The breeding season foraging trip characteristics, foraging distribution and habitat preference of northern fulmars, *Fulmarus glacialis*

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A thesis presented for the degree of
Doctor of Philosophy in Zoology
School of Biological Sciences
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March 2015

Thank you to everyone, human and avian, who assisted with this project

Contents

Author's declaration

I declare that this thesis and the research presented within has been composed and undertaken by myself. No part of this work has been accepted in any previous application for a degree, and all sources of information have been duly acknowledged.

Prof Paul Thompson carried out GPS deployments on Eynhallow during July 2009 – 2012, with the help of numerous field assistants. Subsequent analyses were my own.

Many of the GLS data collected at Eynhallow were from devices started, deployed, recovered and downloaded by Dr Lucy Quinn and Paul Thompson. Subsequent analyses were my own.

Chapter 4 was published in a peer-reviewed journal, and therefore includes edits made by co-authors. In Chapter 4, Dr Ewan Wakefield carried out first-passage time (FPT) analysis on the GPS tracking data from one male fulmar. Other FPT analyses (Chapter 5) were conducted solely by myself.

State-space modelling (Chapter 3) was performed by myself using a published routine by Dr Arliss Winship *et al*. Habitat preference modelling (Chapter 5) was undertaken wholly by myself, whilst incorporating advice from Dr Enrico Pirotta.

Ewan W. J. Edwards, March 2015

Summary

The role of seabirds as indicators of marine conditions is widely acknowledged. As top predators they are vulnerable to environmental change. The study of spatial ecology has been identified as critical to the conservation of seabirds. The studies described within this thesis have for the first time explored in detail the spatial distribution of breeding fulmars. A combination of geolocation (GLS) and GPS tracking during incubation and chick rearing found that fulmars ranged further and for longer during incubation, with little difference between the sexes (Chapter 2). GLS tracking data from this period suggested that some birds were foraging at the Mid Atlantic Ridge, far surpassing the assumed maximum foraging range of this species whilst breeding. This was confirmed from the GPS track of one bird. Search behavior during the trip suggests that this bird exploited prey resources associated with fronts at the Charlie Gibbs Fracture Zone (Chapter 4). Whilst foraging far from the breeding site may allow birds to avoid competition and exploit predictable prey patches, this wide ranging behaviour may expose birds to threats such as fisheries bycatch. The majority of female fulmars tracked during the pre laying exodus foraged within the Norwegian Sea (Chapter 3), where it is estimated that 20,000 fulmars die annually on longlines. A double-tagging study, the first in the North Atlantic region and the first on a petrel species, used a state-space model to estimate the error in GLS data from fulmars and reconstructed the most probably route travelled. These data indicate that during this early period of the breeding season when distribution was virtually unknown, fulmars from a Scottish colony were foraging widely within three broad biogeographical regions. Meanwhile, fine-scale GPS tracking data was collected at three colonies during the chick rearing period. When combined with environmental and fisheries data within a model this facilitated investigation into the habitat preference of fulmars, finding associations between fulmar presence and fisheries activity, as well as oceanography (Chapter 5). This thesis describes how the use of telemetry has for the first time linked breeding season foraging characteristics with spatial distribution and habitat. Tracking has revolutionized our knowledge of fulmar distribution, behavior and habitat preference during the breeding season.

Acknowledgments

I remember being asked in my interview, “What happens if GPS tracking of fulmars fails?” With hindsight it has worked as well as we could have hoped, and I am privileged to have had the opportunity to work with these fascinating birds. I hope that the information I have garnered can assist and inform their future conservation. Many people have assisted me during my PhD to whom I give my utmost thanks.

Firstly to the crew at the Lighthouse Field Station, who always left me wondering where the horror stories that accompany the lives of many PhD students come from? Thanks to Kate Brookes, Sarah Chapman, Barbara Cheney, Line Cordes, Isla Graham, Kelly More, Rachael Plunkett, and numerous BSc/MSc students and volunteers for a constant stream of support, encouragement, amusement and tea and cakes, at the Lighthouse and on fieldwork. You have all contributed to make the entire experience a pleasant one, not least during the latter stages when your proof reading of chapter drafts has been invaluable. Special thanks to Tim Barton, for all your technical support, both IT and fieldwork related. Your time spent rebuilding GPS loggers was critical to the success of the tracking work. Thanks also to Mary-Anne Lea and Helen Bailey, who provided me with invaluable discussion and advice during short visits to Cromarty. Thanks to Mariel ten Doeschate for statistical assistance, wisdom, advice and friendship. Thanks to Debbie Russell, Esther Jones and the group at SMRU for meetings and guidance during my visits to St Andrews.

Many other seabird scientists have become friends throughout the process, and so to everyone with whom I have exchanged ideas – thank you. However, to several individuals I owe a special mention: Ewan Wakefield has inspired me from a very early stage, and has assisted and collaborated throughout. I greatly enjoyed spending time on Bird Island with Richard Phillips, both learning about GPS tracking in the field and am grateful for his advice during my application – his field skills, knowledge and passion were infectious. I also thank James Grecian and Helen Wade, with whom I have had very useful conversations and whom have become great friends.

Fieldwork has been greatly facilitated by both the logistical support provided by the National Trust for Scotland and QinetiQ, allowing me two successful and unforgettable trips to St Kilda. Meanwhile I would never have managed the high success in tracking of fulmars without the capable assistance of Hannah Wood and Gina Prior on St Kilda, and Tessa van Heumen and Sian Tarrant on Eynhallow.

Thanks to Lucy Quinn for unerring support, positivity, humour and kindness. It has been a pleasure to work with you. Your enthusiasm for the fulmars was inspirational and I valued your advice at all stages. Enrico Pirotta has frequently helped me get my head around quantitative analyses and I am infinitely grateful. Rebecca Hewitt has been a kind, thoughtful, organised and appreciated presence at work and at home for the last two years. Whether beautifying a conference presentation, or cooking for me on days when I worked late, Becky, thank you for helping me.

To my supervisors: Coby Needle, your feedback and help in the early days regarding fishing vessel data was extremely useful. To Jason Matthiopoulos, I could not have achieved what I have without your assistance regarding quantitative analysis – thank you for making time and space for me in St Andrews and Glasgow. I would love for you to visit Eynhallow or St Kilda sometime, to see the source of these data! To Paul Thompson, your supervisory support has been just right; your passion for the project, the birds and the shared excitement generated by recovering a GPS from a fulmar that has been away for 14 days has enthused and driven me to the finish; whilst our shared hobbies and enthusiasm for the outdoors have helped me (re)discover some of the greatest parts of Scotland.

I give special personal thanks to my family, for, helping, feeding, loving and caring for me throughout my education. And to Louise, your love and support throughout has given me perspective, enthusiasm and motivation. Your help on St Kilda as a field assistant was priceless. Thank you so much for everything you have done for me, not least working weekends with me during the final weeks and your proof reading of drafts, which has helped beyond my wildest expectations. I look forward to offering the same support to you over the next 18 months!

Chapter 1: General introduction

In their role as abundant, wide-ranging, long-lived top predators, seabirds function as excellent indicators of ecosystem status and performance (Furness and Camphuysen, 1997, Parsons et al., 2008). Changes in seabird distribution, ecology, behaviour and population size can indicate large-scale shifts in prey availability or other environmental variables (Heath et al., 2009). These can affect not just where birds go (Cohen et al., 2014), but also their breeding phenology (Wanless et al., 2009), reproductive performance (Votier et al., 2004) and survival (Sandvik et al., 2012). Breeding success and survival are the two primary components driving life history, and are tied together by the necessity of finding adequate nutrition and avoiding predators.

Seabirds, comprising a broad suite of taxa (Nelson, 1980), exhibit extensive variability in physiology, behaviour, ecology and life history, as well as exhibiting differences in geographical range and habitat (Lewison et al., 2012). They forage at sea where resources can be patchy and sometimes unpredictable (Weimerskirch, 2007). As apical predators they can be particularly sensitive to changes in the environment. They are often specialised in terms of behaviour and/or physiology, relying upon a narrow range of prey types. Seabirds reproduce terrestrially whilst relying on the marine environment for food, so are typically constrained in range at certain times of their breeding cycle (Thaxter et al., 2012). This results in their breeding success potentially being attributed to regional foraging conditions (Daunt et al., 2008).

Anthropogenic activity is causing changes to habitats and ecosystems (Halpern et al., 2008) with direct and indirect effects on marine animals. Harvest of seabirds (Gilliland et al., 2009), changes in fishing practice (Furness and Tasker, 2000), pollution such as oil (Ronconi et al., 2015), light (Rodriguez et al., 2012) or ingestion of macro-plastic fragments (Pierce et al., 2004), invasive species (Cuthbert et al., 2013), and changes in prey availability as an indirect consequence of fisheries (Cohen et al., 2014, Bicknell et al., 2013) or changing ocean conditions (Sandvik et al., 2012), have all been implicated in affecting seabird reproduction, recruitment or survival. Although these issues are known to impact seabird populations, direct interactions with the fishing industry are widely recognised to be one of the greatest threats to seabirds (Prince et al., 2012).

For thousands of years, humans have exploited the oceans with both direct and indirect effects on seabirds (Tasker and Becker, 1992), although not all have been deleterious to populations. Intense exploitation of seabirds sustained some human populations for centuries, which has led to depletion of populations, and even extinctions (Bengtson, 1984). Fishermen utilised piscivorous birds to assist them in locating shoals of fish (Camphuysen, 2001). Industrial advances in shipbuilding and methods of propulsion allowed fishermen to travel further and faster than ever before. Over-exploitation of fish stocks has become a concern as commercial fishing vessels target mainly the larger, more valuable fish using increasingly efficient methods (Pauly et al., 1998, Christensen et al., 2003, Barrett et al., 2004, Worm and Branch, 2012). This top-down control of a significant predatory component of marine trophic systems resulted in increased numbers of juveniles and baitfish (e.g. lesser sandeel *Ammodytes marinus*; Furness, 2003). Until recently these have not been targeted by humans but discarded when caught along with offal. Paradoxically, overfishing may have benefitted some species by providing a patchy yet predictable food source for seabirds foraging around fishing vessels (Fisher, 1952, Tasker et al., 2000).

Whilst fisheries can provide a predictable food source, fisheries interactions often put seabirds at risk. The *Procellariformes* (albatrosses, petrels and shearwaters) are particularly vulnerable. Their wide-ranging behaviour, which brings them into association with fisheries often far from their breeding sites (Gremillet et al., 2015, Petersen et al., 2009), and their scavenging foraging habits lead them to target bait. It has been estimated that 160,000 seabirds are killed annually in longline fisheries (Anderson et al., 2011), whilst more are killed in net-based fisheries (Murray et al., 1994, Sullivan et al., 2006, Žydelis et al., 2009, Žydelis et al., 2013). For example, bycatch in the Norwegian demersal longline fishery alone kills around 20,000 northern fulmars annually (Anderson et al., 2011). Birds are also known to be killed targeting bait at Faroese and Icelandic longline vessels (Løkkeborg and Robertson, 2002).

In recent times policymakers have acknowledged the impacts of the fishing industry. Efforts to conserve the marine environment have focused on spatially explicit protection of marine regions (Winiarski et al., 2014, Lascelles et al., 2012, Skov et al., 1995), to protect certain species, populations or assemblages. For this reason spatial ecology has been identified as a critical area of research. Whilst an understanding of biophysical patterns relating an animal to its distribution is useful, to understand the true drivers of this relationship it is vital to understand the specific processes that influence spatial distribution.

A key aspect of the study of spatial ecology is to understand where birds forage. As central place foragers seabirds must forage during chick rearing to provision their semi-atricial offspring. Consequently, seabirds rely on a good supply of food within a constrained range from their nest. The wide-ranging, pelagic nature of the *Procellaridae*, even during the breeding season (Pollet et al., 2014b, Weimerskirch et al., 1993), poses interesting questions regarding the environmental regimes in which food is found. These seabirds forage for patchy yet often predictable resources, targeting known regions of high productivity (e.g. shelf edges and oceanic fronts) on 'commuting-like' foraging trips (Bost et al., 2009, Pinaud and Weimerskirch, 2007).

Studying seabirds at sea

Studies at seabird colonies can reveal critical information regarding energetics (Weimerskirch, 1990), physiology (Crossin et al., 2012), demographic parameters (Jaeger et al., 2014), attendance patterns (Mallory et al., 2008a) and diet (Phillips et al., 1999, Owen et al., 2013). However, until recently little has been known about the spatial distribution of seabirds at sea, specifically the linkage between individuals from known colonies and foraging sites. Counting seabirds at sea from ships has long been established (Jespersen, 1924, Wynne-Edwards, 1935) and standardised techniques have resulted in this method being commonly used in abundance surveys (Tasker et al., 1984, Garthe, 1997, Skov and Durinck, 2001). Whilst useful at assessing abundance, these methods can seldom determine the colony of origin or breeding status of individuals.

