2001). However, this pattern has not been supported for other albatross species where sexual dimorphism is also present, with both sexes experiencing similar wind speeds (Wakefield *et al.* 2009).

Differences in nutritional requirements, particularly in relation to egg-laying processes may also result in sex differences in foraging. A number of studies have shown it is the female which requires the greatest nutrient input in order to obtain breeding condition and, furthermore, may seek out specific nutrients (such as albumen or calcium) during the egg-forming period (Durant *et al.* 2000; Reynolds, Schoech & Bowman 2003; Boersma, Rebstock & Stokes 2004; Nager 2006). Much less work has been done on post-laying nutritional requirements, however a study on the northern gannet, a monomorphic species which exhibits spatial segregation between the sexes during the chick-rearing period, tentatively suggested that the need for restoration of calcium depletion in the post egg-laying period may lead to female gannets foraging in different areas than males (Lewis *et al.* 2002).

Sex differences may also be ‘context-dependent’, as seen in the Wilson’s storm petrel *Oceanites oceanicus*, where it is only in poor food years that females increase their foraging effort to undergo longer foraging trips and bring in heavier meals (Gladbach *et al.* 2009), or season dependent (Phillips *et al.* 2004a; Owen *et al.* 2013), where sex differences in diet may only exist during a certain time period.

Further to these intrinsic variables of age and sex, extrinsic factors may also play a role in foraging variability and subsequent fitness consequences. Individuals within a colony have the potential to be influenced differentially by geographical variation in climate, dependent on the scale at which they are foraging. An increasing number of seabird studies are demonstrating differential impacts of climate variation change on survival (Barbraud & Weimerskirch 2003; Grosbois & Thompson 2005; Sandvik & Erikstad 2008b) and reproduction (Gjerdrum *et al.* 2003; Sandvik, Coulson & Saether 2008a; Lewis *et al.* 2009), with some species being more ‘at-risk’ to changes than others (Furness & Tasker 2000; Hamer 2010). Studies of the relationship between climate variables and demography at single colonies have demonstrated both positive (e.g. D’Alba, Monaghan & Nager 2010; Rivalan *et al.* 2010) and negative relationships (e.g. Frederiksen *et al.* 2004; Votier *et al.* 2005) between breeding success and/or survival and climatic variables. However, including wintering foraging area as a covariate in analyses with climate variables and population parameters has, to date, rarely been achieved (see Rivalan *et al* 2010).

Whether individuals will be adversely affected by potential changes in food supply over the non-breeding area period depend upon the degree of plasticity that different species have to change their foraging areas. Consistency in foraging area use may arise either due to a heritable component of migration (Robertson & Cooke 1999) or when the benefits of using a known area outweigh the potential risks of finding an unknown foraging area (Thiebot *et al.* 2011). Winter site fidelity has been identified in many different taxa (Kurta & Murray 2002; Bradshaw *et al.* 2004; Kolar, Millspaugh & Stillings 2011), and a high degree of consistency suggests that any effects on an individual's favoured winter foraging area have the potential to influence an individual's fitness.

Population consequences of differing wintering areas

It has long been established that carry–over effects, events in one season affecting events in another season, are likely to occur (Fretwell 1972; Webster *et al.* 2002), and these effects are widespread across taxa (as reviewed in Harrison *et al.* 2011). In the non-breeding period the mediators which most commonly affect subsequent reproduction are winter diet and winter climate. Better food supply in one winter area (or one experimental treatment) compared to another, have led to an increase in breeding output in passerines (Norris *et al.* 2004; Robb *et al.* 2008), mammals (Perryman *et al.* 2002; Cook *et al.* 2004) and fish (Kennedy *et al.* 2008).

These differences in seasonal interactions may impact not only the individual but may have population consequences. Simulations of scenarios in which high quality winter habitat is lost produced declines in population size due to a shift in reproductive output at the breeding site (Norris 2005).

Methodologies employed to investigate spatial distribution and diet

Tracking data

Seabird distributions at sea have traditionally been assessed by a combination of visual surveys and with information from ringing recoveries. Observational data such as ship-based line transect surveys (Durinck & Falk 1996; Oedekoven, Ainley & Spear 2001) or aerial surveys (Garthe 2006; Certain & Bretagnolle 2008) are useful for assessing presence/absence of groups of individuals but only provide a snap-shot of where those individuals are feeding or resting. Similarly, data gained from ringing recoveries are limited because they are biased towards areas where recoveries are higher due to higher population levels or increased fishing effort (Harris *et al.* 2010). More representative data on foraging over larger spatial and temporal scales require the use of bird-borne tracking devices (Wilson *et al.* 2002).

Tracking devices are particularly useful in studies where time of day impedes direct visual observations, for example nocturnal animals (Garshelis *et al.* 1982), or when tracking an animal visually is not feasible due to large distances involved (Guilford *et al.* 2008). In seabird ecology the use of light-based Global Location Sensing loggers (GLS hereafter) (Phillips *et al.* 2004a, Harris *et al*. 2010), satellite tracking Platform Transmitter Terminal (PTT) tags (Jouventin & Weimerskirch 1990; Lecomte *et al.* 2010) and Global Positioning System (GPS) tags (Votier *et al.* 2010) have become the standard for assessing individual differences in foraging. Data from tag-based studies have greatly increased our knowledge of seabird spatial and foraging ecology. For example, wintering foraging areas and migratory patterns for several species have been identified (Guilford *et al.* 2009; Phillips *et al.* 2009; Kubetzki *et al.* 2009; Egevang *et al.* 2010; Harris *et al.* 2010), interactions with fishing vessels established (Weimerskirch *et al.* 1997; Bartumeus *et al.* 2010; Votier *et al*. 2010), and age, sex and colony specific foraging patterns recognized (Grémillet *et al.* 2004; Lecomte *et al.* 2010).

Despite the increasing availability of smaller and more accurate tracking devices, there remain limitations in how many tags can be deployed and recovered with usable data. In particular, the success of recovering data loggers is likely to be much lower for birds with lower reproduction or survival rates. One way of overcoming this is to identify intrinsic geogenic markers that can be used as a proxy of foraging area use and to gain dietary-based information.

Chemical analyses

A distinct advantage of employing chemical analyses rather than tag technologies is that birds need only be caught once to obtain a tissue sample. Furthermore, a considerably larger sample size of individuals (and, hence, a more representative sample of the population as a whole) is possible with tissue sampling. Fingerprinting elements and their isotopes can also provide broader information on an individual's foraging ecology, including data on diet (Forero *et al.* 2005; Käkelä *et al.* 2007; Williams, Iverson & Buck 2008; Ito *et al.* 2009), location (Gonsález-Solís *et al.* 2002; Cherel *et al.* 2006; Anderson *et al.* 2010), and contaminants (Burger & Gochfeld 2000; Bond & Diamond 2009; Ramos *et al.* 2009). A commonly used technique is stable isotope analysis (SIA), often on ratios of ^{15}N to ^{14}N (denoted δ^{15}N) which provides information on the trophic level at which the birds eat. Ratios of ^{13}C to ^{14}C (denoted δ^{13}C) can distinguish between marine and terrestrial sources and also differ between areas of high productivity and areas of lower productivity (Weiss *et al.* 2009). Further to dietary data, δ^{13}C can also provide broad location estimates in areas where a strong latitudinal gradient in δ^{13}C exists, for example, the Southern Ocean (Quillfeldt, McGill & Furness 2005; Cherel & Hobson 2007).

Broad-classifications of individuals using intrinsic markers is commonly used in conjunction with known 'isoscapes' (a map-like isotopic reference, in this case of the sea) (Phillips *et al.* 2009; Jaeger *et al.* 2010) but validation of classifications using tracking data is still in its infancy (Leat *et al.* 2013). One of the objectives of this study is to develop a technique whereby an individual can be classified into differing foraging areas. Utilizing tracking data in conjunction with chemical analyses can inform classifications of non-tagged individuals. There are a number of reasons why individuals may differ in the metal levels found in their tissues. Differences in foraging location are one possible factor but metal concentrations may also differ in relation to: sex (due to females being able to pass contaminants to the developing egg – e.g. Becker *et al.* 2002; Mallory, Braune & Forbes 2006; Taggart *et al.* 2009); hunger state (Sears, Hatch & O'Brien 2009); health status (Debacker *et al.* 2001); age (Bond & Diamond 2009), and tissue type (Anderson *et al.* 2010). Therefore, to develop a technique whereby an individual can be classified into differing foraging areas variation due to these other factors should be explored using data from animals with known foraging locations.

Study species

The northern fulmar, (hereafter 'fulmar'), is a long-lived, pelagic seabird with an extensive range across the northern hemisphere in North Atlantic and North Pacific oceans (Tasker 2009). Due largely to their huge rise in abundance over the 20th century they have been subject to numerous studies relating to a wide-range of topics including: their population spread (Salomonsen 1965; Brown 1970; Thompson 2006), breeding ecology (Carrick & Dunnet 1954; Hatch 1990), factors affecting their survival (Dunnet & Ollason 1978; Grosbois & Thompson 2005), diet (Wang *et al.* 2009; Byers, Smith & Mallory 2010; Owen *et al.* 2013), interactions with pollutants (Thompson, Furness & Monteiro 1998; Mallory, Braune & Forbes 2006; van Franeker *et al*. 2011), interactions with fishing vessels (Furness & Tasker 2000; Dunn & Steel 2001) and climate change effects on their population (Thompson & Ollason 2001; Lewis *et al.* 2009). There is geographic variation in fulmar phenotypes in the Atlantic, with light-phase fulmars (i.e. lighter plumage: L and LL) being more common at lower altitudes and dark-phase fulmars (i.e. darker plumage: D and DD) more common in higher Arctic regions (van Franeker & Wattel 1982). Mixing of these four phenotypes exists, but in this current study only light-phase fulmars were sampled. To give appropriate context for this current study on non-breeding foraging ecology, it is worth discussing; the fulmars annual cycle, the factors which affect their population dynamics and finally their known foraging characteristics.

Annual cycle

Fulmars, in general, begin breeding at around 10 years old (Dunnet 1991), and can continue breeding into old age, with some individuals recorded as still breeding in their mid-40s (P. Thompson, unpub. data). However, fulmars will not necessarily breed every year (Fisher 1952; Ollason & Dunnet 1988). In April, breeders undertake a pre-laying exodus (Macdonald 1977), similar to other procellarids (Warham 1996). From mid to late May females lay a single egg and after a short incubation from the female, the male bird then takes the first main incubation stint (Ojowski *et al.* 2001). The pairs then alternate incubation shifts during the breeding season, generally in stints of around 9 days during the egg incubation period and closer to 5 days during chick-rearing period (Mallory *et al.* 2008b; Gaston *et al.* 2014). Hatching occurs around late June/early July and by mid to late August a fledgling will be ready to leave the nest. During the latter period of chick-rearing it is common for both pair members to forage away from the nest (Mallory *et al.* 2008b). By this stage the fully grown chick has sufficient defences to discourage many predators, with its size and ability to projectile vomit an oily substance being deterrents (Tasker 2009). From September to the end of March fulmars are then defined as being in the non-breeding period of their annual cycle. During the non-breeding period, individuals may visit their breeding colony (Macdonald 1980), but there is a lack of information on seasonal variation in breeding colony visits and indeed what foraging areas are being utilised when away from the colony.

It is during this non-breeding period when adult fulmars carry out the majority of their annual moult, with primary moult beginning late August (Allard *et al.* 2008). Failed breeders or non-breeders at the colony show indications of primary moult before breeders (Carrick & Dunnet 1954; Allard *et al.* 2008). In a typical year, a full wing and tail moult should be completed by the end of February (Ginn & Melville 2000). In unusual years (e.g. 2004, during a winter wreck event), 60% of birds examined from a wreck were still in primary moult in February, compared to 8% in a normal year (van Franeker 2004). It is thought that individuals undergoing wing moult, where up to eight feathers are grown simultaneously, may remain largely flightless for the period of wing moult (Warham 1996; van. Franeker, pers. comm.). It should be noted colony origin is important, as regional differences in moult timings exist between fulmars originating in Canada and those from North Sea colonies (Brown 1988), potentially due to subtle differences in breeding season timings. Body feathers are thought to moult anytime from July to end of February (Ginn & Melville 2000), though evidence for the timing of body moult is lacking in fulmars. It has been suggested that two successive generations of body feathers are present at the same time (Warham 1996; Ginn & Melville 2000). A study of fulmars captured during the breeding period, found only 10% of breeding males and 0% of breeding females with any sign of body feather (specifically belly feather) moult (Allard *et al.* 2008), suggesting that the vast majority belly feathers moult post-breeding.

Population dynamics

Several potential driving forces may explain the fulmar's dramatic population rise from a select few colonies on St Kilda and Iceland in the early 19th century, to 3-4 million pairs currently estimated in the Atlantic (Mitchell *et al.* 2004). An increase in fishery discards is likely to have played a role in providing an easily accessible food resource (Fisher 1952), but cannot fully explain the rise. A change in fulmar harvesting also occurred, particularly in the founding populations of St Kilda and Iceland (Fisher 1952; Thompson 2006). Further to these, a change in climate across the timespan may have affected prey availability (Salomonsen 1965). Most likely, their rise is due to a mixture of these possibilities (Thompson 2006). Although their numbers still remain high in UK and Irish waters, with the latest estimate being 500,000 pairs (Mitchell *et al.* 2004), an overall declining trend of 23% has been noted since the mid-1980s, when their numbers were at a peak, with most of this decline occurring in the last decade (Eaton *et al.* 2013). Canadian fulmar colonies have also shown a steady decrease in population from 1976-2008 at a rate of 1% per year (Gaston *et al*. 2009). Black-legged kittiwakes *Rissa tridactyla* and thick-billed murres *Uria lomvia* at the same colony have either increased or remained at similar numbers over the same period. It is suggested that the wintering grounds may therefore be having an impact on fulmar population trends rather than the summer breeding grounds (Gaston *et al.* 2009). Knowledge of wintering grounds and foraging areas may therefore be key in elucidating the reasons for a decrease in population in the fulmar.

Further to studies on population trends, studies on factors affecting two key elements of population dynamics have demonstrated a link between a large-scale climatic factor, the North Atlantic Oscillation (NAO) on both survival and reproduction. Survival in fulmars, particularly of females, has been shown to be influenced by the NAO (Grosbois & Thompson 2005). Reproductive success at this colony has also been linked to winter NAO and lagged winter NAO, with year to year variation in breeding success strongly related to oscillations in the NAO (Thompson & Ollason 2001; Lewis *et al.* 2009). It is hypothesized that differential winter habitat use may exist between the sexes, which may go some way in explaining the links between a sex difference in survival and reproduction with this large scale climate index.

Foraging characteristics

Fulmars have a wide-ranging prey base (Hobson & Welch 1992; Phillips *et. al.* 1999; Garthe *et al.* 2004; Byers, Smith & Mallory 2010) with seasonal dietary shifts already demonstrated from intrinsic markers in fulmars from Arctic Canada, North Pacific and the North Atlantic (Wang *et al.* 2009; Mallory *et al.* 2010; Owen *et al.* 2013). Fulmars have the potential to forage over large ranges, with fulmars recorded travelling over 2500km from their breeding colony during the incubation period (Edwards *et al.* 2013) and 580km recorded from satellite tracked actively breeding fulmars during the chick-rearing period (Weimerskirch *et al.* 2001). It has long been known that fulmars utilize fisheries discards (Furness & Todd 1984; Hamer, Thompson & Gray 1997; Phillips *et al.* 1999). However, few studies have been able to demonstrate fitness consequences for fulmars utilizing different food resources. Satellite tracking of Canadian fulmars have revealed individual (Falk & Moller 1995; Mallory *et al.* 2008a) and colony-specific post-breeding wintering areas for Pacific fulmars (Hatch, Gill & Mulcahy 2010). However, in all these studies only a few individuals were tagged from each colony and the use of satellite tags was accompanied by the vast majority of fulmars abandoning their breeding attempt either immediately following release or shortly thereafter. Furthermore, some birds did not return to breed the following year. The detrimental effect the satellite tags had in these studies may have affected foraging habitat choice. To assess whether individual and colony-wide differences really do exist in fulmars, a much larger sample size of individuals is required, as is achieved in this current study.

The fulmar, known to forage widely and on a varied prey base, and with links between population dynamics and large scale climatic factors, still has a knowledge gap in its wintering foraging characteristics (Tasker 2009; Mallory *et al.* 2010). It is an ideal study species with which to test the hypothesis that differential wintering areas may play a key role in population dynamics, and to address this question their wintering areas must first be identified.

Thesis Aims

The overarching aim of this thesis was to identify whether there are individual or colony differences in non-breeding strategies in the northern fulmar, and whether these strategies have the potential to influence population dynamics through changes in reproductive success.

In **Chapter 2** I assess the seasonal variation in colony attendance of fulmars, reveal non-breeding distributions of tagged individuals from a single North Sea colony and investigate potential reasons (sex and age) for individual differences in winter foraging area. A further objective was to assess the degree of individual consistency of winter area choice across different years.

In **Chapter 3** I aim to validate the use of body feathers, specifically those from the belly region, as usable proxies for identifying non-breeding areas and in representing dietary information in the non-breeding period. Inter-feather variability, both between feather types and amongst body feathers, is assessed. The most likely time period over which fulmars from the North Sea region moult their body feathers is also investigated.

In **Chapter 4** I compare winter foraging characteristics at two fulmar colonies; one from a North Sea colony (Eynhallow, Orkney) and one from the more southerly part of the fulmar's range (Little Saltee, Ireland), to assess the degree of population mixing between fulmar colonies over winter. This is achieved through use of tagging data. Further to this, I determine the concentrations of a variety of intrinsic markers to establish if there are any colony differences in diet over the same time period.

Chapter 5 expands the colony comparison of Chapter 4 into a broader area, comparing winter foraging characteristics in five fulmar colonies: Iceland, Faroes, St Kilda, Little Saltee and Eynhallow through use of stable isotopes and multi-elemental concentrations. Specific objectives in this chapter also consider whether sex differences in diet are apparent across the differing colonies and whether differences exist in the proportion of birds from each colony utilizing different broad-scale wintering areas.

In **Chapter 6** I assess possible consequences of different wintering areas on average breeding success in; a) both sexes separately and b) tracked pairs, from a single North

Sea colony. A combined approach of tracking data and dietary information from chemical analyses is employed.

I then discuss the main findings and implications of my thesis in a broader context, assess the potential difficulties of this work and finally consider potential future directions for this research.

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CHAPTER 2

Consistent individual and sex-specific variation in non-breeding distribution of the northern fulmar.

Photo: L.Quinn. “Whatchu’ lookin’ at?!”

CHAPTER 2: Consistent individual and sex-specific variation in non-breeding distribution of the northern fulmar.

ABSTRACT

To identify how changes in the distribution of prey in a dynamic marine environment affect marine predator populations we must first understand space use by different individuals within these populations. Tracking technology has allowed greater understanding of seabird habitat use during the non-breeding period. From 2006-2012, we tagged 163 fulmars from Eynhallow, Orkney, to identify their space use over autumn and winter. We obtained 72 tracks and identified four wintering patterns: birds that stayed in the North Sea; birds that travelled to the West Atlantic; birds that travelled to northern Norwegian shelf waters and the Barents Sea; or birds that adopted a mixture of all three. Fulmars visited their breeding colony area throughout the non-breeding period, but particularly from January onwards. We also found that females travelled significantly further west than males, and older individuals tended to remain closer to the colony area. There was a high level of consistency in wintering area between years. Such data now provide the potential to quantify the implications of differing wintering strategies for populations.

INTRODUCTION

Understanding how different individuals in a population utilize space within patchy and variable environments is a crucial step when assessing factors affecting a species' overall population dynamics (Moorcroft 2012). Spatial structuring of predator populations has been affected by changes in the spatio-temporal availability of prey caused by climatic changes (Reid & Croxall 2001; Perry *et al.* 2005; Leaper *et al.* 2006; Grémillet & Boulinier 2009), and predictions of the impact of large-scale changes of their prey therefore require information on where individuals from a population forage (Morris 2003). Where differences in space use exist within the same population, it is particularly important to determine whether individuals have the ability to be flexible in their habitat choice (Abrams 2010).

In the marine environment, the miniaturisation of tracking technologies such as Global Positioning System (GPS) tags, satellite tags, and light based Global Location Sensing (GLS) loggers has greatly increased our understanding of marine predator movements over the last decade (Burger & Shaffer 2008; Wakefield, Phillips & Mattiopoulos 2009; Block *et al.* 2011). As these studies have been expanded to cover year-round assessments of distribution, it has become apparent that over-wintering habitat usage can have carry-over effects for the subsequent breeding season, and hence influence population dynamics (Webster *et al.* 2002; Harrison *et al*. 2011). These technologies have revealed that several seabirds exhibit individual differences in wintering areas used in birds from the same colony (e.g. Furness *et al.* 2006, Bost *et al.* 2009, Kubetzki *et al.* 2009, Kopp *et al.* 2011).

There are a number of potential explanations why individual differences in over-wintering area use may be seen in seabird populations. Sex (Phillips *et al.* 2007), age (Lecomte *et al.* 2010) and body size (Shaffer, Weimerskirch & Costa 2001) may all influence habitat choice. For example, males may outcompete females for food (Gonsález-Solís *et al.* 2000), older individuals may outcompete younger, less experienced individuals (Riotte-Lambert & Weimerskirch 2013), or body size variation may affect flight ability and thus the areas which certain individuals can reach (Shaffer *et al.* 2001). Differences in foraging area can also be accompanied by differences in foraging behaviour and diet (Woo *et al.* 2008) or in foraging activity (Mackley *et al.* 2010).

In many terrestrial and freshwater species, there is known to be strong year-to-year consistency in the use of over-wintering sites by individual birds (Robertson & Cooke 1999; Burton 2000; Latta & Faaborg 2001). Amongst seabirds, individual fidelity to wintering areas has been reported in procellarids (Phillips *et al.* 2005), sulidae (Grecian 2011), stercorariidae (Kopp *et al.* 2011; Magnusdottir *et al.* 2012) and alcids (Guilford *et al.* 2011). It has been suggested that for long-lived species with individual migratory patterns, as seen in seabirds, spatial memory and knowledge of a previously explored area is likely to drive distribution patterns (Guilford *et al*. 2011). Consistency should exist when the benefits of going to a predictable area with known resources outweigh the cost of changing strategies to investigate a new area with unknown resources (Bradshaw *et al.* 2004; Thiebot *et al.* 2011). In a changing marine environment the ability to be flexible in site choice may be advantageous for certain individuals, but this remains difficult to test. In Cory's shearwaters *Calonectris diomedea* 64% remained site faithful in winter, but the remaining birds swapped wintering sites (Dias *et al.* 2011). There is clearly a complexity in why birds forage in certain areas and whether or not they remain faithful to these areas.

In this current study, we have a unique opportunity of having a large sample size of northern fulmars from a long-term study population to study wintering movements, where information on both sex of the individuals and an estimation of breeding age is known. Fulmar foraging movements, particularly from individuals, is lacking. What information there is comes predominantly from ringing recoveries. Immature birds ringed in Britain and Ireland, have been recorded on the coasts of Greenland, Newfoundland, Nova Scotia, Netherlands, Denmark, Iceland and Faroes as well as their natal coasts (Wernham *et al.* 2002), demonstrating that fulmars have the potential to move far afield from their natal colonies. Ringing cannot tell us the main distribution of fulmars when at sea and so remote tracking studies, as this one is, strives to bridge this knowledge gap. It is expected that tracked individuals may travel long distances from the colony. As adults, it is known fulmars attend their colony area over the non-breeding period (Macdonald 1980; Slater 1990), with pairs being seen together (Fisher 1952), suggesting that, at least at some time during the winter period, males and females are together. However, because of the dietary differences noted in the pre-laying period (Owen *et al.* 2013), it is hypothesised that a difference in non-breeding area between the sexes may exist. Satellite tracking studies on adult fulmars revealed differences in area use in the non-breeding period between colonies but samples sizes were too low to compare within a colony (3-5 individuals per colony) (Hatch, Gill & Mulcahy 2010), and adverse tag effects were noted in this study which may have influenced their movements.

It is the aim of this study to: a) assess seasonal variation in colony attendance of breeding adults, b) reveal the main non-breeding distribution for a Scottish population of fulmars; c) identify factors which may explain individual differences in foraging; and d) assess the degree of consistency of use of these non-breeding areas.

METHODS

Study population and Logger deployment

The study was carried out on Eynhallow, Orkney (59°8'N; 3°8'W), as part of a long-term individual-based study of fulmar population ecology (Dunnet 1991). Fieldwork was conducted between 2006-2012, when approximately 100 active nests were recorded annually. Breeding adults were caught at the nest using a hand net or noose, and British Antarctic Survey (BAS) light-based GLS loggers were attached to darvic leg-rings of 163 birds using cable ties. The total device weight (including leg ring) was 3.6g, representing <0.5% of the lightest recorded fulmar's body weight. The average recovery rate for the tags was 46% over one year and 76% over two years.

GLS loggers recorded the maximum received light-levels (lux) in each 10 minute period, from which a time of sunrise and sunset could be calculated. This information was then used to obtain approximate locations, twice a day (one daytime, one nighttime) (see Wilson *et al.* 1992 and Fox 2010 for full methodology). Previous double tagging experiments using these same devices on other seabirds suggest that locations have a mean error of 186km ± 114 km (Phillips *et al.* 2004).

Seasonal variation in colony attendance

General patterns of colony attendance were assessed using time-lapse photography at a sub-set of nests within the colony. Information on individual activity patterns was derived from wet-dry sensors on the GLS loggers.

Time-lapse data were collected using a digital SLR camera in a waterproof casing (www.harbortronics.com). Photographs of a cliff containing approximately 20 nest sites were taken every three hours from July 2010 to July 2011 (see Appendix 1 for example photographs). Valid photos were those with sufficient daylight, not impaired by bad weather and which were of suitable quality to positively identify birds on the cliff. From usable photos, the maximum number of birds from each day was counted and from this a monthly average could be obtained.

GLS loggers recorded whether the tags were wet or dry every 3 seconds. Summary data on the number of wet samples in each 10 minute period were then stored, allowing each 10 minute period to be classified as wet, dry or mixed. Light data were also used to classify each 10 minute sample as day time (when lux=1-64) or night time (when lux=0). These data were then used to calculate the proportion of each day and night that the GLS logger was dry, and the mean proportion of time spent dry was also calculated for each month to explore seasonal differences. Activity data were available for 68 individuals (post-breeding: 33 females, 35 males, non-breeding: 26 females, 29 males).

Non-breeding season distribution

Twice daily locations were obtained for each individual using BASTrak software v.18 with a light threshold level of 10 and an angle of elevation of -3.5. An iterative smoothing process was applied twice to the data to reduce error associated with the resulting tracks (Phillips *et al.* 2004). The non-breeding period was divided into post-breeding (20th August to around 15th September) and non-breeding (around 18th October to 1st March), avoiding equinox periods (i.e. autumn equinox mid September – mid October) for which latitude data are unreliable (Fox 2010). Usable autumn locations were obtained from 72 individuals (34 females, 38 males) and usable wintering locations from 67 individuals (31 females, 36 males). 33 birds had more than one years' worth of wintering data, (23 with 2 years of data, 5 with 3 years, 3 with 4 years, 1 with 5 years of data and 1 with 6 years of data).

Sex and age factors

Sex was determined by molecular analysis of DNA from feathers collected during logger recovery, using P2-P8 primer sequences and Z-002 and CAM-11 markers (Griffiths *et al.* 1998; Dawson 2007). Each individual was assigned to one of three broad age categories based on the number of years since the bird was first recorded breeding to 2012, from the long-term breeding records (see Lewis *et al.* 2009). Age groups were: birds recorded as breeding for; (1) less than 10 years; (2) at least 11 years but less than 21 years; (3) more than 21 years.

Statistical analyses

The tracks were projected in ArcGIS v.9.3 using the North Pole Lambert Azimuthal Equal Area projection. To study overall non-breeding area usage, a point pattern analysis was carried out in ArcGIS on all tracks, with a grid square size of 300km, corresponding to the resolution of the mean logger error plus one standard deviation. This uses a quadrat analysis which calculates the numbers of points per grid square, in order to demonstrate the most densely and least densely used areas (Diggle 2010). For those birds with more than one winter track available, one year was randomly selected. Home range analysis using Hawth's tools was carried out to produce 95% contours for home range use and 50% for core range use for every winter track. Least squares cross-validation was employed, with a 50km cell size and 20km search radius (Phillips *et al.* 2007). To test for an individual's consistency of winter area, centroid values were used in a repeatability estimation using the rptR package (Nakagawa & Schielzeth 2010), using data from birds with two or more years of winter tracks (n = 84 tracks). Too few points were available for an estimation of overall autumn area use as the autumn equinox excluded most points. Summary trip characteristics (maximum distance from colony, average distance from colony, home range (km^2) and core range (km^2)) and activity summaries were compared using t.tests, paired t.tests, ANOVAS and proportion-based tests where applicable. A Fisher's exact test was carried out to test for sex differences in usage of different areas. General linear mixed effect modelling was carried out using maximum likelihood methods in packages nlme and lme4 to investigate factors affecting a bird's average location. Sex and age were considered as fixed effects with year of track considered a random effect. Model selection used Akaike's Information Criterion (AIC) values corrected for by smaller sample size (AICc), in the AICcmodavg package (Burnham & Anderson 2002; Burnham, Anderson & Huyvaert 2011). Model validation was carried out for the top model and model parameters were then calculated for this validated model.

All statistical analyses were carried out using R v2.15.0 (R development Core Team, 2012).

RESULTS

Seasonal variation in colony attendance

Time lapse camera data revealed that the highest number of birds attending the colony were in March and April. Contrasting with this, fewer birds attended the colony between September and December, though nests were attended regularly in the latter part of the winter in January and February. (Figure 1a). In line with these data, the activity data from GLS loggers demonstrated that September to December were also the months in which individual birds spent the highest proportion of their time on the water (Figure 1b). Marked seasonal variation in individual activity patterns was seen in both males and females (Figure 1b), but there were slight differences between the sexes in April and May.

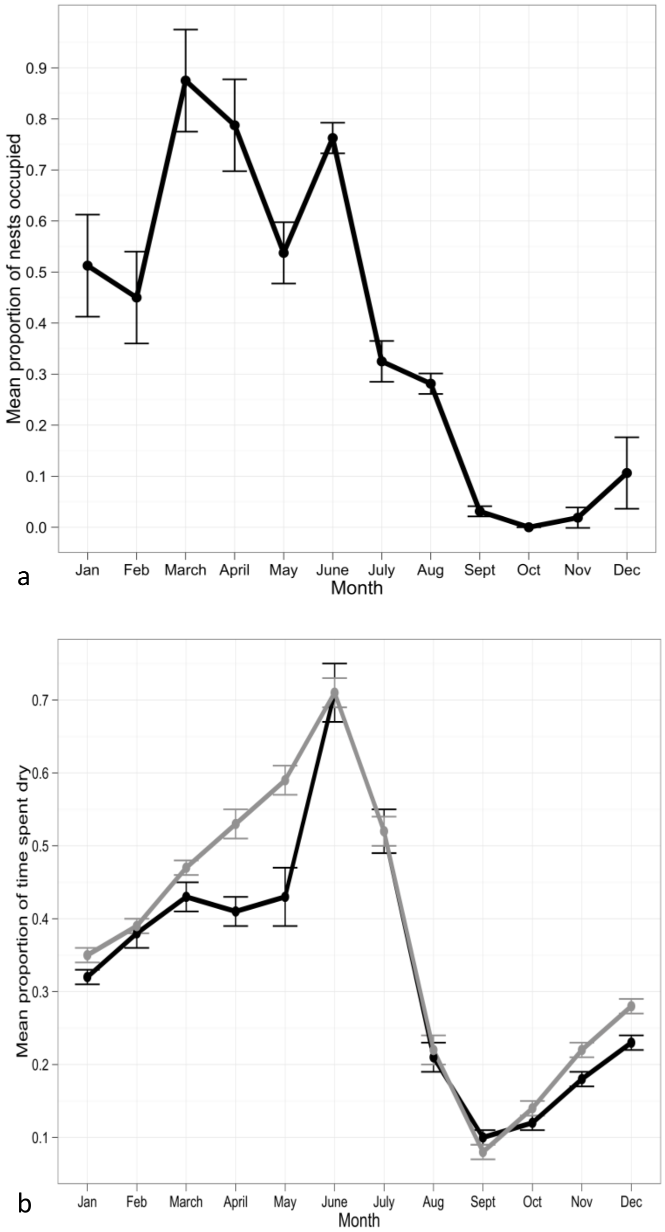

Figure 1. Plots showing; (a) the mean proportion of nests occupied in a study plot (n =20) and (b) the mean proportion of time birds spent dry (n=32 females (black), n=37 males (grey)) in each month of the year. Standard error bars are also shown.

Both sexes spent the highest proportion of time on the water in September (90.5% and 91.5% wet for females and males respectively) and the greatest amount time dry in June (70.9% and 71.0% dry for females and males respectively). In April and May, males appeared to spend slightly less time wet than females, co-incident with the pre-laying exodus and early incubation period, but this was marginally insignificant (prop.test X_1^2=3.38, p=0.06). Focussing on the key non-breeding periods in which data on foraging distribution were available, birds spent a significantly higher proportion of their time on the water in autumn (Aug-Sept) compared to in winter (prop.test $X_1^2=1023$, $p<0.001$). This difference was present regardless of sex or age-group of the bird.

As well as seasonal variation in activity, diurnal variation was also present (Table 1). Significant differences in the amount of time that birds spent wet during the day compared to night were seen in both autumn and winter (Table 1), such that fulmars were more likely to be dry (i.e. flying or on land) during the day than at night. These differences were present regardless of sex or age-group of the bird.

Table 1. Proportion of time birds spend dry, wet and mixed during the day and night in both autumn and winter months (%±sd). Test results of proportion of time spent wet between night and day are shown.

Season	**Dry night (%)**	**Mixed night (%)**	**Wet night (%)**	**Dry day (%)**	**Mixed day (%)**	**Wet day (%)**
Autumn (n=68)	2.7±2.2	9.3±5.8	23.8±7.1	9.6±5.9	19.7±6.6	34.8±11.1
Winter (n=55)	12.5±3.8	26.1±6.7	25.0±6.0	15.8±2.6	12.7±4.6	8.0±2.7
prop.tests	autumn night : autumn day, proportion wet **$X_1^2=133$, $p<0.001$** winter night : winter day, proportion wet **$X_1^2=2010$, $p<0.001$**					

Overall area usage in Scottish fulmars over the non-breeding period

Data from the GLS loggers demonstrated that fulmars from this study colony were distributed across large areas of the North Atlantic during the non-breeding season. Point pattern analysis indicated that there were concentrations of usage within these broader autumn (Figure 2) and wintering (Figure 3) ranges. In both periods, there were two broad areas of high density, one along the shelf waters of the NE Atlantic and the other in the western Atlantic. In the NE Atlantic shelf waters, birds were concentrated along the East coast of the UK and northern North Sea, but Norwegian shelf waters and the Barents Sea were also used extensively. Winter regions were similar to those in autumn, though there is a greater range of area use in winter, most probably due to more data points being available. There are seasonal differences noted, for instance the east coast of England appears less extensively used in winter than autumn, and the Labrador Sea and Davies Straight are utilized in winter but not so in autumn from the data available (Figures 2 & 3).

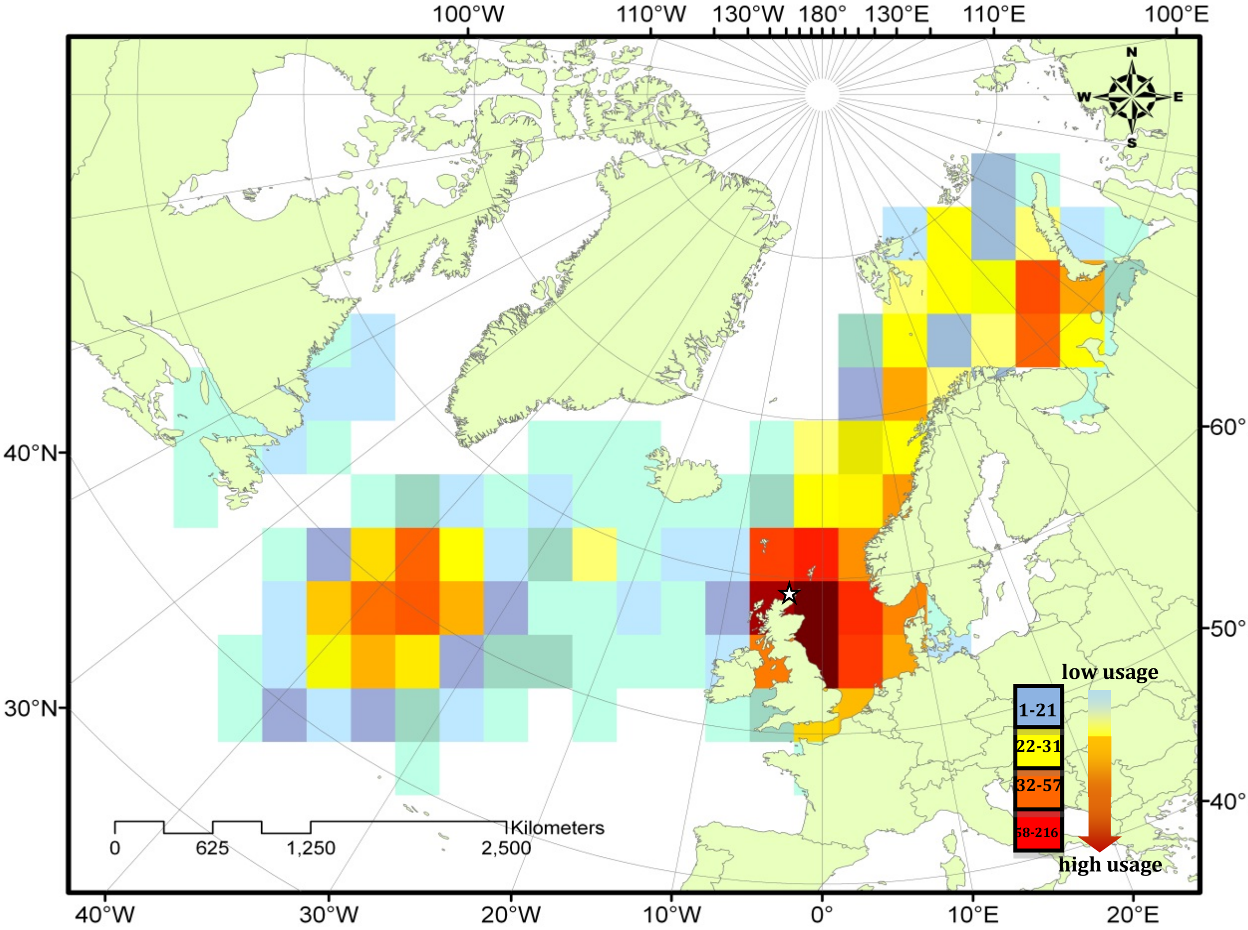

Figure 2. Point pattern analysis of autumn regions used by 72 northern fulmars from Scotland (Eynhallow, starred on map) from 2006-2012. The numbers in the coloured key represent the number of points counted during the analysis.