Recent advances in tracking technology have resulted in the development of a range of lightweight tracking devices that can now be deployed on relatively small (< 50 g; Pollet et al., 2014a, Pollet et al., 2014b) seabirds. These devices now allow tracking of seabirds from their nest sites to offshore foraging areas to better understand the factors influencing their distribution at sea (Egevang et al., 2010, Mosbech et al., 2012, Quillfeldt et al., 2012). Depending upon the type of telemetry device used, the cost and degree of precision varies (Phillips et al., 2004, Hebblewhite and Haydon, 2010). Early studies using VHF radio transmitters (Trivelpiece et al., 1986, Wanless et al., 1991), and later ARGOS satellite transmitters (Jouventin and Weimerskirch, 1990) allowed tracking of seabirds in almost real-time. The last decade has seen great advances in technologies used to track birds at greater accuracies and over longer timescales. The use of small Global Positioning System (GPS) data loggers on seabirds has been facilitated by the development of smaller, lighter and cheaper devices, with longer battery life and greater capacity for data storage or transmission capability (Thaxter et al., 2011).

The advantages and disadvantages of GPS telemetry have been extensively discussed (Hebblewhite and Haydon, 2010). The most frequently stated advantage of GPS is that it can provide accurate position data at a high temporal resolution. Additionally, reduction in the cost of archival data loggers has meant that GPS devices can be < 5% of the price of ARGOS satellite-relay devices, hence higher sample sizes of tracked animals are possible on restricted budgets. This allows for large volumes of data to be generated where both at-sea distribution and fine-scale behavioural responses to factors such as environmental variables can be quantified (Guilford et al., 2008, Votier et al., 2010, Wakefield et al., 2011, Granadeiro et al., 2011, Hamer et al., 2009). This was not previously possible, and has opened up a large field of research (Wakefield et al., 2009). However, telemetry methods, including GPS, have their limitations. One major disadvantage is the fact that the tracking devices have to be retrieved to enable the stored information to be downloaded. In the case of seabird tracking, this involves recapturing birds, which can pose problems of disturbance. Other associated problems are that the sample sizes tend to be small and care needs to be taken to correctly analyse the data to make population level inferences.

Light-level geolocator (Global Location Sensing; GLS) loggers can be more appropriate for smaller, wide-ranging birds (Egevang et al., 2010, Hedd et al., 2012). Location data points from GLS devices are temporally sparse (a maximum of two locations per day) and can be inaccurate due to the process of light-based geolocation, with associated errors in the region of 200 km (Phillips et al., 2004). Even though the errors are large, the small size and weight of the devices can result in deployments over longer time periods and during periods when GPS tracking is not possible (Weimerskirch et al., 2014). Recently developed analytical methods can result in improved accuracy of location estimates (Lisovski and Hahn, 2012, Winship et al., 2012) allowing for improved estimation of distribution. The devices also record wet/dry periods which can be used to differentiate time spent on excursions from time at the colony (Mackley et al., 2011).

Spatial analysis

The interface between statistics and biology has seen rapid development in the last decade (Cagnacci et al., 2010). In recent times habitat preference from telemetry data has been described by increasingly complex statistical modelling approaches. These are reviewed by Tremblay et al. (2009) and include generalised linear modelling (GLM) and generalized additive models (GAM). Mixed-effects approaches which account for individual variation such as generalized linear mixed models (GLMM) and generalized additive mixed models (GAMM) (Wakefield et al., 2011), and generalized estimating equations (GEE) which partition autocorrelated blocks of data (Scales et al., 2014) are finding wider application within the analysis of tracking data. More complex techniques and frameworks involving a combination of approaches are currently under development (Aarts et al., 2013) to deal with the caveats of telemetry and environmental data, such as serial autocorrelation of locations (Fieberg et al., 2010). Covariates can be fixed physical values such as distance from colony/coast, water depth or seabed sediment type and oceanographic factors such as the position of oceanic fronts (Bost et al., 2009, Scales et al., 2014, Miller and Christodoulou, 2014) or sea surface temperature (Wakefield et al., 2011). Biological variables such as chlorophyll-A concentration or plankton data can be monitored from space (Rinaldi et al., 2014) or from ships (Melle et al., 2014). Anthropogenic descriptors (e.g. fishing effort, or distance to nearest fishing vessel) (Votier et al., 2010, Pinet et al., 2011, Suryan et al., 2006) can also be included as an explanatory variable to investigate human links to seabird foraging.

Study species: the northern fulmar

The northern fulmar *Fulmarus glacialis* (L.) (hereafter fulmar) is the northern hemisphere representative of the two species in the genus *Fulmarus*. It is a member of the *Procellaridae* family (the petrels), and often categorised along with six other southern hemisphere species as a *fulmarine petrel*. Three subspecies have been recognised: *F. g. glacialis*, which breeds in the high Arctic regions of the North Atlantic; *F. g. rodgersii,* which breeds in the Pacific Arctic (Siberia and Alaska); and *F. g. auduboni,* which breeds in the boreal North Atlantic. Fulmars breed on grassy slopes and cliffs, in low density but sometimes large colonies, with a southernmost limit in the Atlantic of Brittany, France, ca. 50º N (Kerbiriou et al., 2012), and breeding as far north as Spitsbergen, ca. 80º N, and Franz Josef Land, ca. 81º N (Onley and Scofield, 2013). The global population of all three subspecies of northern fulmar is estimated to be 15 – 30 million individuals (Ekstrom, 2015) with 5 – 7 million birds within the Atlantic (including high Arctic) region. The most recent estimate of total UK breeding population, from Joint Nature Conservation Committee (JNCC) Seabird 2000 colony counts, was 538,000 pairs (Mitchell et al., 2004), with the largest populations around the northern and western coasts and islands of Scotland. The population is estimated to have declined by 13 % between 2000 and 2013 (Hayhow, 2014)

Fulmars are abundant around Scotland, but they experience a diverse habitat due to their wide ranging habits (Hamer and Thompson, 1997, Mallory et al., 2008b). This may expose some individuals and populations to specific threats. Fulmars are suitable for attachment of telemetry devices, as they are large, wide-ranging and return to their nest sites regularly during the breeding season. They are a catholic predator and scavenger (Furness and Todd, 1984, Hamer et al., 1997, Phillips et al., 1999, Lorenz and Seneveratne, 2008, Danielsen et al., 2010), and forage wholly at sea. They are not deep diving birds so largely forage at the surface (Garthe and Furness, 2001). Fulmars are also thought to be one of the species that has benefitted the most from fisheries discards (Fisher, 1952, Garthe and Camphuysen, 1996) and have been shown to consume considerable quantities of discarded offal around trawlers (Hudson and Furness, 1988). Therefore, even though they utilise a reliable source of food, they face the risks associated with interacting with fisheries.

Although fulmar remains have been found at prehistoric sites in Orkney (Serjeantson, 1988), the west of Scotland (Fisher and Waterston, 1941) and Norway (Montevecchi and Hufthammer, 1990), written historic and archaeological findings state that until 350 years ago, fulmars bred at only two sites in the north eastern Atlantic (Grimsey and St Kilda; Fisher, 1952). The Faroe Islands and Foula, Shetland, were colonised during the 19th century, and during the last hundred years fulmars have expanded to breed throughout the coastlines of the British Isles and western mainland Europe (Kerbiriou et al., 2012). The expansion in size and spread seen in the population in the North Atlantic has been well-documented since the establishment of breeding colonies outwith the historic sites in Iceland and on St Kilda, Scotland (Fisher, 1952). Fisher (1952) documented the early expansion throughout Europe. National surveys carried out by the British Trust for Ornithology (BTO) and the JNCC have described the spread in more detail in recent times (Cramp et al., 1974, Lloyd et al., 1991, Mitchell et al., 2004), revealing the extent of the population expansion throughout the 1970s-80s. A study using mitochondrial DNA analysis to determine the origin of the population spread found that most colonisers originated from Iceland although there was weak evidence to suggest St Kilda was also a source (Burg et al., 2003). Meanwhile recent examination of museum specimens also suggests multiple source colonies (Burg et al., 2014). Hypotheses to explain the spread have included reduction in hunting pressure by humans (Thompson, 2006); the provision of an energetically cheap and easily available food source in the form of discards from the fishing and whaling industries (Fisher and Waterston, 1941); indirect anthropogenic factors such as an increase in naturally available prey (e.g. sandeels) since the advent of industrial fishing for predatory species like cod *Gadus morhua* (Furness, 2007); or a response to climate-induced natural changes in food availability in the north-eastern Atlantic, where the population and range expansion has been most pronounced (Salomonsen, 1965).

Several studies have investigated the diet of breeding fulmars to assess the importance on certain food types and trophic levels and gauge the impact of prey type on breeding success. Furness and Todd (1984) compared diet at St Kilda and Foula during the breeding season and found that, whilst the dominant component of the diet of the birds from Foula was fisheries discards, the St Kilda fulmars consumed more pelagic crustaceans. This differs from the findings of Hamer and Thompson (1997) who found that St Kilda birds had a preponderance of small fish in their diet, suggesting a potential dietary shift. A study from the northwest Atlantic showed similar generalist foraging in breeding fulmars (Garthe et al., 2004). Efforts to quantify the importance of fisheries discards as a food source for fulmars have suggested that although discards are important in some areas, less than 50% of the North Sea's fulmars could depend on this means of feeding themselves and provisioning their chicks. This is based on knowledge of discard rates in North Sea fisheries and at-sea observations of fulmars around vessels (Camphuysen and Garthe, 1997, Garthe and Camphuysen, 1996). Whilst on a broad scale fisheries discards cannot sustain the whole fulmar population in the north eastern Atlantic, some colonies show large dependence on discards as a food source. Phillips et al. (1999) found that at some colonies, fisheries discards comprise a significant proportion of the diet during chick rearing. However, although discards are locally important to some colonies, it is unclear how fulmar breeding and foraging distribution may be impacted on a broad scale should the practice of discarding be banned.

Whilst fisheries bycatch of North Atlantic fulmars in European waters is unlikely to have wide-ranging consequences at current population levels, a more specific impact is possible if birds from one colony, region, demographic group or sex are consistently being killed in the fishery. Knowledge of where birds from specific colonies forage is needed to predict the impact of regional disturbance, such as the international management of fisheries. However, investigating and predicting the impact of this disturbance can be challenging as other factors may impact fulmars, including pollution (Heubeck et al., 2003, van Franeker et al., 2011), and construction of offshore renewable energy installations such as wind turbines (Masden et al., 2009, Furness et al., 2013).

Fulmars have been designated an important indicator of the health of the marine environment as a European Ecological Quality Objective (EcoQO) species (OSPAR, 1992), due to their ingestion of plastic debris from the sea. Plastic fragments are ingested when mistaken for prey. Fulmars analysed across a large latitudinal gradient in the North Atlantic region have shown variability in plastic loading, and so variation in their spatial distribution could expose different birds or colonies to varying levels of plastic pollution (Kühn and van Franeker, 2012, Trevail et al., 2015). Annual surveys find that across the North Sea 95% of beached fulmars contain plastic, largely from consumer rather than industrial sources (van Franeker et al., 2011).