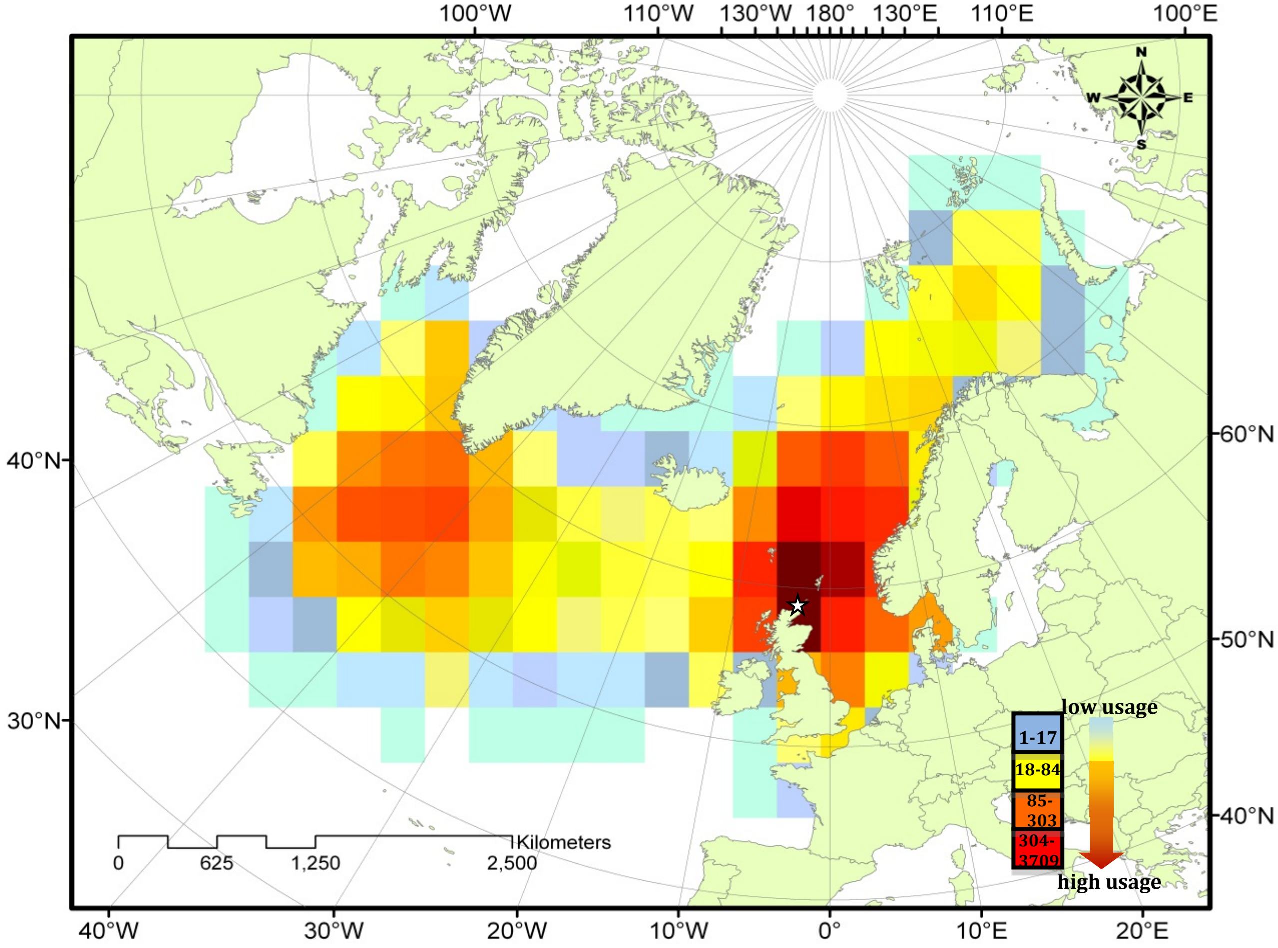

Figure 3. Point pattern analysis of winter regions used by 67 northern fulmars from Scotland (Eynhallow, starred on map) from 2006-2012. The numbers in the coloured key represent the number of points counted during the analysis.

Individual differences in wintering area use

Although large parts of the North Atlantic were used by fulmars from the study colony, there was individual variation in the extent to which different birds used different parts of this range.

Individual tracks revealed four main patterns of area use during the non-breeding season: 1) birds that remained largely within the North Sea waters; 2) birds that used the West Atlantic for part of this period; 3) birds that used northern Norwegian shelf waters and the Barents Sea for part of this period; and 4) birds with a mixed pattern (using both West Atlantic and northern Norwegian shelf waters for part of this period). Example tracks for individuals from each of these groups are shown in Figure 4, and Table 2 presents information on the number of birds adopting each of these four patterns. These data demonstrate sex-differences in the extent to which birds use some different areas, with a significant bias towards males in the North Sea group and females in the West Atlantic group (Fisher's exact test, p=0.009) .

The number of days that individuals spent in each of the three broad areas (see Appendix 2 for definition of boundaries) also differed. Some birds spent only a few days outside the core North Sea area, whilst others spent over 3 months away from these waters (Table 2). Overall, for 54/67 birds (81%) the North Sea was still the area in which they spent the *majority* of their winter, i.e. their time in the North Sea totalled more than their time spent west or east, or combined west and east. Tests revealed that there were significant differences in both sexes in the maximum distance from colony (km) between autumn and winter (females, paired t.test: t_{30}=-4.6, p<0.001; males, paired t.test: t_{35}=-2.8, p=0.007), with the furthest distance from colony noted during the winter period.

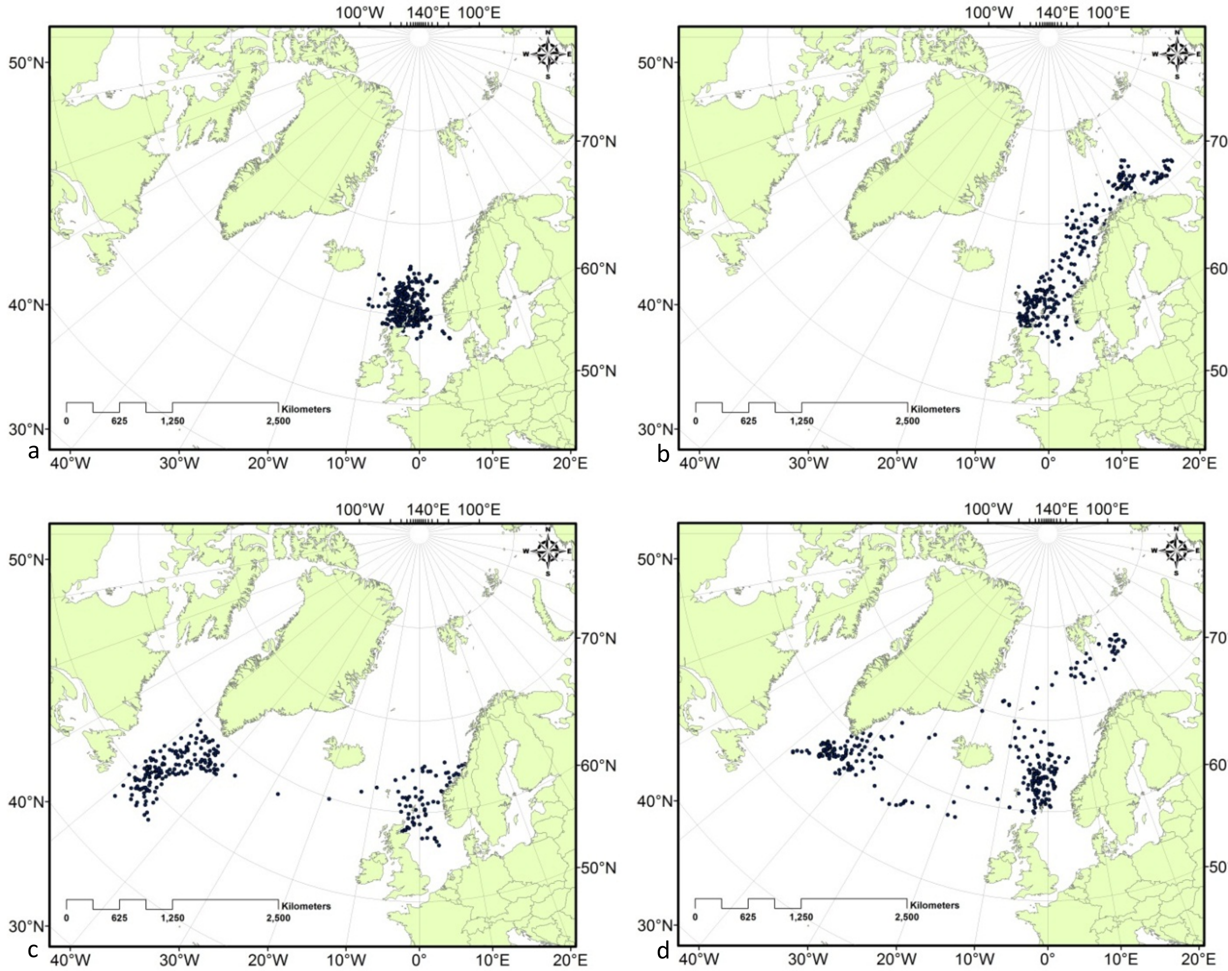

Figure 4. Example tracks of individual differences in wintering patterns. a) Bird 1573; northern North Sea ‘local’ wintering pattern b) Bird 1854; northern Norwegian sea/Barents Sea, ‘eastern’ wintering pattern c) bird 1699; West Atlantic, ‘western’ wintering pattern d) Bird 1878; ‘mixed’ wintering pattern.

The general timing of the birds’ use of these distant foraging areas reflected the time lapse data on colony attendance. This is illustrated in Figure 5, which shows monthly variation in the average distance from the colony for the 41 individuals that foraged outside the core North Sea area. The distance from the colony decreased from October, when the birds were most likely to be furthest away from the colony waters, to February, by which time all birds were within the North Sea area. Due to the low resolution of locations for the GLS loggers it was not possible to determine how regularly these individuals visited the colony. However the activity data compliment these tracking data by revealing that birds are drier for longer periods of time in February than the preceding winter months.

Table 2. Proportion of birds defined in each winter category, with the number of males and females defined in each of these. The range of number of days all tracked birds spent in each area is also shown.

Winter area	**Birds adopting winter strategy (%)**	**No. of individuals**		**Duration in each winter area (days)**
		Female	**Male**	
North Sea	39	6	20	33-135
West	37	17	8	2-108
East	18	6	6	1-60
Mixed	6	2	2	------
total	100%	31	36	135 total winter days

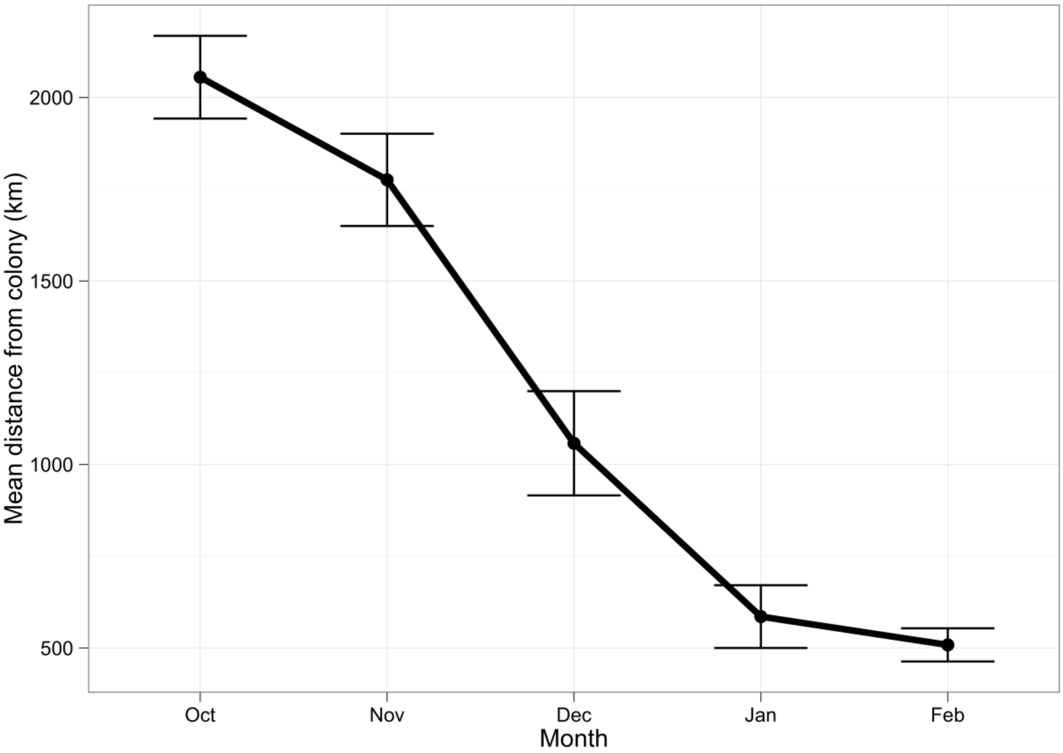

Figure 5. Mean distance from colony from October-February for birds which winter outside the North Sea for part of their non-breeding period (n=41). Standard error bars are also shown.

Factors influencing individual differences in wintering area use

Potential explanations investigated for individual differences in mean wintering location (both latitude and longitude) were; sex and age.

Summary statistics revealed differences between sex and age groups in a number of measures (Table 3). Males and females differed in their average distance from the colony in both autumn (t.test: t_{67}=2.0, p=0.05) and winter (t.test: t_{58}=3.4, p<0.001). Similarly, there were sex differences in their maximum distance from the colony in autumn (t.test: t_{67}=2.5, p<0.020) and winter (t.test: t=3.4_{65}, p<0.001), with females being furthest from the colony in both periods. Females also had, on average, 20% and 21% larger 95% home and 50% core ranges respectively than males, but variability was high and these differences were not statistically significant (95 % home range: t.test, t_{63}=1.65, p=0.104; 50% core range : t.test, t_{65}=1.61, p=0.110).

Age-related differences were also present in the average (ANOVA, $F_{2,64}$=5.07, p=0.009) and maximum (ANOVA, $F_{2,64}$=6.854, p<0.001) distance travelled from the colony during the winter. Tukey's honest significant difference (TukeyHSD) test revealed that the older age group had significantly shorter distances compared to the younger and medium aged birds (av dist: age group 1 versus age group 3: p=0.027, age group 2 versus age group 3: p=0.010; max dist: age group 1 versus age group 3: p=0.004, age group 2 versus age group 3: p=0.005). Both 95% home range (ANOVA, $F_{2,64}$=5.21, p=0.008) and 50% core range ($F_{2,64}$=4.00, p=0.023) were also significantly smaller in the oldest group (95% home range: Tukey HSD p= 0.024; 50 % core range: TukeyHSD p=0.010).

Table 3. Summary of distances travelled (km±standard deviation) and area ranges used (1000 km^2±standard deviation) in autumn (aut) and winter (wint) for each sex (female, male) and each age group (1-3). Values are rounded to three significant figures. No values for 95% and 50% home range for autumn are given due to too few autumn days recorded to give meaningful area results.

	Mean distance from colony(km)	**Mean maximum distance from colony (km)**	**95% home area range (1000 km^2)**	**50% core area range (1000 km^2)**
Female aut n=34	1370±973	1950±1010	-------------	-------------
wint n=31	1080±507	2680±807	2690±968	525±210
Male aut n=38	927±904	1380±909	-------------	-------------
wint n=36	686±418	1900±895	2220±1350	436±243
Age 1 aut n=48	1270±931	1800±971	-----------	------------
wint n=47	905±492	2380±904	2530±119	493±230
Age 2 aut n=11	915±1040	1490±1020	-----------	------------
wint n=9	1120±553	2690±900	3060±134	588±289
Age 3 aut n=13	820±944	1250±987	-------------	------------
wint n=11	490±231	1410±585	1500±474	320±75

Linear mixed models indicated that both sex and age influenced average wintering longitude (Table 4), with females having more western locations than males, and older individuals occurring closer to the colony. Model parameter estimates revealed that these effects were significant between sexes (p=0.012), but not between ages (p>0.05) (Table 5). The best candidate model for mean latitude retained sex in the model (Table 4), but the effect of sex from model parameter estimates was not significant (Table 5).

Table 4. AICc results for the candidate linear mixed models within 2ΔAICc of one another (longitude), and the top model plus second best model (latitude) (in brackets as model more than 2ΔAICc). AICc is the AICc value for the model, ΔAICc is the difference between the candidate models and AICcWt is the weight of relative likelihood of the model given the data and candidate models considered.

Model type	Model parameters	AICc	ΔAICc	AICcWt
Longitude	sex+age	514.15	0.00	0.56
	sex	515.98	1.825	0.22
Latitude	sex	328.58	0.00	0.79
	(sex+age	331.45	2.86	0.19)

Table 5. Model parameter outputs from the optimal linear mixed model, as selected from the AICc values in Table 4.

	Optimal model				
Longitude	Mean Longitude~sex+age				
	Fixed effects:	Estimate	SE	t value	p value
	sex	6.705	2.577	2.601	**0.012**
	agegroup	1.229	1.756	0.700	>0.05
	Random effects:	Intercept	Residual		
	year	0.001	10.15		
Latitude	Mean Latitude~sex				
	Fixed effects:	Estimate	SE	t value	p value
	sex	0.470	0.641	0.732	>0.05
	Random effects:	Intercept	Residual		
	year	0.871	2.55		

Individual consistency in wintering area use

There was significant repeatability between years in an individual's area use (Figure 6a). Thirty-three individuals were tracked over at least two different winters. In all cases, both 95% home ranges and 50% core ranges overlapped between randomly selected pairs of years, with home range overlap ranging from 38-97%, and core area overlap ranging from 27-97%. Area range (km^2) did not differ significantly for home range (paired t.test, t_{32}=-1.51, p=0.140) or core range (paired t.test, t_{65}=1.611, p=0.110) between each year.

Based upon the rptR analysis of the centroids from these home ranges, repeatability for winter longitude was 85% (r=0.85±0.05, p<0.001), and for winter latitude was 66% (r=0.66±0.09, p<0.001). Centroids for these pairs of years are plotted in Figure 5a. Plots of mean longitude (Figure 6b) and latitude (Figure 6c) from one winter against equivalent values for the second winter reveal that there is a strong and significant relationship between the two. Nevertheless, although the overall centroid values demonstrated high repeatability, four individuals did not use the same foraging areas in different years. Of these birds, three used the Western Atlantic area only in the most recent year, whilst continuing to visit areas used in previous years. The fourth bird remained in the North Sea in 2008, but spent some time in the Western Atlantic in each of its following three winters.

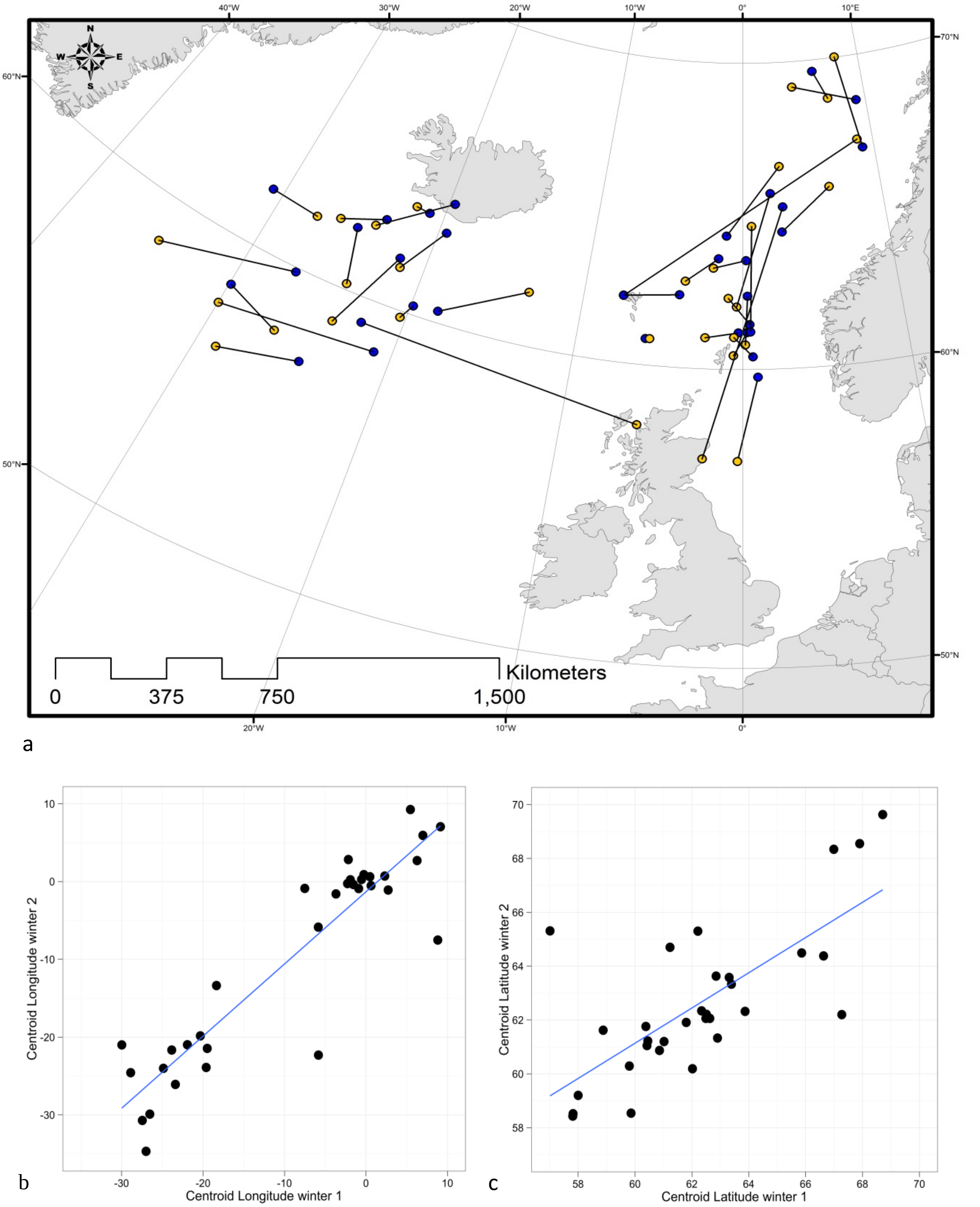

Figure 6. (a) Mean wintering location in the first year of study (blue) in relation to mean wintering location for a subsequent year (yellow) for 33 individuals (b) Relationship between average longitude in the first year of study against that for the subsequent year of study ($r^2=0.84$, $p<0.001$) (c) Relationship between average latitude in the first year of study against that for the subsequent year of study ($r^2=0.56$, $p<0.001$)

DISCUSSION

This study has identified the non-breeding areas used by northern fulmars breeding at a NE Atlantic colony. The data revealed that individual wintering patterns were strongly related to the sex of the bird, with females travelling further west from the colony and spending more time in those distant areas. There was also an indication that age may influence variation in area use, such that older individuals tended to be closer to the colony. Importantly, data from multiple seasons indicated a high level of consistency in the use of different wintering areas by most (>85%) individuals.

Individual differences in the use of non-breeding areas

Following breeding in August, time lapse data indicate that fulmars were largely absent from the colony from September to December (Figure 1a). The complementary activity data also indicate that flight time was reduced during September and October, suggesting that the areas used by these individuals in autumn may correspond to their primary and secondary moulting area. Previous work on fulmars has suggested that moult occurs at this time, (Dott 1973) but information on where birds moult has previously not been available. In both autumn and winter fulmars spend more time on the water at night in winter than during the day, which is similar to other procellarids in the non-breeding season (Mackley *et al.* 2010).

Both the time-lapse data and the activity data also highlight that fulmars return to their colony and surrounding waters throughout much of the non-breeding period. This confirms previous observational studies on colony attendance at UK breeding colonies (Fisher 1952; Macdonald 1980; Slater 1990). In winter, seabirds are clearly not as constrained to return to their breeding colony compared to the summer incubation or chick rearing periods (Bearhop *et al.* 2006; González-Solís *et al.* 2007). Nevertheless, we demonstrate that fulmars return regularly to the colony and spend much of their time in relatively local North Sea waters from January onwards (Figure 5). The increase in the time that these individual fulmars spent in North Sea waters was also accompanied by an increase in the proportion of time that they spent dry (Figure 1b), suggesting that they were spending more time on land.

Historical ringing recoveries indicate that fulmars from UK colonies may travel to the Western Atlantic (Brown 1970, Lyngs 2003; Wernham *et al.* 2002). However, this is the first time that the distribution of active breeders has been described (Figures 2 and 3). Previous ringing recovery studies primarily involved immature birds, whereas here, we demonstrate that adults regularly utilise these areas. Fulmars from colonies in both Greenland (Lyngs 2003) and Canada (Mallory *et al.* 2008) have been reported to use the Newfoundland, Labrador Sea and Davies Straight areas used by many of these Scottish breeders. This confirms the previous suggestion that fulmars may have a 'panmitic' wintering population (Mallory *et al.* 2008), as seen in other seabird species (González-Solís *et al*. 2007; Gaston *et al.* 2011). The West Atlantic region, used by 37% of the wintering fulmars from our study colony, has been identified as an important wintering and stop-over site for many other seabirds (e.g. Egevang *et al.* 2010; Gaston *et al.* 2011; Magnusdottir *et al.* 2012; Stenhouse, Egevang & Phillips 2012), marine mammals (Matthews *et al.* 2011) and large fish species (Kohler *et al*. 2002; Hammerschlag, Gallagher & Lazarre 2011). Why this area is so important to so many species requires further investigation but it is likely that the area's oceanography is such that high biological productivity exists, which can in turn support a large number of biological consumers (Townsend *et al.* 2004; Doney 2006).

For those birds travelling east, the Barents Sea is a similarly productive area biologically (Olsen *et al*. 2010), and supports many top predators (Fauchald *et al.* 2011). The North Atlantic drift keeps the sea ice at bay from July-December (Jakobsen & Ozhigin 2011), so the foraging potential for fulmars in this area may be substantial. Sea-ice itself has also been identified as a good foraging area for fulmars (Mehlum 1997). Here too, it is highly likely that Scottish fulmars will be mixing with birds from the fulmar colonies of Svalbard and Novaya Zemlya. Work on the environmental and habitat characteristics of different areas used by individuals, as has been carried out for other seabird species (e.g. Wood *et al.* 2000; Yamamoto *et al.* 2011), would be useful to further explain why the fulmars exploit these areas.

Sex differences were observed in non-breeding area use, such that female fulmars travelled west more than males and male fulmars were more likely to spend the majority of their winter in North Sea waters. One possibility, as yet untested, that may explain this observation is potential competition between the sexes, with female fulmars forced to forage further afield. Competition between males and females for resources has been shown in other seabirds during the breeding season (González-Solís *et al.* 2000). However, the scale at which we have shown the fulmars can operate over their winter will certainly mean they are in contact with, and potentially in competition with, both male and female fulmars from other populations. Whether the sexes are in the same region, but feeding in different small-scale areas within the larger region remains to be tested, and would benefit from finer-scale tracking work.

Our results also showed that females travelled significantly further from the colony than males (Table 3). Another possibility, therefore, is that females are able to travel more cost-effectively at lower wind speeds due to their smaller body size, as demonstrated in another procellarid species (Shaffer *et al.* 2001). In the mechanics of the gliding-based flight which fulmars adopt (Pennycuik 1960) it is difficult to ascertain whether there should be differential abilities in flight performance between the sexes. Eight male birds did travel to the West Atlantic which demonstrates that males are capable of flying similarly large distances as females, but we do not know if these males may be smaller in comparison to their North Sea wintering conspecifics. Further work to record wing loading may help elucidate if body size may play a role in differing wintering distributions.

A third possibility for sex differences in wintering distribution may relate to their different roles during the subsequent breeding season. Females may be seeking out specific nutrients over the non-breeding period as has been suggested in several seabird species in the pre and post-laying periods (e.g. gannets *Morus bassanus*, Lewis *et al*. 2002; common terns *Sterna hirundo*, Nisbet 1997; and magellanic penguins *Spheniscus magellanicus*, Boersma, Rebstock & Stokes 2004). Previous analyses at this study colony have already demonstrated that there are sex differences in diet in the pre-laying period in the fulmar (Owen *et al.* 2013), and these differences could extend through more of the wintering period. Alternatively, males may focus on defending the nest-site during both breeding and non-breeding periods, as seen in other species (Lundberg 1979; Martindale 1982; Kazama & Watanuki 2010). This is supported by studies of winter attendance at another Scottish fulmar colony, where both sexes visited the colony, but males were more frequent (Macdonald 1980). Future work should consider whether there are concurrent differences in diet between birds utilising different areas, and between the sexes over the non-breeding period, which could be achieved through analysis of stable isotopes of feathers moulted over the non-breeding period.

The return of both males and females to the North Sea area by February, may relate not just to the male's defence of the nest site, but could also be important for maintaining the pair bond or finding new mates. It is recognised that the non-breeding period is an important period for social interactions and pair bonding behaviour in some other seabird species (Kylin 2011) and many freshwater bird species (Robertson & Cooke 1999). It might also be that a desirable food resource becomes available in the North Sea region during these months, which again would require further analysis of winter diet during this period.

In addition to these sex differences in the use of wintering areas, there was an indication that older birds remained closer to the colony in North Sea waters (Table 3). It should be noted that the sample sizes between the age groups were less for middle and older age groups of birds compared to younger birds so the statistically significant differences in mean and maximum distance from the colony detected should be treated with caution. An increase of sample size in the older groups should be advised to see if the pattern remains the same. Nevertheless, it can still be hypothesized why the age differences detected may have arisen.

One possibility is that older birds have reduced physical fitness as has been shown in Cory's Shearwaters (Catry *et al.* 2011). Older shearwaters demonstrated a reduced activity in foraging and in take-offs and landings compared to younger individuals (Catry *et al.* 2011). Age-dependent changes in wintering strategies have been observed in other seabirds such as lesser black-backed gulls *Larus fuscus* (Marques, Sowter & Jorge 2010), but we have no information on where these older fulmars foraged earlier in their breeding history. Although our data suggest that the birds, in general, were consistent in their use of wintering areas, fulmars can breed for several decades and a longer time-series is required to assess whether there are age-dependent changes.

Alternatively, the age-related differences in wintering areas may result from a cohort effect. In larger Procellarid species that have been tracked, albatross fledglings undertake a period of area investigation (Riotte-Lambert & Weimerskirch 2013; R. Phillips pers. comm.). It is possible that fulmar fledglings adopt a similar strategy whereby a range of different foraging areas are investigated once leaving the natal colony. The relative use of those different areas when those birds subsequently recruit to the breeding population could depend either on those individuals selecting the most profitable areas, or through differential mortality of juveniles that use different areas. Tracking of individual fulmar fledglings has not yet been achieved, but UK ringing recoveries support the hypothesis that fulmar fledglings forage widely on leaving their natal colony (Wernham *et al.* 2002). Potentially, the older birds that we studied may have experienced more favourable conditions in the North Sea when they were juveniles, and this then became their 'default' wintering area. However, in more recent decades this area may have been less profitable for juveniles due to changes in food availability supply or increased competition, resulting in greater use of areas outwith the North Sea. For males, there may always be a trade-off between travelling further afield versus staying closer to the colony area to maintain and defend the nest site, potentially explaining why some younger males still utilise the North Sea. Whilst this possibility seems more likely than an energetic-based hypothesis, more data are required to discriminate between these different hypotheses.

Individual consistency in non-breeding strategy

Winter site fidelity was seen in most individuals (29/33) with 2 or more years data on winter foraging areas. Winter site consistency has also been shown for other procellarid species but this work has most commonly been from Southern Ocean studies (Croxall *et al.* 2005; Phillips *et al.* 2005). Individual consistency in wintering area is often studied with only two years of data, but in this current study data were available from 2-6 years, adding strength to the argument for a high degree of consistency. As well as significantly repeatable average locations, similar range sizes between years were shown. This has also been shown in a gannet tracking study (Grecian 2011). However, there is an indication that the story is more complex – for four birds a degree of plasticity is seen. This is not necessarily surprising when considering that the birds are long-lived and capable of making decisions based on previous experiences. Foraging decisions based on memory have recently been postulated in a study of tracked common guillemots *Uria aalge* whose foraging trips were extremely directed (Regular, Hedd & Montevecchi 2013). The guillemot study found no support for the more random search behaviour associated with Lévy search strategies, thought to be an optimal search strategy in a patchily distributed environment (Humphries *et al.* 2010). Fulmars also have the ability to act opportunistically with local conditions, particularly aided by their olfactory abilities (Nevitt 2008).

Whilst these birds were largely consistent within our 6-year data set, this remains short compared with the lifespan of this species (Fisher 1952). Consequently, individuals may switch to other wintering area at longer, decadal scales. Seabirds have been known to switch wintering location based on age, such that birds tend to stay closer to the breeding colony when they are older (Marques *et al.* 2010), and 'context-dependent' foraging strategies exist whereby if food supply changes, birds may subsequently change strategies from their norm (Elliott, Gaston & Crump 2010). If fulmars do indeed have the ability to switch area, as demonstrated by four birds, they may be able to buffer themselves to some degree with a changing marine environment.

Implications for conservation management

The scale at which fulmars are operating means that different individual fulmars will be in contact with differing amounts of pollution, prey type and climatic variables. As different sexes have shown differing survival probabilities in the fulmars at this study colony (Grosbois & Thompson 2005), it also raises the question of whether the differing wintering areas may play a role in differential survival, as has been noted for certain albatross species (Nel *et al.* 2002).

The identification of the wintering areas can now be used in further analyses to assess whether there are concurrent differences in winter diet between individuals in these areas and whether wintering in these distinct areas have subsequent fitness consequences.

Furthermore, the tracking data as a whole can feed into the wider, international tracking data community to increase our understanding of seabird spacial ecology (González-Solís & Shaffer 2009). This data can be used in helping identify key 'hot-spot' areas for seabirds at sea during their non-breeding periods (Grecian *et al.* 2012; Thaxter *et al.* 2012), a period for which we must not ignore for future conservation measures.

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CHAPTER 3

Validating the use of intrinsic markers in body feathers to explore inter-individual differences in moulting and wintering areas of northern fulmars.

Photo: Archive. "You won't catch me…"

CHAPTER 3: Validating the use of intrinsic markers in body feathers to explore inter-individual differences in moulting and wintering areas of northern fulmars.

ABSTRACT

Many wildlife studies use chemical analyses to explore spatiotemporal variation in diet, migratory patterns and contaminant exposure. Intrinsic markers are of particular use when studying marine predators during the non-breeding season when direct methods of investigation are not often feasible. However, any inferences regarding foraging ecology are dependent upon the time scale over which these tissues are formed. In seabirds, the most common tissues used to represent the non-breeding period are feathers. In this study, we validate the use of body feathers for studying non-breeding foraging in the northern fulmar. Body feathers were found to moult predominantly from September to March, encompassing more of the non-breeding timespan than wing feathers (which moulted during September and October) and tail feathers (which moulted between September to January). By randomly sampling several feathers, average values were consistent through the period, despite large inter-feather variability for some elements (particularly Fe and Zn). A discriminant analysis using stable isotopes of carbon and nitrogen correctly assigned 90% of birds to their broad-scale winter area, as verified from tracking data. Thus, body feathers are shown to be an effective samping tool for work on non-breeding foraging diet in the fulmar.

INTRODUCTION

Marine organisms are exposed to a variety of naturally occurring and anthropogenic chemicals. Some of these chemicals have the potential to be biogeochemical markers (e.g. stable isotopes, trace elements and contaminants) that can underpin studies of both spatial and foraging ecology (Ramos & González-Solís 2012). Due to the wide-ranging nature of many marine top predators, these species are likely to be exposed to large spatial variation in the distribution of chemical tracers (Burger & Gochfield 2004; Hobson & Bond 2012). Previous studies have employed intrinsic markers from marine top predators to investigate contaminant levels (Bond & Lavers 2011, Moreno *et al.*

2011), diet (Hooker *et al*. 2001; Fisk *et al*. 2002), and migratory patterns (Hobson, 1999; Seminoff *et al.* 2012). However, interpretation of these results requires information on both where and when those chemicals were incorporated into the target tissues (Burger & Gochfield 2000; Polizzi *et al*. 2013).

Intrinsic marker analysis is particularly suited for seabirds as they can be captured and sampled when they return to their breeding colonies (Furness & Camphuysen 1997). Furthermore, the different tissue types that may be sampled, for instance feather, blood, muscle, relate to different timescales at which the chemicals are assimilated (Pearson *et al.* 2003; Bearhop *et al.* 2004). However, even if a bird's breeding colony origin is known, the bird's prior distribution at sea is often uncertain. This is of particular importance when making colony-level inferences about foraging, because individual differences in wintering areas have been identified at colonies of several seabird species (Kubetzki *et al.* 2009; Harris *et al.* 2010; Kopp *et al.* 2011). Thus, while stable isotopes have been commonly used to study winter foraging ecology in many species (Cherel *et al.* 2006; Dehnhard *et al.* 2011), only a few recent studies have been based upon individuals with known foraging patterns (*cf.* Phillips *et al.* 2009; Jaeger *et al.* 2010; Grecian 2011; Leat *et al.* 2013). Recent advances in tracking technology (see Chapter 2) now provide opportunities to validate these chemical-based methodologies for a wider range of species with different foraging and distribution patterns.

For the majority of temperate and polar seabirds, moult and breeding do not overlap (Quillfeldt, McGill & Furness 2005; Bridge 2006; Allard *et al.* 2008), and the period of feather formation therefore occurs within the non-breeding period. Consequently, feathers are often the preferred tissue for chemical analysis as they are metabolically inert and their composition therefore relates to their period of formation (Inger & Bearhop 2008; Hobson & Bond 2012). Feathers can also be relatively easily collected when birds are at their breeding colony, and can be obtained from the same bird in subsequent years (Bearhop *et al.* 2002). One constraint when using feathers is that information on the study species' moult pattern is required to relate the chemical results to a particular time period or location (Inger & Bearhop 2008). Whilst the pattern of moult in different feathers is well understood in many terrestrial species (Hinsley *et al*. 2003; Ryder & Wolfe 2009; Gargallo 2013), comparable data are rare from seabirds because they spend so much of the year at sea. Furthermore, where data are available, this is most typically for the timing of moult in primary and secondary wing feathers (Ginn & Melville 2000). However, it is not possible to take whole wing feathers from live birds. Consequently, a short section is typically cut from the tip (Cherel *et al*. 2000), but this will relate to just a short period within the time that feather section was grown. To overcome this, it has been suggested that chemical analyses of body feathers may provide a more general indication of foraging activity through the non-breeding period (Bearhop *et al.* 2006). At the same time, this approach may also result in greater inter-feather variability in chemical loadings, and sampling protocols suggest taking a number of different body feathers (Bearhop *et al.* 2002). However, for many species, limited understanding of the timing of moult and variability in the chemical composition of different body feathers constrains the extent to which chemical signatures can be used to understand winter foraging patterns (Larson & Hobson 2009).

Previous isotope studies have typically concentrated on stable isotopes of carbon ($^{12,13}C$) and nitrogen ($^{14,15}N$) (Ramos & Gonsález-Solís 2012). Differences in ratios of these isotopes (denoted as $\delta^{13}C$ and $\delta^{15}N$) have provided information on inshore versus offshore and benthic versus pelagic feeding (Davenport & Bax 2002; Moreno *et al.* 2013; Hipfner *et al.* 2014), and on the trophic level of feeding (Atwell *et al.* 1998; Jaeger *et al.* 2013). In the Southern Oceans, available isoscape data have been used to make broad scale inferences about spatial patterns of foraging during the non-breeding season (e.g. Quillfeldt, McGill & Furness 2005; Cherel & Hobson 2007). In contrast, there is less background information on biogeochemical distributions in the North Atlantic (see Graham *et al.* 2010). Whilst $\delta^{13}C$ and $\delta^{15}N$ may also be informative in this region, there are *a priori* reasons to expect variation in other stable isotopes to provide valuable information on the spatial distribution of marine predators. In particular, lead isotopes ($^{206,207,208}Pb$) vary dependent on the geographic source of lead (Hamelin *et al.* 1990). The importance of these isotopes for pollution studies (e.g. Scheuhammer & Templeton 1998; Meharg *et al.* 2002) has resulted in extensive studies on the distribution of natural and anthropogenic sources of lead throughout both northern and southern hemispheres (Bollhöfer & Rosman 2001; Bollhöfer & Rosman 2002). Because lead isotopes are under geological control and are unaffected by dietary processes (Flegal & Smith 1995; Born *et al.* 2003), they may provide an important indicator for assessing broad scale geographic variation in winter foraging activity.

Recent tracking data has demonstrated that there can be marked individual differences in the wintering locations of northern fulmars breeding at the same North Atlantic colony (Chapter 2). Furthermore, individual birds were distributed widely but tended to be consistent in their use of one of three over-wintering areas (the West Atlantic, the North Sea and the Barents Sea/northern Norwegian Sea) that are likely to differ in their biogeochemistry. This study system therefore provides a rare opportunity to integrate analyses of feather chemistry with tag-based data on individual distributions, and to test whether there are concurrent spatial differences in chemicals. However, to achieve this, additional work is first required to confirm that the chemical composition of body feathers that can be collected from breeders is representative of the time at which birds are absent from the colony over winter. Existing information on moult patterns in fulmars is limited, and based either on observations of birds at breeding colonies (Carrick & Dunnet 1954; Allard *et al*. 2008) or analysis of beached or by-caught individuals outside the breeding season (van Franeker 2004b). In some years, poor food availability may slow down or arrest moult (van Franeker 2004a). More typically, adult moult begins post-breeding (late August) (Carrick & Dunnet 1954; Allard *et al.* 2008) and is thought to be completed by the end of February (Ginn & Melville 2000). Data from activity loggers indicate that the birds spend most time on the water during September and October (Chapter 2), suggesting that wing moult is most likely to occur in this period. If there is co-variation in chemical composition in wing feathers and body feathers it would suggest growth of these different feathers occurs over a similar period. In contrast, if body feathers grow later in the winter, they may be more similar in composition to tail feathers, as fulmars are known to initiate tail moult when wing moult is around 75% complete (Ginn & Melville 2000).

This study aimed to validate the use of body feathers, specifically those from the belly region, to assess individual and spatial variation in trace metals and stable isotope markers over the non-breeding period. Using a combination of tracking and chemical analyses, the specific objectives were to: a) assess inter-feather type variability in moult timings and chemical loadings, b) assess inter-feather variability which may occur when sampling belly feathers c) to validate the use of belly feathers as usable proxies for identifying non-breeding areas and in representing dietary information in the non-breeding period.

METHODS

Feather moult data

Data on feather moult were collected from carcasses during a long-term study of plastic pollution by Jan Andries van Franeker (see van Franeker 2011). Full details of the techniques used can be found in the Fulmar Litter EcoQO Manual Part 1: Collection and dissection procedures (van Franeker 2004b). Primary, tail and body moult scores were recorded for each bird using criteria developed by the British Trust for Ornithology (BTO) (Ginn & Melville 2000). Moult scores for primary and tail feathers were based upon external inspection of the feather, where an old feather was scored as 0 and a new, fully developed feather as 5. The maximum primary moult score for a fulmar was therefore 100, as fulmars have a total of 20 primary feathers. The maximum tail moult score was 70, as fulmars normally have 14 tail feathers. For the purposes of this study, April 1st was used as the reset date for the completion of moult, after which new plumage (total score 100 or score 70) must become old plumage (score 0) before the next moult cycle. Body moult was scored by internal assessment of the degree of body moult after dissection: 0 = no new feather shafts present; 1 = a few feather shafts present and 2 = feather shafts present over the majority of the internal body surface. Data were available from 725 adult fulmars which were defined as breeders based upon internal examination (see Appendix 3 for month by month sample sizes). These birds were either by-caught on Faroese or Icelandic long-lines, or hunted, but were otherwise recorded as being in apparently healthy condition based upon body condition scores during dissection (see van Franeker 2004b). It is assumed for the purposes of this study that moult data from the birds caught off the Faroes are representative of the moult pattern of birds from Eynhallow, the study colony. There are only two degrees difference in latitude between the colonies so a latitudinal difference in moult pattern is unlikely (Hemborg, Sanz & Lundberg 2001).

Study site and logger deployment

Data on winter-distribution and feather chemistry were collected from fulmars breeding on Eynhallow, Orkney (59°8'N; 3°8'W). Fieldwork was conducted between 2006-2012, when approximately 100 active nests were recorded annually. Breeding adults were caught at the nest using a hand net or noose, and British Antarctic Survey

(BAS) light-based GLS loggers were attached to the darvic leg-rings of 163 birds using cable ties. The total device weight (including leg ring) was 3.6g, representing <0.5% of the lightest recorded fulmar's body weight. The average logger recovery rate was 46% over one year and 76% over two or more years. After re-capture, a randomly selected sample of six to ten belly feathers were taken from tagged individuals. Complete winter tracks were available from 67 individuals. Data on trace metals and Pb isotopes in feathers grown over the same winter were available from 46 birds. Concurrent data on C and N isotopic data were also available from 38 birds.

Element analyses

Feathers were washed with Milli-Q water prior to oven drying at 65^{o}C for >12 hours. Aristar nitric acid (0.5ml) was added to each feather sample and left overnight to digest. Aristar hydrogen peroxide (1ml) was then added, before a 75 minute microwave digest (CEM Microwave Technology Ltd.) in which a peak of 95^{o}C was held for 30 minutes. Samples were then diluted to 10ml with ultrapure deionized Milli-Q water, and 19 element total concentrations were measured from a sub-sample using an ICP-MS 7500 (Aglient Technologies), using the reaction cell with hydrogen gas. Bovine liver (National Institute of Standards and Technology) 1557b was used as the certified reference material (CRM). Standards made from Multi-Element solution 2 were run every 30 samples, from which standard curves could be calculated. In a few samples, some elements (V, Mn, As, Cd, Pb) were below the limits of detection (LoD). Following standard procedure (Anderson *et al*. 2010), these samples were given a value of half the LoD.

$\delta^{206,207,208}$Pb isotope analyses

^{206,207,208}Pb isotopes were measured using an ICP-MS (Element 2, Thermo Scientific, Bremen, Germany), using a subsample from the digested feather samples. Pb standard solutions were run every two samples to correct for instrumental mass bias. Each feather was analysed separately so that inter-feather variability could be assessed prior to taking an average value for each bird.

$\delta^{13}C$ and $\delta^{15}N$ Stable isotope analyses

For $\delta^{13}C$ and $\delta^{15}N$ isotope analyses, feathers were washed with Milli-Q water prior to oven drying at 65°C for > 12 hours. Samples were then homogenised in a ball mill (Mixer Mill type MM 200, Retsch of Haan, Germany). Sub-samples of 1.3mg material were then loaded into 5 x 3.5mm tin cups (Elemental Microanalysis Ltd.). Total N and C values and the ^{15}N:^{14}N and ^{13}C:^{12}C isotope ratios of milled dried material were determined using a Flash EA 1112 Series Elemental Analyser connected via a Conflo III to a Delta^{Plus} XP isotope ratio mass spectrometer (all Thermo Finnigan, Bremen, Germany). Isotope ratios were calculated using CO_2 and N_2 reference gasses injected with every sample. The isotopic values of these gasses were directly referenced against IAEA reference materials USGS40 and USGS41 (both L-glutamic acid); certified both for $\delta^{13}C$ (‰ $_{VPDB}$) and $\delta^{15}N$ (‰$_{air\ N_2}$). Long-term precision of a quality control standard (milled flour) was: $\delta^{13}C$ -25.5 ± 0.29 ‰ and ^{15}N 0.367 ± 0.0002 atom % (mean ± sd, n = 200).

Between-feather variation in chemical composition

Samples of feathers from ten birds that were by-caught on Faroese long-lines were used to assess within-individual variation in chemical composition using four different types of feathers: primary (inners), secondary (first secondaries), tail (central retrices) and belly (selection) feathers. Average sample weights were: primary (0.043±0.009), secondary (0.040±0.006), tail (0.051±0007) and belly (0.025±0.003). Data were available for associated trace metals and Pb isotopes for between-feather comparisons, but not for C and N isotopic data.

Between-feather variability in the chemical composition of belly feathers was assessed using independent analysis of four or five feathers from ten individual birds from Eynhallow.

Tracking data

Individual tracks were produced from light-based GLS loggers using BASTrak software v.18, using a light threshold of 10 and an elevation angle of -3.5. An iterative smoothing process was applied twice to the data to reduce error associated with the tracks

(Phillips *et al.* 2004). Over-winter tracks were projected in ArcGIS v.9.3 using the North Pole Lambert Azimuthal Equal Area projection.

These data were then used to assign each individual bird to one of the three wintering regions (the West Atlantic, the North Sea and the Barents Sea/northern Norwegian Sea) in two different ways. First, a mean location was calculated for each individual over the whole winter period (October-February). Second, the overall winter distribution from all points over the winter was assessed to see if the mean location reliably represented the bird's main winter location (see Appendix 2 for winter location divisions). This second approach was particularly useful for those birds whose mean location was borderline between groups. To maintain independence, when a bird had data from multiple years, only one year was randomly chosen for analysis to ensure that each bird only had one locational point and one group of metal and isotope results.

Statistical analyses

Mean moult scores for each feather type were calculated for each month of the year. These were then converted into a proportion of numbers of birds with complete moult per month with associated standard errors.

Median concentrations of all elements above the limits of detection (LoD) were calculated for each feather type. Due to unequal variances between feather types, data were ranked (Langin *et al.* 2007) before performing repeated-measure ANOVAS. Feather type was the explanatory variable in the ANOVA, with each metal(loid) and Pb isotope tested separately as the response variable. Individual bird ID was included as an error term to account for non-independence of individuals with repeated measures of feather types. Model fits were verified and pair-wise comparisons were made between each feather type using Tukey's honest significant difference tests.

To assess within-individual variation in feather chemistry, the coefficient of variation (CV) was calculated in each metal(loid) for the ten birds in which there were measurements from multiple feathers. For comparison with individuals in which measurements were based solely upon analyses of two belly feathers, two belly feathers were randomly sampled from each of these 10 birds and the mean value calculated for each element (mg/kg). This process was then repeated for another two belly feathers and the two means were compared against each other. Pearson's product moment correlation coefficients were calculated for each bird.

To explore how feather chemistry varied in relation to individual location, a linear discriminant analysis (lda) was carried out in the 'MASS' package in R (Venables & Ripley 2002) using C and N stable isotope data from belly feathers. Cross validation techniques were employed to produce jackknifed predictions (Leat *et al.* 2013). Predictions were initially based upon birds being assigned to one of three wintering areas using location data from October-February. However, due to the small sample size for birds wintering in the Barents Sea/northern Norwegian Sea, the analysis was repeated using data for just the two main wintering areas (West Atlantic and North Sea). A MANOVA was also carried out on all elements against location group to assess for differences in trace metal(loid)s between location groups.

Statistical analyses were performed in R v.2.15.0 (R Core Development Team 2012).

RESULTS

Inter-feather type variability in moult timings and chemical concentrations

Timing of moult

Analysis of moult scores revealed that primary moult occurred during September and October and was complete by November in all healthy adults dissected (Figure 1). No overlap with the breeding period in either wing or tail moult was recorded. Active tail moult was seen over a longer period, from September to January, and was completed by February. Internal body moult was seen from September onwards, with the highest levels of active moult recorded in birds caught in October and December. However, these data indicate that active body moult occurs throughout the non-breeding period (September to March) (Figure 1).

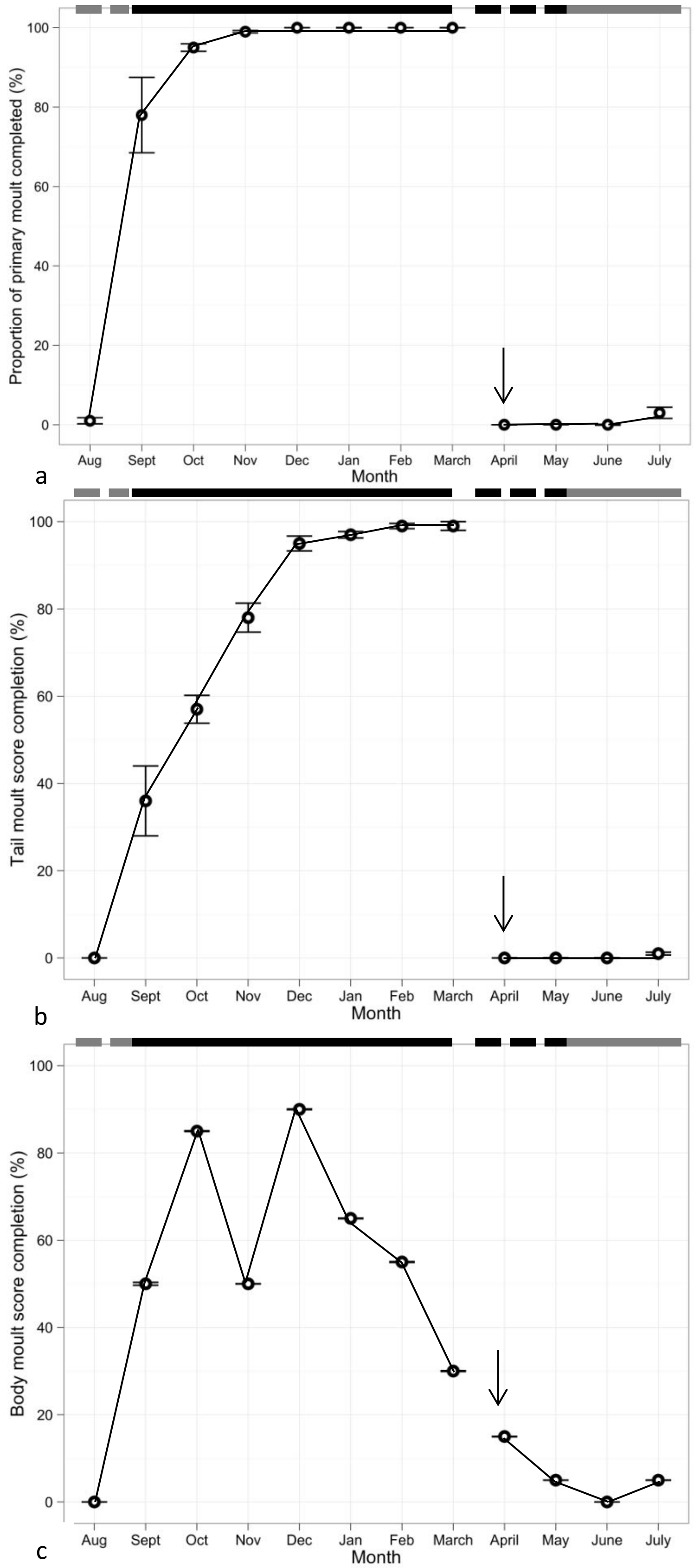

Figure 1. Proportion of adult fulmars that had completed their moult in each month for a) primary (n=704), b) tail (n=703) and c) body (n=725). The arrow represents the reset date on April 1st. Standard error bars are also shown. Black solid line represents the non-breeding period, black dashed line the pre-laying period, grey solid line the breeding period and grey dashed line the end of breeding period.

Variation in chemical composition of different feather types

Instrumental quality results for the chemical analyses are shown in Table 1. The percentage recovery for each element was excellent, with two elements (Se and Sr) being above the 100% recovery, which relates to analytical interferences.

Table 1. Limits of Detection (LoD) for feather samples (μg/g) and percentage recovery of the elements, using Bovine liver certified reference material (CRM) with the expected and obtained values (μg/kg).

Element	*LoD(μg/g)*	*Expected CRM value (μg/kg)*	*Obtained CRM value (μg/kg)*	*% recovery for element*
As	0.061	50	41	81
Cd	0.043	500	460	92
Cu	2.104	160000	143836	90
Fe	15.510	184000	175396	96
Mn	0.318	10500	9420	90
Pb	0.332	129	127	98
Se	0.174	730	856	117
Sr	0.794	136	221	163
V	0.088	123	119	96
Zn	4.097	127000	114089	90

In general, belly feathers demonstrated smaller ranges in element concentrations than primary, secondary and tail feathers (Table 2). Fe and Zn, two essential elements, had the highest concentrations of all elements studied and demonstrated large ranges (Table 2). Results of statistical comparisons of differences between the feather types are presented in Table 3. All elements except As demonstrated a high degree of variability between feather types. Tail feathers were consistently different from all other feather types in pair-wise comparisons. Tail feathers also tended to have highest median concentrations of all elements compared to belly, primary and secondary feathers, except for As, Se and Sr. Primary and secondary feathers were not significantly different for any metal(loid) concentrations except in V. Overall, the belly feathers showed similar median concentrations with primary feathers in all but two elements (V and Sr).

Median values for Pb isotopes were generally similar in different feather types (Table 2). The exceptions were $Pb^{206.207}$ ratios, where tail feather concentrations were higher than those in primaries. Tail feathers also showed the largest range of values in Pb isotopes.

Table 2. Median concentrations of each element and Pb ratios in mg/kg (range in brackets), for each feather type. Values are given to 2 decimal places.

Element	***Feather type***			
	Belly n=10 median(mg/kg) (range)	*Primary n=10* median(mg/kg) (range)	*Secondary n=10* median(mg/kg) (range)	*Tail n=10* median(mg/kg) (range)
V	0.21 (0.11-0.45)	0.433 (0.27-5.55)	0.281 (0.23-1.19)	1.563 (0.75-3.48)
Mn	0.92 (0.56-9.29)	1.738(0.51-34.20)	1.916(0.56-6.59)	4.794 (3.05-16.93)
Fe	131.72(43.48-389.00)	97.71(45.52- 1440.04)	158.32(32.79-2468.77)	777.30(357.50-4215.83)
Cu	10.12 (8.55-11.62)	10.02 (7.94-77.95)	8.96 (6.35-13.97)	12.62 (9.85-27.51)
Zn	81.35(59.84-102.26)	67.01(51.93-184.87)	84.76(68.35-127.88)	127.38(44.36-326.22)
As	0.96 (0.48-1.92)	1.16 (0.33-17.61)	1.05 (0.24-3.01)	1.12 (0.46-6.74)
Se	3.87 (2.41-4.31)	5.23 (3.89-8.97)	5.64 (4.60-9.68)	3.44 (2.56-6.90)
Sr	15.03 (10.64-19.65)	30.82 (25.37-43.55)	29.15 (21.02-41.20)	28.21 (25.75-38.05)
Cd	0.22 (0.13-1.08)	0.16 (0.04-0.37)	0.11 (0.03-1.07)	0.47 (0.26-1.12)
Pb	0.53 (0.41-1.41)	1.35 (0.25-4.84)	0.66 (0.25-4.63)	4.36 (2.71-22.16)
Pb206.207	1.14 (1.13-1.15)	1.13 (1.11-1.16)	1.14 (1.11-1.20)	1.17 (1.04-1.20)
Pb208.206	2.13 (2.11-2.15)	2.15 (2.08-2.23)	2.13 (2.07-2.19)	2.07 (1.78-2.19)
Pb208.207	2.43 (2.41-2.42)	2.43 (2.32-2.54)	2.43 (2.38-2.55)	2.33 (2.10-2.55)

Table 3. Results from repeated measure rank-based ANOVAs for each element/isotope ratio and feather type. Pairwise comparisons between feather type groups are also shown where B=belly feather; P=primary feather; S=secondary feather and T=tail feather. Significance is taken to be < 0.05.

Element/ Isotope ratio	**Model**			**Significantly different pairwise comparisons between feather types**
	Feather type			
	F	df	Pr(>F)	
V	36.11	3	**<0.001**	All
Mn	15.71	3	**<0.001**	Tail vs B,P,S
Fe	9.53	3	**<0.001**	Tail vs B,P,S
Cu	9.95	3	**<0.001**	Secondary vs B,T
Zn	4.40	3	**0.012**	None
As	0.72	3	0.551	None
Se	40.15	3	**<0.001**	All except P&S,B&T
Sr	19.24	3	**<0.001**	Belly vs P,S,T
Cd	8.32	3	**<0.001**	Tail vs P,S
Pb	18.58	3	**<0.001**	Tail vs B,P,S
Pb206.207	3.82	3	**0.021**	Tail vs P
Pb208.206	2.56	3	0.076	None
Pb208.207	0.86	3	0.475	None

Inter-feather variability in the chemical composition of belly feathers

Coefficients of variation were often high when multiple belly feathers were measured from the same bird (Table 4). However, variation between individuals was generally much greater. Thus, when two different means were assessed for correlation between random pairs of feathers from the same individual, there was a significant relationship between these repeat measurements in the majority of the elements (Table 4). The overall correlation between the two different sets of feather means was highly positive.

Table 4. Mean concentrations of elements are shown and the coefficient of variation as an indicator of variance between samples. Means were taken from 5 feathers for each bird, apart from birds 1015, 1153 and 1890, where n=4. Correlations between two different means is shown with significance p<0.05 in all cases.

Bird	**Element**																				
	V		Mn		Fe		Cu		Zn		As		Se		Sr		Cd		Pb		Mean 1 vs Mean 2 correlation
	Mean (mg/kg)	CV (%)	Mean (mg/kg)	CV (%)	Mean (mg/kg)	CV (%)	Mean (mg/kg)	CV (%)	Mean (mg/kg)	CV (%)	Mean (mg/kg)	CV (%)	Mean (mg/kg)	CV (%)	Mean (mg/kg)	CV (%)	Mean (mg/kg)	CV (%)	Mean (mg/kg)	CV (%)	
1015	0.35	23	17.85	39	193.74	28	8.95	9	54.09	8	0.17	42	0.10	11	5.91	20	0.03	7	1.17	67	r=0.99
1136	0.22	3	1.70	11	113.67	6	9.29	14	52.46	10	0.06	69	1.27	6	7.08	13	0.02	4	0.71	95	r=0.99
1153	0.15	9	0.91	58	38.69	43	7.08	8	47.90	21	0.05	65	1.14	12	6.72	22	0.02	7	0.85	38	r=0.98
1367	0.15	20	1.27	19	53.42	47	7.25	10	59.52	15	0.08	56	1.29	14	7.13	16	0.06	39	1.15	89	r=0.94
1597	0.47	13	8.87	26	172.58	14	8.04	4	48.76	11	0.44	36	1.01	8	6.71	8	0.06	45	1.06	25	r=0.99
1631	0.17	7	1.06	23	40.88	21	11.07	8	48.03	7	0.03	7	1.14	9	10.64	23	0.02	4	0.99	28	r=0.99
1854	0.23	16	1.16	14	116.83	18	8.30	19	50.29	11	0.04	28	1.33	11	7.26	27	0.03	28	0.94	41	r=0.99
1876	0.18	14	1.25	40	82.82	23	9.17	7	52.91	13	0.03	8	0.94	15	5.60	16	0.02	14	1.01	40	r-0.98
1880	0.25	7	1.23	15	85.96	15	10.25	8	63.15	29	0.18	102	1.68	32	6.20	25	0.26	85	1.25	18	r-0.81
1890	0.31	69	7.59	50	191.49	85	8.63	18	62.13	22	0.20	75	2.03	9	7.83	33	0.03	38	0.77	30	r=0.99

Validation of spatial assignment using intrinsic markers

The mean locations of birds for the overall winter time period (October-February) are plotted in Figure 2, together with the wintering region that each bird was assigned to. Most birds were assigned to the North Sea or West Atlantic category.

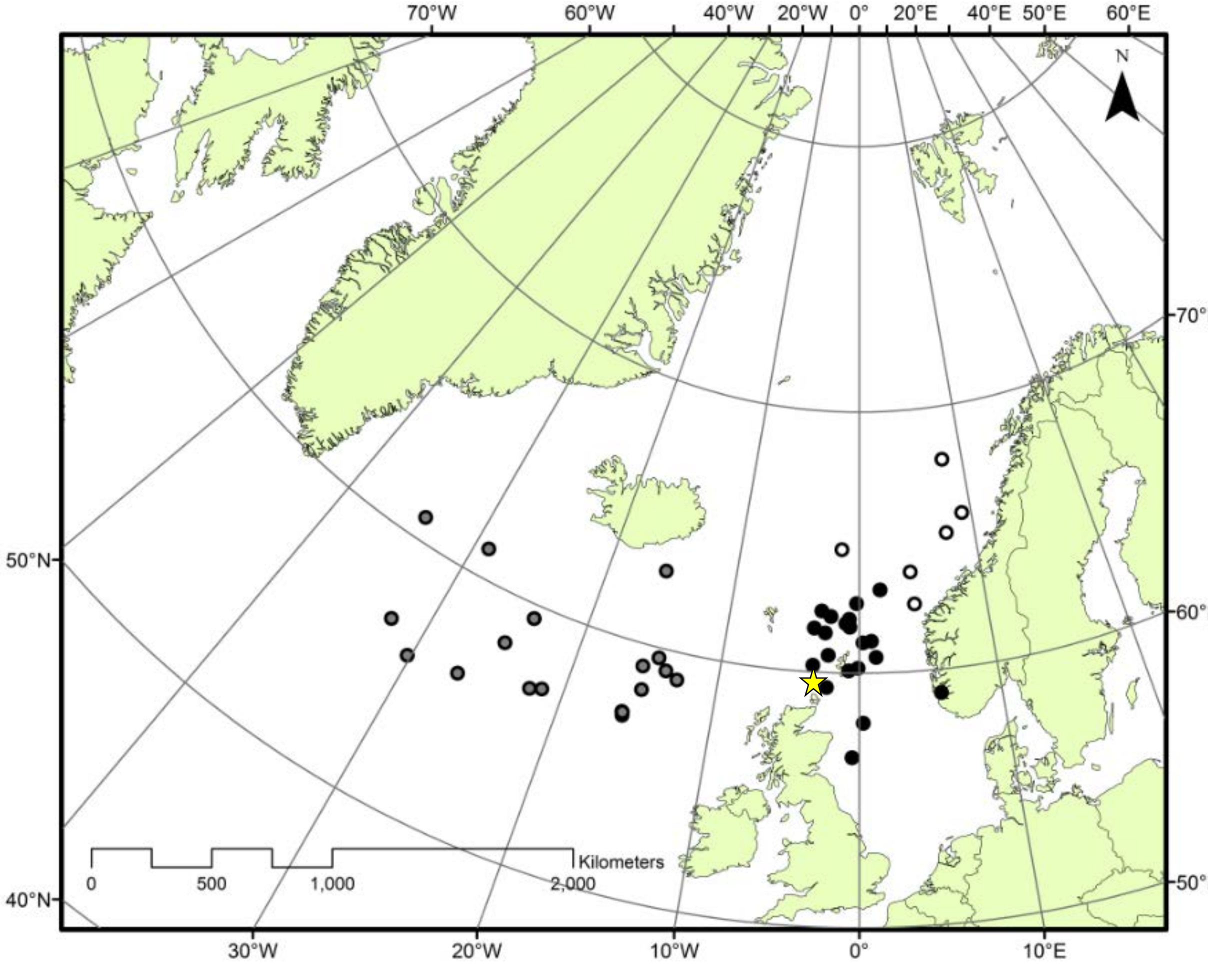

Figure 2. Map of mean bird locations for the 46 birds which have feather chemistry values relating to their winter track (average location from mid-October to end of February). Location groups represented as circles (West Atlantic=grey, North Sea=black, East=white). Colony location is marked (yellow star).

Considering each element separately, levels of many elements were broadly similar between location groups (Table 5). No significant differences between the groups was apparent when all elements were considered together (MANOVA: Pillai = 0.42, $F_{2,18}$=1.08, Pr(>F)=0.393).

What is of particular note is that Pb isotope ratios do not differ between location groups (ANOVA, $^{206/207}$Pb, $F_{2,44}=1.29$, $p=0.286$; $^{208/206}$Pb, $F_{2,44}=0.34$, $p=0.717$; $^{208/207}$Pb, $F_{2,44}=2.39$,$p=0.104$). As the multi-elemental and Pb isotope analysis revealed no clear differentiation between location groups, they were not included in the discriminant analysis.

There were significant differences in $\delta^{15}N$ between location groups (ANOVA, $F_{2,36}=19.54$, $p<0.001$) and borderline significant differences in $\delta^{13}C$ between location groups (ANOVA, $F_{2,36}=2.88$, $p=0.070$).

Table 5. Median values of metal(loid) or isotope concentration in mg/kg (range given in brackets) for each location group. For element and Pb isotopes n=18 (West Atlantic), n=22 (North Sea) and n=6 (East/Barents Sea). For C and N isotopes n=14 (West Atlantic), n=21 (North Sea) and n=3 (East/Barents Sea). Values are given to two decimal places.

Element/ Isotope	***Location group***		
	West Atlantic median mg/kg (range)	*North Sea median mg/kg (range)*	*East/Barents median mg/kg (range)*
V	0.21 (0.09-0.80)	0.21 (0.09-0.50)	0.20 (0.09-0.35)
Mn	2.69 (0.32-17.21)	2.37 (0.32-29.4)	1.57 (0.68-5.12)
Fe	113.82 (22.28-435.09)	107.06 (16.35-132.38)	96.93 (51.31-211.61)
Cu	9.03 (7.27-11.85)	9.84 (5.30-12.51)	8.47 (7.54-9.63)
Zn	60.04 (42.25-80.00)	61.50 (34.27-176.13)	51.54 (49.05-66.85)
As	0.16 (0.04-0.46)	0.12 (0.04-0.33)	0.06 (0.01-0.20)
Se	2.60 (0.03-12.59)	1.74 (0.95-2.74)	1.43 (0.84-2.08)
Sr	8.37 (5.94-12.70)	7.98 (3.96-22.10)	8.58 (5.98-10.41)
Cd	0.08 (0.03-0.42)	0.05 (0.01-0.48)	0.05 (0.01-0.08)
Pb	0.67 (0.38-8.31)	0.95 (0.27-2.37)	0.63 (0.34-0.97)
Pb 206.207	1.16 (1.14-1.18)	1.16 (1.14-1.17)	1.16 (1.16-1.17)
Pb 208.206	2.11 (2.06-2.12)	2.11 (2.06-2.13)	2.11 (2.07-2.13)
Pb 208.207	2.44 (2.41-2.47)	2.44 (2.40-2.45)	2.46 (2.41-2.48)
δ^{13}C	-17.18 (-17.87,-16.91)	-17.22(-18.14,-16.13)	-17.82(-17.82,-17.75)
δ^{15}N	14.27 (13.93,15.46	15.63 (14.65,17.00)	15.38(15.27,15.83)

The discriminant analysis assessed how well birds could be classified into their location group based on their C and N isotopic signatures in belly feathers. The analysis was carried out twice: once with all three winter groups, and secondly with only North Sea and Westerly groups as the Easterly group had a much smaller sample size compared to the other location groups. The discriminant analyses demonstrated a high proportion of true westerly birds were assigned correctly using their C and N isotope data (Table 6 & 7). Misclassifications occurred most commonly between North Sea groups and easterly groups.

Table 6. Classification results from discriminant analysis carried out using three location groupings (West Atlantic, North Sea, East) with C and N isotopes.

Allocated group	*True group*		
	west	*north*	*east*
west	13	3	0
north	1	14	1
east	0	4	2
total n	14	21	3
proportion correct	0.93	0.67	0.67

Table 7. Classification results from discriminant analysis carried out using two location groupings (West Atlantic, North Sea) with C and N isotopes.

Allocated to group	*True group*	
	west	*north*
west	13	3
north	1	18
total n	14	21
proportion correct	0.93	0.86

DISCUSSION

This study has demonstrated that the chemical composition of body feathers can be used to make inferences about winter foraging ecology, and that stable isotope chemical markers differed in groups of fulmars with contrasting winter distribution patterns. Analysis of data from post-mortem investigations confirmed the time period over which body feathers grow in this species, thereby validating their use in diet and distribution studies over this period. Despite high inter-feather variability, mean values from pairs of belly feathers provided a robust measure of individual variation in chemical loadings.

Variation in the moult and chemical composition of different feather types

The moult data indicate that body feathers moult over a longer time span than primary feathers (Figure 1), thus making them more representative sample for assessing dietary information over the non-breeding period. This pattern of a shorter period of primary moult post-breeding, in conjunction with a more protracted period of body feather moult is seen in other, similar-sized seabirds (Furness *et al.* 1986; Bridge 2006). However, it is by no means universal in fulmarine petrels (see Barbraud & Chastel 1998) and will depend upon breeding status (Allard *et al.* 2008). A shorter period of wing moult maximises winter foraging opportunities as wing moult is known to impede flight ability in certain species (Hedenström & Sunada 1999; Bridge 2006). Activity data from fulmars from this study colony indicates that flight was constrained during this same period as this was when birds spent most time on the water (Chapter 2). In contrast, a longer period of body moult is possible because it should not impede flight capabilities. These data also found no overlap between the breeding period (April to August) and either wing or tail moult initiation. This confirms results from a study of High Arctic breeding fulmars (Allard *et al*. 2008). Similar patterns are found in other bird species, both terrestrial and marine (Weimerskirch 1991; Hemborg, Sanz & Lundberg 2001), though exceptions in overlapping breeding period and moult exist (see Barbraud & Chastel 1998; Ramos *et al*. 2009).

Chemical concentrations in belly feathers were similar to those found in primary feathers (Table 3), suggesting the feathers were grown under similar conditions with respect to time, place or dietary intake. This concurs with other studies which demonstrated similarities in certain isotope levels between primary and breast feathers in wandering albatrosses *Diomedea exulans* (Jaeger *et al.* 2009) and common guillemots *Uria aalge* (Becker *et al*. 2007). In contrast, there were some differences between tail feathers and the remaining feather types, with tail feathers having larger median concentrations of most elements. In fulmars, tail moult occurred in the latter half of winter months, but this pattern of tail moult occurring after wing moult is not ubiquitous amongst other petrel species (see Hedd & Montevechhi 2006). Observed differences in chemical loadings in tail feathers could result from biological factors, such as differences in moult pattern or area; or fundamental differences the sequestering of elements in tail feathers. Alternatively, differences may result from methodological issues related to feather preparation.

If differences in elemental loadings between tail feathers and other feathers are the result of the later moult in tail feathers, one would also expect greater variation in belly feathers, which are also still moulting during late winter. However, this was not detected and it seems unlikely that observed differences are solely due to differences in moult timing, and hence area, as seen in other seabird species (Nisbet *et al.* 2002). Different rates of sequestration of elements occur depending on the moult sequence, with those feathers at the beginning of the moult sequence commonly showing higher values of metals than those towards the end of the moult sequence (Dauwe *et al.* 2003). However, in fulmars the tail feathers demonstrated higher values than other feathers in most elements despite being moulted after, so this hypothesis is also unlikely.

Another possibility is external contamination of the tail feathers. Tail feathers have a more complex structure than belly feathers, and it is possible that, despite the Milli-Q water washing stage, external dust may have remained embedded in the feather. A comparison of feather washing methods in warbler feathers demonstrated that some particles remained after a Milli-Q bath, but not after being cleaned using nitrogen gas (Font *et al.* 2007). External contamination of certain elements, commonly Fe, Hg, Ni and Zn, has been suggested in other feather studies (Dauwe *et al.* 2003) and it is known that preen oil does contain heavy metals which may affect chemical loadings (Goede & de Bruin 1984; Jaspers *et al.* 2008). In our study, lead levels were significantly higher in the tail feathers. However, if tail feather structure makes them more susceptible to external contamination, we might also expect to see higher lead values in primary feathers which also have a more complex structure than belly feathers. This was not the case, but it is possible preen oil may play an unknown role in external contamination. It has also been suggested that between-feather variability in metal concentrations may be an artefact of different sample weights (Bortolotti 2010). This may also be why the chemical concentrations in belly feathers tended to have smaller ranges compared to other feather types (Table 2), possibly reflecting both a lighter feather and a difference in growing duration of each type.

Calculations to obtain the mg/kg of sample take the original weight of the sample into consideration, but it should be noted that tail feather section sampled, though of a similar size to the belly feathers sampled, had larger weights. Whilst it is difficult to distinguish between the reasons for tail feathers having higher metals concentrations we cannot rule out the possibility role of external contamination and differing sample weights playing a role.

Inter-feather variability within a bird

Large coefficients of variation were demonstrated between individual body feathers (Table 4). Nevertheless, strong positive correlations between the two differing means gives us confidence in using mean values of body feathers for further studies on northern fulmars and biogeochemicals. This confirms what is often assumed in other studies utilising seabird body feathers (Bearhop *et al*. 2000; Cherel *et al.* 2006).