Study sites

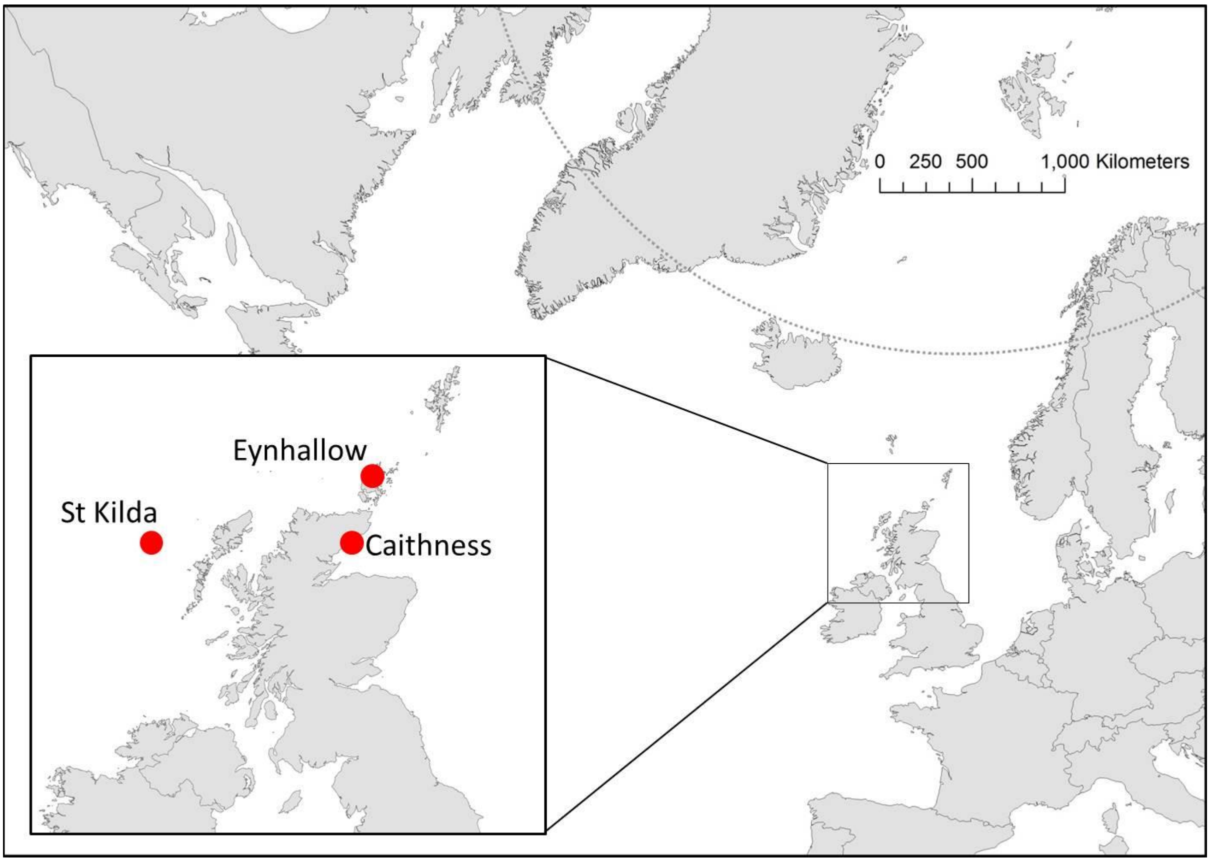

Fig. 1.1 Map illustrating the location of Scotland within the wider NE Atlantic. The zoomed insert shows the location of the three tracking sites around the Scottish coast. The Arctic Circle (66° 23' North) is marked as a grey dashed line.

Information on reproductive rates and survival of fulmars in the North Atlantic is based heavily upon a single individual-based study at a colony on Eynhallow, Orkney (59.14° N, 3.12° W, *Fig. 1.1*; Dunnet, 1991). Annual studies of colour-ringed fulmars at this site have resulted in a unique time series that continues to this day. Marking (ringing) of individuals began in 1950, revealing in due course that fulmars can breed annually (Carrick, 1954). Recoveries of birds ringed at Eynhallow later revealed that individuals of this species range widely across the North Atlantic (Macdonald, 1977). Data collected on Eynhallow have revealed links between climate variability over winter and breeding success as well as individual survival (Grosbois and Thompson, 2005, Lewis et al., 2009, Thompson and Ollason, 2001).

Eynhallow is a natural choice of study site for these investigations of fulmar spatial ecology since much is already known about the individual birds and nest sites at the colony, with three field trips to the island each year. The trips are made in late May, post-laying, to count the number of eggs laid; in mid-July, during chick rearing, to determine hatching success; and in late August, to count and ring fledglings. In addition to the demographic studies, tracking work has previously been carried out on Eynhallow, including the deployment of geolocator devices for an overwinter distribution study (Quinn, 2014).

Lately the Eynhallow fulmar population has shown a decline in size and breeding success, from a peak of ca. 200 nests per year in the mid-1990s, to ca. 100 nests during the last four years. Reasons for this decline remain uncertain, and it is likely that there have been multiple factors acting upon this colony and fulmars in general (Thompson, 2006). However the reduction in numbers of birds observed at Eynhallow has occurred concurrent with a decline in the availability of natural prey (e.g. sandeels) in the northern North Sea (Furness, 2007, Furness and Tasker, 2000) and a reduction in discard availability due to diminishing commercial fishing effort in the region (Fernandes et al., 2011).

This study also tracked fulmars from two additional colonies. Two visits were made to Hirta (57.81° N, 8.59° W, *Fig. 1.1*), within the St Kilda archipelago, 100 km west of the Scottish mainland. St Kilda is renowned as one of only a handful of sites occupied by fulmars during the 19th century, prior to the population expansion. The fulmar population at St Kilda has remained fairly steady during the second half of the 20th century (Cramp et al., 1974, Mitchell et al., 2004), following centuries of exploitation by the islanders, which ceased in 1930 (Fisher, 1966). The St Kilda archipelago was, at last count, home to 14 % of the UK fulmar breeding population, with 68,448 apparently occupied sites counted (Mitchell et al., 2004). In addition, fulmars were also tracked from the coast of Caithness, Scotland, as part of the environmental impact assessment for an offshore windfarm in the Moray Firth (Moray Offshore Renewables Ltd), The nest sites were within the East Caithness Cliffs SPA (around 58.8° N, 3.5° W, *Fig. 1.1*), designated as ‘a seabird assemblage of international importance’ (EC, 2009).

No tracking work had been carried out at this colony previously, although the Caithness coast was surveyed during the three national seabird censuses (Cramp et al., 1974, Lloyd et al., 1991, Mitchell et al., 2004). During Seabird 2000, 20,269 nests were counted on the east Caithness coast (Mitchell et al., 2004).

Aims

This thesis aims to address knowledge gaps in the at-sea spatial ecology of breeding northern fulmars, using a combination of data from tracking and monitoring at the colonies, and explored through statistical modelling.

In **Chapter 2**, GPS and GLS tracking data were used to investigate the spatial distribution and foraging trip characteristics of fulmars through the breeding season, from early incubation until fledging. Sex differences were examined, and differences between trip characteristics for the two tracking methods were compared. Distance from the colony was also compared with respect to breeding status (i.e. whether birds were successful or failed breeders, or skipped breeding).

In **Chapter 3**, a state-space modelling framework was used to estimate errors in latitude and longitude for GLS data, using both GLS and GPS data from birds during incubation trips. The state-space model was then fitted to GLS-only data from the pre-laying exodus to improve the accuracy of location estimates from this technology and reconstruct the most likely path of pre-laying exoduses. This allows investigation of the distribution of fulmars during this early, yet critical, period of the breeding season.

In **Chapter 4**, the fine-scale movements and activity of one particular fulmar was considered in detail as part of a broader scale study of the Mid Atlantic Ridge region (Priede et al., 2013). This individual was tracked using GPS to the Charlie-Gibbs Fracture Zone, during an incubation-period foraging trip. The activity patterns, route, and foraging regions visited during this long excursion from the nest were investigated in relation to remotely sensed environmental data.

In **Chapter 5**, GPS tracking data and first-passage time analysis were used to identify fulmar foraging locations during chick rearing excursions from the colony. A habitat preference model was created to investigate the role of environmental covariates and explain the relationship between fulmars from the three colonies and their environment. Habitat association was quantified to assess which factors dictate where the birds forage. Particular attention was given to the relationship with areas of commercial fishing activity. The model was validated using additional tracking data and predicts the distribution of Orkney, St Kilda and Caithness fulmars.

In the final chapter the findings of my research are discussed, within the context of more general spatial ecology and seabird conservation. The limitations and problems of the work are assessed and related future research suggested.

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Chapter 2: The distribution, range and foraging trip durations of northern fulmars through the breeding season: insights from tracking technology

Abstract

Identifying the distribution and range of seabirds at sea is critical to identifying important marine areas, on which conservation measures can be focused. Whilst monitoring attendance of individuals at the colony can provide detail on foraging trip durations which can be used to estimate range, relatively few studies have directly assessed how spatial distribution of a seabird species changes throughout the breeding season.

Unlike many seabird species in north western Europe, earlier studies indicate that fulmars are not restricted to local waters within the breeding season. The conservation implications of such behaviour reinforce the importance of determining the patterns of distribution during the breeding season. This chapter uses telemetry data to establish the foraging distribution of northern fulmars breeding at a Scottish colony and describes the effect of sex, breeding success, stage of breeding and type of data logger on foraging trip characteristics.

We used GLS and GPS data loggers to track fulmars during the breeding season to assess the characteristics of foraging trips during both the chick rearing and incubation periods. Mixed-effects models suggest that foraging trips were longer in range and duration during incubation than during chick rearing. No significant difference was found in foraging trip characteristics between the sexes during incubation or chick rearing. Type of data logger used did not appear to affect trip characteristics. Some birds foraged in the north western Atlantic Ocean and the Kattegat when actively breeding on Eynhallow, although during chick rearing the range is largely focused on the Scottish continental shelf and northern North Sea. This study shows that during the breeding season, Scottish fulmars forage over a wide area and potentially face threats such as the risk of fishery bycatch.

Introduction

Identifying the distribution and range of seabirds at sea is critical to identifying important marine areas, on which conservation measures can be focused (Thaxter et al., 2012, Lewison et al., 2012). Monitoring attendance of individuals at the colony can provide detail on foraging trip durations which can be used to estimate range (Hamer et al., 1997) but relatively few studies have directly assessed how spatial distribution of a seabird species changes throughout the breeding season.

Fulmars are known to consume discards at fishing vessels from both visual observations (Garthe and Camphuysen, 1996) and diet studies from birds caught at colonies (Phillips et al., 1999). It has been hypothesised that male giant petrels compete more effectively for discards than female birds, due to their larger size (Thiers et al., 2014), although dietary differences from fatty acid analysis of fulmar samples suggested that females consumed more demersal prey than males (Owen et al., 2013). Sex differences in distribution have been identified in other seabirds such as gannets (Stauss et al., 2012) and albatrosses (Wakefield et al., 2009b). This could lead to sex-specific survival rates if, for example, one behavioural strategy leads to increased mortality (Ryan and Boix-Hinzen, 1999, Patrick and Weimerskirch, 2014a). Foraging strategy and thus distribution has also been linked to personality whereby bold birds undertake shorter foraging trips which can have consequences for fitness (Patrick and Weimerskirch, 2014b). Foraging around fishing vessels carries the risk of injury or drowning through collision or bycatch (Anderson et al., 2011, Løkkeborg and Robertson, 2002) thus variation in foraging strategy between individuals could lead to differences in survival.

The fulmar is protected under the EC Wild Birds Directive (EC, 2009) and has been named as a bird of conservation concern in the UK (Eaton et al., 2009). It has been demonstrated that fulmar population dynamics and demographics are affected by climate variability (Thompson and Ollason, 2001, Grosbois and Thompson, 2005), and breeding success has been seen to be highly variable between years (Lewis et al., 2009). Unlike many seabird species in north western Europe, preliminary studies indicate that fulmars are not restricted to local waters within the breeding season

(Edwards et al., 2013). This suggests that a distribution extending outwith EU jurisdiction may have conservation implications and reinforces the importance of establishing the patterns of distribution during the breeding season.

Space-use by animals is a function of habitat accessibility and preference (Matthiopoulos, 2003), meaning that many factors may interact to determine where animals forage. For example, habitat accessibility during the breeding season varies inversely with distance from the breeding site, whilst being influenced by the energetic and temporal costs of travel (Wakefield et al., 2009a). Preference for foraging habitat in a diverse marine environment relates to food availability, which can be influenced by oceanographic determinants such as sea surface temperature or seabed slope (Aarts et al., 2008). It can also be affected by biotic influences such as primary production (Block et al., 2011) or intra- or interspecific competition for resources (Wakefield et al., 2013).

As central place foragers during the breeding season, seabirds have to balance the demands of energy intake for both self- and offspring-provisioning, whilst constrained to return regularly to their nest site. The spatial range of foraging trips is strongly linked to this central place constraint, and is related to the efficiency with which birds can travel to foraging areas. Meteorological conditions (Furness and Bryant, 1996), barriers to movement e.g. land or industrial developments in the sea (Masden et al., 2009); intraspecific competition (Lewis et al., 2001, Wakefield et al., 2013) and foraging success during the trip can influence distance covered and flight speed. A further consequence of this central place constraint is that foraging trip duration varies between stages of the breeding cycle (Weimerskirch et al., 1993, Shaffer et al., 2003). For example, macaroni penguins *Eudyptes chrysolophus* undertake 10 – 26 day foraging trips during incubation, whilst during the chick-rearing period 80% of trips lasted less than 48 hours (Barlow and Croxall, 2002). Another study showed that mean foraging trip duration and maximum distance from the colony in kittiwakes *Rissa tridactyla* was greater during incubation than chick rearing. However in this species, trip durations were rarely longer than one day during both periods (Robertson et al., 2014). In the case of Procellarids (petrels), it has been suggested that the ability of an incubating adult to sustain weight loss during fasting is critical in facilitating extended incubation shifts (Weimerskirch, 1990), whilst frequent provisioning of the chick is important in sustaining chick growth rates (Quillfeldt et al., 2007).