Studies on intra-individual variation in chemical loadings between feathers have mostly concentrated on comparisons between different feather types (Thompson & Furness 1995; Deben *et al.* 2012). However, rarely have studies considered the advantages and disadvantages of using an averaged value for a pooled sample of body feathers compared to average values from feathers that have been subjected to independent analysis (see Jaeger *et al.* 2009). Although homogenising several body feathers is still often recommended, we demonstrate that, for certain trace metals, pooling data may lose information. It can be important, for example, to know which metal(loid)s show the most inter-feather variation, as this may affect subsequent analyses. Fe and Zn demonstrated large variations between feathers, as shown in other seabird studies (Jerez *et al.* 2011). It is perhaps not surprising that Fe values are highly variable, as large amounts of this element are required for feather formation (Honda *et al*. 1990). Circulating levels of hepatic Fe will be highly dependent on diet at that time, as seen with other essential elements (Stewart *et al.* 1994). Therefore, if body feathers are growing at slightly different periods over winter, different amounts of Fe may pass into the feather tract during development.

Analyses of body feathers involved taking the whole belly feather, rather than taking a sample of larger wing or tail feathers, as often carried out in seabird dietary work (Barrett *et al.* 2007; Kouwenberg *et al.* 2013). Moreover, it was possible to sample several belly feathers from the same bird to provide an average estimate of metal loadings. Furthermore, due to the less complex feather structure it is possible belly feathers are less likely to have chemical loadings influenced by external contamination. This study suggests that belly feathers therefore provide a suitable sampling unit when using feather chemistry to study the overwintering ecology of fulmars.

Combining location data with metal(loid) and isotope data

Combining tracking data with chemistry data demonstrated that C and N isotopes have the potential to distinguish between wintering areas, with relatively good predictions, as has been shown in previous studies of large procellarids (Phillips *et al.* 2009) and Great skuas *Stercorarius skua* (Leat *et al.* 2013). In particular, predictions between birds wintering in the West Atlantic were correct 93% of the time. The misclassifications between North Sea groups and East groups may be due to a number of factors. The small sample size of the easterly group in comparison to the North Sea group is likely to have affected the discriminant analysis. In future it would be useful to obtain more C and N data from birds known to utilise easterly areas to assess whether an increased number could help distinguish these areas better. It may also be due to easterly birds overlapping with the North Sea birds for a large proportion of their non-breeding time, which has been shown in a previous tracking study (Chapter 2).

It is also possible that sex is a confounding factor in distinguishing between these groups. Female fulmars travel further from their colony on average than males (Chapter 2), and sex differences in diet inferred from chemical analyses have been noted across marine taxa (Ruiz-Cooley *et al*. 2004; Bearhop *et al.* 2006; Tucker *et al.* 2007). Considering if dietary differences between the sexes exist in the fulmar over this non-breeding period in subsequent analysis, coupled with an increase in sample size of easterly foragers may help to differentiate between the North Sea and easterly groups for future analyses.

There was no evidence of differences in Pb isotopes in groups of birds wintering in different areas. This was contrary to expectations as these ocean basins are known to differ in Pb isotopic signatures due to variation in naturally occurring and anthropogenically produced lead sources (Hamelin *et al.* 1990; Born *et al.* 2003). Tracked fulmars from this same colony demonstrated that 81% of birds spent the majority of their time in the North Sea over the winter period, despite individuals spending time west and east of the colony (Chapter 2). Therefore, it is possible that Pb ratios better reflect feeding conditions in the colony region (i.e. North Sea), rather than geographic differences in winter distribution within a single colony. It would be useful to compare values from this Scottish colony with other fulmar colonies to assess whether Pb isotope ratios are more closely related to breeding colony, as has been shown in Great skuas for persistent organic pollutants (Leat *et al.* 2013, see Chapter 5). The $^{206/207}$Pb ratio average of 1.16 in each location group, is at the higher end of the range of recorded in $^{206/207}$Pb levels from atmospheric aerosol measurements in northern Europe (1.10-1.16) and higher values of $^{206/207}$Pb may reflect a subarctic signature (1.16-1.18) (Bollhöfer & Rosman 2001).

Implications for future work

As the use of intrinsic biogeochemical markers in elucidating migratory patterns and dietary information increases, it is paramount we gain a greater understanding of both the chosen tissue sample, and the environmental spatial distribution of our selected markers. Detailed knowledge on moult patterns are still not commonly studied amongst the seabird fraternity (Bridge 2006), despite the frequent use of feathers as the chosen sample. Future studies, where possible, should utilise by-caught or beached birds (as also used in Ramos *et al.* 2009) to validate their chosen sample's formation period coupled with location based on tracking data. Once this has been achieved there remains a powerful tool for use in seabird ecology. There is the ability to greatly increase sample sizes compared to tagged individuals (as in Phillips *et al.* 2007; Leat *et al.* 2013), and the study organism need only be captured once to obtain the sample and not re-captured to retrieve a tag as is the case for many commonly used data loggers (Hobson & Norris 2008). This may be of particular importance when there is within colony variation in wintering strategies where retrieval may be biased to more successful individuals. Carefully thought-out feather sampling regimes can provide a non-lethal sampling technique with the ability to vastly increase our knowledge of a seabird's foraging during the non-breeding period. The use of body feathers as opposed to wing feather samples, the sampling of which may impair flight capabilities or be limited in the amount which can be sampled, may be considered a useful alternative. Body feathers may therefore act as proxies for identifying non-breeding area and in representing dietary information in the non-breeding period.

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CHAPTER 4

Contrasting non-breeding strategies at two northern fulmar colonies identified through geo-spatial and isotopic tracking.

Photo: H.Dombrowe. “The fight”

CHAPTER 4: Contrasting non-breeding strategies at two northern fulmar colonies identified through geo-spatial and isotopic tracking.

ABSTRACT

Understanding differential foraging strategies in highly mobile species, such as seabirds, is crucial for assessing a species' overall population dynamics and conservation requirements. In this study, northern fulmars were tracked from two colonies: Eynhallow, a North Sea fulmar colony, and Little Saltee, a southerly Irish Sea fulmar colony. Tracking data revealed that Eynhallow fulmars had a larger winter home range and many individuals spent considerable amounts of time in the West Atlantic and in oceanic waters. Little Saltee fulmars predominantly remained in the Irish and Celtic Seas around the core colony area in the winter period, and foraged in neretic waters. Stable isotope analysis and elemental profiling revealed differences in $\delta^{13}C$ such that Little Saltee fulmars had a more benthic signature in their diet, and were feeding on prey items with higher values of $\delta^{15}N$ than Eynhallow fulmars. It is hypothesized that differences in isotopic signatures may relate to a differential use of fishery discards between the two colonies.

INTRODUCTION

In many species, mortality risk increases over winter (Harris & Wanless 1996) and winter habitat quality can strongly influence subsequent breeding seasons (Harrison *et al.* 2010). Understanding foraging movements outside the breeding season and establishing whether there are inter- and intra-colony differences in movements between breeding and non-breeding grounds is therefore crucial to understanding a species' population dynamics (Webster *et al.* 2002). Identifying whether aggregations of non-breeders contain individuals from different breeding populations can also have important conservation implications for species which use particular areas for foraging (Elphick & Oring 2003; González-Solís *et al.* 2007) or pair bond formation during the non-breeding season (Kylin 2011; Robertson & Cooke 1998).

Seabirds have often been considered useful ecological indicator species as they 'integrate' a wide habitat range, have long lifespans, and can be caught on land at their breeding colonies (Furness & Camphuysen 1997). However, studying foraging distribution in marine organisms is problematic due to the scale of marine systems, and uncertainty over their distribution at sea has often constrained their potential value as ecological indicators. Work over the last decade has started to overcome this issue through a considerable increase in the number of seabird tracking studies (e.g. Egevang *et al.* 2010; Hedd *et al.* 2012), many using light-based geolocation technology (GLS loggers). These GLS loggers have revolutionised our knowledge of seabird migration and movements over the non-breeding period. Concurrent advances in the chemical analysis of tissue samples have also provided opportunities to infer migratory patterns from specific chemical markers (Cherel, Hobson & Weimerskirch 2000; Rubenstein & Hobson 2004), and to assess foraging differences between (Anderson *et al.* 2010) and within seabird species (Rey *et al*. 2012).

Multi-colony tracking studies are of particular interest in assessing differing patterns between populations. Colony segregation in breeding season habitat choice may be predicted due to constraints of central-place foraging with breeding birds having to return to the breeding colony, as noted in gannets *Morus bassanus* (Wakefield *et al.* 2013), black-browed albatrosses *Thalassarche melanophris* (Huin 2002) and blue-eyed shags *Phalacrocorax atriceps* (Wanless & Harris 1993), for example. In contrast, considerable overlap in wintering distributions of birds from different breeding colonies is predicted and has been shown in several species including black-legged kittiwakes *Rissa tridactyla* (Frederiksen *et al.* 2012), Cory's shearwaters *Calonectris diomedea* (Gonsález-Solís *et al*. 2007) and guillemots *Uria spp.* (Tranquilla *et al.* 2013). Examples of distinct colony-specific wintering areas in colonies within an individual's foraging range are rare (see Gaston *et al.* 2011). Whilst these tracking studies are of great use to define distribution patterns, the level of overlap between colonies cannot be used to determine whether or not dietary preferences differ between colonies. Combining tracking data with elemental profiling and stable isotope analysis can help overcome this, but has predominantly been carried out during the breeding season (Votier *et al.* 2010; Moseley *et al.* 2012). Those studies which have been carried out during the non-breeding period have concentrated on differences between species breeding at different colonies (Phillips *et al.* 2007; Phillips *et al.* 2009; Linnebjerg *et al*. 2013) or differences in birds from single colonies with individual differences in broad scale winter area (Hedd *et al.* 2012). Rarely has a study compared both inter- and intra-colony differences in winter distribution and foraging patterns (see Grecian 2011).

Stable isotopes can be used to infer differing trophic levels of foraging due to the stepwise enrichment of $\delta^{15}N$ with each trophic level and can also be used to infer benthic or pelagic foraging based on $\delta^{13}C$ signatures (Hobson 1999). Foraging differences may also be detected by varying times spent in separate bathymetric regimes, which can relate to productivity differences. Seabirds in temperate and polar environments are known to feed in productive shelf waters (Catry *et al*. 2009) where upwelling systems make it a profitable environment in which to forage. Comparisons between proportions of bathymetric domain usage have typically been carried out from at-sea surveys (Yen, Sydeman & Hyrenbach 2003; Nur *et al.* 2011) on individuals of unknown breeding origin. Some tracking studies have considered species differences in bathymetric habitat choice (Suryan & Fischer 2010), but the few comparisons between individuals from the same colony area have lacked concurrent dietary information (Wakefield *et al.* 2011).

For an individual to be defined as having a particular foraging strategy, that individual has to have a preference to forage in a particular area (Weimerskirch *et al.* 2005) or for particular prey items (Gonsález-Solís, Croxall & Wood 2000). In this current study, a non-breeding foraging strategy is defined as an individual's use of a preferred foraging area over the non-breeding area and the dietary composition obtained within this chosen area.

This study aimed to compare winter foraging characteristics at two northern fulmar colonies; one from a North Sea colony (Eynhallow, Orkney) and one from the southerly part of the fulmar's range (Little Saltee, Ireland). Tracking data from Eynhallow has demonstrated individual differences in foraging location over the non-breeding period, and sex-differences in foraging distances from the colony, such that females travel furthest from the colony on average (Chapter 2). Individual consistency in these non-breeding habitat choices has also been shown (Chapter 2), but it is not known to what extent birds from different colonies may overlap in their wintering range. A previous satellite tracking study on Pacific fulmars from four Alaskan colonies demonstrated colony-specific wintering areas, though sample sizes between colonies were small (up to 5 individuals per colony, some with incomplete winter data) (Hatch, Gill & Mulcahy 2010). For the majority of tagged Pacific fulmars, tag deployment was accompanied by breeding abandonment, which may have affected timings of non-breeding distributions, as has been noted in failed breeders in kittiwakes (Bogdanova *et al.* 2011). Previous dietary studies on fulmars in the breeding period suggest that there are colony differences in the extent to which birds may rely on fisheries (Hamer, Thompson & Gray 1997; Phillips *et al.* 1999). Whilst fulmars have long been associated with fishing vessels for obtaining by-catch (Fisher 1952; Garthe & Huppop 1994), they also consume many natural prey items (Thompson, Furness & Lewis 1995) and are also associated with large-scale oceanographic features (Edwards *et al*. 2013; Renner *et al.* 2013), where both fisheries and natural prey items may reside. However, it is not known whether colony differences in diet, as measured from stable isotope ratios, exist in the non-breeding period or whether differences may exist due to wintering foraging area.

This study aimed to: a) use tracking data to compare the non-breeding distribution of fulmars from two colonies and b) determine the concentrations of a variety of intrinsic markers in belly feathers to establish if there are any colony differences in dietary proxies over the same time period.

METHODS

Fieldwork and feather sampling collection

Forty-four BAS GLS tags were deployed on breeding adult fulmars on Little Saltee, Ireland (52º7'N, 6º41'W) in June and July of 2010, and a total of 28 of these were recovered in May 2011 and June 2012. Of these 28, all 28 tags had autumn tracks and 27 had complete winters. Fifty-seven GLS tags were deployed on breeding adults on Eynhallow, Orkney (59º8'N, 3º7'W) in 2010 with 43 being recovered in 2011 and 2012, all of which had autumn and complete winter data. Eight to ten belly feathers were taken from around the brood patch on recapture, which related to the previous overwinter period (Chapter 3). Of these feathers, 2 were randomly selected for elemental analyses and 2 or 3 were selected for stable isotope analyses of C and N. Feathers were stored dry in envelopes at room temperature until analysed. Sexes were determined molecularly using P2-P8 primer sequences using a Z-002 marker (Griffiths *et al.* 1998; Dawson 2007).

Tracking data

Twice daily locations for each bird were produced using BASTrak software v.18, with a light threshold level of 10 and an angle of elevation of -3.5. An iterative smoothing process was applied twice to the data to reduce error associated with GLS tracking data (Phillips *et al.* 2004). The autumn period was taken to be from 20th August, when most breeders have completed their breeding cycle, to mid-September. The winter non-breeding period was taken to be from end of October to end of February, thus avoiding any equinox periods for which latitude data are unreliable (i.e. mid- September to mid-October) (Fox 2010). Tags were recovered from 25 males and 18 females in Eynhallow, and 22 males and 6 females in Little Saltee. Six Little Saltee birds also had data available for a second winter, adding to the 33 Eynhallow birds which also have data from 2 or more years (see Chapter 2).

$\delta^{13}C$ and $\delta^{15}N$ Stable isotope analyses

Feathers were washed with Milli-Q water prior to oven drying at 65°C for > 12 hours. The samples were then homogenised in a ball mill (Mixer Mill type MM 200, Retsch of Haan, Germany). Sub-samples of 1.3mg of material were then loaded into 5 x 3.5mm tin cups (Elemental Microanalysis Ltd.). The total N and total C contents and the ^{15}N:^{14}N and ^{13}C:^{12}C isotope ratios of the milled dried material were determined using a Flash EA 1112 Series Elemental Analyser connected via a Conflo III to a Delta^{Plus} XP isotope ratio mass spectrometer (all Thermo Finnigan, Bremen, Germany). The isotope ratios were calculated using CO_2 and N_2 reference gasses injected with every sample. The isotopic values of these gasses were directly referenced against IAEA reference materials USGS40 and USGS41 (both L-glutamic acid); certified both for $\delta^{13}C$ (‰$_{\text{VPDB}}$) and $\delta^{15}N$ (‰$_{\text{air N2}}$). Long-term precisions for a quality control standard (milled flour) were: $\delta^{13}C$ -25.5 ± 0.29 ‰ and ^{15}N 0.367 ± 0.0002 atom % (mean ± sd, n = 200). In 2010, data were available from 30 Eynhallow birds, and from 18 Little Saltee birds for C and N stable isotope analyses. In addition, 14 birds from Eynhallow had C and N isotope data from other years and 20 Eynhallow and 10 Little Saltee birds had 2 years of C and N data available.

Element analyses

Feathers were washed with Milli-Q water prior to oven drying at 65°C for > 12 hours. Aristar nitric acid (0.5ml) was then added to each feather sample and left overnight to digest. Aristar hydrogen peroxide (1ml) was then added, before using a 75 minute microwave digest (CEM Microwave Technology Ltd.) with a peak of 95°C that was held for 30 minutes. The samples were then diluted to 10ml with ultrapure deionized Milli-Q water, a sub-sample of which was used for measuring 19 element total concentrations using an ICP-MS 7500 (Aglient Technologies), with the reaction cell used with hydrogen gas. The certified reference material used was bovine liver (National Institute of Standards and Technology) 1557b. Standards made from Multi-Element solution 2 were run every 30 samples, from which standard curves could be calculated.

Statistical analyses

Tracking data

The tracks were projected in ArcGIS v.9.3 using the North Pole Lambert Azimuthal Equal Area projection. Overall area usage of birds from each colony was calculated from home range analysis in Hawth's tools (Beyer 2004), using least squares cross-validation, with a 50km cell size and 200km search radius (Phillips *et al.* 2007). Home range was defined as the 95% usage contour and core range area was defined as 50% usage contour. Overlap in home and core ranges was measured by calculating the area of intersect between Eynhallow and Little Saltee home and core ranges. Point pattern analysis was also carried out in ArcGIS to demonstrate hotspots of area use across the winter locations with a grid square size of 300km, corresponding to the resolution of the mean logger error plus one standard deviation (Phillips *et al.* 2004). This uses a quadrat analysis which calculates the numbers of points per grid square, in order to demonstrate the most densely and least densely used areas (Diggle 2010). To calculate the proportion of time spent within waters nearby the colony, points within 300km of each colony were counted (similarly based upon mean logger error plus one standard deviation). A proportion was used because individuals differed in the number of days that they were tracked, primarily because some days had to be excluded due to error in the light data (ranging from 0-30 days being excluded from a possible 135 'winter' days and 0-13 days being excluded from a possible 28 'autumn' days). A chi-squared test was used to compare differences in proportions of time spent in each region between each colony. The average and maximum distances travelled from the colony were calculated for each bird, and differences between sexes and colonies were analysed using Mann Whitney U tests. For Little Saltee and Eynhallow birds with two years of winter data a repeatability estimation was calculated using the rptR package (Nakagawa & Schielzeth 2010).

General Bathymetric Chart of the Oceans (GEBCO) data was obtained from the British Oceanographic Data Centre (BODC) (https://www.bodc.ac.uk/data/online_delivery/gebco/) using the one arc-minute grid resolution (Suryan & Fischer 2010). These data were overlaid with tracking data, and time spent in different bathymetric regimes was calculated for each colony and each sex. Classifications of bathymetric regimes were: neretic (less than the 200m continental shelf), shelf break (from 200m shelf to the 1000m beginning of continental slope) and oceanic (greater than 1000m) (Wakefield *et al*. 2011).

Each bird that was tracked was assigned to a wintering area based upon the amount of time they spent in a particular foraging area. Wintering areas categories were: North Sea; Irish Sea; West Atlantic; and Barents Sea/northern Norwegian Sea (see Appendix 2 for map of regional divisions).

Isotope and element data

For elements where a few samples were below the limits of detection (LoD) (V, Mn, As, Cd, Pb) in feathers, those samples were given a value of half the LoD value, as is standard procedure (Anderson *et al.* 2010). All other elements reported had values that were all above the LoD. For each of the chemical elements and stable isotope ratios, a median and range were calculated for each sex within each colony. Linear models were carried out for each element, with colony, sex, and wintering as explanatory variables. Model fits were checked using standard plots and the most parsimonious model was chosen based on AIC values, corrected for by small sample size in the AICcmodacg package (Burnham, Anderson & Huyvaert 2011; Burnham & Anderson 2002).

All statistical analyses were carried out in R v.2.15.0 (R development Core Team, 2012).

RESULTS

Comparison of non-breeding areas between Eynhallow and Little Saltee colonies

The tracking data revealed overlap in the overall winter distribution of fulmars from Eynhallow and Little Saltee (Figure 1). However, there were marked colony-differences in the core areas used, as revealed by the point pattern analyses (Figure 1 a and b). At each colony, areas of highest use were in waters surrounding the colony: Orkney and Shetland region for Eynhallow birds and the Irish and Celtic Sea regions for Little Saltee birds. This result was also reflected in the percentage of the winter that birds spent within local colony waters (Table 2). Little Saltee birds spent significantly more time in colony waters (70%) compared to Eynhallow birds (40%) in winter, with the differences being present in both sexes. The home ranges (95% kernel) of the two colonies overlapped by 38% but there was no overlap in core range (50% kernel) (Table 1 and Figure 1). Home and core ranges for Eynhallow birds were more than double the size of home and core ranges of Little Saltee birds (Table 1). This difference remained when tested with equal sample sizes by randomly selecting 27 Eynhallow birds (home and core ranges still over 2 times bigger).

The larger ranges in Eynhallow birds were also reflected in the summary statistics, as Eynhallow birds travelled significantly further in terms of both maximum distance from colony and average distance from colony (Table 2).

Sex differences detected in Eynhallow birds, with females travelling significantly further than males on average, were not detected in Little Saltee birds (Table 2). Little Saltee females still showed a tendency to travel further from the colony than males, but potentially due to the much smaller sample size of females, no statistical significance was apparent. No differences in the mean number of days males and females spent within the core colony area were detected for either Eynhallow or Little Saltee birds.

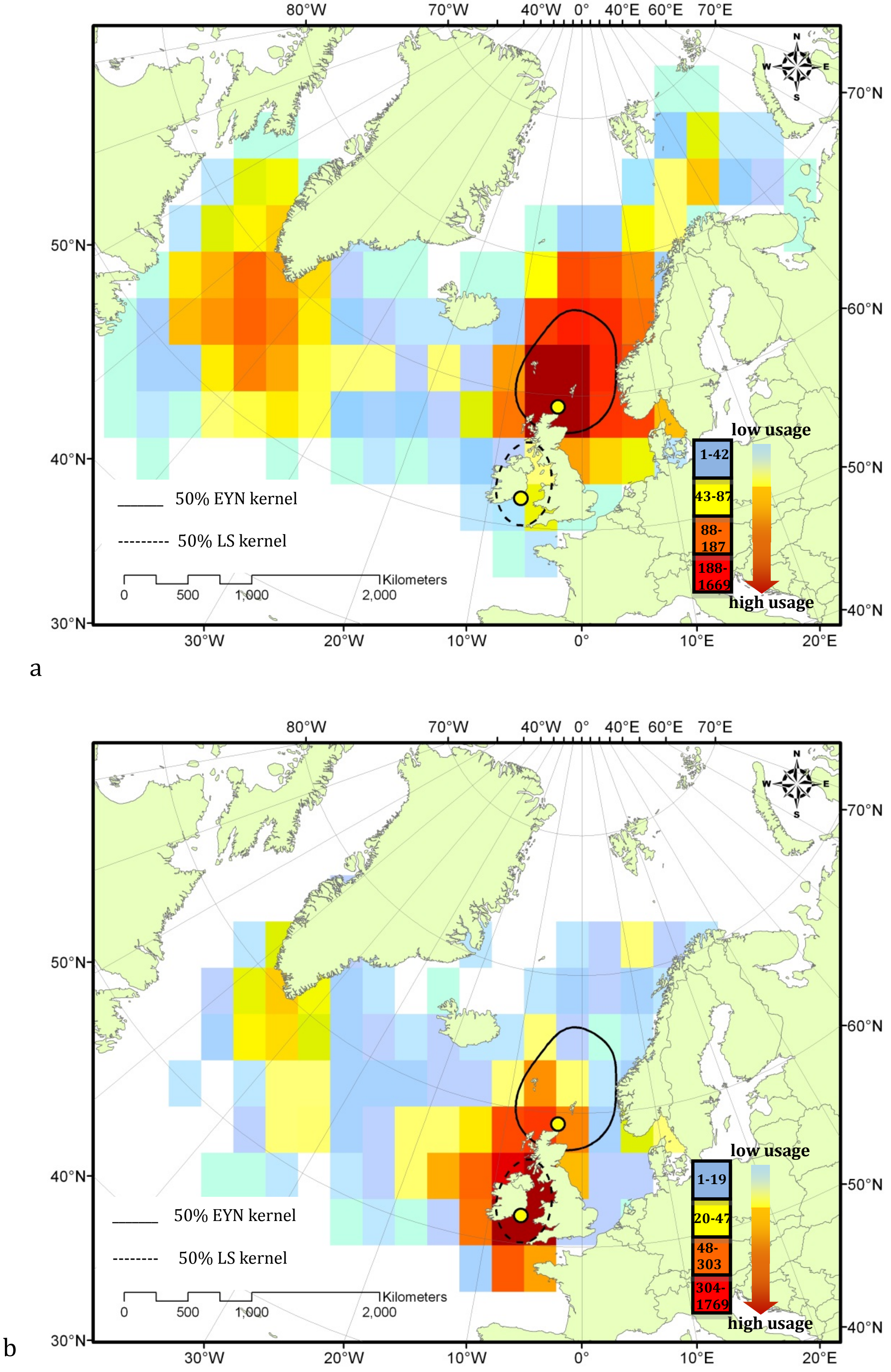

Figure 1. Eynhallow (EYN) (a) and Little Saltee (LS) (b) point pattern analysis of area use over winter (end Oct-end Feb). Fifty % core area kernels are shown for EYN (solid black line) and LS (dashed black line). Areas of high usage are shown as dark red colours and lower area use shown as lighter blue colours. The numbers in the coloured key represent the number of points counted during the analysis.

Table 1. Home range and core range area use in Eynhallow and Little Saltee birds with overlapping percentage shown for home range. No overlap in core range was noted.

Colony	**95% home range (km^2)**	**50% core range (km^2)**
Eynhallow (Eyn)	6,500,000	590,000
Little Saltee (LS)	3,300,000	220,000
Extent of Overlap (%)	**38%**	**0%**

Table 2. Winter track summary characteristics for Eynhallow and Little Saltee. Mann-Whitney U and chi-squared test results are shown for comparisons between and within colonies.

	Mean distance travelled from colony (km)	**Mean maximum distance travelled from colony (km)**	**Mean no. of days spent within colony area (% of total winter days)**
Eynhallow all (n=43)	**830±500**	**2200±900**	**54±25 (40%)**
Little Saltee all (n=27)	**360±240**	**1500±790**	**87±17 (70%)**
Test between EYN/LS	W=1023, $p<0.001$	W=847, $p=0.001$	$X_1^2=21.73, p<0.001$
Eynhallow males (n=25)	**640±400**	**1770±840**	**58±26 (44%)**
Little Saltee males (n=21)	**330±180**	**1560±1100**	**87±16 (71%)**
Test between EYN/LS males	W=458,$p<0.001$	W=352, $p=0.049$	$X_1^2=18.05, p<0.001$
Eynhallow females (n=18)	**1100±510**	**2810±580**	**49±23 (36%)**
Little Saltee females (n=6)	**490±370**	**1940±990**	**88±21 (67%)**
Test between EYN/LSfemales	W=92, $p=0.009$	W=85, $p=0.040$	$X_1^2=25.20, p<0.001$
Eynhallow females vs. males	W=354, $p=0.001$	W=370, $p<0.001$	$X_1^2=1.42, p=0.233$
Little Saltee females vs. males	W=89, $p=0.140$	W=81, $p=0.316$	$X_1^2=0.23$ $p=0.634$

On an individual level, birds from both colonies utilised West Atlantic regions in winter. Though fewer Little Saltee birds foraged in the west (Eynhallow; 21 birds, Little Saltee; 9 birds) (Table 3), no difference in the proportion of birds from each colony travelling west was detected (prop.test X_1^2 =1.056, p=0.304). Only one Little Saltee bird spent a considerable amount of time foraging in the Norwegian and Barents Sea area (> 44 days). This contrasted to Eynhallow birds with six individuals making long visits to these areas east of the colony (> 35 days) and 11 individuals spending shorter periods of time in this area (Table 3). However, again no difference in proportion of bird's using this area extensively from each colony was detected (prop.test X_1^2 =0.965, p=0.326).

Consistency in wintering foraging area, previously identified in Eynhallow birds (Chapter 2), was also confirmed for six Little Saltee birds with two years of winter tracks. Low sample size excluded the ability to produce a repeatability estimation for Little Saltee birds alone, so their location data were combined with previous Eynhallow data (Chapter 2). Both mean longitude (r=0.84±0.048, p<0.001) and mean latitude (r=0.83±0.049, p<0.001) were highly repeatable between the two years.

A striking difference was seen between the autumn (end August - mid September) and winter (end October - end February) foraging strategies of birds from Eynhallow and Little Saltee. Individuals from Eynhallow were more mixed in their autumn strategy: some left North Sea waters in autumn (18/43 birds), others remained with North Sea waters (25/43). Between October and December, Eynhallow birds then foraged further afield than Little Saltee birds. In January, the majority of Eynhallow birds returned to within approximately 500km of their colony (Figure 2). In contrast, Little Saltee birds tended to forage furthest from their colony during the autumn compared to their winter (Figure 2 & Table 2), with the mean distance from the colony over autumn close to the maximum distance recorded during winter (Table 2). Significantly more Little Saltee birds travelled outwith their colony area of the Irish Sea compared to those remaining in the Irish Sea for the autumn (19/28 birds and 9/28 birds respectively, prop.test X_1^2=5.786, p=0.016). From November, Little Saltee birds remained close to their colony waters (Figure 2).

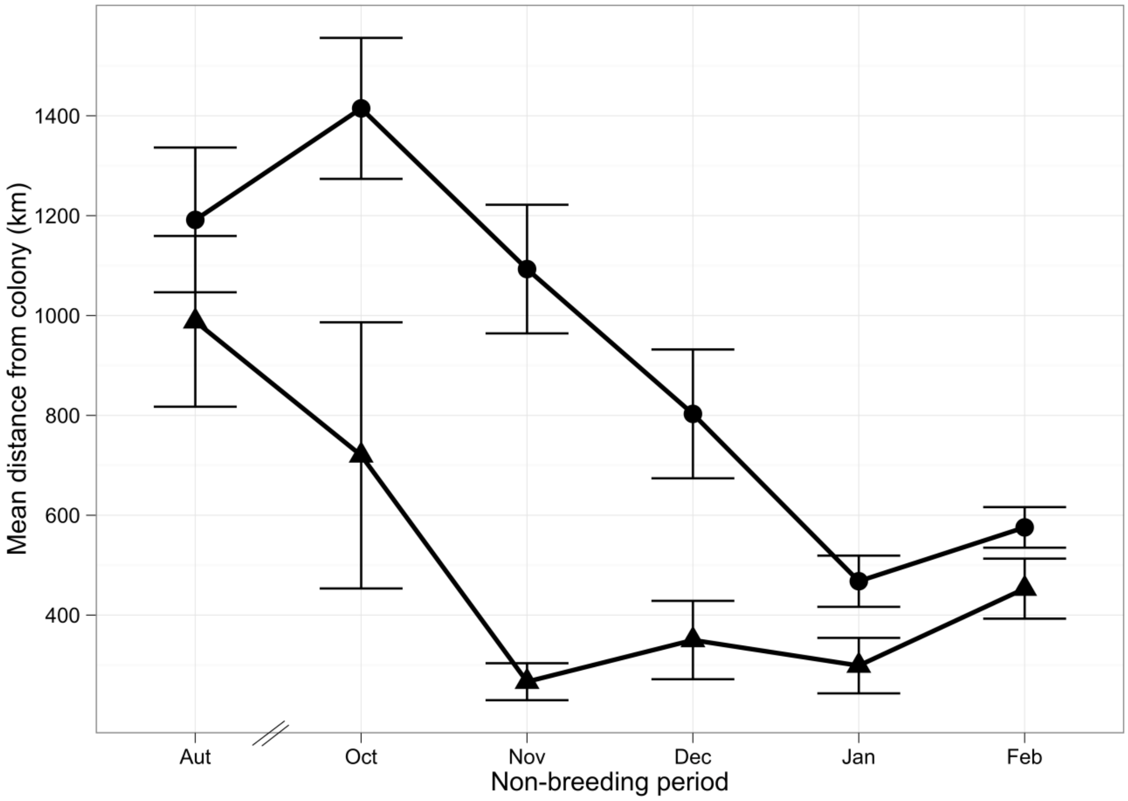

Figure 2. Mean distance from colony (km) in Eynhallow fulmars (black circle) and Little Saltee (black triangle) fulmars across the non-breeding period, with standard error of the mean shown as error bars. The lines between Aut (Autumn) and Oct (October) represent the fact some data is missing during this time period due to the autumn equinox period.

Table 3. Mean proportions of time spent in each broad scale area for Eynhallow (EYN) and Little Saltee (LS) fulmars over both autumn and winter. Range of days spent in each area is also given. The numbers of individuals which spend time in each area are also shown: note that this does not represent the number of individuals classified in each of the broad scale groups, but represents those which use these areas at some point over their non-breeding period.

Broad non-breeding foraging area	**Mean proportion of time: autumn (%) (range of days)**		**Mean proportion of time: winter (%) (range of days)**		**No. individuals utilising areas**	
	EYN	**LS**	**EYN**	**LS**	**EYN**	**LS**
West Atlantic	19	29	18	6	21/43	9/28
	(7-26)	(9-28)	(17-108)	(1-58)		
North Sea	61	1	74	49	43/43	20/28
	(2-25)	(1-6)	(33-135)	(2-31)		
East/Barents Sea	17	0	7	<1	17/43	1/28
	(3-28)	(0)	(1-51)	(1-26)		
Irish Sea	3	70	1	84	2 /43	28/28
	(2-4)	(6-25)	(1-42)	(58-122)		

Figure 3 demonstrates the differences between Eynhallow and Little Saltee birds in their use of differing bathymetric regimes in both autumn and winter. In autumn, Eynhallow fulmars spent more time in neretic waters (prop.test, X_1^2=52.72, p<0.001) and shelf break waters (prop.test, X_1^2=87.29, p<0.001) compared to Little Saltee birds. Little Saltee birds spent longer in oceanic waters (prop.test, X_1^2=180.83, p<0.001). In contrast, in winter, Little Saltee birds spent more time in neretic waters than Eynhallow birds (prop.test, X_1^2=5219.05, p<0.001), which spent longer in oceanic (prop.test, X_1^2=2685.28, p<0.001) and shelf break (prop.test, X_1^2=1198.90, p<0.001) waters. General linear models revealed that there were significant colony differences in the depths of water used in both autumn ($F_{1,2778}$=391.17, p<0.001) and winter ($F_{1,18381}$=2893.3, p<0.001). Furthermore, females foraged in deeper waters than males in both autumn ($F_{1,2778}$=76.67, p<0.001) and winter ($F_{1,18381}$=1311.4, p<0.001).

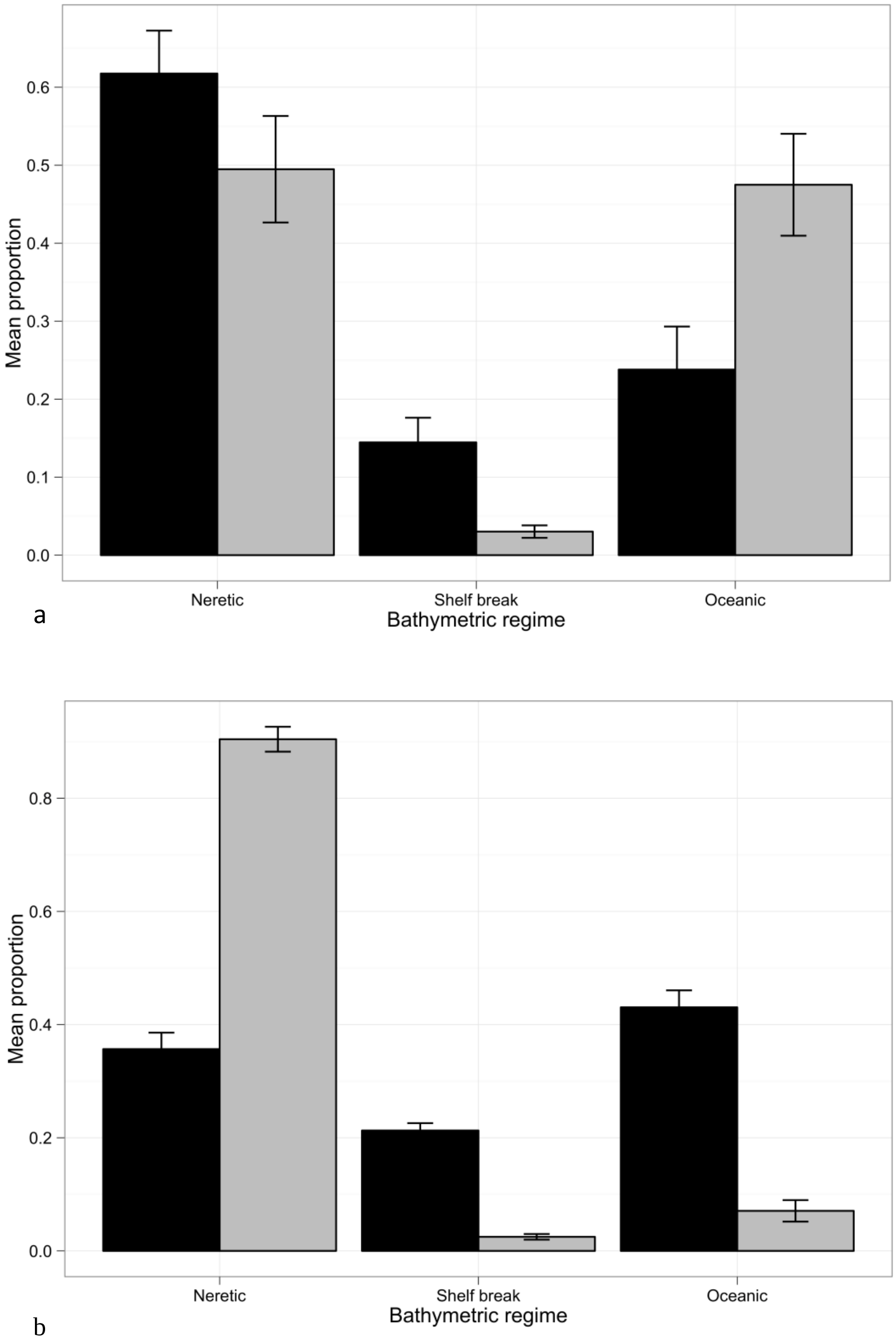

Figure 3. Differences in proportional use of neretic (<200m), shelf break (200-1000m) and oceanic (>1000m) waters between Eynhallow (black) and Little Saltee (grey) birds in both autumn (a) and winter (b). Error bars are included, being the standard error of the mean proportion of time spent in each regime.

Wintering differences in intrinsic markers between Eynhallow and Little Saltee fulmar colonies

Instrumental quality results

The percentage recovery for each element was excellent, with two elements (Se and Sr) being above 100% recovery which relates to analytical interferences.

Table 4. Limits of detection (LoD) for feather samples (*μg/g*). Bovine liver certified reference material (CRM) expected and obtained values (*μg/kg*) are shown, along with the percentage recovery for each element.

Element	*LoD(μg/g)*	*Expected CRM value (μg/kg)*	*Obtained CRM value (μg/kg)*	*% recovery for element*
As	0.061	50	41	81
Cd	0.043	500	460	92
Cu	2.104	160000	143836	90
Fe	15.510	184000	175396	96
Mn	0.318	10500	9420	90
Pb	0.332	129	127	98
Se	0.174	730	856	117
Sr	0.794	136	221	163
V	0.088	123	119	96
Zn	4.097	127000	114089	90

Differences in element concentrations between Eynhallow and Little Saltee colonies

Element concentrations were generally similar between the two colonies, the most notable exceptions being the essential elements Fe and Cu, and the non-essential element As. Little Saltee fulmar feathers contained significantly larger Fe and Cu values than Eynhallow birds (Table 5). Sex differences were not detected in any element except Cu, with females having significantly lower Cu values than males within each colony.

Table 5. Median concentrations (and ranges) of elements (mg/kg) in fulmar feathers from Eynhallow (EYN) and Little Saltee (LS) colonies are shown, split into males and females. Linear model results are also shown with colony and sex as explanatory variables, only those with significant differences detected between the colonies and/or sexes are shown. Values are shown to two decimal places. Significance taken to be <0.05.

Colony	**V (mg/kg)**	**Mn(mg/kg)**	**Fe (mg/kg)**	**Cu (mg/kg)**	**Zn(mg/kg)**	**As(mg/kg)**	**Se (mg/kg)**	**Sr(mg/kg)**	**Cd(mg/kg)**	**Pb (mg/kg)**
EYN males	0.18 (0.08-0.52)	2.01 (0.37-29.44)	90.96 (11.99-435.09)	9.80 (8.59-12.51)	62.35 (49.30-9.95)	0.09 (0.02-0.33)	1.95 (0.84-3.56)	7.80 (4.95-22.10)	0.04 (0.02-0.20)	0.86(0.21-2.37)
females	0.21 (0.10-0.64)	2.97 (0.68-17.21)	110.87 (25.50-98.71)	8.78 (7.27-11.85)	60.01 (49.05-7.83)	0.07(0.03-0.38)	2.43 (1.38-3.84)	9.07(6.57-11.54)	0.08(0.02-0.42)	0.72(0.23-2.85)
LS males	0.28(0.11-0.74)	4.40(1.53-17.68)	211.05(66.47-78.34)	10.65(7.96-14.56)	63.37(50.26-74.86)	0.17(0.10-0.49)	1.80(1.31-2.44)	7.06(5.40-10.04)	0.03(0.02-0.12)	0.72(0.42-3.72)
females	0.28(0.11-0.53)	2.50(1.38-7.30)	205.44(73.70-75.60)	10.48(8.89-12.18)	63.23(58.29-78.04)	0.19(0.09-0.35)	1.59(1.50-2.27)	6.94(5.58-9.54)	0.03(0.02-0.08)	0.63(0.31-2.84)
Model										
Colony	**n/s**	**n/s**	**$F_{1,56}$=8.59,**	**$F_{1,56}$=10.60,**	**n/s**	**$F_{1,56}$=8.05,**	**n/s**	**n/s**	**n/s**	**n/s**
			p=0.005	**p=0.002**		**p=0.006**	**n/s**	**n/s**	**n/s**	**n/s**
Sex	**n/ s**	**n/s**	**n/s**	**$F_{1,56}$=5.30,**	**n/ s**	**n/s**				
				p=0.025						

Differences in δ^{13}C and δ^{15}N between Eynhallow and Little Saltee colonies

Analysis of stable isotopes from feathers of breeding adults from the two colonies revealed significant colony and winter location differences in both δ^{15}N and δ^{13}C (Tables 6 and 7). West Atlantic foragers had the lowest δ^{15}N values and Irish Sea foragers had the highest δ^{15}N values (Table 6). Differences in δ^{13}C in wintering location were apparent between Irish Sea foragers and the other three wintering locations (West Atlantic, North Sea, Barents Sea) (Table 6).

In a univariate model, the bathymetric regime also explained variation in δ^{15}N with oceanic birds having a significantly lower δ^{15}N value than predominantly neretic birds ($F_{2,37}$= 11.09, p<0.001). No differences in δ^{13}C ratios were detected amongst the differing bathymetric regions ($F_{2,37}$=1.16, p=0.325).

For the birds which had more than one year of C and N isotope data, their isotopic values were strongly positively correlated between years (Pearson's correlation of δ^{13}C = 0.70, p<0.001; Pearson's correlation of δ^{15}N = 0.83, p<0.001).

Table 6. Median and range of δ^{13}C and δ^{15}N values for each winter group of fulmars from both Eynhallow and Little Saltee colonies.

Winter group	**Median (Range) δ^{13}C**	**Median (Range) δ^{15}N**
West Atlantic	-17.17 (-17.87, -15.40)	14.59 (13.69, 17.79)
North Sea	-17.15 (-18.02, -16.13)	15.62 (14.24, 16.96)
Barents Sea	-17.50 (-18.14, -16.40)	15.79 (15.27, 16.44)
Irish Sea	-15.47 (-18.03, -14.92)	17.81 (15.18-18.37)

Table 7. Median and range of $\delta^{13}C$ and $\delta^{15}N$ values for Eynhallow and Little Saltee males and females. Results from linear modelling with winter location (North Sea, West Atlantic, Irish Sea, East/Barents Sea), colony (EYN or LS) and sex (male or female).

Colony	**Median (Range) $\delta^{13}C$**	**Median (Range) $\delta^{15}N$**
Eynhallow: male n=17	-17.25 (-18.14,-16.41)	15.70 (14.18,16.25)
female n=13	-17.31 (-18.58,-16.13)	14.81 (14.02,16.96)
Little Saltee male n=17	-15.50 (-18.04,-14.92)	17.82 (15.92,18.72)
female n=4	-15.68 (-16.55,-15.02)	17.79 (14.43,18.02)
Model		
winter location	$F_{3,36}$=17.72, p<0.001	$F_{3,36}$=48.76, p<0.001
colony	$F_{1,36}$=10.41, p=0.003	$F_{1,36}$=20.46, p<0.001
sex	n/s	$F_{1,36}$=9.07,p=0.004

A plot of $\delta^{13}C$ and $\delta^{15}N$ in feathers shows the range of isotopic ratios within each colony (Figure 4). The plot also reveals a separation in isotopic values between Little Saltee and Eynhallow birds with the exception of four birds. Three of these four Little Saltee birds spent a large proportion of time (range of 25 to 58 days) over their autumn and winter period in shelf break and open water bathymetric zones in the West Atlantic. The remaining fourth bird was the one Little Saltee bird which spent a substantial amount of time in the Barents Sea (44 days).

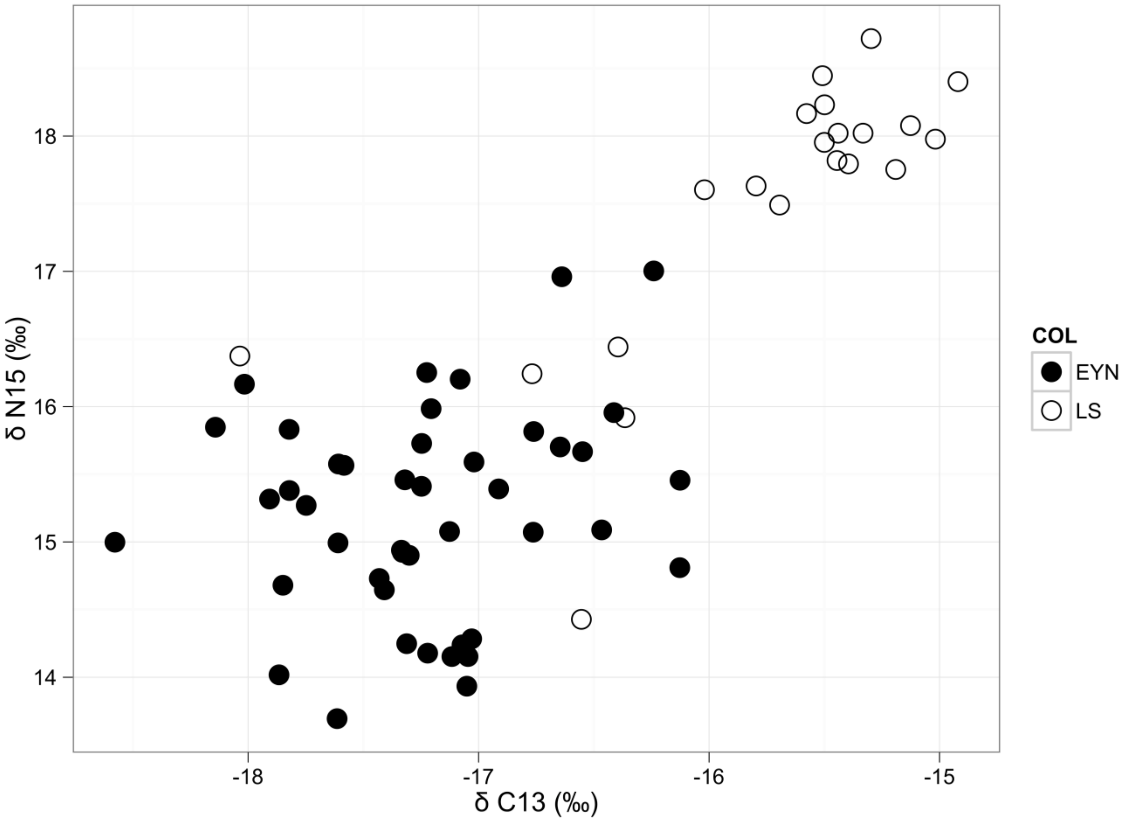

Figure 4. Plot of $\delta^{13}C$ and $\delta^{15}N$ between Eynhallow (EYN) and Little Saltee (LS) colonies.

DISCUSSION

This study presents novel information on spatial partitioning and concurrent intrinsic marker information for two fulmar colonies over the non-breeding period. Though there was a 38% overlap in home range between the colonies, the colonies demonstrated separate core area use and differences in preference of bathymetric domain and location in both autumn and winter. Furthermore, diet composition differences, as measured by feather isotopic and elemental content, exist between the two colonies with Little Saltee fulmars feeding at predominantly higher $\delta^{15}N$ values and with a more benthic signature of $\delta^{13}C$ compared to Eynhallow birds.

Inter-colony differences in non-breeding area use

The tracking data demonstrated overlap in home ranges (95% kernels) between the Scottish (Eynhallow) and Irish (Little Saltee) colonies; however, there was no overlap in the core area usage (50% kernels). To have some degree in overlap in home ranges between two colonies which are geographically approximately 780km apart (straight line distance) is not surprising given that fulmars may range over 2000-3000km from their colony in both the breeding season (Edwards *et al.* 2013) and over winter (Chapter 2). Overlap in non-breeding habitat distributions have been demonstrated both within (Frederiksen *et al.* 2012) and between seabird species (Linnebjerg *et al*. 2013). However, there were some distinct differences between autumn and winter foraging strategies at the two colonies. Eynhallow birds tended to remain within coastal waters nearer to the colony in autumn and moved to deeper shelf break and oceanic waters during the winter period (Figure 3). Little Saltee birds, by contrast, foraged more in shelf break and oceanic waters in the autumn, further from the colony than during their winter when the majority of birds foraged within coastal, neretic Irish Sea waters (Figures 2 and 3).

Studies on breeding seabirds have previously demonstrated that both foraging distance (Pettex *et al*. 2012) and trip duration (Lewis *et al*. 2001) at different sized colonies increases with increasing colony size. The greater foraging ranges in Eynhallow birds cannot be explained by a difference in breeding colony size, as both our study colonies were of a similar size (108 occupied nests for Eynhallow and 160 occupied nests for Little Saltee in 2010 respectively). However, there were differences in the regional populations surrounding these colonies. The waters in which Eynhallow birds breed, have a highly dense population of fulmars, with a total of approximately 332,000 breeding fulmars in Orkney, Shetland, and Northern Scotland waters (Mitchell *et al.* 2004). Little Saltee birds, in contrast, are on a coastline with substantially less densely populated fulmar colonies around the southern Irish and Welsh coastlines with approximately 4600 breeding fulmars in the region (Mitchell *et al*. 2004). It is possible that competition for local food resources in the winter may force birds from densely populated areas such as Orkney to winter elsewhere, whereas Little Saltee birds may be able to remain closer to the colony. This theory would require further investigation to test its importance in explaining differences in wintering areas utilized. It has been suggested in other seabird species that avoidance of competition in the off-breeding period may explain why Great skuas from two different major colonies have different over winter migratory strategies (Magnusdottir *et al*. 2012). Differences in immediate post-breeding (autumn) foraging strategies between two colonies have also been seen in Cory's shearwaters which shared winter grounds, but had slightly different autumn movements, potentially relating to resource availability and intra- and inter-specific competition (Catry *et al.* 2011).

In one of the few cases where tracking studies have been conducted at multiple colonies, kittiwakes from colonies off Ireland and Wales remained closer to their breeding colony over winter. In contrast, those breeding at Svalbard, northern Norway, Iceland, Greenland and North Sea colonies predominantly utilised West Atlantic waters by the Mid-Atlantic ridge and Labrador Sea (Frederiksen *et al.* 2012). This pattern is a remarkably similar result to this current study's results from fulmars, despite marked differences in the foraging energetics and life-history characteristics of these two species. It suggests that other species of seabirds may show a similar pattern with those nesting in the North Sea seabird breeding colonies potentially showing differences in winter habitat choice than their conspecifics breeding in the Irish Sea region. Furthermore, differences between colonies with some individuals remaining closer to the breeding colony and others foraging much further afield may have differing population consequences at these two colonies. This could be investigated further with long-term data on both reproduction and survival at these colonies.

Inter- and intra-colony differences in intrinsic markers over winter

As theory predicts that animals will forage in areas which are the most energetically beneficial (Pyke 1984), birds are only likely to remain in more local waters if they are able to forage on a predictably good resource. It was not possible to collect prey items from each area to assess direct winter diet, but a proxy of winter diet was measured by carrying out chemical analyses on feathers grown during the winter period.

Carbon stable isotopes confirmed the more coastal association of the Little Saltee fulmars, as identified from the tracking data, with significantly higher values being measured in the Irish birds (Figure 5). The higher carbon isotope values are also indicative of a benthic-based diet rather than a pelagic diet (Hobson 1999). The Irish and Celtic Sea fishery region predominantly lands demersal species, mostly the shellfish *Nephrops*, but also fish such as cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* (Elliott *et al.* 2012). The more benthic and demersal carbon signature of the Little Saltee birds suggests the birds could be utilising the benthic shellfish and demersal fisheries as a food resource from fishery discards. It has been estimated that 47% of total catch of *Nephrops* is discarded in this region including by-catch of haddock, juvenile whiting *Merlangius merlangus* and megnium *Lepidorhombus whiffiagonis* (ICES 2012). It was estimated that in 2011, over 1000 tonnes of juvenile whiting alone was discarded in the Irish Sea (ICES 2012). It has been hypothesised that fulmars at the southern range rely more on fisheries (Phillips *et al.* 1999), and this current study provides some evidence that this may be the case for southern Irish birds. A recent tracking study utilising bird-bourne cameras on gannets foraging within the Irish Sea also found that fulmars were the predominant species in multi-species groups (Votier *et al.* 2013). Thus, evidence does exist of fulmars feeding extensively off fishing vessels in this region.

Further evidence that the Irish birds may be utilising fisheries as a prey resource is seen in nitrogen stable isotopes. Little Saltee fulmars were feeding on prey with significantly higher values of $\delta^{15}N$ (Table 6). This may simply reflect a difference in nutrient cycling between the different oceanographic regimes that birds from these two colonies feed within (Figure 1). However, based upon published maps of variation in $\delta^{15}N$ across the Atlantic Ocean (Graham *et al.* 2010), it appears that Irish and Scottish birds are probably feeding in similar base-line regimes. If there is any difference, the Irish Sea region has a slightly lower baseline $\delta^{15}N$ (‰) (Graham *et al.* 2010), suggesting that the difference in nitrogen isotope values should reflect genuine differences in the trophic level at which these birds are feeding (Hobson 1999). The difference of nearly 5‰ between the lowest value for an Eynhallow bird versus the highest value for a Little Saltee bird reflects a 1-2 trophic level difference (Hobson 1999).

The range of $\delta^{15}N$ values within the Eynhallow colony also demonstrate that some individuals are feeding at entirely different trophic levels than others within the colony. If individual Eynhallow birds are taking advantage of fisheries and others are feeding on lower trophic natural prey items, it might explain the intra-colony difference in $\delta^{15}N$ levels.

The difference in autumn and winter strategies as determined by tracking data may also in part be due to the timings of the peak landings of key prey species. Pelagic prey, such as mackerel Scombridae, reach their peak in late autumn in the North Sea sector and also have a January peak off North-west Scotland, when 54% of all mackerel landings occur (Elliott *et al*. 2012). If individual Eynhallow birds are feeding on pelagic fishery discards this perhaps explains why some birds remain closer to North Sea waters in autumn before heading further away from the colony in October, then returning to colony waters during January, when the second large peak for pelagic species landings occur. Further tracking work at this colony over autumn confirmed this hotspot of usage in the North Sea, particularly off the east Scotland of northern England and Scotland (Chapter 2). In contrast, *Nephrops* reach their peak landings during July, before dipping in the autumn months (Elliott *et al*. 2012), which perhaps explains why Little Saltee birds move further away from the coast during autumn to forage on potentially different prey items. The *Nephrops* fishery is nonetheless carried out throughout the whole year (ICES 2012), potentially providing a reliable food source for fulmars to exploit across seasons.

Although these data indicate that discards may be more important for fulmars from Little Saltee, one cannot rule out the possibility that these birds are also foraging on naturally caught fish from the surface. The four Little Saltee birds which demonstrated overlap in carbon and nitrogen isotope values with Eynhallow birds provide some evidence for this. These individuals spent a large amount of time outwith the Irish Sea: three moving into the West Atlantic and one in the Barents Sea and high Arctic. Therefore, it is perhaps not surprising that the stable isotope ratios in these four birds overlapped with the Eynhallow range (Figure 5) as these birds did not spend as much time within the Irish Sea area as their breeding colony conspecifics.

From comparisons of wintering areas and stable isotopes, those fulmars foraging in the West Atlantic had the lowest $\delta^{15}N$ values (Table 6), suggesting they are feeding at a lower trophic level than fulmars foraging elsewhere in winter. Comparison to another high arctic fulmar colony demonstrates that reliance on a *Calanus,* pelagic food chain produces lower $\delta^{15}N$ signatures (Dahl *et al.* 2003), which suggests that the West Atlantic foragers are feeding on a similar food chain.

Whether birds are feeding on natural or discarded prey would require a more detailed dietary study on likely prey items in each area, as has been carried out in studies using stable isotope mixing models (e.g. shearwaters *Puffinus spp*., Ronconi *et al.* 2010). Samples collected from fishing boats could provide an indication of fishing by-catch isotopic signatures and natural prey items may be sampled from surface waters. Dietary techniques, such as fatty acid analysis may also distinguish between prey items, as has been carried out for fulmars during the pre-breeding and breeding period (Owen *et al.* 2013). However, as we have shown the large geographic range over which fulmars forage, prey sampling in each area would be an inherently difficult task.

A further possibility for the variation in stable isotope values noted between the two colonies is due to the latitudinal gradient in carbon isotopes that exists. Differences in the temperature gradient between the geographic regions influences cell turnover rates which leads to regions of higher latitude having more depleted $\delta^{13}C$ values (Cherel & Hobson 2007; MacKenzie *et al.* 2011). Whilst this certainly should be taken into consideration when explaining potential reasons for the colony differences in stable isotopes noted, published carbon isoscapes of the Atlantic Ocean reveal that there is a similar baseline of $\delta^{13}C$ values between Eynhallow and Little Saltee (Graham *et al.* 2010). Therefore, in comparing Eynhallow and Little Saltee, latitudinal differences in baseline are unlikely to strongly influence the variation in $\delta^{13}C$ values that exists between birds from these two colonies.

Consistencies in wintering diet (Phillips *et al.* 2007; Grecian 2011) and area (Croxell *et al.* 2005; Kopp *et al.* 2011) have been noted for many species. However, what was of particular interest from both tracking and stable isotope data was that not only were consistencies noted in wintering habitat choice in both Eynhallow (Chapter 2) and Little Saltee birds, consistencies in diet were also noted, as measured by C and N isotopes. This suggests fulmars feed on prey items within a similar isotopic range in similar winter sites each year. This consistency in both area and isotopic signatures across years has also been noted in a study of gannets tracked from two different colonies (Grecian 2011), but this current study and the study on gannets are, to date, rare examples of this.

Implications for future analyses

Many seabird populations are known to be in decline in both numbers (Croxall *et al.* 2012) and breeding success (Mavor *et al.* 2006). With a highly dynamic marine environment inducing prey item changes (Hays, Richardon & Robinson 2005; Perry *et al.* 2005) and changes in discard practices likely to occur in the near future (Bicknell *et al.* 2013), it is likely some seabirds will adapt to foraging changes better than others (Furness & Tasker 2002; Votier *et al.* 2004). Therefore, it is more pertinent than ever to have knowledge of foraging areas of differing seabird populations across as wide a geographic area as possible in order to make predictions about how food supply changes may be affecting population dynamics. Combining tracking and chemical analyses will aid in detecting potential foraging differences between breeding colonies over the non-breeding period and will greatly increase our predictive knowledge of those breeding populations at higher risk than others to changes in food supply.

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CHAPTER 5

Stable isotope and elemental analyses reveal colony and sex differences in winter foraging characteristics of NE Atlantic fulmars

Photo: H.Dombrowe. “The winner”

CHAPTER 5: Stable isotope and elemental analyses reveal colony and sex differences in winter foraging characteristics of NE Atlantic fulmars.

ABSTRACT

Intrinsic markers, such as stable isotopes and metal(loid)s, can provide information on foraging characteristics. Here, the chemical composition of feathers grown in the non-breeding period was compared across five fulmar colonies in the North Atlantic: Iceland, Faroes, St Kilda, Orkney and Ireland. Multi-elemental analyses revealed large variation in several elements between the colonies, with Icelandic birds having a more distinct dietary cluster. Stable isotope analysis revealed a large difference in both $\delta^{13}C$ and $\delta^{15}N$ signatures between the Irish colony and the remaining colonies, with Irish birds having significantly more enriched values of $\delta^{15}N$ and $\delta^{13}C$ signatures, more related to inshore and higher trophic foraging. Consistent sex differences in non-breeding diet were noted across all colonies, with females having significantly lower $\delta^{15}N$ values than males. Using predicted non-breeding foraging areas, it is demonstrated there are differences in the relative frequency of area use between colonies. More female fulmars were classified as having a signature indicative of a West Atlantic forager than males. This study suggests an overlap in wintering areas between fulmars from differing colonies over the non-breeding period, with individual differences in foraging seen both between and within colonies.

INTRODUCTION

Naturally occurring and anthropogenically elevated elements vary widely in their concentrations in the environment, and this variation can be used diagnostically in ecological investigations (Rubenstein & Hobson 2004). The use of intrinsic markers such as metal(loid)s and stable isotopes in wildlife studies has underpinned knowledge of migration (Militão *et al*. 2012; Trueman, MacKenzie & Palmer 2012), diet (Fisk *et al.* 2002; Quillfeldt, McGill & Furness 2005) and regional differences in pollution (Burger & Gochfeld 2004; Mallory & Braune 2012) in marine ecosystems. As different tissue types each reflect the time over which the elements were sequestered (Hobson 1999), it is possible to use these markers to study the non-breeding season diet and distribution of key indicator species, such as marine top predators (Furness & Camphuysen 1997; Ramos & Gonsález-Solís 2012).

The most common chemical markers used to assess geographic and dietary variation are naturally occurring stable isotopes of carbon ($^{12,13}C$) and nitrogen ($^{14,15}N$). Differences in carbon ratios (denoted as $\delta^{13}C$), relate to differences in prey items from inshore and offshore habitats; benthic and pelagic habitats; and also latitudinal differences across oceans (Hobson, Piatt & Pitocchelli 1994; Cherel & Hobson 2007a). Differences in nitrogen ratios (denoted as $\delta^{15}N$), provide an indication of trophic level (Hobson, Piatt & Pitocchelli 1994). Studies have utilised these two stable isotope ratios to study broad scale patterns of wintering area use through comparison with tracked individuals (Phillips *et al.* 2009; Leat *et al.* 2013) and reference isoscapes (Quillfeldt, McGill & Furness 2005). Different geographic regions are also known to have differing stable isotopes of lead ($^{206,207,208}Pb$) due to underlying geogenic features and/or from different sources of anthropogenically produced lead (Bollhöfer & Rosman 2001; Henderson & Maier-Reimer 2002). Lead isotopes can be used to identify different sources of lead, which may be particularly important for supporting conservation management of at-risk species (Meharg *et al* 2002; Finkelstein, Gwiazda & Smith 2003; Finkelstein *et al.* 2010; Scheuhammer & Templeton 1998).

Further inferences about diet can be drawn from essential and non-essential trace elements, which can demonstrate differences in foraging between species (Elliot 2005; Anderson *et al.* 2010) and regions (Savinov, Gabrielson & Savinova 2003). Whilst elements are often analysed separately, most commonly those potentially toxic such as mercury, cadmium and lead (Thompson, Furness & Monteiro 1998; Bond & Diamond 2009), concurrent multivariate analyses of trace metals can demonstrate differences between groups in overall elemental loadings (Borga *et al.* 2006).

To understand geographic, dietary and pollutant level differences across a species' range, samples should ideally be taken from known breeding sites and comparisons made across regions. Very few studies have achieved this across a wide scale to date (see Bond & Lavers 2011; Polito *et al.* 2011). Those studies which have compared across sites have collected samples at sea in differing regions (Savinov, Gabrielson & Savinova 2003), for which breeding provenance of the bird is unknown, or have concentrated on breeding diet, lethally sampling from different breeding colonies within the same broad geographic area (Braune & Scheuhammer 2008). Breeding site information is key if we are to then investigate differences in foraging characteristics across a species' range, the differences of which may have population implications. The northern fulmar is an ideal study species to investigate colony-wide comparisons of non-breeding foraging as they have a large range across the Atlantic.

Fulmars regularly visit their colony area over the non-breeding period (Macdonald 1980; Chapter 2), but birds from different colonies also show high overlap in wintering range (Chapter 4). Belly feathers have proved to be an ideal sample tissue for investigating non-breeding foraging as these feathers moult over the non-breeding period, and have shown discrimination in broad winter area based on isotopic differences (Chapter 3). Tracking data over the non-breeding period has revealed individual differences in foraging with some fulmars ranging over 3000km from their breeding colony, whilst others remain closer to colony waters (Chapter 2). Sex differences in winter foraging have also been noted such that, on average, females travel further from the colony than males (Chapter 2). Dietary differences between the sexes also exist during the pre-laying period (Owen *et al. 2013*) at some colonies. Whether this sex difference in foraging is consistent across other fulmar colonies is yet to be tested. As males forage more locally around their colonies over the non-breeding period than females, sex differences in diet might be expected. Furthermore, colony-specific dietary markers may be greater in males than females.

Spatial differences in the diet of fulmars have already been noted during the breeding period (Furness & Todd 1984; Phillips *et al.* 1999; Cherel *et al.* 2001; Mallory *et al.* 2010), with different colonies varying in the extent to which they forage on discards from fishing vessels versus foraging on more natural prey. However, a regional assessment of fulmar diet over winter is still currently lacking (Mallory *et al.* 2010). It is predicted that colonies closer together may show more similarities to one another than colonies further apart due to the increased likelihood that they share the same wintering area. As tracking data has revealed overlap in geographic distribution between fulmars from two different colonies (Chapter 4), concurrent overlap in dietary proxies is expected. Further to this, lead isotopes have demonstrated a similarity in values between individuals from the same colony (Chapter 3), therefore it is hypothesised that lead isotopes demonstrate more variation due to differing colonies rather than amongst a single colony.

The aim of this study was to assess whether there are broad-scale winter foraging differences in northern fulmars in intrinsic markers: a) between colonies; b) between males and females; and c) in the proportion of birds from each colony utilising different wintering areas.

METHODS

Fieldwork and feather sampling collection

Fieldwork took place on: Eynhallow, Orkney (59º8'N, 3º7'W) (2006-2011), Little Saltee, Ireland (52º7'N, 6º41'W) (2010-2011), St Kilda, Scotland (57º5'N, 8º34'W) (2011), Vestmannaeyjar, Iceland (63º25'N, 20º17'W) and Grímsey, Iceland (66º33'N, 18º0'W) (both 2011) (Figure 1). At each of these colonies a selection of 8-10 belly feathers were sampled around the brood patch from breeding adults, caught at their nests using a hand net or noose. Belly feathers moult during the non-breeding period (Chapter 3) and therefore relate to wintering diet. In addition to live caught birds, feathers were sampled from long-line victims off Hornstrandir, Westfjord, Iceland (2011) and from birds hunted for consumption (off Vidareidi, Faroes) or long-line victims off the Faroes (2011). For samples from dead birds, only those defined as currently breeding adults were used in analysis. Breeding status was determined by identification of the status of the gonads during the dissection procedure (see methodology by J.A. van Franeker (van Franeker 2004)). Furthermore, only those birds caught in the breeding period were considered for this analysis (April for Icelandic Westfjord birds, May for Faroese birds). For each individual bird, 2 feathers were randomly selected for element and Pb isotope analyses, and 2 or 3 feathers were selected for stable isotope analyses of C and N. Feathers were stored dry in envelopes at room temperature until analysed.

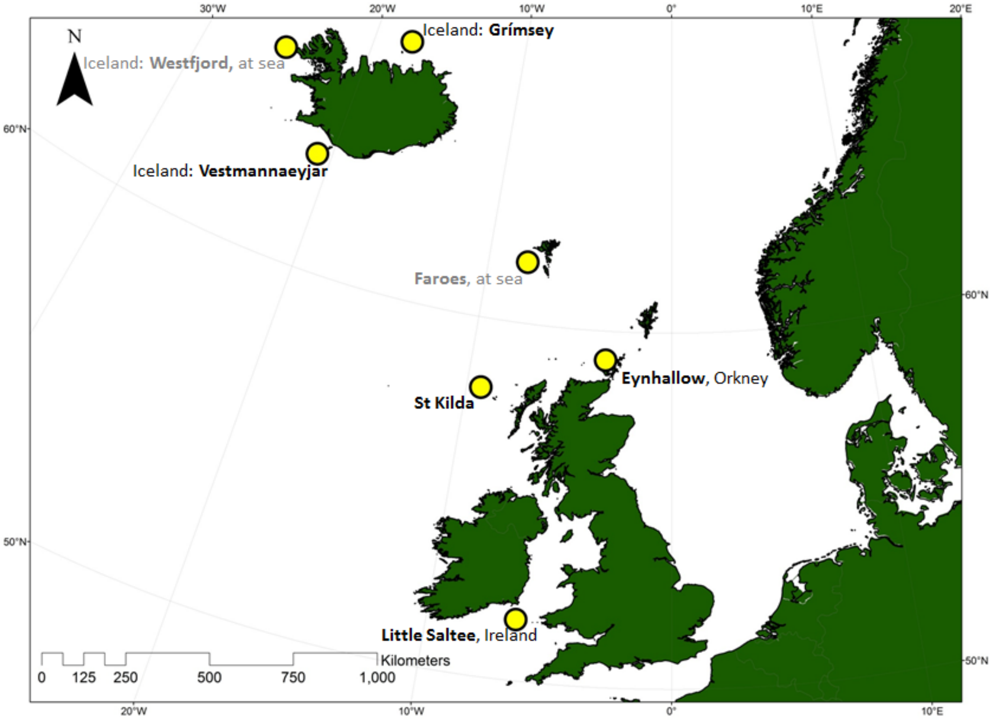

Figure 1. Map of fulmar colony locations where feather samples were taken from live-caught breeding adults (black text) and sampled from fulmars caught at sea during the breeding period (grey text).

Element and δ^{206,207,208}Pb isotope analyses

Individual feathers were analysed separately, and an average value for each individual bird was assumed to be representative of the belly feather moult period (Bearhop *et al.* 2004; Chapter 3). Feathers were washed with Milli-Q water prior to oven drying at 65°C for > 12 hours. Aristar nitric acid (0.5ml) was then added to each feather sample and left overnight to digest. Aristar hydrogen peroxide (1ml) was then added, before using a 75 minute microwave digest (CEM Microwave Technology Ltd.) with a peak of 95°C that was held for 30 minutes. The samples were then diluted to 10ml with ultrapure deionized Milli-Q water, a sub-sample of which was used for measuring 19 element total concentrations using an ICP-MS 7500 (Aglient Technologies), with the reaction cell used with hydrogen gas. The certified reference material used was bovine liver (National Institute of Standards and Technology) 1557b. Standards made from Multi-Element solution 2 were run every 30 samples, from which standard curves could be calculated. ^{206,207,208}Pb isotopes were then measured using an ICP-MS (Element 2, Thermo Scientific, Bremen, Germany), using another subsample from the digested feather samples. Standard solutions were run every two samples to correct for instrumental mass bias.

$\delta^{13}C$ and $\delta^{15}N$ Stable isotope analyses

Feathers were washed with Milli-Q water prior to oven drying at 65°C for > than 12 hours. The samples were then homogenised in a ball mill (Mixer Mill type MM 200, Retsch of Haan, Germany). Sub-samples of 1.3mg of material were then loaded into 5 x 3.5mm tin cups (Elemental Microanalysis Ltd.). The total N and total C contents and the ^{15}N:^{14}N and ^{13}C:^{12}C isotope ratios of the milled dried material were determined using a Flash EA 1112 Series Elemental Analyser connected via a Conflo III to a Delta^{Plus} XP isotope ratio mass spectrometer (all Thermo Finnigan, Bremen, Germany). The isotope ratios were calculated using CO_2 and N_2 reference gasses injected with every sample. The isotopic values of these gasses were directly referenced against IAEA reference materials USGS40 and USGS41 (both L-glutamic acid); certified both for $\delta^{13}C$ (‰ $_{VPDB}$) and $\delta^{15}N$ (‰ $_{air\ N_2}$). Long term precisions for a quality control standard (milled flour) were: $\delta^{13}C$ -25.5 ± 0.29 ‰ and ^{15}N 0.367 ± 0.0002 atom % (mean ± sd, n = 200).

Table 1. Sample sizes for each colony area for the three differing type of chemical analyses.

Breeding colony		**Elemental & Pb isotopes**		**C & N isotopes**	
		male	**female**	**male**	**female**
Eynhallow	**(EYN)**	41	40	24	20
Little Saltee	**(LS)**	33	14	17	4
St Kilda	**(SKIL)**	14	15	14	15
Faroes	**(FAE)**	16	30	15	15
Iceland:					
Westfjord	**(ICE)**	30	18	10	10
Vestmannaeyjar	**(ICEV)**	14	9	12	8
Grímsey	**(ICEG)**	17	7	13	7
total		165	133	105	79

Statistical analyses

Multi-elemental analyses

Trace elements with mean concentrations (μg/g) below the limits of detection (LoD) for the majority of the samples (Li, Cr, Co, Ni, Rb, Cs) were excluded from statistical analysis. For those elements with a few samples below the LoD (V, Mn, As, Cd, Pb), these samples were given a value of half the LoD value, as is standard procedure (Anderson *et al*. 2010). As there were several different batch runs, half of the highest LoD value from all batch LoDs (in μg/g) was used.

Given the aim was to consider broad-scale regional differences, the three different Icelandic colonies were grouped together when modelling colony and sex differences.

However, as regional differences in Icelandic fulmar diet has been noted previously (Thompson *et al.* 1999), the three differing colonies were considered separately for the multivariate analysis. For each element their median (mg/kg) and range values were calculated for each colony. ANOVAs were then used to test for colony and sex differences. For those elements where differences between colonies were found to be significant, post-hoc Tukey's honest significant difference tests were conducted. Normality and model fits were verified for all elements. A multivariate analysis on the element dataset was used to assess whether certain colonies had a particular signature for metal(loids). A Principle Components Analysis (PCA) was carried out in the package MASS, using the correlation method due to differences in scale between the elements (Crawley 2007).

Stable Isotope analyses

Whilst the majority of feather samples were taken in 2011 (163 out of 184), birds from Eynhallow and Little Saltee had samples from different years (Eynhallow: 2009-2011; Little Saltee: 2010-2011). Data from all years were used to maximise the number of different individuals available for analysis, but MANOVAs were carried out for both colonies to test if isotopic trends differed between sampling years, before pooling years.

ANOVAs were carried out to test for differences in C and N ratios between Icelandic colonies, before grouping them into one group, as for the trace element analyses. For C, N and isotopic ratios a MANOVA was first carried out followed by separate models for C and N to test for differences in isotopes across colonies and between sexes.

To test whether use of wintering areas differed between colonies, discriminant functions derived from a discriminant analysis using data from GLS tracked birds from Eynhallow and Little Saltee (Chapters 3 and 4) were used. Using C and N stable isotope data from Eynhallow birds with known wintering locations, a discriminant analysis correctly assigned North Sea winter foragers 86% of the time, and birds utilising the West Atlantic region over winter were correctly assigned 93% of the time (Chapter 3). Little Saltee birds were correctly identified as foraging in the Irish Sea 94% of the time. We used a combined discriminant function to assign untracked birds from Orkney, Little Saltee, St Kilda, Faroes and Iceland to one of three groups. Group 1 had a signature that appeared to reflect use of a shelf-sea wintering area. Group 2 had a signature that reflected use of West Atlantic areas. Group 3 had a signature that reflected the use of Irish Sea nearshore foraging (see Appendix 4 for map of broad group divisions). Only those birds which had a probability of more than 80% in being correctly assigned to one of these groups had subsequent proportion-based tests carried out. For values below 80%, 50% of birds with known winter location were incorrectly assigned. In contrast, above 80%, 97% of birds with known winter location were correctly assigned. The linear discriminant function was carried out in the 'MASS' package in R.