Most previous studies of fulmar foraging distribution and foraging trip characteristics have relied upon recoveries of ringed birds (Macdonald, 1977a, Dunnet and Ollason, 1982), at-sea surveys (Camphuysen and Garthe, 1997, Garthe, 1997, Garthe, 2006) and observation at colonies (Dunnet et al., 1963, Furness and Todd, 1984, Hamer et al., 1997, MacDonald, 1977b, Phillips and Hamer, 2000). These studies suggest that there is substantial variation in incubation trip duration, with birds from high arctic colonies generally taking longer incubation shifts than boreal breeders. Incubation trips up to 14 days have been recorded in the Arctic and in Eynhallow, Scotland (Mallory et al., 2008) albeit with substantial individual variation (1 – 14 days). One study on Foula, Scotland from late incubation reported mean incubation trip duration of 32.5 h (Ojowski et al., 2001). Whilst these previous studies at colonies across the population range have shown a difference in foraging trip durations between the incubation and chick rearing periods, the spatial distribution of breeding fulmars is virtually unknown.

More recent technological advances have opened up the potential to identify connectivity between colonies and particular offshore foraging areas. Satellite derived location estimates (e.g. ARGOS, GPS) from bird-borne tracking devices can provide high accuracy location data (Guilford et al., 2008), although devices tend to be heavy and limited by battery life, which restricts the species able to carry them. Meanwhile light-level Global Location Sensing (GLS) and activity dataloggers can record for more than one year whilst deployed on birds as small as 45 g (Pollet et al., 2014), but location accuracy is low (ca. 200 km; Phillips et al., 2004).

Three limited studies have demonstrated potential breeding foraging range from telemetry (Falk and Møller, 1995, Weimerskirch et al., 2001, Edwards et al., 2013), but their sample sizes were very small (n = 3, n = 2 and n = 1 respectively). A tracking study using ARGOS satellite tags (Platform Terminal Transmitters; PTT) on fulmars at Pacific colonies revealed a late breeding season range of 250 – 400 km but breeding success was not determined (Hatch et al., 2010).

The study presented here seeks to use telemetry data to establish the foraging distribution of northern fulmars breeding at a Scottish colony and aims to address four primary questions: (1) what is the spatial distribution of fulmars during the incubation and chick-rearing periods, (2) are there differences in trip characteristics between males and females, (3) how does foraging range vary with breeding status, and (4) do estimates of foraging trip duration and range vary dependent on the type of data logger the bird is carrying?

Materials and Methods

Study site

Fieldwork was carried out during the years 2007-2013 on Eynhallow, Orkney, Scotland (59.14° N, 3.12° W), the site of an individual based fulmar study for more than 60 years (Dunnet, 1991). Demographic data were recorded during three individual field trips every year: a nest census around 1 June (early incubation period) to count eggs laid/active nests; a visit in mid-July (early chick-rearing period) to count hatched chicks; and a late-August census of pulli, from which breeding success is calculated. In addition to the population monitoring work, recent studies have carried out telemetry device deployments on fulmars nesting on Eynhallow (Edwards et al., 2013, Quinn, 2014).

Monitoring during colony visits involved circuits of the island, observing all locations where fulmars were known to nest, and identifying active nest sites. Each colony visit involved multiple circuits of the island, to try and resight as many pairs of individuals as possible. Sections of coast were initially observed from a distance to identify sites where birds were nesting. Closer approaches were then made, to either attempt to read colour ring sequences of individually marked birds, to capture birds to read metal ring numbers or to deploy/recover tracking devices. Breeding status (whether the nest is still active or failed) and stage (egg or chick) was recorded at each nest site on each visit.

Device deployments

Fulmars were caught on the nest using a fleyg net or monofilament noose during early incubation (May 20 – June 5) and early chick rearing (July 10 – July 20) in the years 2007 - 2013. Birds were sexed using biometric measurements (Dunnet and Anderson, 1961) or from analysis of DNA from feathers (Griffiths et al., 1998, Dawson, 2008). Two different types of tracking device were used in this study. Geolocators (Global Location Sensing (GLS); British Antarctic Survey Mk5/Mk9/Mk15; Phillips et al., 2006, Egevang et al., 2010, Quinn, 2014) were set up using supplied software (*BASTrak* suite, British Antarctic Survey) and deployed using cable tie attachment on to Darvic leg rings (*Fig. 2.1(a)*). GLS devices collect two types of data: light level and wet/dry activity data. The device samples light level every three seconds and records the highest light level for every 10 min period (a single value between 0 – 64). The activity data consists of a value between 0 – 200, corresponding to the number of three second intervals (in a 10 min period) when the logger was immersed in water. Mass of the GLS logger and attachment was approx. 5 g and the deployments lasted 8 – 24 months. Some GLS deployments spanned an entire breeding season, some only comprised part of a breeding season, whilst some birds were captured mid-season and had a new logger attached, meaning that GLS data were combined from successive deployments.

GPS loggers (MobileAction® iGot-U GT-120) were repackaged to reduce weight and height, and were attached to mantle feathers using Tesa® tape as per Edwards et al. (2013) (*Fig. 2.1(b)*). The mass of the GPS logger and attachment was approx. 24 g. The devices were programmed to record one location every 10 min during short chick-rearing deployments. To conserve battery life the resolution was reduced to one location per hour during longer incubation deployments. Loggers were set up and downloaded using supplied software (*@trip*, MobileAction®).

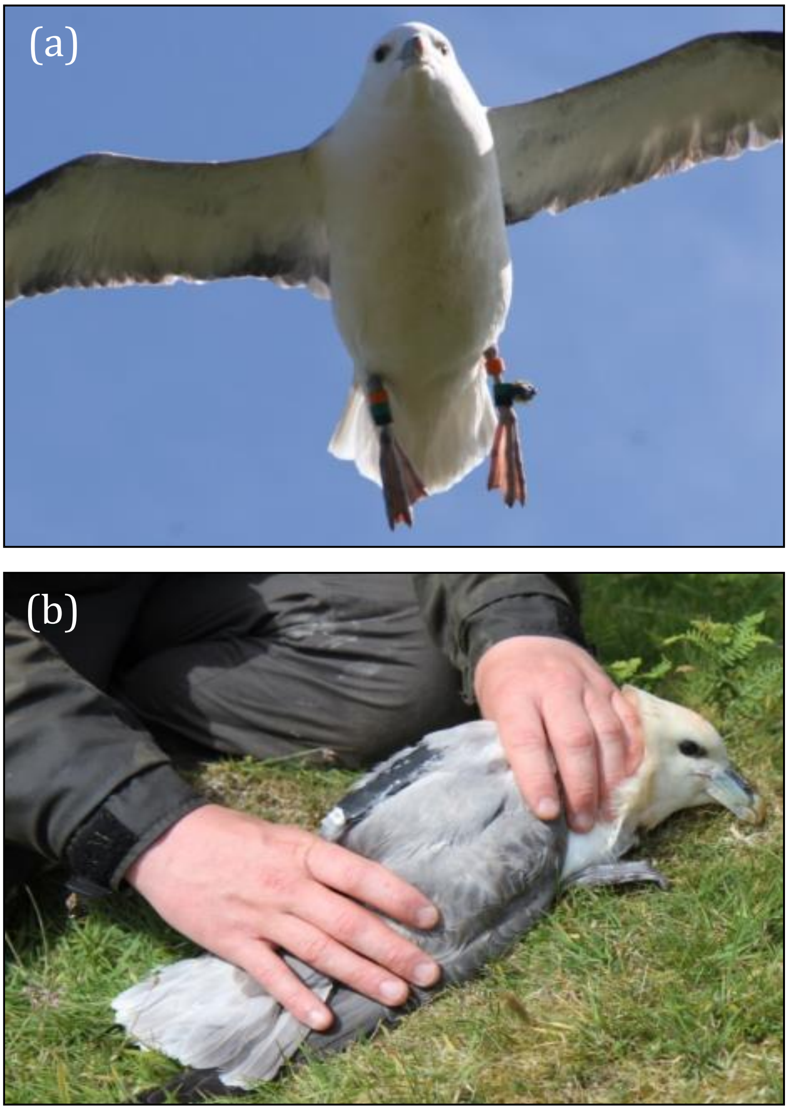

Fig. 2.1. Photographs showing (a) a GLS data logger attached to a plastic leg ring using a cable tie; (b) a GPS data logger attached to the mantle feathers of a fulmar, using Tesa® tape

Data processing and analysis

Light and activity data files from GLS dataloggers were extracted and processed using *BASTrak* software. Data from both types of tracking device covering the period 15 May – 20 August (incubation and chick rearing periods) were analysed for this study (*Fig. 2.2*).

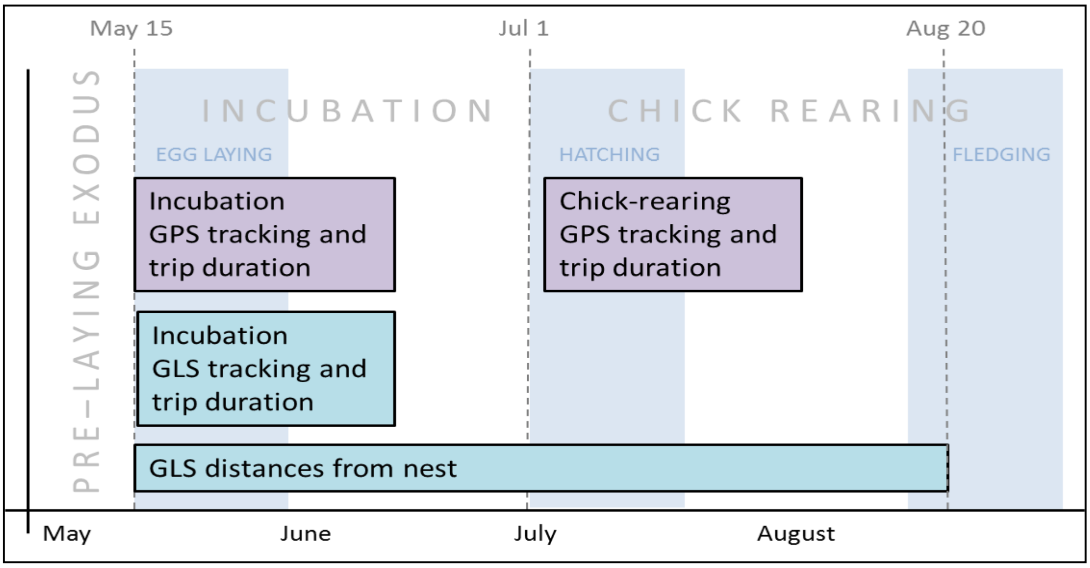

Fig. 2.2. Diagram showing a timeline of the fulmar breeding season from egg laying to fledging, indicating periods when data from various sources used in this study were collected.

A bird from a pair that successfully fledged a chick (i.e. chick seen alive during the August colony visit) was classified as *successful*. A bird that attempted to breed (egg seen during May/June visit, or chick seen during July visit) but that did not fledge a chick (based on the August visit) was recorded as having a *failed* breeding attempt. A bird from a pair that was not seen to attempt to breed, where 1) neither the tracked bird nor their partner from the previous year had been seen at their previously occupied nest site, or 2) failed before either it or its partner from a previous year was seen at a nest site, was classified as *not seen at the colony* and data were not included in this part of the study. These were deemed to be putative non-breeders in the study year.

Light traces from GLS devices were examined visually using *TransEdit* software (British Antarctic Survey) where sunrises/sunsets were identified manually at a predetermined threshold level of 10, and solar elevation of -3.5° (Quinn, 2014). Where the sunrise/sunset transition was noisy or poorly defined, for example when the bird was on the nest, the associated location was removed from the dataset.

The length of day and night was used to estimate latitude, and time of local noon and midnight to estimate longitude. Where two locations were available for one day, these were averaged to produce one location per day. ESRI® Arc GIS 10.0 was used to visualise the data and generate maps. Erroneous locations in the GLS locations (i.e. where there was >1000 km between two consecutive locations) were manually filtered from the dataset, to retain only realistic estimations of location.

Data from the GPS loggers were downloaded from the device using *@trip* software. The data were used to generate maps in Arc GIS 10.0, which could be examined to see when birds left and returned to the nest site. Location data from periods when the birds were on the nest were discarded. Where birds had been tracked during more than one foraging trip, each trip was examined individually. No further filtering or smoothing was applied to the GPS data.

There is evidence that whilst at sea fulmars frequently alight upon the water even during extended transits (Chapter 4), whilst other *Procellariformes* also land regularly, even during migration (Mackley et al., 2011, Mackley et al., 2010). Extended dry periods were therefore used to distinguish incubation shifts at the nest from foraging trips to sea. Incubation trip durations for birds with GLS loggers were estimated from the wet/dry activity data. Activity traces were examined manually for each bird. Where a bird remained dry for > 6 hours before the start of a period of mixed/wet activity of > 1 day, the time of the first wet activity value was assumed to represent the start of a foraging trip. When a bird remained dry for > 6 hours following a period of > 1 day of mixed/wet activity, indicative of being at the nest site, the time of the first dry activity value was assumed to represent the end of the foraging trip and the start of an incubation shift. Only the first two incubation foraging trips per bird per year were considered from the GLS data, as these correspond to the period in early incubation when most GPS incubation tracking data were collected (*Fig. 2.3*).

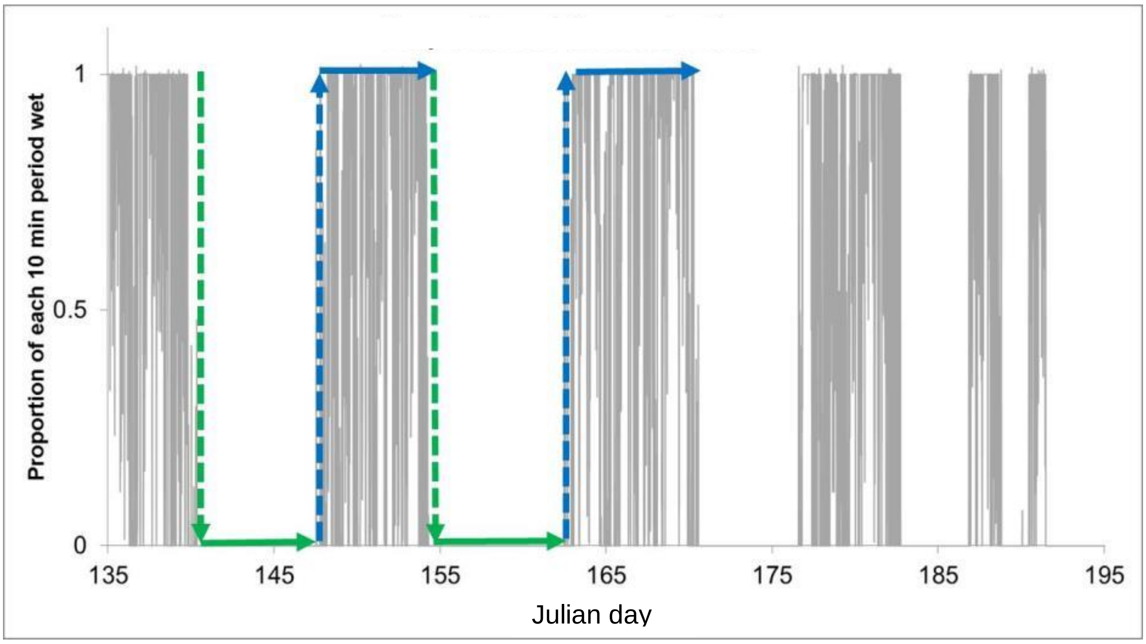

Fig. 2.3. Graph illustrating an example of how activity data were used to calculate incubation trip duration. Green dashed (vertical) arrows indicate the final wet record preceding a dry period > 24 h. This signifies the end of a foraging trip and start of an incubation bout. Blue dashed (vertical) arrows indicate the time of the first wet record after a dry period > 24 h. This signifies the end of the incubation bout and the start of a foraging trip. Solid green (horizontal) arrows demarcate time on the nest, whilst solid blue (horizontal) arrows indicate the duration of the foraging trip. Two incubation bouts and two foraging trips are indicated.

Data analyses were carried out in Microsoft Excel and R 3.0.0 (R Core Development Team, 2013) to identify trip durations (h) and maximum great-circle distance from nest per foraging trip (km). A linear model was fitted to data to compare the relationship between maximum range from the colony and trip duration, between the incubation and chick rearing periods. Foraging trip parameters between groups and periods of the breeding season were compared using non-parametric statistical tests in R. Differences in distance from the colony between birds of different breeding status were compared using generalized linear mixed-effects models (GLMM), using the glmmPQL() function within the R package ‘MASS’ (Venables and Ripley, 2002). GLMMs were fitted to the data for each breeding period. A random effect was included for individual birds. An AR1 correlation structure was included to account for temporal autocorrelation. A Gamma probability distribution was chosen as the distribution that best fitted the data. Linear mixed-effects models used to compare differences within foraging trip characteristics were implemented using the ‘lme4’ (Bates et al., 2015) and ‘lmerTest’ (Kuznetsova et al., 2015) packages. Maps were generated in Arc GIS 10.0 to visualise distributions. Kernel density estimates were generated in Geospatial Modelling Environment v0.7.2.0 (SpatialEcology$^{\mathrm{TM}}$).

Results

GLS data analyses utilised data from two subsets of birds. For analysis of the distance from colony through the whole breeding season, a subset of 35 birds where GLS light data were available through the whole breeding season were used (*Table 2.1*). For analysis of foraging trip durations and maximum foraging ranges during the incubation period data were included from all those birds which attempted to breed (whether successful or not) and which had light level geolocation *and* activity data during the incubation period.

GPS data were collected during the incubation periods of 2011 and 2012, and the chick rearing periods of 2009 – 2011. Of 31 GPS deployments during the incubation period, 14 devices were recovered and included in this study (*Table 2.1*). The recovery rate improved from 2011 to 2012 due to an improved recapture technique. During the chick rearing period, a total of 39 GPS loggers were deployed in early- to mid-July in 2009 – 2011, of which 27 were recovered and the associated data were used in this analysis. Devices that were not recovered were either lost by the bird before recapture or the bird could not be recaptured during the season of deployment.

Table 2.1. The number of individual birds included in different stages of analysis.

	GPS incubation trip duration/range	**GLS incubation trip duration/ range**		**GPS chick rearing duration/ range**	**GLS distance from colony through season**		
	Analysed (deployed)	Successful breeders	Failed breeders	Analysed (deployed)	Successful breeders	Failed breeders	Not Seen
2007	-	-	-	-	-	1	-
2008	-	4	1	-	4	-	1
2009	-	2	1	6 (11)	3	2	-
2010	-	13	4	10 (13)	8	4	-
2011	1 (9)	5	9	11 (15)	-	7	5
2012	13 (22)	1	1	-	-	-	-
Total	**14 (31)**	**25**	**16**	**27 (39)**	**15**	**14**	**6**

Distance from colony through the breeding season

GLS location data from birds that were tracked through the whole breeding season (n = 35) were used to examine variation in the estimated distance from the colony in relation to breeding status and breeding period (*Fig. 2.4*). These were divided according to three breeding status categories: birds that successfully fledged a chick, birds that suffered breeding failure, and six birds that were not seen at the colony during the season in which they were tracked (*Table 2.1*).

During the incubation period the data suggest that there was no significant difference in distance from the nest between the birds which attempted to breed (successful or failed). However, birds that were not seen at the colony were significantly closer to the nest (*Table 2.2(a)*).

During the chick rearing period, birds that were actively rearing chicks remained closer to the colony than birds that had failed and birds that had not been observed breeding in that season. There was no significant difference in distance from colony between non-breeders and failed breeders (*Table 2.2(b)*).

Table 2.2. Model coefficients for two generalized mixed-effects models, fitted to daily distances from the colony in the breeding season, for (a) the incubation period and (b) the chick rearing period. P-values in bold indicate significant results at 95 % confidence level.

(a)

Distance from nest during incubation period for successful, failed and not-seen birds

	Estimate	**SE**	**DF**	**t**	**P**
Intercept	-0.000443	0.00150	818	-0.295	0.77
Julday:failed	0.0000158	0.00000979	818	1.611	0.10
Julday:notseen	0.0000106	0.00000428	818	2.481	**0.013**
Julday:success	-0.00000181	0.00000201	818	-0.898	0.37

(b)

Distance from nest during chick rearing period for successful, failed and not-seen birds

	Estimate	**SE**	**DF**	**t**	**P**
Intercept	0.00744	0.00139	1264	5.36	**< 0.001**
Julday:failed	-0.0000298	0.00000626	1264	-4.76	**< 0.001**
Julday:notseen	0.000000590	0.00000101	1264	0.586	0.558
Julday:success	0.00000749	0.00000151	1264	4.96	**< 0.001**

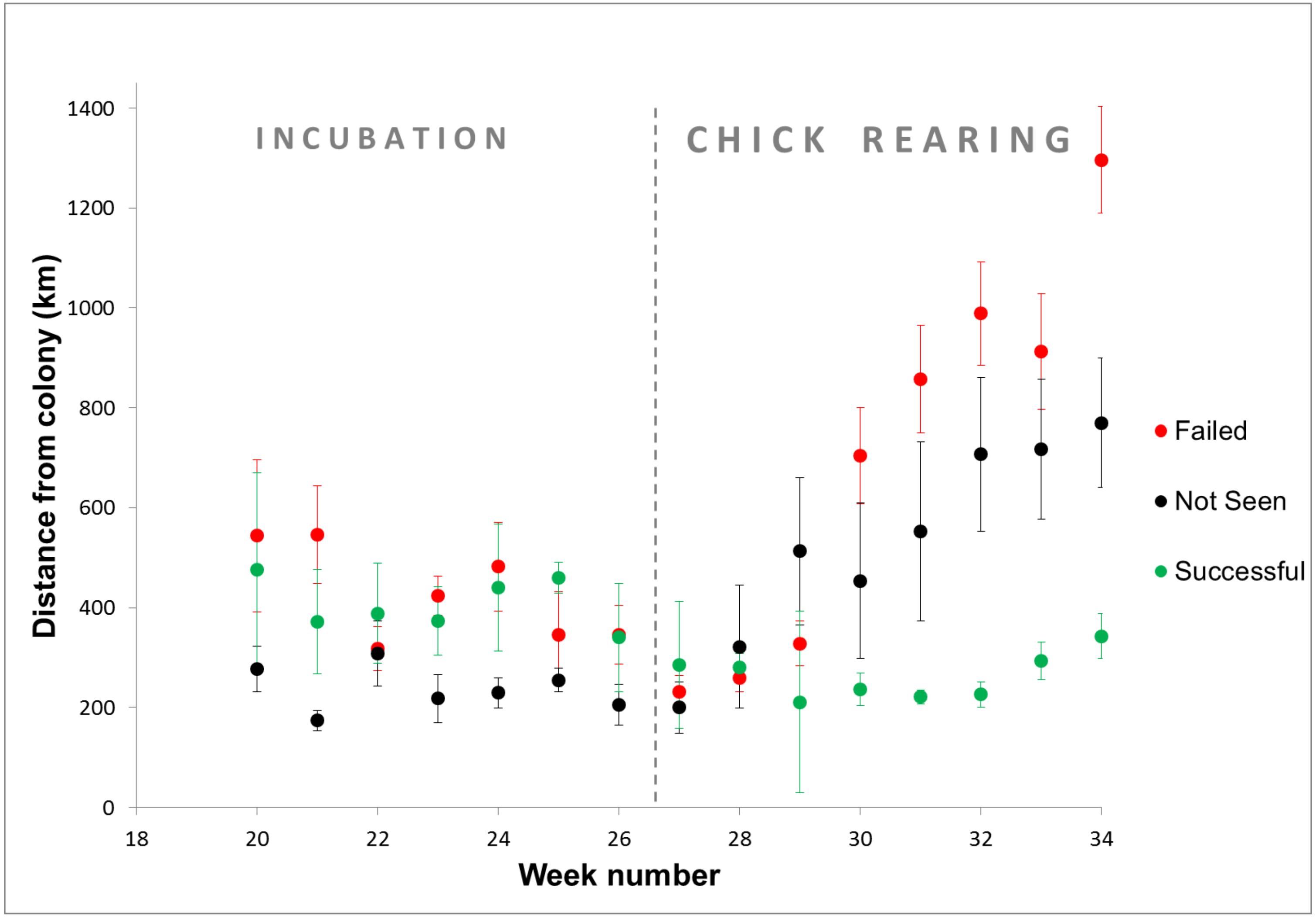

Fig. 2.4. A scatterplot showing weekly median distances from the colony (± SE) for the three groups of birds: successful breeders (n=15), failed breeders (n=14) and birds not seen at the colony (n=6) during the season of study. The grey vertical dashed line indicates July 1, which for the purposes of analysis was taken as the boundary between incubation and chick rearing.

Incubation period foraging trips

Data collected using both GPS and GLS data loggers were used in the analysis of foraging range and trip duration during incubation. Birds carrying GLSs were either successful breeders, or carried out a minimum of one foraging trip before the breeding attempt failed. Birds that were not seen at the colony during the year of study were not included. Locations were determined from light-level geolocation or GPS data and foraging trip durations were derived from GLS activity data or GPS locations. Data were analysed for the period 15 May to 30 June.