General linear models were carried out with colony, latitude and sex as explanatory variables and C and N ratios as the response variables. Model selection was performed in the package AICcmodavg using AICc values (Burnham, Anderson & Huyvaert 2011). Model plots were carried out to verify model fit.

All statistical analyses were carried out in R v.2.15.0 (R development Core Team, 2012).

RESULTS

Instrumental quality results

The percentage recovery for each element was excellent, with two elements (Se and Sr) being above 100% recovery which relates to analytical interferences.

Table 2. Limits of detection (LoD) for feather samples (*μg/g*). Bovine liver certified reference material (CRM) expected and obtained values (*μg/kg*) are shown, along with the percentage recovery for each element.

Element	*LoD(μg/g)*	*Expected CRM value (μg/kg)*	*Obtained CRM value (μg/kg)*	*% recovery for element*
As	0.061	50	41	81
Cd	0.043	500	460	92
Cu	2.104	160000	143836	90
Fe	15.51	184000	175396	96
Mn	0.318	10500	9420	90
Pb	0.332	129	127	98
Se	0.174	730	856	117
Sr	0.794	136	221	163
V	0.088	123	119	96
Zn	4.097	127000	114089	90

Differences in essential and non-essential elements between 5 fulmar colonies

Regional differences in average elemental loadings were shown between the 5 fulmar colonies (Table 3). As there is a high degree of variability between the colonies in many elements only those which are of greater biological interest from a dietary or contaminant perspective are discussed further.

Fe, an essential element, had the highest average concentrations in feathers in Little Saltee birds but Iceland had the largest range of Fe values and the highest absolute values (Table 3). In the PCA analysis, the higher Fe values pull apart select individuals from Grímsey and Vestmannaeyjar (Figure 2). Only Zn and Cu demonstrated a sex difference in concentration as well as a colony difference, with females tending to have higher values of Zn than males, but lower values of Cu than males on average.

Se showed similarities between Faroes, St Kilda and Iceland but differences between these colonies and Eynhallow and Little Saltee, with the latter group having lower Se loadings on average. Iceland had the highest absolute value of Se found in feathers (up to 14.86 mg/kg). Pb concentrations were highest in Eynhallow and Little Saltee, with

Eynhallow values being significantly higher than Faroes, Iceland or St Kilda colonies (Table 3).

Tukey post-hoc tests demonstrated that Iceland had more significantly different concentrations of elements in pair-wise comparisons of all colonies. Iceland also represented the furthest straight-line distance from the other colonies. Faroes and St Kilda were the most similar, with the least number of significant pairwise comparison differences (only difference in level of As) (Table 3).

PCA 1 explained 31% of the variation, PCA 2 an additional 17% and PCA 3 an additional 14%. Westfjord-caught Icelandic birds demonstrated a huge degree of similarity with one another, whilst Grímsey and Vestmannaeyjar Icelandic birds had a similar spread of values with each other. Little Saltee, Eynhallow, St Kilda and the Faroes all overlapped with one another, but some individuals from the Faroes and Eynhallow were pulled out by larger Pb values (Eynhallow) and higher As and Zn values (Faroes).

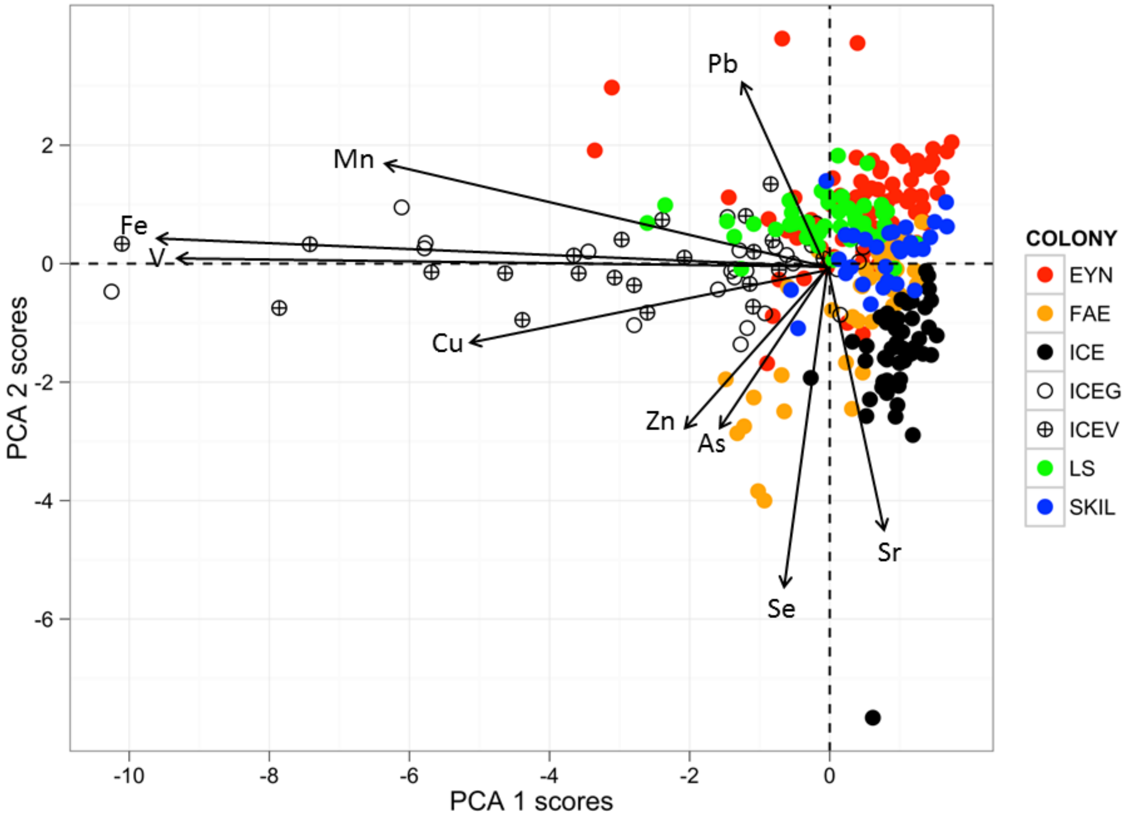

Figure 2. Plot of Principle component scores 1 against Principle component scores 2. Where EYN is Eynhallow; FAE is Faroes; ICE are Icelandic birds from Westfjords; ICEG, Icelandic birds from Grímsey; ICEV, Icelandic birds from Vestmannaeyjar; LS, Little Saltee birds, and SKIL, St Kilda birds. Labelled arrows are those elements influencing the separation with longer arrows being more influential in the separation (Oksanen 2013).

Table 3. Median concentrations (and range) of elements (mg/kg) in fulmar feathers from five different breeding colony areas: Eynhallow (EYN), Little Saltee (LS), St Kilda (SKIL), Faroes (FAE) and Iceland (ICE). ANOVA results are also shown with colony and sex as explanatory variables, along with the significant pair-wise comparisons between colonies made from post-hoc Tukey's honestly significant differences (TukeyHSD). n/s represents non significance in the tests.

Colony	V (mg/kg)	Mn (mg/kg)	Fe (mg/kg)	Cu (mg/kg)	Zn (mg/kg)	As (mg/kg)	Se (mg/kg)	Sr (mg/kg)	Cd(mg/kg)	Pb(mg/kg)
EYN malesn=41	0.16 (0.07-0.59)	1.36 (0.37-60.10)	79.44 (11.99-35.09)	9.46 (6.11-12.51)	59.05 (44.39-76.13)	0.08 (0.02-0.38)	1.75 (0.84-3.56)	7.41 (2.77-22.10)	0.04 (0.02-0.30)	0.75 (0.15-8.60)
females n=40	0.18 (0.06-0.64)	2.72 (0.48-60.32)	88.41 (21.49-98.71)	8.88 (5.62-11.85)	63.11 (48.33-88.74)	0.09 (0.03-1.19)	2.13 (0.13-3.84)	7.88 (4.24-11.54)	0.07 (0.02-0.42)	0.82 (0.20-8.31)
LS males n=33	0.27(0.10-0.74)	3.83(1.02-26.41)	207.77(66.47-78.34)	10.62(7.96-14.56)	63.69(45.11-99.73)	0.17(0.08-0.49)	1.75(1.31-2.44)	6.79(4.14-10.04)	0.03(0.02-0.17)	0.69(0.26-3.72)
females n=14	0.18(0.08-0.71)	2.50(1.18-8.74)	118.40(28.71-59.74)	9.64(7.57-12.60)	68.64(50.26-83.67)	0.14(0.08-0.44)	1.68(1.45-3.05)	6.95(5.38-10.04)	0.03(0.02-0.13)	0.48(0.20-2.84)
SKIL males n=14	0.13(0.05-0.48)	1.29(0.25-4.79)	47.71(14.48-339.80)	9.49(7.16-12.84)	64.51(43.47-74.29)	0.07(0.03-0.55)	2.45(1.90-3.64)	7.79(5.38-11.22)	0.04(0.02-0.12)	0.38(0.17-3.25)
females n=15	0.12 (0.08-0.38)	1.04(0.54-13.24)	38.39(25.51-175.40)	9.06(4.99-11.95)	63.75(51.35-80.20)	0.06(0.04-0.13)	2.75(2.41-4.37)	7.28(5.04-12.30)	0.03(0.02-0.12)	0.22(0.16-0.57)
FAE males n= 16	0.13 (0.05-0.45)	0.58 (0.11-7.53)	42.90 (8.63-388.99)	10.40 (8.55-21.66)	66.27 (56.86-02.26)	0.14 (0.03-1.64)	2.75 (2.22-4.27)	13.49 (3.90-8.46)	0.04(0.02-1.08)	0.16 (0.13-14.05)
females n= 30	0.12 (0.07-0.33)	0.77 (0.14-11.50)	46.90 (20.84-10.91)	9.26 (6.71-11.61)	73.50 (49.34-90.12)	0.12 (0.03-1.92)	3.09 (1.93-4.31)	6.36(3.27-19.65)	0.03(0.02-0.63)	0.17 (0.15-1.03)
ICE males n=64	0.28(0.12-5.48)	1.88(0.17-48.16)	67.60(12.23-595.27)	10.42(6.74-18.65)	62.60(44.93-89.02)	0.12(0.04-1.11)	3.11(1.63-14.86)	15.90(6.10-2.22)	0.05(0.02-0.38)	0.28(0.13-3.51)
females n=34	0.33(0.13-5.24)	1.70(0.32-23.38)	95.75(18.62-632.06)	9.33(6.77-13.05)	69.09(57.28-100.66)	0.13(0.05-0.30)	3.11(1.72-4.46)	16.46(6.02-8.49)	0.06(0.02-2.40)	0.21(0.15-3.63)
Model										
Colony	**$F_{4,178}$=16.60, p<0.001**	**$F_{4,178}$=3.86, p=0.004**	**$F_{4,178}$=10.84, p<0.001**	**$F_{4,178}$=6.61, p<0.001**	**$F_{4,178}$=4022, p=0.002**	**$F_{4,178}$=7.94, p<0.001**	**$F_{4,178}$=29.88, p<0.001**	**$F_{4,178}$=42.19, p<0.001**	n/s	**$F_{4,178}$=8.44, p=0.001**
Sex	n/s	n/s	n/s	**$F_{1,178}$=22.16, p<0.001**	**$F_{1,178}$=6.40, p=0.012**	n/s	n/s	n/s	n/s	n/s
TukeyHSD	**ICE vs** all colonies (all p<0.001)	**FAE vs** ICE (p=0.005)	**ICE vs** EYN, FAE, SKIL (all p<0.001)	**EYN vs** FAE (p=0.037),ICE (p=0.011), LS(p=0.001)	**FAE vs** EYN (p=0.001), SKIL (p=0.020)	**FAE vs** all colonies: EYN, ICE SKIL (all p<0.001), LS (0.047)	**EYN vs** FAE, ICE, SKIL (all p<0.001) **LS vs** FAE, ICE, SKIL (all p<0.001)	**ICE vs** all colonies (all p<0.001)	N/A	**EYN vs** FAE (p<0.001), ICE (p=0.001), SKIL (p=0.003)

Differences in Pb isotope ratios between 5 fulmar colonies

For Eynhallow, a MANOVA on combined Pb isotopes revealed differences between years (MANOVA: Pillai = 0.141, $F_{1,3}$=4.213, Pr(>F)<0.001). However, when post-hoc tests were carried out it was revealed the significant difference in years were being driven by a significant difference between the years for $^{208/206}$ Pb isotope ratio (ANOVA, $F_{1,79}$= 12.802, p<0.001). For Little Saltee, there were no significant differences in combined Pb isotopes between the years (MANOVA: Pillai = 0.149, $F_{1,3}$=1.512, Pr(>F)=0.235). Therefore all years were treated as one for the subsequent analyses.

ANOVAs revealed no sex differences between Pb isotope ratios in any of the colonies. $^{206/207}$Pb and $^{208/206}$Pb signatures showed significant differences between all colonies (Table 5). $^{208/207}$Pb showed significant differences between Little Saltee and Eynhallow, St Kilda and Iceland. Pb isotopic ranges from the literature are shown in Table 4.

Table 4. $^{206/207}$Pb broad area characteristic signatures from the literature.

Broad regime	**$^{206/207}$Pb range**	**Reference**
European boreal	1.09-1.14	Church *et al.* 1990
Northern Europe	1.10-1.16	Hopper *et al.* 1991
Saharan & Mediterranean	1.15-1.18	Véron *et al.* 1994
Canadian and subarctic	1.15-1.18	Bollhöfer & Rosman 2001
US eastern	1.20-1.22	Church *et al.* 1990

Table 5. Mean, standard deviation and ranges of each of the Pb isotopes (^{206,207,208}Pb) measured for each colony and between the sexes. Results from ANOVAs carried out are shown and Tukey's honest significant difference pairings are also shown.

Colony	**206/207Pb**	**208/207Pb**	**208/207Pb**
	mean±sd (range)	mean±sd (range)	mean±sd (range)
Eynhallow male n= 41	1.157±0.008 (1.138-1.173)	2.104±0.019 (2.051-2.137)	2.434±0.018 (2.393-2.480)
(EYN) female n=40	1.160±0.009 (1.139-1.185)	2.101±0.017 (2.066-2.132)	2.437±0.014 (2.408-2.470)
L.Saltee male n=33	1.167±0.011 (1.148-1.189)	2.109±0.009 (2.090-2.125)	2.461±0.018 (2.413-2.496)
(LS) female n=14	1.165±0.009 (1.152-1.184)	2.115±0.013 (2.0951-2.151)	2.464±0.023 (2.437-2.506)
St Kilda male n=14	1.129±0.018 (1.094-1.166)	2.157±0.028 (2.114-2.234)	2.435±0.017(2.402-2.465)
(SKIL) female n=15	1.128±0.008 (1.115-1.139)	2.153±0.016 (2.131-2.175)	2.428±0.010(2.406-2.445)
Faroes male n=16	1.152±0.010 (1.137-1.174)	2.113±0.016 (2.074-2.134)	2.435±0.008 (2.425-2.456)
(FAE) female n=30	1.151±0.010 (1.128-1.166)	2.113±0.014 (2.085-2.149)	2.432±0.011(2.402-2.449)
Iceland (all) male n=61	1.148±0.010 (1.109-1.166)	2.123±0.018 (2.059-2.169)	2.436±0.015 (2.385-2.460)
(ICE) female n=34	1.149±0.008 (1.137-1.179)	2.121±0.014 (2.077-2.142)	2.438±0.010(2.418-2.460)
Model			
Colony (col)	**$F_{3,195}$=109.48, p<0.001**	**$F_{3,195}$=73.76, p<0.001**	**$F_{3,195}$=32.73, p<0.001**
Sex	n/s	n/s	n/s
TukeyHSD	**all cols** p<0.001 with each other	**all cols** p<0.02 with each other	**LS vs** EYN,ICE & SKIL (all (p<0.001)

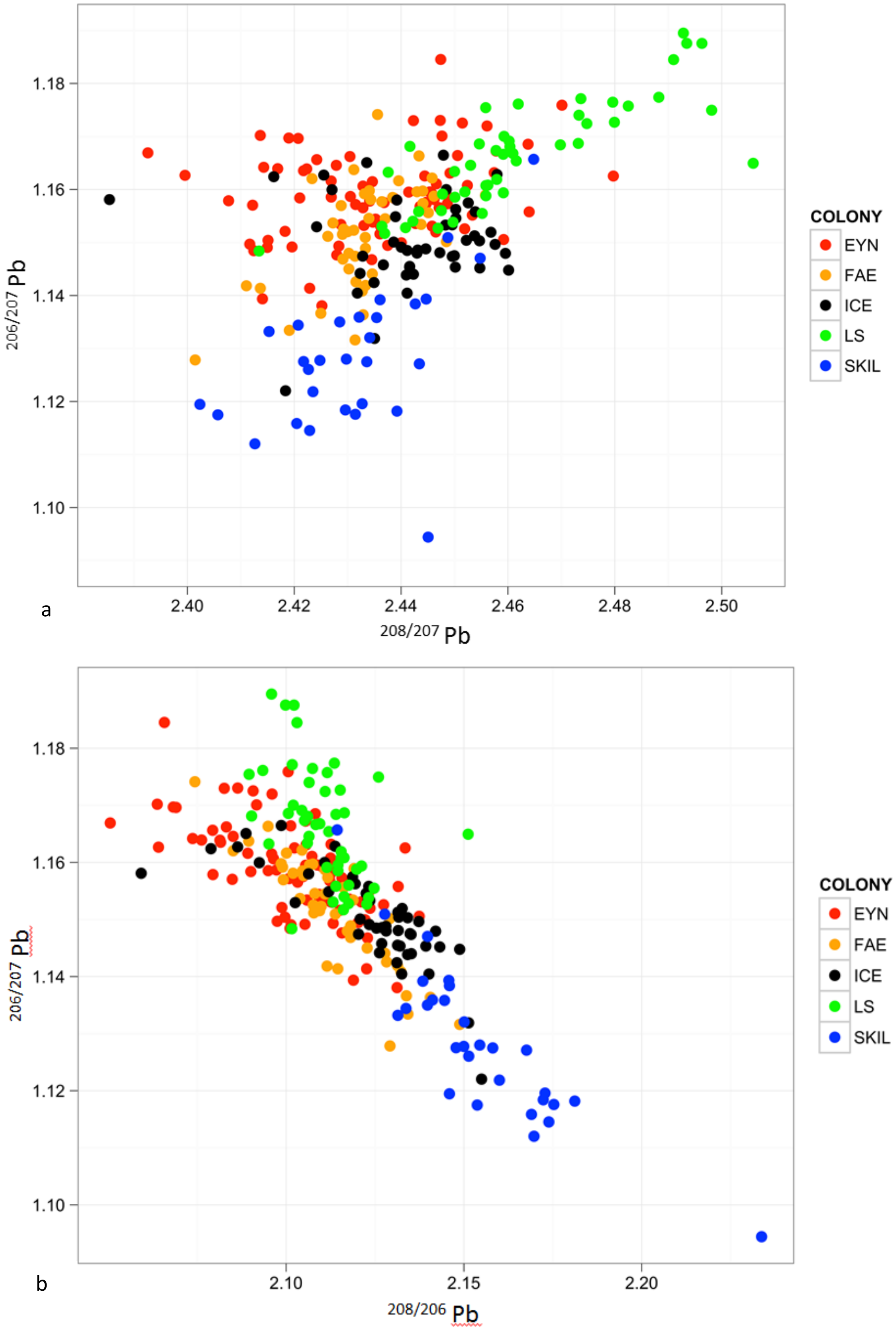

Figure 3. Three-way isotopic plots showing the range of (a) $^{206/207}$Pb and $^{208/207}$Pb, and (b) $^{206/207}$Pb and $^{208/206}$Pb. Where EYN is Eynhallow; FAE is Faroes; ICE is Iceland; LS is Little Saltee; and SKIL, St Kilda.

Differences in δ^{13}C & δ^{15}N between 5 fulmar colonies

There were no significant differences between years for either δ^{15}N (ANOVA $F_{2,42}$=0.003, p=0.96) or δ^{13}C (ANOVA $F_{2,42}$=1.117, p=0.297) in samples from Eynhallow birds. Therefore years were pooled for subsequent analyses.

No significant differences in δ^{15}N values between the three Icelandic colonies were seen (ANOVA: $F_{2,40}$=1.13, p=0.329). In δ^{13}C values, there were differences noted (ANOVA: $F_{2,40}$=7.78, p=0.001), between the northern most (Grímsey) and the southernmost (Vestmannaeyjar) colonies (TukeyHSD: p=0.010). The means for each group were -17.60 (Grímsey) and -17.26 (Vestmannaeyjar). However, as this increase in C enrichment was low (Hobson 1999), Icelandic colony data were pooled for overall colony-wide comparisons.

A MANOVA revealed there were statistically significant differences between the colonies in δ^{15}N and δ^{13}C (MANOVA: Pillai = 0.95, $F_{4,8}$=39.06, Pr(>F)<0.001) and between the sexes (MANOVA: Pillai = 0.19, $F_{1,2}$=19.82, Pr(>F)<0.001).

In investigating realtionships between the explanatory variables it was apparent that colony and latitude were collinear. Because of this only colony was used for subsequent modeling. For separate C and N models, model selection for GLMs revealed two models within two Δ AICc values of each other for δ^{13}C. The best fitting model retained colony and sex as predictors (AICc weight 0.62, AICc value 228.78). The second best model included colony only (AICc weight 0.33, AICc value 230.05).

For models on δ^{15}N values, only one model provided any evidence of explaining variation in δ^{15}N. From AICc values, colony and sex were again retained as explanatory variables (AICc weight 0.97). The second best model had AICc values more than two Δ AICc values of each other. The final model revealed that in all colonies there were consistently higher δ^{15}N values in males compared to females.

Table 6. Mean and standard deviations (ranges in brackets) of δ^{15}N and δ^{13}C values (‰). Results from the model with colony and sex differences are shown.

Colony	**Mean δ^{13}C**	**Mean δ^{15}N**
Eynhallow: male n=24	-17.16±0.520 (-18.14,-16.13)	15.49±0.523 (14.18,16.25)
female n=20	-17.31±0.575 (-18.58,-16.13)	14.88±0.201 (13.69,17.00)
Little Saltee male n=17	-15.76±0.758 (-18.04,-14.92)	17.62±0.848 (15.92,18.72)
female n=4	-15.73±0.690 (-16.55,-15.02)	17.01±1.730 (14.43,18.02)
St Kilda male n=14	-16.68±0.309 (-17.18,-16.14)	15.37±0.642 (14.13,16.23)
female n=15	-17.03±0.336 (-17.45,-16.16)	14.46±0.349 (13.81,15.08)
Faroes male n=15	-17.98±1.360 (-22.72,-16.86)	15.27±0.383 (14.66,15.50)
female n=15	-17.67±0.348 (-18.44,-17.00)	14.92±0.432 (14.29,15.85)
Iceland male n=35	-17.39±0.255 (-18.04,-16.76)	14.83±0.693 (13.66,17.00)
female n=25	-17.51±0.355 (-18.28,-16.88)	14.19±0.516 (13.28,15.06)
Final GLM		
colony	$F_{4,174}$=70.80, **p<0.001**	$F_{4,174}$=78.50, **p<0.001**
sex	$F_{1,174}$=3.36, p=0.0.067	$F_{1,174}$=39.80, **p<0.001**

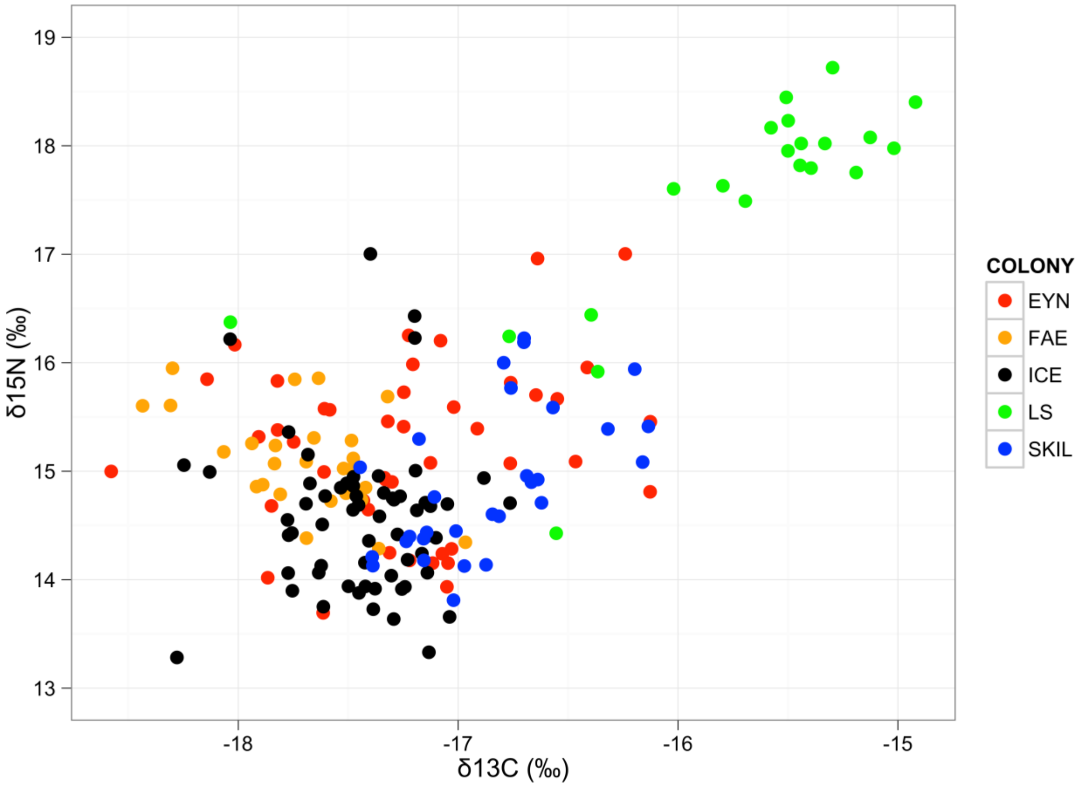

Figure 4. Range of δ13C and δ15N ratios (‰) seen between and amongst each colony.

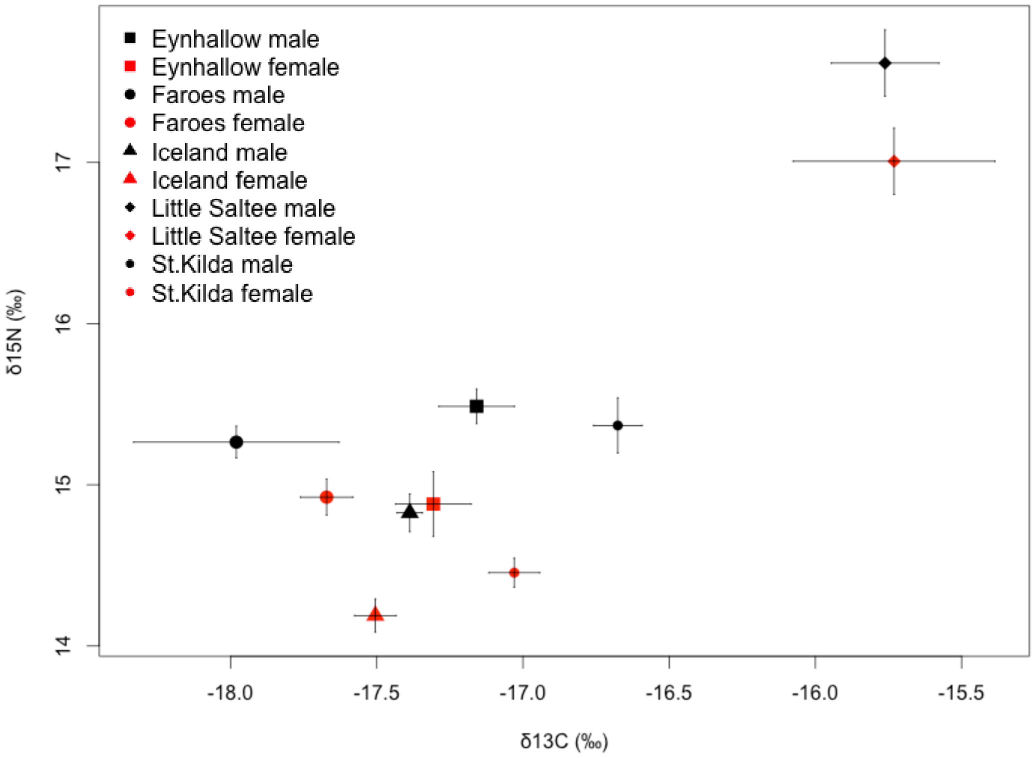

Figure 5. Differences in mean δ13C and δ15N (‰) between males (black) and females (red) from each colony. Standard error bars are also shown.

The numbers of birds assigned to each winter group at the different colonies are shown in Table 7. There was a striking difference in the number of females classified as being in group 2 compared to group 1. There were also between colony differences seen with Iceland containing the largest number of birds classified in group 2 (Figure 6). No birds other than Little Saltee birds were classified as being group 3.

Table 7. Number of birds classified in each winter group (1, 2 or 3). Only those birds with a predicted correct classification of 80% or higher are included. A chi-squared test demonstrating the difference in proportion of males and females classified in each group is shown.

Breeding colony	**Predicted group 1**		**Predicted group 2**		**Predicted group 3**	
	male	**female**	**male**	**female**	**male**	**female**
Eynhallow	19	8	4	11	0	0
Faroes	4	2	1	9	0	0
Iceland (all)	4	0	25	21	0	0
Little Saltee	0	0	2	1	14	3
St Kilda	8	0	2	13	0	0
Total no. of birds	35	10	34	55	14	3
	X_1^2=25.60, **p<0.001**		X_1^2=9.00, **p=0.002**		X_1^2=11.76, **p<0.001**	

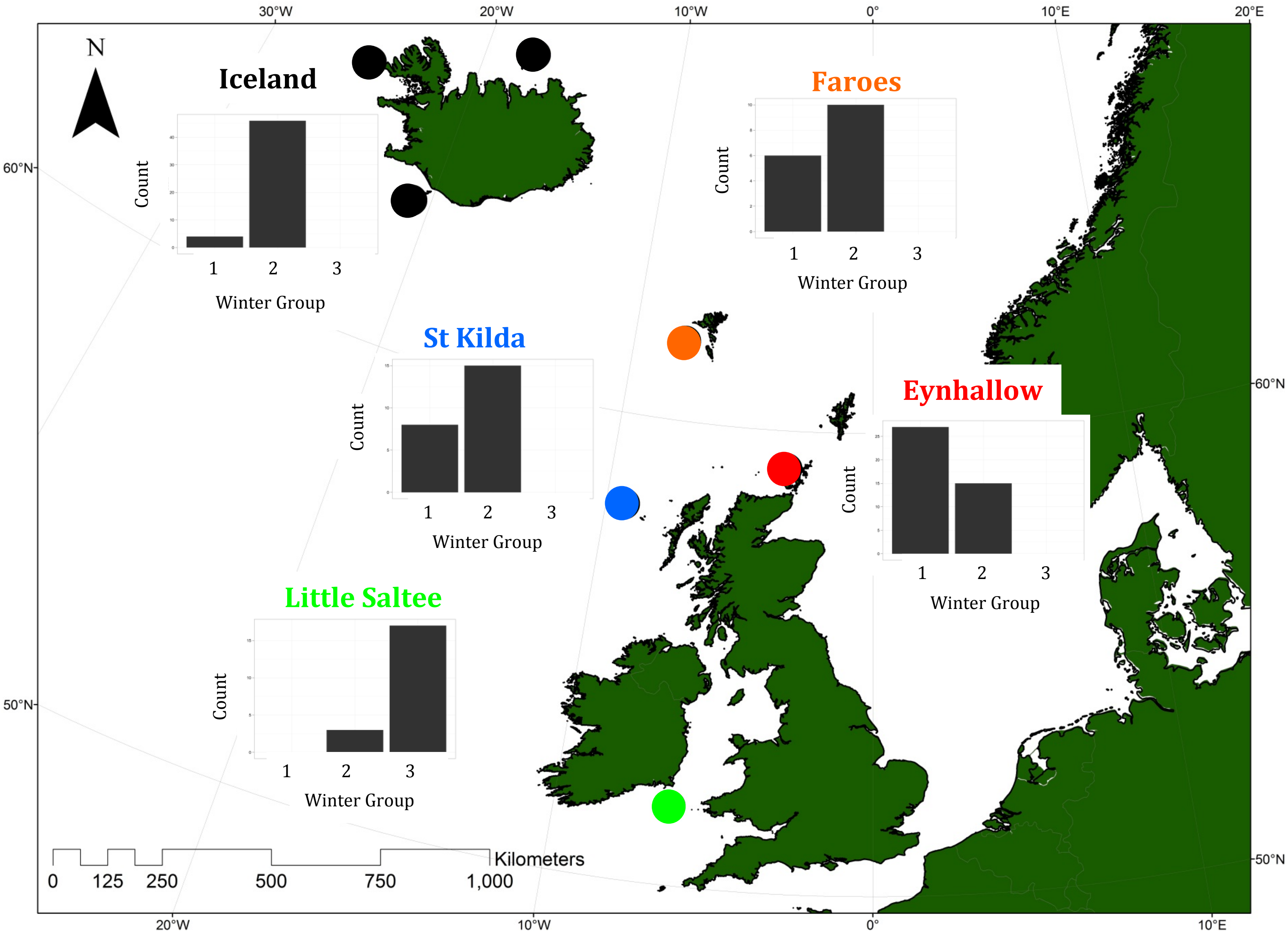

Figure 6. Map of colony differences in winter group counts, as predicted from discriminant analysis. Colony locations circles are colour co-ordinated with colony names. Winter group 1 represents birds associated with a North Sea/shelf signature, group 2 with a West Atlantic signature and group 3 with an Irish Sea signature.

DISCUSSION

Using a combination of intrinsic markers, this study suggests that fulmars from five broad breeding regions have overlapping wintering diets. Nevertheless, there were notable inter and intra-colony differences, and sex differences were recorded in both winter diet (as measured by $\delta^{15}N$) and in relative area use (as predicted by a discriminant function). Further to the dietary-influenced ratios of N and C, the geogenically-influenced Pb isotopes revealed a striking difference in Pb isotopes in St Kilda birds.

Differences in essential and non-essential trace metal(loid)s

Multi-variate analysis of essential and non-essential elements revealed overlaps between colonies: Faroes and St Kilda; Eynhallow and Little Saltee, in particular. Icelandic birds from the Westfjords clustered together with virtually no overlap with other colonies (Figure 2). Vestmannyjaer and Grímsey colonies were similar to one another with several individuals having large absolute values of Fe. Icelandic birds showed the greatest difference in elemental loadings compared to the other colonies (Table 3).

This may relate to differences in wintering area, as has been shown in univariate analysis of trace metals in flesh-footed shearwaters *Puffinus carneipes* (Bond & Lavers 2011), or differences in the prey items consumed. Conventional diet sampling during the breeding period has previously demonstrated colony differences in diet composition (Phillips *et al.* 1999). Overlap in winter distribution is likely to exist due to the far-ranging potential for fulmars over winter (Chapter 2), but the elemental analyses suggests that Icelandic birds may feed on different prey items. It is known fulmars spend extensive periods of time around colony waters over winter (Chapters 2 and 4); potentially the Icelandic birds remain at higher latitudes over the non-breeding period and do not travel as far east from their colony into the North Sea regions. Predictions from discriminant functions add to this suggestion with more Icelandic birds being classified as winter group 2 than group 1 (Table 7). In birds tracked from Eynhallow birds classified as group 2 reflected the use of West Atlantic regions in wintering foraging, whereas group 1 birds reflected the use of North Sea regions. The current breeding population of fulmars in Iceland is estimated to be 1-2 million pairs

(Mitchell *et al.* 2004), around 2-4 times the size of the UK and Irish population. It is therefore possible that due to increased competition, fulmars from the other NE Atlantic colonies will avoid foraging in these waters, as seen in other seabird species during the breeding season (Wakefield *et al.* 2013). Indeed, from tracking data of Eynhallow and Little Saltee birds, very few individuals spent any time over winter in Icelandic waters (Chapter 2, Chapter 4).

Little Saltee birds have the largest Fe concentrations on average, and the highest absolute values of Fe occur in Icelandic birds. Large Fe values have previously been shown in procellarid species (Anderson *et al.* 2010). Generally, Fe concentrations in fish species increase with both size and age (Burger & Gochfeld 2000). Thus, it is possible that individuals with the highest Fe levels have been feeding predominantly on fish rather than lower trophic level prey items (Sydeman & Jarman 1998), such as plankton, crustaceans, and squid, which fulmars are also known to consume (Phillips *et al.* 1999), which will have lower Fe levels.

Trace metal(loid)s can also inform us if there are differences in pollutant loadings between colonies and indiviudals. Se levels differed with geographic area with western colonies (Iceland, Faroes, and St Kilda) having higher levels than Eynhallow and Little Saltee. High Se levels in fulmars from Canada have been noted (Braune & Scheuhammer 2008), suggesting prey items in the further west of the Atlantic contain higher Se levels on average, though caution in comparing across tissue types should be noted (Bond 2010). Icelandic birds showed the largest Se values (maximum of 14.86 mg/kg). Depending on the species, Se levels as low as 3.8mg/kg can pose a health risk and inhibit reproduction (Lemly 2004; Burger *et al.* 2007). Whilst all birds were caught as breeders, suggesting these higher levels of Se has not caused impaired reproductive ability, it is possible that these levels may have longer-term detrimental consequences. However, element regulation is known to affect element accumulation (Borga *et al.* 2006). As such, fulmars may use their feathers to get rid of a high Se burden, as has been shown for other potentially toxic metals, for instance, Hg (Monteiro & Furness 1995). The high Se values may be reflecting a diet containing higher levels of Hg, as there is a known role in Se in reducing Hg toxicity (Enhus, Boalt & Bignert 2011). To confirm this, Hg measurements from birds in these differing regions could be tested.

Pb is known to bioaccumulate in feathers, thus they are a good tissue sample to consider Pb totals (Kim *et al.* 1998; Jerez *et al.* 2011). Though the average concentrations of all colonies remained within the considered background concentration level, 0.51-1.68 mg/kg in feathers, (Seco Pon *et al.* 2011), some individuals within all colonies demonstrated much larger Pb concentrations. Eynhallow and Little Saltee fulmars had the highest total Pb (mg/kg) values (Table 5). Relatively high concentrations of Pb have been found in marine mammals from the Irish Sea (Law *et al.* 1992), so it is not unexpected the Little Saltee birds, known to utilise the Irish Sea region over winter (Chapter 4), may be exposed to Pb in their food chain. Some Eynhallow birds have values above a potentially damaging level (defined as more than 4 mg/kg in feathers) (Burger & Gochfeld 2004; Seco Pon *et al.* 2011). These larger levels of Pb suggest extended foraging in more anthropogenically polluted waters than their colony conspecifics. The more remote colonies of Iceland and Faroes had lower Pb concentrations on average. An increase in Pb corresponding to an increase of human-based activities has also been shown in penguin feathers in Antarctica (Jerez *et al.* 2011).