The highest densities of fulmar foraging locations during incubation were to the north west of Orkney, and in the northern North Sea between Scotland and Norway (*Fig. 2.5(a)*). Some longer trips extended north into the Faeroes-Shetland channel, and several birds (including three tracked with GPS) foraged in the eastern North Sea and Skagerrak, to the north of Denmark. Five birds tracked with GLS, and one tracked with GPS, foraged in the central North Atlantic, 2-3000 km west of the British Isles. The core range (50% kernel density contour) of Eynhallow fulmars during the incubation period covered an area of 603,971 km^2, corresponding to a large part of the northern North Sea and North Atlantic Ocean surrounding the Northern Isles.

The characteristics of 55 foraging trips were analysed for the incubation period (*Table 2.5 (a)* and *(b)*). When dataloggers were attached during more than one foraging trip, only the first trip was included in subsequent analyses. Linear mixed-effects models were used to determine the influence of datalogger type and sex upon trip duration and distance from the colony. Neither sex nor logger type affected maximum foraging range (*Table 2.3 (a)*) or trip duration (*Table 2.3 (b)*).

Table 2.3. Fixed-effect coefficients from two linear mixed-effects models investigating foraging trip parameters during the incubation period.

(a)

Linear mixed effects model: max. distance from colony ~ sex + logger type + (1|year)

	Estimate	**SE**	**DF**	**t**	**P**
(intercept)	972.08	168.17	5.83	5.78	**0.0013**
Male	-199.83	152.84	50.92	-1.31	0.20
GPS	-425.86	251.74	14.32	-1.69	0.11

(b)

Linear mixed effects model: trip duration ~ sex + logger type + (1|year)

	Estimate	**SE**	**DF**	**t**	**P**
(intercept)	199.82	34.35	4.7	5.82	**0.0026**
Male	-41.44	21.46	49.27	-1.93	0.059
GPS	-50.62	40.60	41.32	-1.25	0.22

Chick rearing period foraging trips

Data from 42 deployments were used in the analysis of chick rearing foraging range and trip duration (25 GPS, 15 GLS). Birds carrying GLSs were all successful breeders during the season during which they were tracked. Locations were determined from light-level geolocation and GPS data and foraging trip durations were estimated from the GPS data. Data were analysed for the period 1 July to 20 August.

The highest density of fulmar foraging locations during early chick rearing was to the NW of Orkney, with some longer trips into the northern North Sea between Scotland and Norway (*Fig. 2.5(b)*). The core range of Eynhallow fulmars during this period covers an area 255,825 km^2 in the north western North Sea, including the outer Moray Firth, and to the north-west of the islands of Orkney.

Data from 25 foraging trips were analysed to investigate sex differences (*Table 2.5 (c)* and *(d)*). Based on the GPS data, there were no significant differences between maximum distance from colony (*Table 2.4 (a)*) or foraging trip duration (*Table 2.4 (b)*) between males and females.

Table 2.4. Fixed-effect coefficients from two linear mixed-effects models investigating foraging trip parameters during the chick rearing period.

(a)

Linear mixed effects model: max. distance from colony ~ sex + (1|year)

	Estimate	**SE**	**DF**	**t**	**P**
(intercept)	75.30	23.07	6.59	3.26	**0.015**
Male	2.82	27.15	22.97	0.10	0.92

(b)

Linear mixed effects model: trip duration ~ sex + (1|year)

	Estimate	**SE**	**DF**	**t**	**P**
(intercept)	19.80	3.66	8.46	5.41	**< 0.001**
Male	2.16	4.26	23.0	0.51	0.62

Table 2.5. Foraging trip duration and range summary data.

(a) Maximum distance from colony (km) during incubation

	N	**Median**	**Range**
M	34	475.5	35 – 2373
F	21	702	110 – 2736

(b) Foraging trip duration (h) during incubation

	N	**Median**	**Range**
M	34	111.3	24.4 – 335.5
F	21	174.5	41.3 – 367.7

(c) Maximum distance from colony (km) during chick rearing

	N	**Median**	**Range**
M	17	64	8 – 258
F	8	56	14 – 222

(d) Foraging trip duration (h) during chick rearing

	N	**Median**	**Range**
M	17	19.5	9 – 40.6
F	8	21.3	5.5 – 41.8

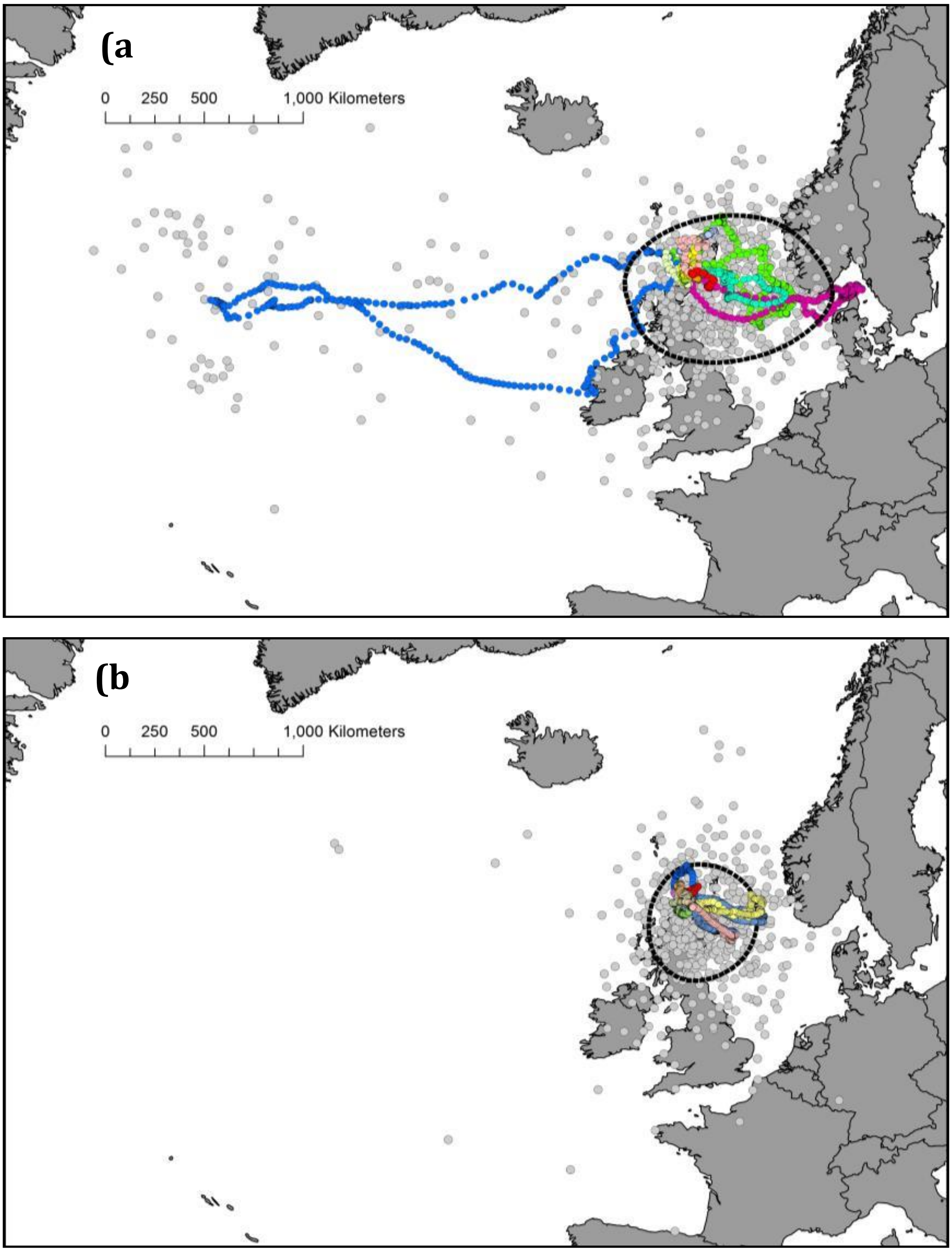

Fig. 2.5. Map showing distribution of tracked fulmars from Eynhallow during (a) incubation and (b) chick rearing. Coloured dots show tracks from individual birds tracked using GPS loggers (incubation, n = 14; chick rearing, n = 23). Grey dots show locations of birds tracked using GLS between 15 May and 30 June (incubation, n = 27; chick rearing, n = 15). Black dashed line shows 50% kernel density (LSCV) contour, generated from GLS locations.

Comparison of incubation and chick rearing trip ranges and durations

All available telemetry data were used to compare the differences in duration and foraging ranges of fulmars between periods of the breeding season. The data show that maximum distance from colony was significantly higher during incubation by 609.8 km ± 116.7 (t(77.2) = 5.23, $p < 0.001$). Foraging trip duration was also shown to be significantly longer during incubation by 114.19 hours ± 16.87 (t(76.2) = 6.77, $p < 0.001$) *(Fig 2.6)*.

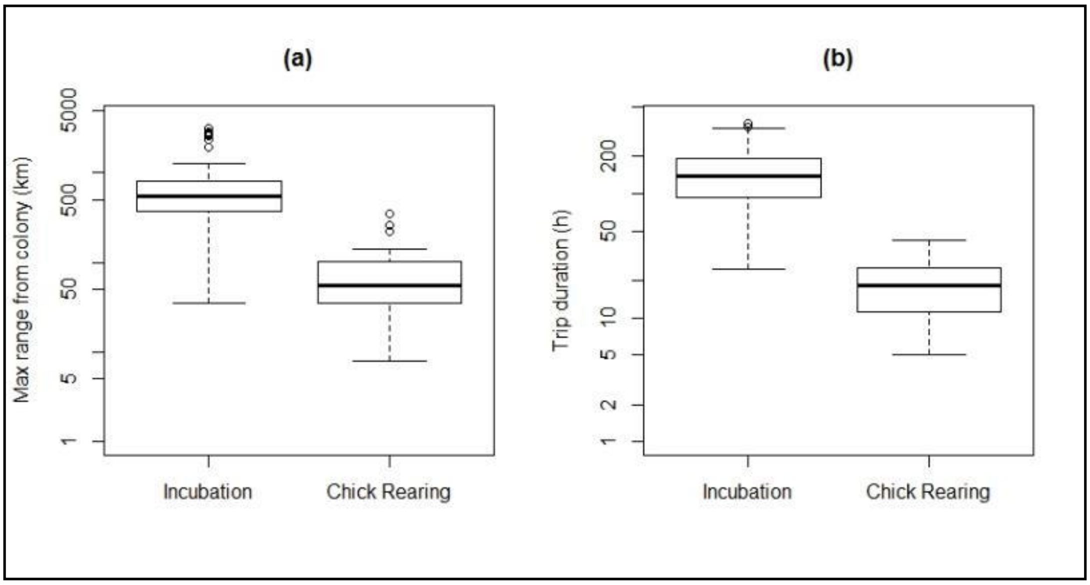

Fig. 2.6. Comparison between stages of the breeding season (incubation and chick rearing): (a) maximum distance from the colony and (b) foraging trip duration (drawn on a $\log_{10}$ Y-axis).

A linear model fitted to the data suggested that whilst there is a strong relationship between trip duration and maximum foraging range, there is no significant difference in this relationship between the incubation and chick rearing periods (*Table 2.6*). However, during incubation maximum foraging ranges show large variation, especially foraging trips > 200 h (*Fig. 2.7*).

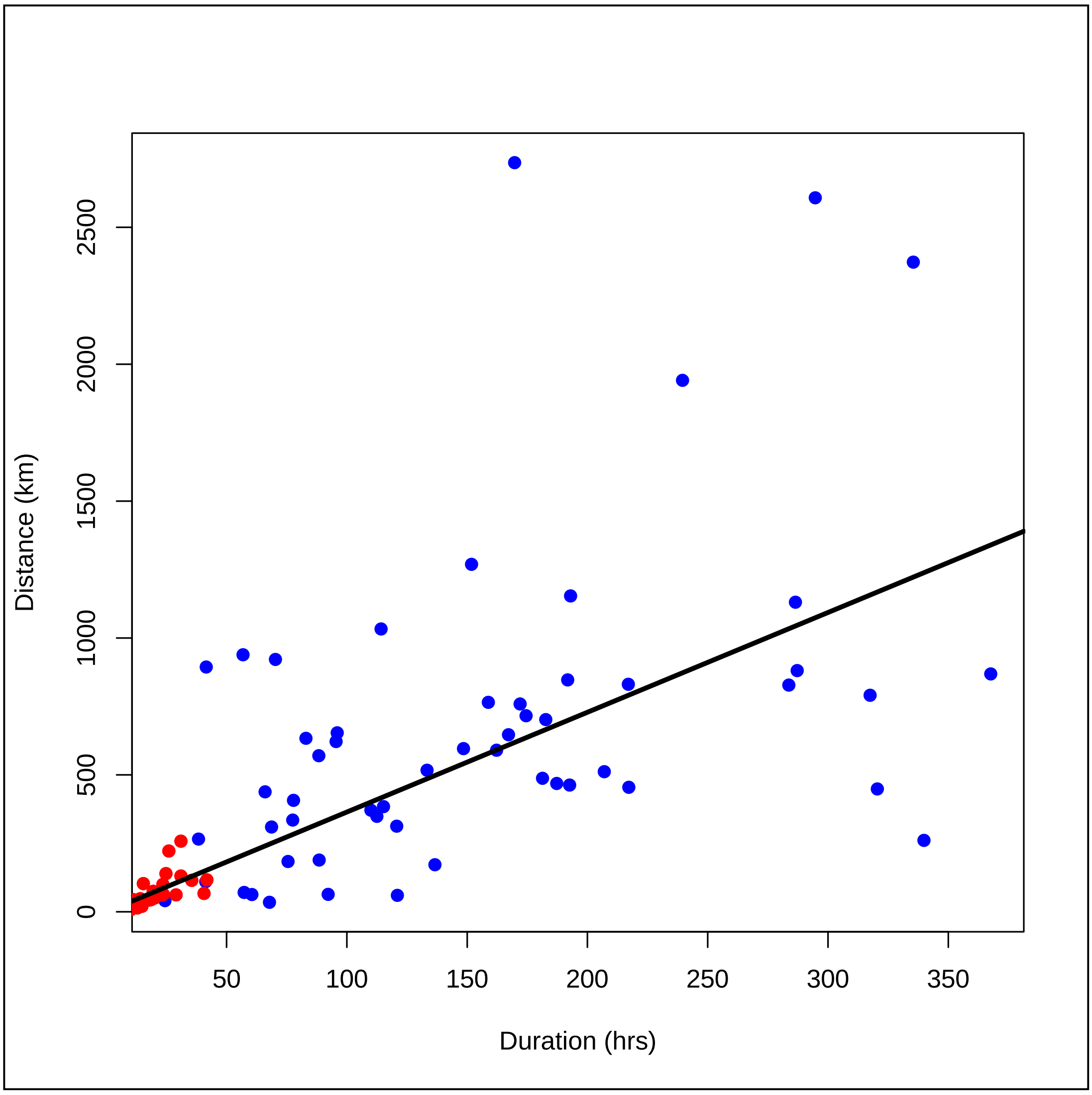

Fig. 2.7. The relationship between maximum distance from nest (km) and foraging trip duration (h), for the chick rearing (red circles) and incubation (blue circles) periods. The black line illustrates the model detailed in Table 2.6.

Table 2.6. Linear model comparing relationship between maximum distance from colony and trip duration, for two periods of the breeding season.

(c)

Comparison of relationship between maximum distance to colony and foraging trip duration

Coefficients	**Estimate**	**SE**	**t value**	**P**
duration:incubation	4.07	0.33	12.28	**< 0.001**
duration:chickrearing	3.64	3.75	0.97	0.33

Discussion

Whilst post-breeding migration tracking has been successfully carried out using both satellite transmitters (Mallory et al. 2008) and light level geolocation (Quinn 2014), this is the first study to use telemetry data to compare fulmar distribution and foraging trip characteristics between the incubation and chick rearing periods of the breeding season.

Comparison between incubation and chick-rearing foraging trips

Using a combination of GPS and GLS data loggers, this study characterised the patterns of distribution and foraging trips of fulmars during the incubation and chick rearing periods of the breeding season. Our data show that breeding fulmars forage in both the North/Norwegian Sea and the central Atlantic Ocean during the incubation period, two regions with very different oceanographic characteristics (Laughton et al., 1975, OSPAR, 1992) and undoubtedly different prey availability to surface-feeding seabirds. The maximum distance from the colony was more than 2700 km, confirming their high mobility even during the breeding season. Fulmars have not been tracked during the incubation period before, and the maximum foraging range for a breeding fulmar was previously estimated to be only 580 km (Thaxter et al., 2012), based on their potential range for a foraging trip duration of 29 h during chick rearing (Furness and Todd, 1984). This more extensive range could have serious implications for the breeding success and survival of Scottish populations, as approximately 20,000 fulmars die as bycatch in the Icelandic, Faeroese and Norwegian commercial longline fisheries every year (Anderson et al., 2011), a figure that is potentially a gross underestimate (Brothers et al., 2010).

Analysis of GLS and GPS data indicated that median maximum distance from the colony was significantly greater during incubation than chick rearing. However the GPS data also highlight that some incubation period foraging trips remained within 100 km of the colony for the duration of the trip. Birds foraging during the incubation period made longer duration excursions from the nest than a chick-rearing trip of similar range, suggesting that birds encountering profitable prey patches in the locality of the colony do not need to travel further from the nest site (Weimerskirch, 2007), but can exploit those patches for longer as there is less pressure to return to the nest before chick provisioning has commenced. Despite this, some incubation foraging trips were recorded in excess of 2500 km from the colony. Foraging over such large distances is likely to require suitable wind patterns to facilitate the fast efficient flight of Procellarids (Furness and Bryant, 1996, Wakefield et al., 2009b, Weimerskirch et al., 2012). Therefore, it is possible that the shorter range of some foraging trips during incubation could be due to meteorological conditions at that time preventing travel further from the colony. Long distance foraging trips during the breeding season are potentially a high-risk strategy in terms of breeding success, as the probability of an incubating bird abandoning the nest, causing failure of the breeding attempt, increases with trip duration of its partner (Weimerskirch, 1990). This and other studies have shown that ca. 14 d is the maximum recorded incubation trip duration for fulmars (Mallory et al., 2008). Therefore, should wind conditions fail to permit a foraging bird to return from a distant foraging trip within approximately two weeks, it is likely that its partner will cease incubation and will abandon the nest.

The maximum recorded foraging range during chick rearing in this study was largely comparable to predictions made by Hamer et al. (1997) based on the average ground speed recorded by Falk and Møller (1995). At approximately 250 km in 40 h, this suggests that, even when constrained during the early chick-rearing period, fulmars from Eynhallow can forage widely over the Scottish continental shelf and potentially into the waters of Ireland, Iceland, the Faroe Islands, Denmark and Norway.

During the incubation period, median trip duration (5.8 d) was comparable to that observed at Eynhallow from 2003 – 2005 (7 d), and at other boreal and high arctic sites (Mallory et al., 2008, Gaston et al., 2014). Nevertheless there was considerable variation in trip duration, with the maximum recorded duration also similar to the 13.8 d reported from Eynhallow in 2003 (Mallory et al., 2008). Incubation trip durations from this study were however approximately four times longer than those observed at Foula and Unst (Shetland) during 1998 and 1999 (Ojowski et al., 2001). In recent years breeding success in many seabird species in Scotland has been poor, largely as a result of lower availability of prey such as sandeels (Votier et al., 2004). Because fulmars are more able to cover long distances at high speed (Chapter 4) on foraging trips than some other seabird species, this increase in foraging trip duration could potentially be a response to diminished availability of prey locally. Fulmars are known to scavenge for discards and offal at fishing vessels (Camphuysen and Garthe, 1997, Phillips et al., 1999), and the reduction in discarding from the Scottish whitefish and *Nephrops* trawl fishery (Fernandes et al., 2011) could explain the increase in foraging effort (trip duration and distance from colony) over the past decade. However as the earlier Shetland study monitored attendance at nests from 23 June (Ojowski et al., 2001), it was highly biased towards late incubation. The data presented in this chapter suggest that median distance from the colony decreases through time during incubation (*Fig. 2.4*) and thus these late incubation trips may not be directly comparable with our trips from throughout the incubation period.

Foraging trips during chick rearing were shorter in duration than those during incubation. The median foraging trip duration for both males (19.5 h) and females (21.3 h), as calculated from GPS tracking data, were shorter than the mean estimated trip duration of 31 h reported from Fair Isle by Phillips and Hamer, 2000). One plausible reason for this is that observations from that study included those collected into late chick rearing (> 50 d post-hatching), when birds may undertake slightly longer-range trips from the colony. Increases in trip range as the season progresses (*Fig. 2.4*) were also seen in our GLS tracking data and in a previous study (Weimerskirch et al., 2001). It is thus likely that trips during the brood/guard period (mid-July), such as those in this study, are shorter (in duration) than those occurring when the chick is unguarded. Chick rearing trip durations reported from Foula in 1998 and 1999 during a similar time period, mid – late July were closer to those reported in this study (mean 11.2 h; Ojowski et al., 2001). Studies during the past 25 years at other north east Atlantic colonies have reported comparable trip durations (see *Appendix 1*).

Although the GPS locations in this study were highly accurate, the GLS data were less so. The use of such data requires some subjective decisions and assumptions to be made. GLS locations are calculated based upon length of day (and night) to estimate latitude, and time of noon (and midnight) to estimate longitude. For these locations to be estimated, solar transitions (sunrise and sunset) were manually identified. Although care was taken to only include locations calculated from sunrises and sunsets where the logger recorded a clean transition from light to dark (or *vice versa*), factors such as cloudiness can affect estimation of location (Phillips et al., 2004, Lisovski et al., 2012).

The GLS activity data were used to estimate foraging trip duration during the incubation period. Because trip duration using activity data were calculated based on the last 10 min period where the activity value was equal to zero, the initial flight from the nest and the final flight returning to the nest were likely included with time on land. This means that trip duration from activity data may have been slightly underestimated. In Chapter 4, more detailed analysis of a single bird suggests that a fulmar on a flight to the Mid Atlantic Ridge seldom flew for longer than 30 min without landing on the water. A study using GLS devices on white-chinned petrels *Procellaria aequinoctialis* in South Georgia, a similar sized species, reported breeding season flight bout durations between 62 – 85 min (Mackley et al., 2011). Assuming comparable behaviour in fulmars, it is unlikely that GLS activity-derived trip durations were underestimated by more than 3 h per trip. Indeed, estimates of incubation trip durations were similar for GLS and GPS loggers, suggesting that this error was negligible.

Comparison between male and female birds

Data collected and analysed in this study suggest that during incubation, male and females perform trips of similar range and duration. This is in contrast to a study on the two giant petrel species *Macronectes spp.* (large fulmarine petrels) in the Southern Ocean, which showed that females tend to disperse more widely than males (Thiers et al., 2014), whereas wandering albatrosses *Diomedea exulans* have been shown to forage in very different oceanographic zones, separated by sex (Patrick and Weimerskirch, 2014a). Further tracking work, of a larger sample of tracked individuals, especially during incubation, would facilitate a more robust comparison of sex differences in relation to their potential impact on sex-specific survival rates. During GPS tracking in early chick rearing, ranges and durations of foraging trips were very similar for both sexes, possibly due to the central place constraint from the requirement for both members of the pair to regularly provision the chick.

Comparison between types of logger

In this study the mass of the GPS logger and attachment was 3% of the mean mass of adult fulmars weighed at Eynhallow (males 884 g, females 706 g; (Dunnet and Anderson, 1961)). Mass of the GLS logger and attachment was less than 1 % of the mean mass of adult fulmars. Birds tracked with GLS loggers in this study were found to make trips of a similar range and duration to birds tracked with GPS. Attachment of data loggers has been shown to affect flight of albatrosses and petrels, prolonging foraging trip duration and inducing high rates of breeding failure, particularly when logger mass was more than 3% of the bird's body mass (Phillips et al., 2003). The sample of GPS tracked birds in this study was likely to be biased towards large birds, at accessible nest sites, which were easier to catch than others. Black browed albatrosses have been shown to demonstrate variability in personality and foraging range, where increased boldness may help individuals compete for food (Patrick and Weimerskirch, 2014b). A more appropriate control for the tagging effect would be remote monitoring of untagged birds at nest sites using camera traps to assess trip duration without capturing and tagging the birds (Gaston et al., 2014).

Breeders vs. non-breeders

The GLS data used in this study suggest that birds that were not seen attempting to breed remained closer to the colony throughout the incubation period (*Fig. 2.4*). Observation of the light and activity traces from the GLS devices does not show an obvious pattern of foraging trips. This indicated that these unseen birds were not simply breeding at an alternative colony. The increased distance between failed/non-breeding birds and active breeders during the latter part of the breeding season suggests that birds that are not actively breeding depart for wintering regions before the end of the breeding season. In these circumstances fulmars have no obligation to remain close to the colony, and it is probable that the birds depart to exploit more productive foraging areas in other regions away from the colony. This may be a response to inter- or intraspecific competition for prey on the continental shelf;

especially as gannets and gull species are known to compete with fulmars for discards from fishing vessels in north west European waters (Camphuysen and Garthe, 1997, Garthe and Camphuysen, 1996, Hudson and Furness, 1988).