Colony-specific Pb isotope signatures

Whilst there are overlaps in Pb isotopic range between colonies, significant differences in average Pb isotope ratios exist between colonies (Table 5). This suggests that Pb isotopes may be more closely related to colony area than individual differences in wintering area within a single colony. This pattern has also been seen for organic pollutants in Great skuas, where breeding colony was more influential than wintering area for pollutant loadings of persistent organic pollutants (POPs) (Leat *et al.* 2013). Fulmars over the non-breeding period spend a substantial part of their winter around their colony waters and return to their colonies throughout the winter (Macdonald 1980; Chapter 2), thus Pb isotope influences surrounding the colony area have time to be assimilated over the non-breeding period as well as during the breeding period.

The majority of the samples reflected the background range of values expected in Northern Europe ($^{206/207}$Pb: 1.10-1.16) (Bollhöfer & Rosman 2001). The exception was Little Saltee birds, where the majority of samples fell above 1.16. From tracking data at this colony, it is known these birds utilise the Irish and Celtic Seas and the Bay of Biscay extensively (Chapter 4), and so it is more likely their Pb isotopes reflect a Saharan and Mediterranean range ($^{206/207}$Pb 1.15-1.18) (Véron *et al.* 1994) than a subarctic signature (also $^{206/207}$Pb 1.15-1.18) (Bollhöfer & Rosman 2001).

One of the most distinct patterns emerging from the Pb isotope data was St Kilda birds had little overlap with other colonies, and lower $^{206/207}$Pb values (Figure 3). Lower $^{206/207}$Pb (less than $^{206/207}$Pb 1.2) values generally relate to more industrial lead signatures, whereas higher values (more than $^{206/207}$Pb 1.6) relate to more radiogenic signatures (Hopper *et al.* 1991; Bollhöfer & Rosman 2001). Potential reasons for a difference in St Kildan signatures may either relate to Pb isotope values being assimilated from their specific colony area or relate to a specific area in which they are feeding.

Soil data from St Kilda revealed atmospheric deposition of Pb since the Industrial Revolution and ash from peat and turf burning played a role in influencing $^{206/207}$Pb signatures (Meharg *et al.* 2006). The majority of the fulmar feather $^{206/207}$Pb signatures fit within the range of the St Kilda soil range (above 20cm, $^{206/207}$Pb of 1.02-1.15). One possibility is that contamination from nesting in the cleats on St Kilda has influenced the fulmar's Pb isotope signature. In Laysaan albatrosses *Phoebastria immutabilis* nesting on an island with a decommissioned military base, birds were found to have a highly contaminated Pb isotope signature (Finkelstein *et al.* 2003). Feather sampling birds from other parts of St Kilda may help elucidate if it's a nest-site specific signature that is being seen, as all birds caught in this study were from one region on St Kilda. Alternatively, the low Pb isotopes signatures in individual St Kildan birds may reflect the signature of waters close to St Kilda and the west coast of Scotland. This could be tested by tracking individuals from this colony across their winter period, as has been carried out for the Scottish and Irish colonies (Chapter 2 and 4).

Colony and sex-differences in wintering foraging revealed by C and N isotopes

Discrimination using C and N isotopic data revealed that there are differences in the relative frequency of wintering strategies between colonies. The further west the colony, the more individuals were predicted as wintering in group 2. This winter group 2 reflected West Atlantic foragers in tracked Orkney birds. Concurrently, the isotope data revealed within and between colony differences in diet. Overlap in δ^{13}C and δ^{15}N values between colonies suggests individuals from different colonies may be feeding on prey items with similar isotopic values or are feeding in similar regions. Overlap in wintering grounds from birds of differing breeding colonies has also been noted in tracked Cory's shearwaters (González-Solís, Croxall, & Ruiz 2007), and it is likely the fulmars in this current study also overlap in winter foraging areas. Regional differences in diet composition have been shown to exist in fulmars, particularly during the breeding period (Hamer, Thompson & Gray 1997; Phillips *et al.* 1999; Ojowski *et al.* 2001; Wang *et al*. 2009; Mallory *et al*. 2010). However, winter diet has, until now, been less extensively studied (see Thompson *et al.* 1999).

In δ^{13}C isotopes, Faroese and Icelandic birds in particular showed the strongest pelagic C signatures of all colonies (Table 6), which is perhaps not surprising as both are furthest from other land masses. In contrast, Little Saltee birds had the most enriched δ^{13}C isotope values of the five colonies, which indicate a more inshore, benthic foraging strategy (Hobson, Piatt & Pitocchelli 1994). Tracking data from several individuals from this colony supports this supposition (Chapter 4). As there is a known latitundinal variation in C isotope values due to temperate influencing cell turnover rates (MacKenzie *et al.* 2011), another potential explanation for observed variation in δ^{13}C is differences in latitude between the colonies. However, from published isoscapes of the Atlantic Ocean the colonies have similar baseline δ^{13}C contours with the exception of Iceland which has a more depleted baseline (Graham δ^{13}C 2010). Our data revealed that the largest difference in δ^{13}C was between Little Saltee and the other, more northerly colonies. As Little Saltee has a similar baseline δ^{13}C values with all colonies except Iceland, it seems likely that the differences observed are due to a difference in dietary intake or winter distribution rather than due to colony latitude alone.

There was a range of δ^{15}N isotopic values seen, with some individuals feeding at a lower trophic level than others (lowest value δ^{15}N 13.28, highest value δ^{15}N 18.72), relating to a 1-2 trophic level difference (Hobson 1999). For St Kildan birds a comparison between winter diet in the 1990s with this current study reveals an increase in δ^{15}N from 13.65 in the early 1990s (Thompson, Furness & Lewis 1995), to 14.91 presently. A similar increase in δ^{15}N in Orkney birds from 1990s to present day is also seen (14.18 in 1990s to an average of 15.19 currently) (Thompson, Furness & Lewis 1995). This suggests there may have been a prey switch during this 20 year period at these colonies.

Lower $\delta^{15}N$ have previously been related to a pelagic, *Calanus* food chain in high arctic fulmars (Dahl *et. al.* 2003), suggesting the lower signatures recorded in this current study may relate to birds feeding predominantly within this food chain. Further to the enriched $\delta^{13}C$ signatures in Little Saltee birds, this colony also separated with its enriched $\delta^{15}N$ signatures. Previous studies have hypothesised that more southerly populations of fulmars consume more discards (Phillips *et al.* 1999) and it is possible that the Little Saltee birds, which spend a large proportion of their winter around colony waters (Chapter 4), take advantage of fishing vessels in the area. The area where Little Saltee fulmars forage overwinter is known to be an important area for fisheries, particularly for *Nephrops* (Elliott *et al.* 2012), which have high discard rates (ICES 2012). Gannets are known to utilise discards from this area (Votier *et al.* 2010), and fulmars have even been filmed feeding off fishing vessels in this region (Votier *et al.* 2013). No significant difference in N isotopes, was noted between the Icelandic colonies in this study. This is in contrast to previous work on diet during the breeding season in Iceland between the northern colonies, thought to be more reliant on capelin, and the southern colonies, thought to be more reliant on fishery discards (Lilliendahl & Solmundsson 1997; Phillips *et al*. 1999; Thompson *et al.* 1999). If individuals within one colony are feeding predominantly on fishery discards compared to smaller, pelagic fish we might also expect there to be consequences in terms of contaminant loadings the birds will receive depending on these two food resources. The smaller pelagic fish are likely to have fewer contaminants than offal from larger, discarded fish (Arcos *et al*. 2002; Cipro *et al.* 2014). This may also help explain why we see such variation in metal concentrations between individuals (Table 3).

As well as colony differences, marked sex differences were present in the $\delta^{15}N$ isotope data, with females having significantly lower $\delta^{15}N$ values than males across all colonies, with St Kildan birds demonstrating the largest difference in $\delta^{15}N$ values between the sexes (Table 6). Females have been shown to consume prey of lower $\delta^{15}N$ values in other seabird species (Bearhop *et al.* 2006; Stauss *et. al.* 2012), but this is more commonly observed in the breeding period (Forero *et al.* 2002; Ramos *et al.* 2009). The majority of seabird dietary studies, including those on other Procellariiformes, have found no sex differences in proxies of diet over the non-breeding period (e.g. Cherel *et al.* 2007b; Phillips *et al.* 2009).

Female fulmars may therefore be feeding on different prey than males, or are utilising different areas than males. It is known from tracking data from Orkney that sex differences in winter habitat do exist (Chapter 2), and from this study's discriminant analysis there were sex differences in assignment to winter area group (Table 7). It is possible that differences in morphology may play a role in prey items consumed as females are known to have smaller beaks (Dunnet & Anderson 1961) and individual variation in beak size and shape have been noted within a single colony (P. Thompson, pers comm.). Beak morphology has been shown to effect prey consumption in shags, with males being able to consume larger prey items (Cook *et al.* 2007). Wing loading may also differ between the sexes which may determine how far each sex travels, as shown in other petrels (Shaffer, Weimerskirch & Costa *et al.* 2001). To test this, wing loadings of fulmars caught could be measured and compared to their wintering area, as has been tested in gannets where a body size index differed with geographic area (Grecian 2011). Whilst all fulmars caught in this present study were a light-phase phenotype, it should be remembered that geographical variation in different phenotypes of fulmars (light phase and dark phase) exist. Across the northern fulmar's range this may confound the sex differences noted in this study, as male-dark phase fulmars can be smaller than female light-phase fulmars (van Franeker & Wattel 1982), demonstrating the importance of considering regional differences in mixed phenotypes.

Sex differences in fulmar diet measured with fatty acid (FA) analysis at Eynhallow, have been shown in the pre-laying period. These differences do not continue in the incubation and chick rearing periods, which show similar dietary profiles (Owen *et al.* 2013). Females had higher proportions of prey species linked to a demersal signature in their FA profile than pelagic prey species at a single colony (Owen *et. al.* 2013). Whilst it has been suggested that demersal signatures are likely to relate to a diet based on fishery discards (Owen *et. al.* 2013), this constrasts with this current study which demonstrated females feeding at lower δ^{15}N values than males over winter (Table 6). Furthermore, their smaller size potentially could impede their competitive ability in feeding on discards, known to be a highly competitive environment. Thus, it is unlikely females consume more discards than males over this period. It is therefore proposed that the observed relationship between fatty acid signatures and a pre-laying sex difference in diet actually reflects a difference in wintering area use, as demonstrated previously (Chapter 2). The demersal signature recorded in the fatty acid study was determined from North Sea-based fatty acid reference values (Owen *et al.* 2013). It is therefore possible that the West Atlantic region where many females forage (Chapter 2) has a different fatty acid reference system than the North Sea.

It has been previously proposed that females lower their trophic level in winter months (Mallory *et al*. 2010) and fulmars have shown a reduced trophic level from summer to winter diet at a high Arctic colony (Hobson & Bond 2012). This current study also confirms a differentiation between summer and winter diet when compared to previous work on summer diets. For example, Icelandic diet over summer had values of δ^{13}C -20.00 (Thompson *et al.* 1999), whereas this study had values of -17.39. This suggests this is a colony-wide characteristic of fulmar foraging shifting during the wintering months, though caution in comparing across timespans should be noted in this instance.

Conclusions and future directions

Overall, it has been shown that fulmars from colonies across their North Atlantic range demonstrate a wide range of dietary differences both within and between colonies. Sex differences in diet, such that females were feeding at lower values of δ^{15}N, were noted across the fulmars range.

In addition to more conventional C and N isotope analyses carried out, we also present for the first time results from a wide-ranging species using Pb isotopes, spanning differing colonies. We demonstrate that Pb isotopes can potentially provide us with different information about the areas over which fulmars may forage in the winter, showing they will be exposed to differing regional differences in potential pollutants. To further explain the differences observed in the St Kilda birds it would be useful to track individuals from this colony to see the extent of their use of colony waters over winter and to further explore possible routes of Pb isotopes into their feathers.

Further to these conclusions, we demonstrate the ability to use non-destructive sampling of belly feathers to assign untracked birds to a potential winter region. Knowing the far ranging potential in fulmars both over breeding and wintering periods means overlap in foraging ranges with birds from differing breeding provenances exist and therefore sampling birds of unknown origin may obscure true results of differences between colonies.

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CHAPTER 6

Different winter strategies affects reproductive success in an iteroparous breeder

Photo: Archive. “Future forager”

CHAPTER 6: Different winter strategies affects reproductive success in an iteroparous breeder

ABSTRACT

Carry-over effects from the non-breeding period can affect subsequent breeding success as a result of extrinsic or intrinsic factors. In this study, individual fulmars tracked within a single study population had known differing wintering foraging strategies. Whether these differences in non-breeding location influence the probability of successfully producing an egg and in turn successfully producing a fledgling, was considered for females, males and pairs. Winter diet in both males ($\delta^{13}C$) and females ($\delta^{15}N$) contributed to average breeding success at both egg and fledgling stages. Tracked pairs revealed that a pair's winter strategy contributed to average breeding success (from 2005-2012) at both breeding stages. The most successful pairs were those where the male foraged closer to the colony area, in the North Sea. The least successful strategy was when both members of the pair foraged extensively outwith the North Sea. This is the first tracking study to date which has assessed a pair's wintering area as a possible influence on subsequent breeding success and demonstrates the complexity of influences on an individual's reproductive output.

INTRODUCTION

Understanding the factors that explain variation in an organism's reproductive fitness is a fundamental question in ecology (Krebs & Davies 1997). For mobile organisms with distinct breeding and non-breeding seasons, individuals from the same population may differ in their geographical distribution both between and during these seasons. Given current interest in the influence of climate change on future population dynamics, mobile, migratory and partial-migratory species are of particular interest because individuals may experience different climatic regimes in the non-breeding seasons, which could lead to carry over effects in the subsequent season (Webster *et al.* 2002). These carry-over effects may contribute substantially to explaining individual fitness (Harrison *et al*. 2011) and hence investigating the processes underlying these effects is key to understanding a species' overall population dynamics.

Non-breeding, winter ecology has demonstrated links to subsequent reproductive consequences during the breeding season through a variety of mechanisms. Winter diet and food availability plays a particularly important role (Cook *et al.* 2004; Robb *et al.* 2008), with profitable winter food supply allowing individuals to maintain body condition required for reproduction.

Winter climate can also have a population-level effects on a species' reproduction and survival. For example, the winter North Atlantic Oscillation (NAO) is known to affect several species, in both terrestrial (Costantini, Carello & Dell'Omo 2010) and marine realms (Frederiksen *et al*. 2004). Winter NAO has been linked to both survival (Grosbois & Thompson 2005; Sandvik, Erikstad & Saether 2012) and reproduction (Lewis *et al.* 2009) in many seabird species. Whilst links between large-scale climatic variables have been noted, it is often difficult to assess the reasons for the linkage, but it is likely to relate to the area in which they feed, and their diet within these foraging areas.

Understanding winter distribution and winter diet in marine organisms can be particularly challenging. However, with the ability to track animals across their yearly cycle using data loggers, combined with dietary proxies based on intrinsic markers, winter distribution and diet can now be investigated for many marine top predators (Ramos & Gonsález-Solís 2012; Linnebjerg *et al.* 2013). Ratios of stable isotopes of both carbon, ^{13}C to ^{12}C (denoted as δ^{13}C), and nitrogen, ^{15}N to ^{14}N (denoted as δ^{15}N), can provide information on the trophic level at which an individual feeds (δ^{15}N) and a distinction between inshore and offshore diets (δ^{13}C) (Hobson 1999).

When individuals within a single colony have differing wintering distributions, concurrent differences in diet may exist (Grecian 2011). Research is lacking in fitness consequences of differing winter foraging characteristics within a colony. In a study using wintering areas from five colonies based on ringing recoveries, no strong link between winter area and survival differences between colonies were noted (Harris *et al.* 2005). However, ringing recoveries provide a biased picture of a colony's winter distribution, and subsequent work has demonstrated that differences in wintering area can exist in within single puffin colonies (Harris *et al.* 2010). A study of tracked gannets demonstrated that those birds which wintered closer to the breeding colony were in better body condition for the breeding period (Grecian 2011), though a direct assessment of breeding success was not measured in this case.

Further to individual differences, wintering strategies may also differ within a pair, but this has rarely been considered. In a study on Balearic shearwaters *Puffinus mauretanicus*, activity data revealed the most successful pairs were those which were the most synchronous in colony visits over the non-breeding period (Guilford *et al.* 2012). Though differing wintering distributions between pairs were not considered in this study, the work did indicate how pair wintering strategy may be important over the non-breeding period.

In this current study, there is a unique opportunity to test the prediction that a pair's wintering strategy may influence reproductive success. Northern fulmars, well-documented as having a population rise from the 1900s to 1980s (Thompson 2006), have fallen in numbers since the 1990s. UK-breeding fulmars are currently amber-listed as a species of moderate concern due to their breeding localisation and their decline in breeding population (Eaton *et al.* 2009). Both fulmar survival (Grobois & Thompson 2005) and reproduction (Lewis *et al.* 2009) have been linked to winter NAO, with year to year variation in breeding success strongly related to oscilliations in the NAO. Further to this extrinsic influence on breeding success, intrinsic influences of pair bond duration and previous pair reproductive success are also known to influence an individual's reproductive output (Lewis *et al.* 2009). Individual differences in wintering areas exist from this same study colony and individuals are highly consistent in their choice of wintering area (Chapter 2). In this current study, it is argued differences in wintering strategy may also need to be taken into consideration when considering reproductive success.

This study investigated whether winter foraging strategy influences average reproductive success in a) females b) males and c) within a pair.

METHODS

Study population

Long-term data on occupied nests have been recorded since 1950 at Eynhallow, Orkney (59°8'N; 3°8'W) and data on individual breeding adults have been collected since 1958. This island currently has approximately 100 occupied nests within a defined study area. Nest sites are found in differing habitats across the island: on cliffs, at ground-level on beaches, on or amongst abandoned buildings; and underneath rocks. Fieldwork was conducted at this site with British Antarctic Survey (BAS) light-based Global Location Sensing (GLS) loggers (loggers hereafter) deployed on darvic leg-rings on 163 breeding adults caught by net or noose at the nest between 2006-2011 and recovered from 2007-2012. The average logger recovery rate was 46% over one year and 76% over two or more years. The total device weight (including darvic leg ring) was 3.6g, representing less than 0.5% of the lightest recorded fulmar's body weight. A selection of 6-10 belly feathers were plucked from around the brood patch of each tagged individual for winter dietary analysis. Sex was determined by molecular analysis of DNA from feathers collected during logger recovery, using P2-P8 primer sequences and Z-002 and CAM-11 markers (Griffiths *et al.* 1998; Dawson 2007).

Tracking data

Individual tracks were produced from the loggers using BASTrak software v.18, using a light threshold level of 10 and an elevation angle of -3.5. An iterative smoothing process was applied twice to the data to reduce error associated with GLS tracking data (Phillips *et al.* 2004). The winter, non-breeding period was taken to be from end of October to end of February, thus avoiding any equinox periods for which latitude data are unreliable (Fox 2010). There were 117 usable winter tracks across all years from 67 individuals (31 females and 36 males). These data were used to assign each individual bird to one of the three wintering regions (the West Atlantic, the North Sea and the Barents Sea/northern Norwegian Sea) in two different ways. First, a mean location was calculated for each individual over the whole winter period. Second, the overall winter distribution from all points over the winter was assessed to verify the mean location reliably represented the bird's main winter location. Each bird was then grouped either in group 0 (spends its winter either in the West Atlantic or Barents Sea) or in group 1 (spends its winter predominantly in the North Sea). Sample sizes for each year are shown in Table 1.

Table 1. Sample sizes for tracked individuals in each year, with only one year per individual being included.

Year	Female	Male
2006	1	1
2007	3	3
2008	5	4
2009	3	2
2010	18	25
2011	1	1
Total	31	36

Of these 67 individuals, 22 were members of pairs with tracking data. It was assumed for the purposes of the model that winter location remained the same within individuals between years, as previous tracking work at this colony has shown high winter site fidelity (Chapter 2). This enabled the maximum number of tracked pairs available as even if tracks were from separate years within each pair (as in n=11 pairs), a winter location could still be assigned for each member. Two pairs contained members which swapped partners during the study period.

δ^{13}C and δ^{15}N stable isotope analyses

Feathers were washed with Milli-Q water prior to oven drying at 65°C for > 12 hours. The samples were then homogenized in a ball mill (Mixer Mill type MM 200, Retsch of Haan, Germany). Sub-samples of 1.3mg material were loaded into 5 x 3.5mm tin cups (Elemental Microanalysis Ltd.). Total N and C contents and the ^{15}N:^{14}N and ^{13}C:^{12}C isotope ratios of milled dried material were determined using a Flash EA 1112 Series Elemental Analyser connected via a Conflo III to a Delta^{Plus} XP isotope ratio mass spectrometer (all Thermo Finnigan, Bremen, Germany). Isotope ratios were calculated using CO_2 and N_2 reference gasses injected with every sample. The isotopic values of these gasses were directly referenced against IAEA reference materials USGS40 and USGS41 (both L-glutamic acid); certified both for $\delta^{13}C$ ($‰_{\mathrm{VPDB}}$) and $\delta^{15}N$ ($‰_{\mathrm{air\ N_2}}$). Long-term precisions of a quality control standard (milled flour) were: $\delta^{13}C$ -25.5 ± 0.29 ‰ and ^{15}N 0.367 ± 0.0002 atom % (mean ± sd, n = 200). Of the tracked birds, 16 females and 22 males had concurrent isotope data available.

Reproductive data

Eynhallow has a long-term dataset on fulmars spanning since 1950. BTO-ringed breeding adult fulmars have been given a unique colour ring combination. From 1958, the colony has been visited on three occasions in each breeding season to collect individual-based reproductive data: late May/early June to count occupied nests with eggs, mid-July to count nests with hatched eggs, and mid-August to count and ring fledglings. In years 1997-2000 no data was available on fledgling numbers as no trips were made over this period. A previous study on factors affecting breeding success at the same study site focused on data from 1958-2005 (Lewis *et al.* 2009). Assessment of change in breeding success was extended in this current study from 1958-2012, with a regression smoother (loess) applied to the data (Cleveland, Grosse & Shyu 1992), and an overall trend line calculated.

For assessment of winter foraging strategies in conjunction with breeding success, this study concentrates on average breeding success during recent years (from 2005-2012) for each of the recovered logger birds. Average breeding success rate was taken from 2005 for two reasons. Firstly, in the winter of 2003/2004 there was a mass wreck of fulmars (van Franeker 2004), which caused the lowest breeding success of the entire time series. Secondly, we did not want to make assumptions about an individuals' wintering area prior to the period when tracking studies were conducted. Although previous tracking work has shown a high degree of consistency in winter area choice (Chapter 2), it is not inconceivable that an individual may have wintered in a different area at a different stage of its life history.

Statistical Analysis

Separate sex models

Tracked male and female birds were considered separately in binomial generalized linear models (glm) with a logit-link function. The binomial response variable was the average breeding success for each bird, considering both the probability of successfully producing an egg and the probability of successfully producing a fledgling. Explanatory variables were: winter location of the individual (0 = outwith North Sea, 1 = North Sea), dietary components as measured by $\delta^{13}C$ and $\delta^{15}N$ values; nest site type (rock (1), cliff (2), beach/ground (3), or, on or within buildings (4)); and age group of the individual. Age group was assigned based upon the minimum number of years that an individual had been recorded breeding at the study site, and included 59 birds of unknown age and eight individuals of known age, having being ringed as chicks. Each individual was assigned to one of three broad categories: 1: bird recorded as breeding for less than 10 years; 2: bird recorded as breeding for at least 11 years but less than 21 years; 3: bird recorded as breeding for more than 21 years. A quasi-binomial function was used to correct for over dispersion where this occurred. Further linear regression analyses were carried to explore relationships between explanatory variables.

Pair-based models

For each tracked pair, the pair's average success rate was used as the binomial response variable. Separate models were run for the probability of producing an egg and the probability of producing a fledgling. Explanatory variables were: the winter location for each member of the pair (as in single sex models), pair strategy (1: female member remains in NS during winter, male member travels outwith NS area; 2: male member remains in NS during winter, female member travels outwith NS area; 3: both pair members travel outwith NS area; 4: both pair members remain within the NS area over winter); age group of each member of the pair (as single sex models); winter diet of each member of the pair, as measured by $\delta^{13}C$ and $\delta^{15}N$ values; and minimum number of years the pair has been together, ascertained from the long-term database (see Appendix 5 for pair locations and number of years the pair has bred together).

Model selection was carried out using Akaike's Information Criterion (AIC) values corrected for by smaller sample size (AICc), in the package AICcmodavg (Burnham & Anderson 2002). The covariates retained in models within 2∆ AICc of each other were further investigated using binomial glm summary functions. Models were verified using standard plots and packages lme4 and nlme were used.

All statistical analyses were carried out using R v.2.15.0 (R development Core Team, 2012).

RESULTS

Long-term breeding data for Eynhallow fulmars

Following on from Lewis *et al.*'s 2009 study, we extended the data on long-term trends of breeding pairs on Eynhallow from 1950 to 2012 (Figure 1). The colony increased steadily from 1950 with 8 breeding pairs in the study area up to a peak in 1984 of 200 breeding pairs in the study area. The most recent count had 99 pairs in the colony (as of 2012).

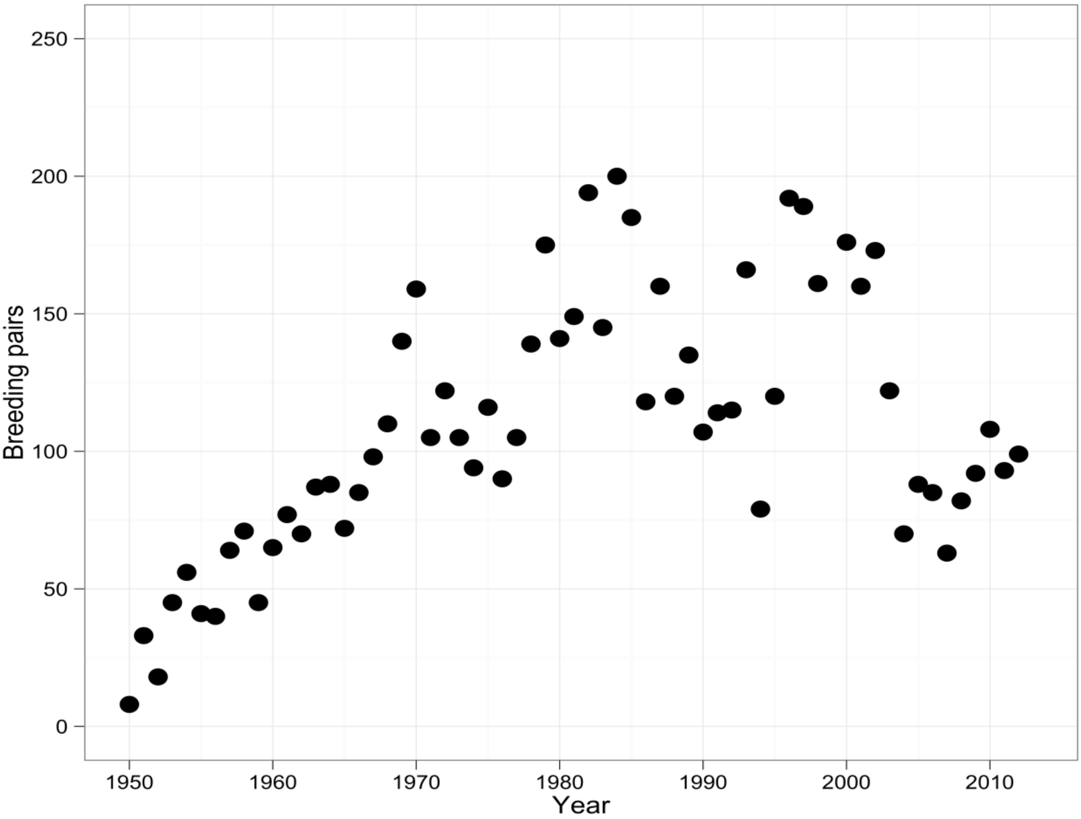

Figure 1. Changes in the numbers of breeding pairs of northern fulmars on Eyhallow, Orkney between 1950 and 2012.

Breeding success, as defined by the proportion of fledglings produced from the number of eggs laid, has fluctuated decadally from 1958-2012. The lowest breeding success was in 2004, when less than 10% of eggs laid successfully reached the fledgling stage. Overall, there has been a decline in breeding success over the time period (Figure 2) ($F_{1,49}$=9.806, Pr(>F)=0.003).

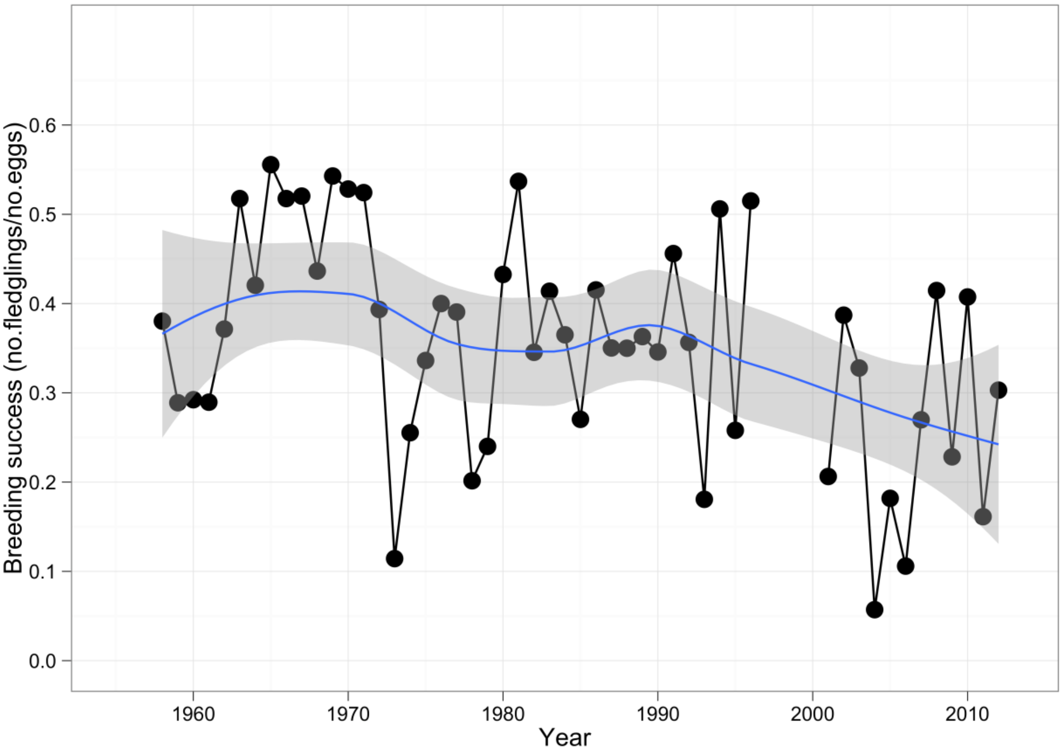

Figure 2. Changes in breeding success, as measured by the number of breeding attempts to reach fledgling stage, of northern fulmars on Eynhallow, Orkney between 1958-2012. The overall downwards trend is shown using a non-linear smoothing method, with 95% confidence interval shading. Missing data from 1997-2000 was due to no trips being made during the fledgling survey period.

Effects of wintering strategies on average breeding success

For males, binomial GLMs predicting the probability of successfully producing an egg revealed three models within two ΔAICc values of each other, relating to $\delta^{13}C$, $\delta^{13}C$*winter interaction and $\delta^{15}N$ (Table 2a). Model estimates from the strongest model revealed that the lower the $\delta^{13}C$ signature in males, the higher the success in producing an egg (Table 2a and Figure 3b).

The probability of males producing a fledgling was again associated with $\delta^{13}C$ signatures (Table 2a and Figure 4b). In addition, nest site characteristics affected this measure of breeding success (Table 2a). Having a nest on a cliff was significantly worse than having a nest under a rock (binomial GLM; z=-2.566, se=0.547, p=0.010) and borderline significantly worse than having a nest on a beach or on the ground (binomial GLM; z=-1.876, se=0.583, p=0.06). The second best model also included age group as a predictor. Whilst older males appeared to have higher chance of breeding success in their median values (42% probability of successfully producing a fledgling in the oldest age group, compared to 36% in younger age groups), evidence was not strong for this pattern (quasi-binomial GLM z=0.779, se=0.186, p>0.05). Further linear regression analysis did reveal $\delta^{13}C$ was significantly related to age group of males ($F_{2,19}$= 4.198, p=0.031), such that older birds had lower $\delta^{13}C$ signatures.

For females, the strongest models for the probability of producing both eggs and fledglings were associated with $\delta^{15}N$ (Table 2b). Model estimates revealed that the lower the value of $\delta^{15}N$, the higher the chance of successfully producing both an egg and fledgling (Figure 4a and Table 3b).

Plots showed the differences seen at the egg stage between male and female location, with female birds wintering outwith the North Sea having a higher probability of producing an egg, and males wintering outwith North Sea having a lower probability of producing an egg (Figure 3a and b).

Table 2. AICc results for the candidate models within 2Δ AICc of each other, predicting breeding success at the egg and fledgling stages for a) males, b) females and c) pair data. AICc is the AICc value for the model, Δ AICc is the difference between the candidate models and AICcWt is the weight of relative likelihood of the model given the data and candidate models considered (Cherry *et al.* 2013)

Model type	Model parameters	AICc	Δ AICc	AICcWt
a) Males				
Egg Success	$\delta^{13}C$	44.50	0	0.36
	$\delta^{13}C$ + winter interaction	45.44	0.94	0.23
	$\delta^{13}C + \delta^{15}N$	45.89	1.40	0.18
Fledgling Success	$\delta^{13}C$+nest site	81.23	0	0.29
	$\delta^{13}C$ + age group	81.43	0.20	0.26
	$\delta^{15}N$	81.97	0.75	0.20
b) Females				
Egg Success	$\delta^{15}N$	48.02	0	0.94
Fledgling Success	$\delta^{15}N$	48.15	0	0.75
c) Pairs				
Egg Success	pair strategy	46.00	0	0.51
	pair strategy + male age group	46.26	0.27	0.44
Fledgling Success	pair strategy	73.64	0	0.55
	pair strategy + male age group	74.84	1.20	0.30

Table 3. Model parameter outputs from the top model, as selected from the AICc values in Table 2.

	Parameter	**Estimate**	**Std.Error**	**Pr(>|z|)**
a) Males				
Egg success	$\delta^{13}C$	1.254	0.618	**0.042**
	intercept	23.819	10.737	0.026
Fledgling success	$\delta^{13}C$	0.268	0.369	>0.05
	nest	-0.413	0.269	>0.05
	intercept	5.484	6.251	>0.05
b) Females				
Egg success	$\delta^{15}N$	-0.446	0.216	**0.039**
	intercept	7.586	3.286	0.021
Fledgling Success	$\delta^{15}N$	-0.621	0.190	**0.006**
	intercept	9.250	2.917	0.008
c) Pairs				
Egg success	pair strategy	-0.105	0.309	>0.05
	intercept	2.013	0.834	0.015
Fledgling success	pair strategy	-0.160	0.585	>0.05
	intercept	-0.009	0.222	>0.05

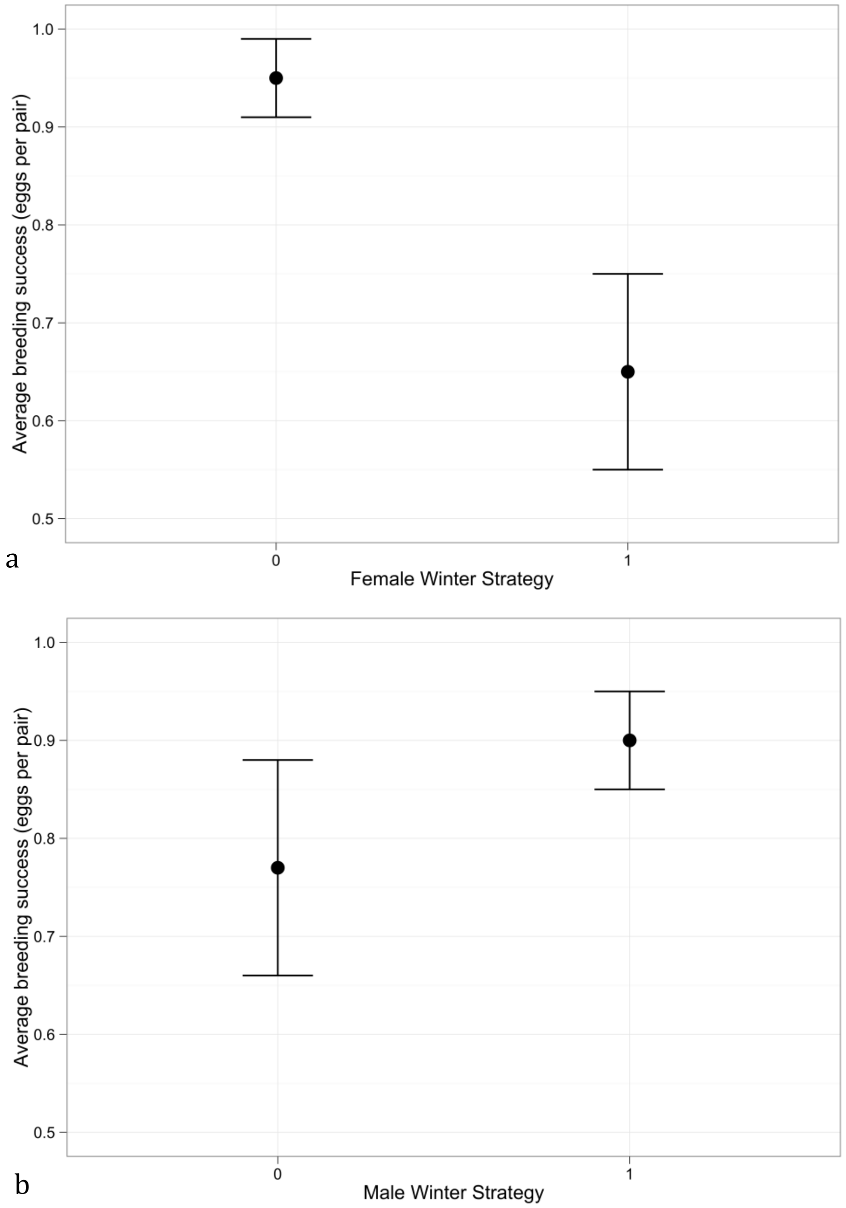

Figure 3. Average probability of successfully producing an egg in a) females and b) males, against winter strategy, where 0=winters outwith the North Sea, and 1= winters within the North Sea area. Standard errors are also shown.

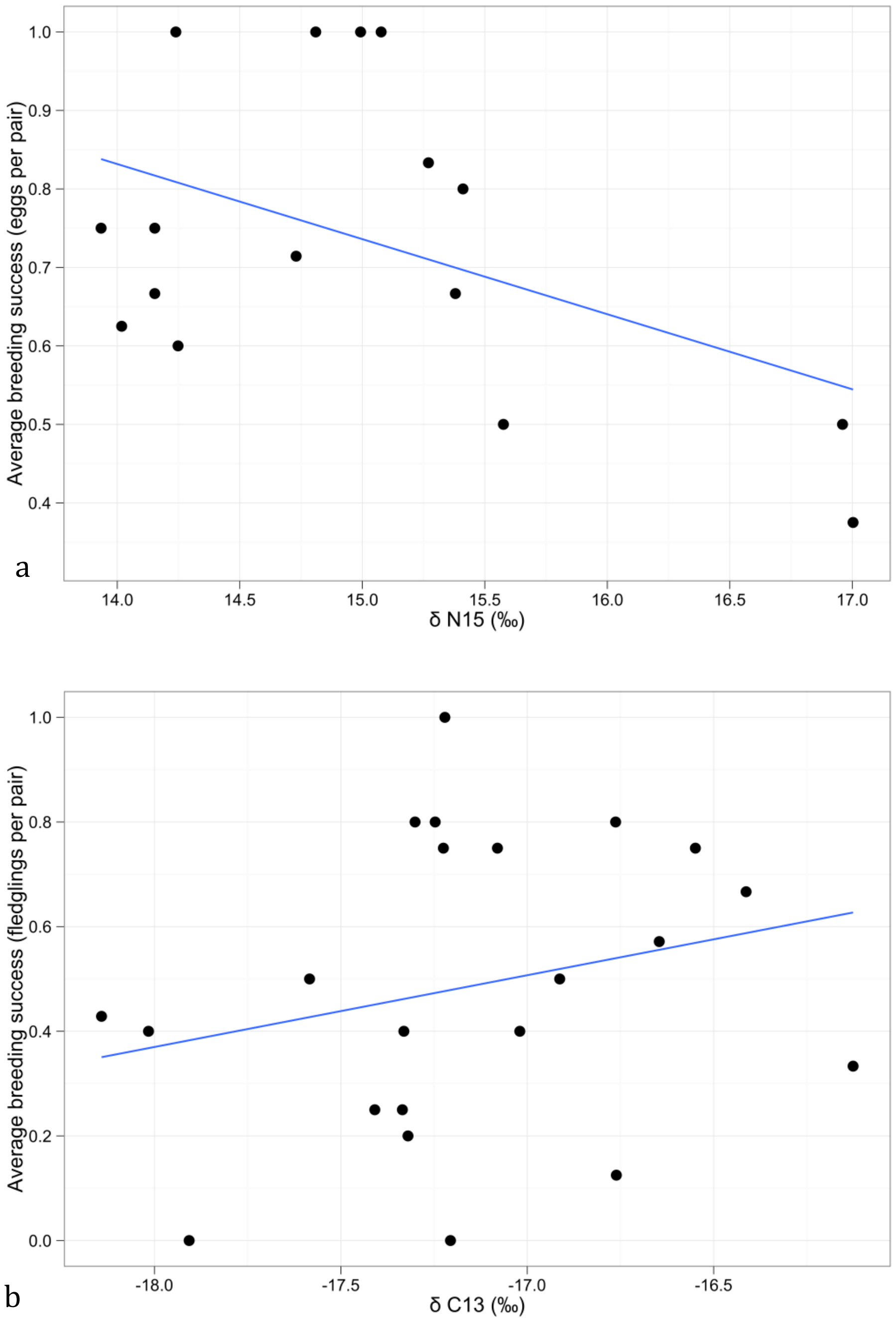

Figure 4. Effects of winter diet as measured by $\delta^{15}N$ and $\delta^{12}C$ in (a) the egg stage, as measured from females; and (b) the fledgling stage, as measured from males.

GLMs revealed that a pair's average breeding success at both egg and fledgling stages was related to their winter strategy (Tables 2c, 3c). The least successful strategies were those involving the male wintering away from the North Sea (Figure 5). At the egg stage, the probability of successfully producing an egg is increased if the female winters outside the North Sea and the male winters within the North Sea (binomial GLM, z=2.888, se=1.169, p=0.003). At the fledgling stage, having both members of the pair within the North Sea significantly improved the chances of successfully reaching the fledgling stage of breeding (binomial GLM, z=-2.431, se=0.892, p=0.015).

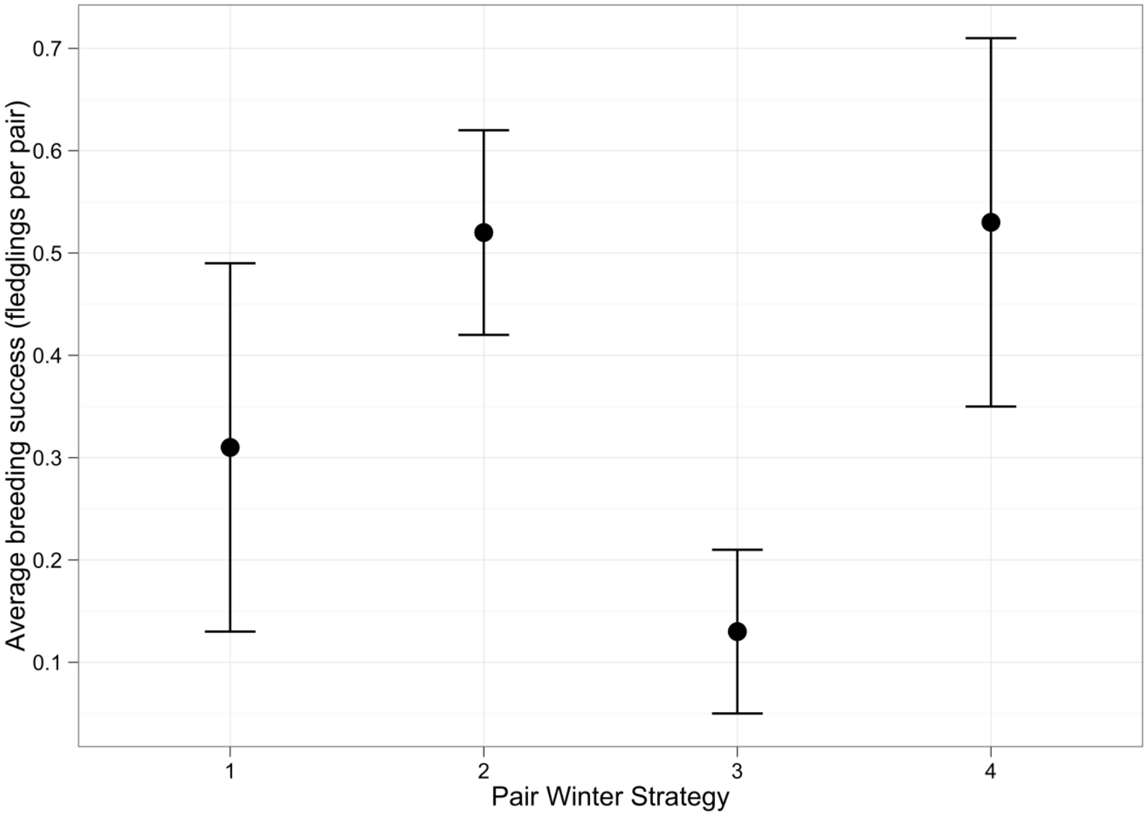

Figure 5. Probability of a pair successfully producing a fledgling from their breeding attempt against differing pair winter strategies where; 1 = female winters in NS, male winters outwith NS; 2 = female winters outwith NS, males winter in NS; 3 = pair members winter outwith NS; 4 = both pair members winter in NS. Standard errors of the average values are also shown.

DISCUSSION

This study demonstrated that winter strategies can affect both an individual's and a pair's average breeding success. The winter distributions of tracked pairs revealed that pairs were more successful when males remained closer to the colony area over winter and females travelled outwith the North Sea. Both female and male winter diet, measured by stable isotope analysis, influenced breeding success with female isotopic signatures potentially relating to improved diet for egg production and male isotopic signatures reflecting a benefit in having a more nearshore signature. The decline in the number of breeding fulmars in the UK has been reflected at the local scale in this study (Figure 1), confirming previous results from Lewis *et al.* 2009. Breeding success has also shown an overall decline during the study (1958-2012), although breeding success was highly variable between years (Figure 2).

Effects of winter foraging strategy on breeding success

Previously, winter NAO was seen to have an effect on inter-annual differences in breeding success (Lewis *et al.* 2009). Here, average breeding success was shown to be influenced by differences in winter foraging strategy. It is possible individuals from the same colony will experience different environmental conditions depending on their wintering location. Winter NAO has been shown to affect plankton abundance (Planque & Taylor 1998), which will in turn affect prey abundance at higher trophic levels (Arnott & Ruxton 2002). Winter NAO is also known to influence weather patterns and has demonstrated links with wind speeds (Scaife *et al.* 2005). Wind speed affects fulmar flight patterns and energetic costs (Furness & Bryant 1996), therefore changes of wind speeds under differing winter NAO regimes may differentially affect fulmars in different wintering areas.

The least successful females to produce an egg were those where the female remained within the North Sea (Figure 3(a)). Countering this female pattern, the most successful males to produce eggs were those males which foraged in the North Sea (Figure 3 (b)). In a pair winter strategy comparison, the worst strategy for successfully reproducing was when both male and female wintered outwith the North Sea (Figure 5). Reasons for this may relate to differences in diet between the areas and differences in roles of each sex, which single-sex models helped elucidate.

Fulmar pairs are seen at colonies over the winter period (Fisher 1952; Macdonald 1980; Chapter 2), suggesting an importance in pairs meeting during the non-breeding period. Pairs where the male winters outwith the North Sea may decrease the likelihood of males and females arriving at the nest site over the winter together. Arrival synchrony in sexes which do not winter together has been shown to be important in migratory shorebirds (Gunnarsson *et al.* 2004). Potentially pair bonds are reiterated, and are required, over the non-breeding period, as has been noted in other seabird species (Kylin 2011). It could also be indicative of good coordination between the pair during the breeding season itself, known to be important for breeding success (Choudhury 1995). In a rare study with tracked pairs, shearwater activity data revealed males and females highly synchronous in their visits to the colony, with the pair with the lowest synchrony also being the pair with the poorest breeding performance, suggesting a link between the two (Guilford *et al.* 2012). Furthermore, synchrony (the synchronous timing of individuals being at the colony at the same time) with other individuals at the colony over the non-breeding period may lead to subsequent pair bonds. Two non-paired shearwaters that were synchronous during the winter became partnered the following breeding season when one of their partners did not return (Guilford *et al*. 2012).

Winter diet was revealed as one possible cause for differential wintering areas having an effect on successful egg production (Table 3). Individual females with lower $\delta^{15}N$ values, i.e. those values indicating feeding at a lower trophic level (Hobson 1999), had increased probability of successfully laying an egg (Figure 4). Lower $\delta^{15}N$ values reflecting a superior diet has been seen in Cassin's auklets *Ptychoramphus aleuticus*, which demonstrated that females feeding on the lower, copepod trophic level bred earlier and had larger eggs than females feeding on a higher trophic level rockfish *Sebastes spp* (Sorensen *et al.* 2009). It is known from a previous study on winter location and diet at this current study's colony that $\delta^{15}N$ values are significantly linked to winter area (Chapter 4), with higher $\delta^{15}N$ values in birds feeding in the North Sea compared to the West Atlantic region. Thus, those females with higher $\delta^{15}N$ values, and consequent lower probability of producing an egg, were from birds feeding in the North Sea regions. Females which forage over the non-breeding period may be seeking nutrients required for egg production later on in the non-breeding season and those with lower $\delta^{15}N$ values may obtain better body condition, as has been proposed for the pre-laying exodus foraging strategy in females (Mallory *et al.* 2008). As females are more variable in their winter foraging area strategy (Chapter 2), it is possible females also experience differing levels of pollutants within their broad winter areas, as has been noted in skuas (Leat *et al.* 2013), which may in turn affect body condition (Ryan 1987; Debacker *et al.* 2001). For females, specific dietary requirements may be the driver in differential foraging area and the West Atlantic area in which many females visit (Chapter 2) potentially offers an advantage in food supply over a female remaining in the North Sea. In conjunction with this, females remaining in the North Sea may be subject to increased intra-and inter-specific competition. For males, it may be beneficial to remain within the North Sea area closer to the colony area to defend the nest site territory over the non-breeding period. Nest site defense is important for many species (Montgomerie & Weatherhead 1988; Carrillo & Gonzalez-Davila 2013) and is traditionally a role males achieve (Fisher 1952). Differential sex roles have also been proposed in a study of sooty shearwaters *Puffinus griseus* where sexes spatially segregated during the pre-breeding period (Hedd *et al.* 2014). Further possibilities in explaining reasons for successful egg production may relate to differential flight costs in traveling to different foraging areas or could also relate to some direct effect of weather in these different areas, both of which are nkown to affect procelliiforms (Shaffer *et al*. 2001; Weimerskirch *et al.* 2012).

For males, $\delta^{13}C$ was important in explaining variation in successful egg production (Table 3). Lower $\delta^{13}C$ values, reflecting a more inshore signature (Hobson 1999), had a higher probability of producing an egg. More inshore $\delta^{13}C$ signatures were also related to the age group of males, with older males having more inshore signatures. Though age group itself was not significant in its model parameter estimation, age group did contribute to explaining some of the variation in breeding success (Table 2). Many studies have shown increased breeding success with increased age up to a point which senescence may cause a decrease in breeding success (Daunt *et al.* 2007; Reed *et al.* 2008). These studies have predominantly taken place in the breeding period and have demonstrated increased foraging efficiency and delivery rates in older, more experienced individuals (Daunt *et al.* 2007). It has been shown that younger individuals may be competitively excluded from foraging grounds (Greig, Coulson & Monaghan

1983; Bertellotti & Yorio 2000). However, it could also reflect the study itself. There are fewer older birds in this study compared to the younger age group class, and the older birds remaining may be of intrinsically higher quality. Any lower quality, older males may have died off during the winter. To increase the sample of older individuals it may be possible to sample feathers from known older individuals and classify their wintering area using stable isotope analysis, the technique of which has been utilized in this colony (Chapter 3).

Further to winter location effects on breeding success, clearly factors during the breeding season will play a large role in reproductive output. Nest site differences in this study demonstrated that nests under rocks, i.e. with better protection from both weather and known predators on the island, were the most successful in successfully producing a fledgling. It is possible though that the nest sites themselves are linked to an intrinsically fitter parent. The more desirable nest sites may require greater defence and could be limited dependent on the area, as seen in an island population of kestrels *Falco tinnunculus* (Carrillo & Gonsález-Davila 2013). Further to nest site difference, differences in summer foraging will play a role in breeding success variability too (Suryan, Irons & Benson 2000). It should also be noted that winter foraging location of an individual may also be an indication of summer foraging location. It has been previously demonstrated that a northern fulmar tracked over winter travelled to a similar area during egg incubation (Edwards *et al.* 2013). Ongoing fine-scale tracking work will be able to elucidate the differences in summer foraging areas and how this may affect reproductive output. Whilst factors during the breeding season will undoubtedly influence a pair's reproductive success, as will year to year variations in climate, this study has demonstrated the importance of including wintering foraging strategy as a component of explaining an organism's reproductive fitness.

Conclusions and future analyses

Seasonal interactions may play a key role in understanding some of the dramatic population changes that are currently taking place for many species (Croxall *et al.* 2012). This study has demonstrated that winter area can affect the average breeding success in an iteroparous, pelagic seabird, the northern fulmar, mediated through differences in diet and potentially differences in climate experienced in these areas. To further explore the possibility of winter strategy affecting reproductive success, the dataset should be combined with the breeding season dataset to assess the relative importance of winter foraging in conjunction with breeding season factors. This could be achieved through further analysis of current tracking data and by utilising feather sampling techniques to assign more individuals to broad-scale foraging areas (as verified in Chapter 3). One huge asset in this specific study is the study colony's long-term dataset, as it will be possible to specifically target birds of interest from their known breeding histories.

Further work on this current fulmar dataset utilizing both activity data and time-lapse cameras could be used to give an indication of when the pairs are together at the colony over the non-breeding period. Studies on non-breeding pair synchrony and its potential effects on reproductive output are still in their infancy in ecological studies, but may play a greater role than previously imagined.

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CHAPTER 7

GENERAL DISCUSSION

Photo: L.Quinn, “True Love”

CHAPTER 7: GENERAL DISCUSSION

Marine ecosystem management requires an understanding of how natural fluctuations in prey populations as well as human-induced changes to prey distribution affect marine predators. To better our understanding of a pelagic top predator's space use, individual-based studies, such as this, can prove invaluable. With an increased understanding of predator distributions, we can then make informed predictions on their requirements from this dynamic marine environment. Knowledge of at-sea distribution has been identified as one of the research priorities for seabird conservation and management (Lewison *et al.* 2012). In many species, mortality risk increases over winter (Harris & Wanless 1996) and winter habitat quality can strongly influence subsequent breeding seasons (Harrison *et al.* 2011). As such, understanding foraging movements outside the breeding season is crucial to understanding a species' population dynamics (Webster *et al.* 2002).

In this thesis, intra- and inter-colony differences in non-breeding strategies were considered across five colonies spanning the fulmar's North-east Atlantic range.

Implications of this study

Previous to this study knowledge of fulmar wintering areas was limited to a few individual fulmars from different colonies, primarily from the Pacific (Hatch, Gill & Mulcahy 2010) and a few indiviudals from a Canadian colony (Mallory *et al.* 2008). At-sea distributions and observations of colony attendance had been described (Macdonald 1980; Camphuysen & Garthe 1997), but no information on an individual's habitat use can be attained from this data. Ringing data had indicated that fulmars from the North Sea may have ventured across the Atlantic (Wernham *et al.* 2002), but until now this had not been confirmed. Previous satellite tracking of Pacific northern fulmars had demonstrated colony differences in wintering area (Hatch, Gill & Mulcahy 2010), but due to the small sample size within-colony variation could not be investigated. This current study has demonstrated that fulmars from a single colony forage widely across the Atlantic with individual differences in wintering foraging strategies (Chapter 2). These wide-ranging and variable strategies over the non-breeding period mean that fulmars from the same colony will be exposed to different prey populations, varying levels of pollutants and differences in local climatic conditions, all of which may have downstream population-level consequences.

Different foraging preferences within the same study population have previously been shown to have potential conservation consequences for a number of Procellariiforme species. This is particularly so where sex differences in risk of being by-caught in long-line fisheries exist (Weimerskirch & Jouventin 1987; Murray *et al.* 1993; Ryan & Boix-Hinzen 1999). With the majority of female fulmars foraging further from the colony than males, and favouring foraging in the West Atlantic, changes in food supply or by-catch risk in this area is likely to have differential consequences on males and females from Scottish colonies. Furthermore, the observed reproductive benefit to females foraging in the West Atlantic (Chapter 6), presumably mediated through a better food supply or lower competition in these areas, indicates likely population level effects if this area of the West Atlantic became less profitable in the future. The discovery that female and some male fulmars, are utilising this area in the West Atlantic also adds to the body of evidence which suggests this area is a key area for foraging in many marine species, including other seabirds (Gaston *et al.* 2011, Magnusdottir *et al.* 2012), sharks (Kohler *et al.* 2002), turtles (Watson *et al.* 2005) and cetaceans (Baumgartner & Mate 2005). In some respects, if a species contains individuals with differing foraging strategies, it may buffer the population as a whole against large-scale population changes. However, within different populations there may be contrasting changes in abundance depending on the relative use of different wintering areas. This study has demonstrated that this will vary depending on colony location (Chapter 5).

Whether individuals are consistent in their habitat or dietary choices also has implications for their ability to buffer themselves against a changing environment. This study is the first to show that individual fulmars favour specific foraging areas with over 85% of fulmars returning to the same wintering area (Chapter 2). Also, for those with concurrent dietary information a strong correlation between isotopic values in different years was found (Chapter 4). Winter site fidelity has been identified across many taxa including; phocids (Bradshaw *et al.* 2004), sharks (Jorgensen *et al*. 2010), antelopes (Kolar *et al.* 2011), bats (Kurta & Murray 2002) and waterfowl (Robertson &

Cooke 1999). Four individual fulmars (out of 33) expanded their original wintering area in subsequent winters, suggesting that some fulmars have a degree of plasticity (Chapter 2). It is known that fulmars are opportunists in their feeding and will scavenge on surface waters (Phillips *et al*. 1999), suggesting these individuals took advantage of a different food resource.

Key to the successful use of feather sampling in this study to assess the aforementioned dietary information was the confirmation of the most likely period when body feathers moulted and the subsequent validation of their use in assigning non-tracked individuals to broad winter foraging areas (Chapter 3). This process was crucial, as the period of moult is often uncertain and validation of geographic assignment is seldom achieved in avian studies, particularly in the use of body feathers. The use of body feathers, specifically those plucked from the belly region in this study, proved a successful non-lethal sampling technique. The concurrent information on breeding area origin was central to the comparison between colonies (Chapter 5). Studies which utilize samples from birds lethally obtained at sea (e.g. Fisk *et al.* 2001; Savinov, Gabrielsen & Savinova 2003; Braune *et al.* 2005) must be questioned, not only from an ethical point of view but also from a data perspective. This study has demonstrated that fulmars from differing colonies mix at sea, particularly during the winter months, thus any information on regional differences in pollutants or other chemical analyses from birds sampled at sea will be confounded by potential inherent differences in breeding colonies. This was seen both in the Icelandic birds in this study which had a distinctive elemental concentration composition, and also in the birds breeding on St Kilda, which had distinctive lead isotope signatures (Chapter 5). Thus, it has been demonstrated that carefully thought-out sampling at the breeding season, coupled with the use of opportunistically obtained by-caught or beached birds, is an informative methodology to employ.

A particularly unique aspect of this current study was the inclusion of pair-based tracking data (Chapter 6). Even in terrestrial systems it is rare to know where each member of the pair has been foraging and only a few tracking examples exist in the literature (Dufty 1982; Guilford *et al.* 2012), with neither of these examples including concurrent information on the pair's average reproductive success. The finding that pair wintering strategy was related to breeding success is one of this study's key results (Chapter 6), though will require further work to elucidate reasons for this. The non-breeding period has been shown to be a crucial time in many species as a time to reiterate pair bonds (Kylin 2011), establish or hold territory (Salomonson & Balda 1977) and to gain the necessary body condition for the energetically demanding breeding season (Chastel, Weimerskirch & Jouventin 1995).

Potential difficulties arising from this work

An integral part of the research process is to recognize that there may be inherent biases in the data obtained or uncertainties in the data itself. It is therefore important to consider issues which arise from this current study and to assess how these could be addressed.

Telemetry data, for which recapture of the datalogger is required, is known to be biased in its nature as it will often be the stronger individuals which return to the colony the following year (Daunt *et al.* 2006). This bias may be particularly prominent in Chapter 6, where the stronger individuals may also be those which breed more successfully. There may also be a 'catchability' bias with certain individuals having a higher tolerance for stress than others. In this study, we have shown that body feathers can be used to geographically assign individuals to broad-scale areas (Chapter 3), and so it is possible an increased sample size could be achieved in this manner. In addition, a wider sampling regime could include non-breeders and failed breeders.

Whilst every measure possible is taken to minimize the stress of capture and handling, there is no doubt that many individual fulmars will experience stress that they would not otherwise have undergone. Reducing the number of times an individual wild bird is caught should therefore be a goal for all avian ecologists. Feather sampling only requires the bird to be caught once and thus may help alleviate the stress of repeated captures. Improved remotely downloaded dataloggers could undoubtedly further revolutionize the field, if costs and weight-constraints allow.

It is also possible that remotely downloaded tags may alleviate some of the problems of GLS loggers, which have unreliable data during the equinoxes and lose their light data when under high Arctic conditions. In this study, this meant some individuals had fewer autumn or winter days available for use, depending on their foraging area. Nevertheless, in the context of this study, which concentrated on broad-scale area use, the GLS loggers proved an invaluable tool.

Whilst feathers proved valuable in providing an indication of broad dietary differences both between colonies and sexes in this study (Chapters 4 & 5), no direct data on potential prey was obtained. The tracking data demonstrated how wide-ranging these fulmars are and therefore obtaining prey samples from across the Atlantic may prove difficult from a practical perspective. However, if we aimed to distinguish the differences in wintering diet between the sexes we could concentrate on one area, for example the North Sea. Furthermore, prey samples obtained from the Irish and Celtic Seas could be obtained to better understand the striking difference in isotopic values noted between fulmars in Ireland and Scotland (Chapter 4). Stable isotope mixing model approaches, and their variations, are commonly used in dietary studies across terrestrial and marine systems (Ben-David, Flynn & Schell 1997; Phillips, Newsome & Gregg 2005; Wilson *et al.* 2013) and can distinguish between the main prey groupings.

Future directions

One of the most exciting aspects of research are the new questions that arise from each study and there are a number of key areas from this study that could be developed further.

The dietary differences between the Irish and Scottish fulmar populations suggested a differential usage of fishery discards over the non-breeding period (Chapter 4), which poses an interesting question of how changes in this food source may affect seabird populations in these regions differently in the future. To some extent certain seabird populations, including the fulmar, may have been bolstered by anthropomorphic changes in food supply (Furness, Edwards, Oro 2007) and current fluctuations in fulmar population size may be a return to a more ‘natural’ population size. With the European Union (EU) Common Fisheries Policy resulting in further changes in fishery discard practices, this is likely to differentially affect species and individuals within and between colonies depending on their relative use of fisheries as a food source (Bartumeus *et al.* 2010; Bicknell *et al.* 2013). Discards have already decreased in some fisheries due to a decrease in fish stock (ICES 2012a, ICES 2012b) and in fishing mesh sizes (Fernandes *et al*. 2011), and potentially differences are already being seen in seabird populations utilizing this resource. A knock-on effect could be that a decrease in food supply may lead to an increase in competition between both conspecifics and different species utilizing the same prey resource. Changes in prey resources affecting predator populations have already been seen in Great skuas which prey-switched, increasing their predation on other seabirds (Votier *et al.* 2004). This study would benefit from further dietary work on these populations to ascertain the prey type birds in each region consume to confirm or reject the hypothesis that Irish fulmars are more reliant on fishery resources.

Further to a more detailed look at dietary differences between the two tracked colonies, additional work on within colony differences could focus on the question of pair synchrony. This would require further analysis of activity data, a valuable, but often underused, aspect of GLS loggers. Activity patterns over winter on a day by day basis could be considered when both pairs are tracked to within colony waters. Periods when both members of the pair are recorded as being dry for a large proportion of the day could be considered as an indication of individuals being back at land. Further time-lapse camera footage would complement this data by measuring how often pairs are seen together over the non-breeding period at the same nest site.

Whilst reproductive success was considered in this study, one important aspect of an animal's life; survivorship, was not. In order to gain information on enough individuals for a survivorship analysis an increased feather sampling regime of known birds at the Eynhallow colony, followed by stable isotopic discrimination to wintering groups, as carried out in Chapter 3, could provide the necessary sample size. This would be particularly useful in investigating the hypothesis that different wintering areas may help explain the link between a large scale-climatic factor, the winter North Atlantic Oscillation, and survivorship which is known to exist in fulmars (Grosbois & Thompson 2005).

Ultimately, the major goal of future research should be to integrate data from both breeding and non-breeding seasons. Predictions can then be made on how population fluctuations vary with climate and how food supply changes across an animal's yearly cycle. Fine-scale GPS tracking work is currently being carried out on this study population, and has already identified linkage between summer and winter foraging areas in one individual tracked from Scotland (Edwards *et al.* 2013). Finer-scale work makes it possible to answer the questions of why an individual may be choosing a certain area, and modelling used to explore associations with environmental covariates and external food sources such as fishing vessels. Combining the two data sets will substantially add to the knowledge on how a wide-spread, pelagic feeding top predator utilizes different oceanic regimes.

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APPENDICES

APPENDIX 1

Time lapse image examples from (a) January 10th 2011, with counts of 8 occupied nests and (b) March 28th 2011, with counts of 20 occupied nests.

a

b

APPENDIX 2

Map of each area of division for assignment to winter groups: West Atlantic, North Sea and Barents Sea/northern Norwegian Sea for Chapter 2. For Chapter 4, these same divisions were used in classifying wintering area with an additional 'Irish and Celtic Sea' box added. The North Sea section of the sea then excluded the area encompassed by Irish/Celtic Seas.

This map also includes the bathymetric contour lines which were used in Chapter 4's comparison of usage of different bathymetric zones between nearshore (up to the 200m line, light grey on map), shelf (between 200-1000m, dark grey line on map) and oceanic waters (>1000m, beyond the dark grey line on map).

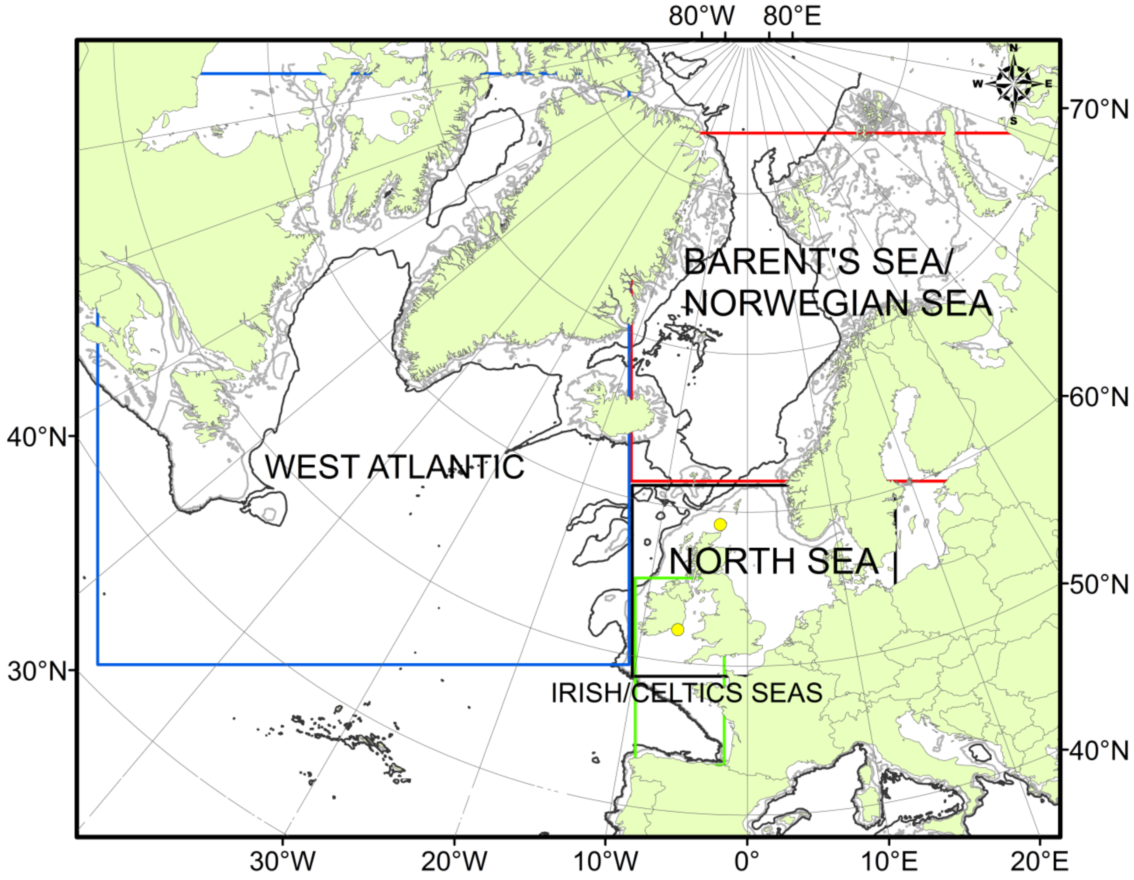

Figure 1. Map of winter area divisions, with West Atlantic, North Sea, Irish and Celtic Seas, and Barents Sea/northern Norwegian Sea shown. Colony locations of Little Saltee and Eynhallow are also shown on the map (yellow circles) as are baythymetric contour lines (200m, light grey and 1000m, dark grey).

APPENDIX 3

Table 1 represents the number of birds sampled in each month for use in Chapter 3's moult analysis.

Table 1. Numbers of birds sampled per month for moult data in each feather type.

Month	**Primary (no. of birds)**	**Tail (no. of birds)**	**Body (no. of birds)**
January	103	103	102
February	78	78	77
March	45	45	45
April	107	106	104
May	104	104	130
June	17	17	17
July	100	100	100
August	11	11	11
September	10	10	10
October	61	61	61
November	30	30	30
December	38	38	38
Total	704	703	725

APPENDIX 4

Map of classification groups based on discriminant analyses used in Chapters 3 and 5. Group 1 is classified by shallower, water areas (lighter grey colouration), which in Eynhallow tracked birds represented usage of the North Sea region; Group 2 is classified by deeper, oceanic waters (darker grey colouration), which in Eynhallow tracked birds represented usage of West Atlantic regions; and Group 3, classified as nearshore, shallow waters surrounding the Irish and Celtic Sea waters, which in Little Saltee tracked birds represented usage of these regions (encompassed by green line).

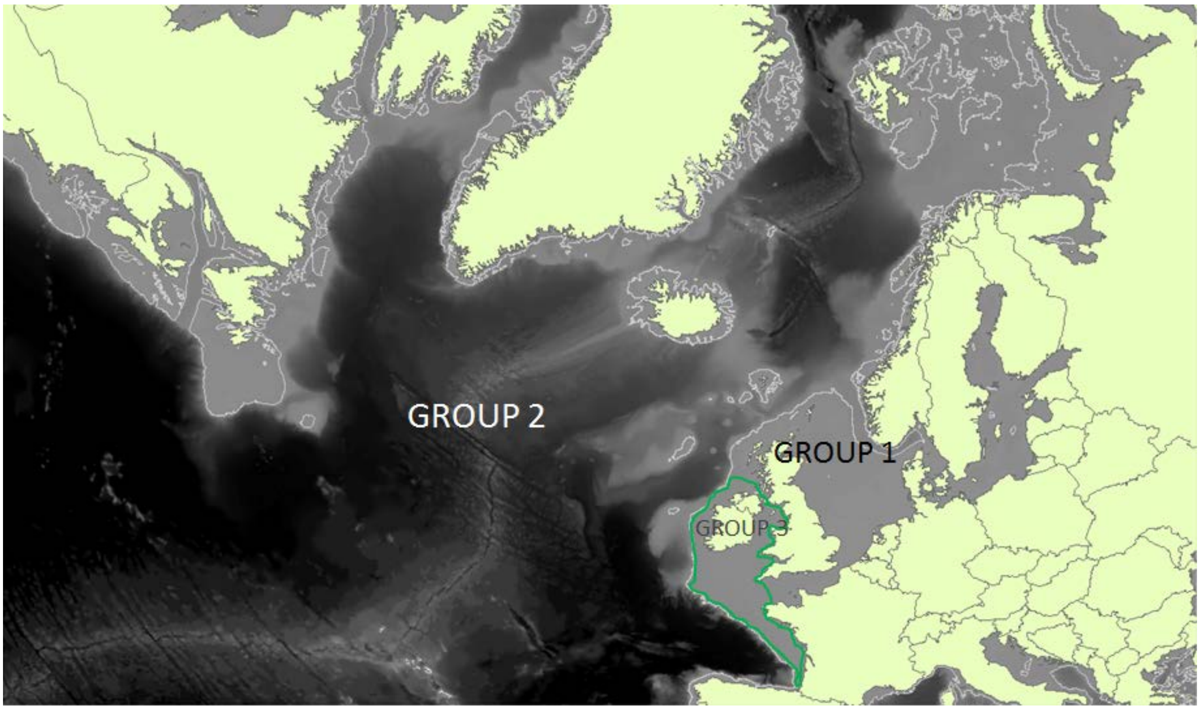

Figure 2. Map of classification groups based on discriminant analysis carried out using stable isotopes. Water depths are also shown on the map, with darker colourations representing deeper waters. The 200m shelf line is shown as pale grey. Group 1 represents shallower shelf waters; Group 2, deeper oceanic waters in the West Atlantic; and Group 3, Irish and Celtic Seas in shallow waters.

APPENDIX 5

Table 2 shows information on: winter areas of each pair member, minimum number of years of pair bond, as used for part of the analysis for Chapter 6. The number of years in which the pairs skipped a breeding attempt since 2005 is also shown.

Table 2. Pair wintering locations, split into North Sea, West (representing a westerly trip from the colony into the West Atlantic, reaching as far as the Labrador Sea and Davies Straight); and East (representing an easterly trip from the colony into the north Norwegian Sea and into the high Arctic in the Barents Sea). These classifications defined the pair strategy. Information on minimum pair bond years is also given, and the number of years breeding skipped since 2005.

Pair number	Male No.	Male winter	Female No.	Female winter	No. years skipped breeding since 2005.	Minimum total years of pair bond
1	865	West	1838	West	2	10
2	1149	West	1867	North Sea	0	2
3	1153	North Sea	1614	West	0	8
4	1355	North Sea	1876	East	1	4
5	1489	West	1015	North Sea	4	8
6	1490	West	1868	West	0	5
7	1496	North Sea	1139	North Sea	0	5
8	1525	North Sea	1597	North Sea	0	3
9	1557	North Sea	1588	West	0	4
10	1631	North Sea	1680	West	0	3
11	1641	North Sea	1883	West	0	4
12	1672	North Sea	1859	North Sea	1	4
13	1706	North Sea	1707	West	0	4
14	1735	North Sea	1495	West	0	4
15	1823	West	1867	North Sea	1	4
16	1852	North Sea	1858	East	0	4
17	1852	North Sea	1877	West	0	3
18	1866	North Sea	1595	North Sea	1	3
19	1869	West	1827	West	0	4
20	1873	East	1562	East	0	5
21	1875	North Sea	1854	East	0	4
22	1889	North Sea	1862	West	0	5