Conclusion

This study found considerable variation in the foraging trip range and duration of northern fulmars during the incubation period, but less variation during chick rearing when the necessity to return to the nest frequently restricts the distance travelled from the breeding site. As a result, foraging trips tend to be longer in range and duration during incubation than during chick rearing. Sex appeared to be unimportant in influencing maximum foraging range and trip duration during incubation or chick rearing, although due to limited sample sizes the power to detect sex-specific and interannual differences was low. Data logger type also appeared to have no affect on foraging range or duration. Some birds foraged in the north western Atlantic Ocean and in the Kattegat whilst actively breeding on Eynhallow, although during chick rearing the range is largely focused on the Scottish continental shelf and northern North Sea. Even during the breeding season, Scottish fulmars are potentially facing threats such as the risk of fishery bycatch. Larger sample sizes of tracked birds would improve the robustness of statistical comparisons, such as the effect of year on foraging trip characteristics.

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Chapter 3: State-space modelling of geolocation data reveals within-colony differences in the use of different North Atlantic management areas by breeding northern fulmars.

Abstract

Effective management and conservation of marine predators frequently requires information on connectivity between specific breeding colonies and at-sea foraging areas. Whilst Global Positioning System (GPS) loggers can now provide high resolution data on seabird foraging characteristics, their use is generally restricted to incubation and chick rearing periods. Smaller Global Location Sensors (GLS) deployed in previous years could provide valuable data during earlier phases of the breeding season, but additional information on their accuracy is required to assess this potential.

We used incubation trip tracking data from 11 double-tagged (GPS/GLS) fulmars tagged at a Scottish colony within a state-space modelling framework (SSM; Winship et al. 2012) to estimate the error around GLS locations. The SSM was then fitted to a larger sample of GLS tracking data from the pre-laying exodus, using the mean of these error estimates. Outputs from the SSM were then used to characterise their spatial distribution, and assess the extent of within-colony variation in the use of different OSPAR management regions.

During the pre-laying exodus, fulmars from a single Scottish colony foraged across several biogeographic regions, up to 2900 km from the colony. Males spent significantly less time away from the colony ($\bar{x}$ = 18 days, n = 20) than females ($\bar{x}$ = 25, n = 19), and most (60 %) males remained within the North Sea region. In contrast, most (68 %) females flew north, foraging within Norwegian and Barents Sea, A small subset of birds (15 %) travelled to the central North Atlantic.

Within-colony variation in ranging behavior during the breeding season may result in sex differences in exposure to threats such as fisheries bycatch and marine plastics, with birds from a single colony dispersing over several OSPAR management areas.

These patterns also have implications for interpreting trends from colony-based monitoring, and EU Marine Strategy Framework programmes that use northern fulmars as an indicator species for monitoring trends in marine litter.

Introduction

The study of spatial ecology is one of the highest priorities for seabird conservation for the coming years (Wakefield et al., 2009, Lewison et al., 2012). In European waters, the European Commission Birds Directive obliges member states to maintain populations of wild birds by designating and managing networks of Special Protection Areas (SPA) for rare, vulnerable and migratory species (EC, 2009). Alongside these measures, the General Obligations of the OSPAR Convention state that member states must conserve marine ecosystems by taking necessary measures to protect their maritime area against the deleterious impacts of human activity such as pollution (van Franeker et al., 2011). Such measures are managed by OSPAR across five broad biogeographic regions, from the Barents Sea to the Bay of Biscay and west to the Mid Atlantic Ridge. However, as a result of their highly mobile nature, most seabird species are unlikely to remain in either the maritime area of individual OSPAR nations, nor indeed to wider EU waters (Fijn et al., 2013).

Whilst extensive information on the distribution of seabirds at sea exists from visual surveys (Durinck and Falk, 1996, Garthe, 1997, Garthe, 2006), this cannot be used to understand the link between specific breeding colonies and key foraging areas. Similarly, at-sea survey data can only rarely be used to understand within-species variability in the use of potential foraging areas by birds of different age or sex (Weimerskirch and Jouventin, 1987). Northern fulmars *Fulmarus glacialis*, are considered one of the most abundant and widely distributed of North Atlantic seabirds. This has led to their use as one of the primary indicator species for plastic contamination under the EU Marine Strategy Framework Directive (EU, 2008). Efforts to understand the factors leading to variations in plastic contamination in this species, and potential population consequences, require better information on connectivity between particular breeding colonies and different OSPAR regions.

Early studies using sightings of marked individuals at sea (Tickell, 1968) and recoveries of ringed individuals (Macdonald, 1977a, Harris, 1984, Hunter, 1984, Croxall and Prince, 1990) revealed that many species of seabirds could travel several thousand kilometres during their post-breeding migration. More recently, the tracking of seabirds using miniaturised telemetry devices has resulted in a wealth of data that demonstrate that foraging may occur many hundreds of kilometres from the colony, even during the breeding season (Phillips et al., 2007, Guilford et al., 2008, Edwards et al., 2013, Thiers et al., 2014). A broad suite of studies has now highlighted the importance of distant waters for many seabird species. However, wider scale conservation efforts are often constrained by uncertainty over the extent to which birds from particular colonies use these different areas within different phases of the annual cycle (Lascelles et al., 2012, Camphuysen et al., 2012).

Many *Procellariformes* (petrels) such as northern fulmars are absent from their colonies for long periods during the early breeding season (MacDonald, 1977b, Mallory et al., 2008, Phillips et al., 2006, Pollet et al., 2014b). This extended departure from the nest site during the pre-laying exodus is likely to represent a critical point of the annual cycle for these species, especially since females must access nutritional resources to develop an egg that is large relative to body size compared with many other bird species (Tickell, 1962, Lack and Gillmor, 1966). Furthermore, both partners must acquire sufficient energy reserves to support long fasts during the incubation period (Weimerskirch, 1990, Mallory and Forbes, 2008). The importance of foraging during this period was highlighted in a study from Alaska, which showed that male fulmars that spent more time at sea during the pre-laying exodus had a higher hatching success (Hatch, 1990a).

Despite the likely importance of this period for successful reproduction, knowledge of distribution during the pre-laying exodus is sparse for most *Procellariformes*. The only information on northern fulmars distribution during this period is from limited ringing recoveries (Wernham, 2002). These data are often biased to regions where birds may be recovered from beaches, or where they are by-caught in areas with high fishing effort (Harris et al., 2010). Furthermore, the breeding status of these birds is seldom known.

Bird borne transmitters and loggers are especially valuable for understanding colony- and individual-specific foraging patterns. Such data can permit conservation managers to evaluate the extent to which different age- or sex-classes from particular colonies may interact with specific threats such as renewables developments (Wade et al., 2014), oil and gas infrastructure (Ronconi et al., 2015), fisheries bycatch (Anderson et al., 2011, Løkkeborg and Robertson, 2002) or pollution events (Montevecchi et al., 2012). However, previous tracking work has typically been through short-term deployments during the chick-rearing period. At this time, birds are easier to capture and re-capture, but their foraging ranges are also constrained whilst provisioning chicks (Guilford et al., 2008, Votier et al., 2010). Earlier in the breeding season, distribution may vary more greatly, when these central-place constraints are weaker (Chapter 2). Consequently chick-rearing tracking data are likely to under-represent the full extent of these birds' spatial distribution over a complete breeding season.

Following courtship and mating, many seabirds are only loosely attached to their nest site and prone to flushing (Safina and Burger, 1983, Rojek et al., 2007). Capturing or recapturing birds to deploy or recover devices is therefore difficult or impossible until breeders start to sit more tightly on eggs or young chicks. Light-based Global Location Sensing (GLS) loggers, deployed in preceding seasons, provide the potential to better understand distribution and foraging trip characteristics during these periods when short-term deployments of high-resolution data loggers are not possible. GLS loggers can be ring-mounted and recovered after one or more years whereas devices that are attached to feathers may be lost more readily during longer deployments (Phillips et al., 2003). GLS loggers have the additional advantage that their small size (< 5g) means that they can be deployed on even very small seabird species, such as Arctic terns *Sterna paradisaea* (86-127 g; Egevang et al., 2010) thin-billed prions *Pachyptila belcheri* (130 g; Quillfeldt et al., 2012) and Leach's petrels *Oceanodroma leucorhoa* (ca. 45 g; Pollet et al., 2014a).

As previously discussed (Chapter 2) the primary disadvantage of GLS devices is that the accuracy of tracking data is low, with errors in the region of 200 km (Phillips et al., 2004). Consequently, these data have tended to be used to describe broad-scale patterns of distribution. It remains unclear to what extent even complex modelling of these data (Jonsen et al., 2005, Thiebot and Pinaud, 2010, Lisovski and Hahn, 2012) can be used to characterise finer scale movements within individual foraging trips. Previously, only three studies have directly assessed the accuracy of these devices on seabirds using a combination of light-level geolocator and satellite-derived location estimates.

In the first of these, an early light-level geolocator study involving double-tagged albatrosses revealed that a simple two-stage iterative smoothing algorithm could reduce the mean error of location estimates (Phillips et al., 2004). Twelve breeding black-browed albatrosses *Thalassarche melanophrys* were tracked with both GLS and ARGOS PTT devices, during a total of 138 complete (and 12 incomplete) foraging trips. The mean distance between contemporary GLS and PTT locations was 186 km, with SDs of ± 1.66° latitudinal and ± 1.82° longitudinal error around the GLS locations. After double smoothing, errors were reduced by 9 %, to a mean of 169 km.

Subsequently, a study on Laysan and black-footed albatrosses in the Pacific Ocean compared both light-level and SST-derived geolocations with ARGOS telemetry locations (Shaffer et al., 2005). This study found that the mean distance between light-derived geolocations and satellite-derived locations was 400 ± 298 km. This was reduced to 202 ± 171 km when light-based longitude and sea-surface temperature (SST)-derived latitude was used to estimate position.

Finally, a recent study used a suite of data from double-tagged marine predators (pinnipeds, birds and fish) within a two-stage Bayesian state-space model to estimate geolocation error and improve location estimates (Winship et al., 2012). The state-space model (for a detailed description, see Jonsen et al. 2005) was fitted to both high-precision satellite-derived locations (GPS and ARGOS) and low-precision GLS data from each double-tagged individual. The primary output from stage one of the model was a mean error, in both latitude and longitude, between the raw geolocation data and the locations estimated by the state-space model (fitted to both satellite-derived and GLS data). This resulted in mean SDs from two species of albatross (n = 27) of between 1.9 – 3.9° longitude, and 1.2 – 1.9° in latitude.

At boreal colonies, northern fulmars typically make regular visits to their breeding colony through the spring (Fisher, 1952, Hatch, 1990b). However, there is evidence of a longer absence from the colony prior to egg-laying and subsequent incubation. Observed attendance at the breeding colony on Eynhallow, Scotland, dropped to 3 – 10 % of the breeding population (based on number of eggs laid) in the weeks prior to commencement of laying, whilst pre-laying absences in excess of three weeks have been recorded at Scottish colonies (Dunnet et al., 1963). It is hypothesised that the stronger attachment of the male to the nest site is due to mate-guarding and avoidance of extra-pair copulation (Hatch, 1987, Hatch, 1990a). Whilst these characteristics of pre-laying exodus durations have been identified, knowledge of spatial distribution of fulmars at this time of year is virtually non-existent.

This chapter aims to (1) use data collected from simultaneously-deployed GLS and GPS dataloggers during long incubation trips within a state-space model (SSM), to estimate the error around GLS tracking locations from fulmars; (2) fit the SSM (using previously determined errors) to GLS-only data from the pre laying exodus; and to (3) compare the spatial distribution of males and females from a single UK colony to assess the extent to which these birds use different North Atlantic management regions during the pre-laying exodus.

Methods and materials

Device deployments

Fieldwork was carried out on Eynhallow, Orkney Islands, Scotland (59.12° N, 3.1° W), where regular colony visits were made each year to collect data for individual based demographic studies (Dunnet et al., 1979, Dunnet, 1991, Thompson and Ollason, 2001, Grosbois and Thompson, 2005, Lewis et al., 2009). Typically, this work involved colony visits in late May, when birds had completed laying, during the early chick rearing period in July, and immediately prior to fledging in mid-August.

The double-tagging experiment was carried out during the breeding seasons of 2011 and 2012. To attach and recover dataloggers, breeding fulmars were caught under licence (PPL 60/3689) on the nest using a net or noose in late May. Birds were fitted with a GPS logger (attached to mantle feathers using six strips of Tesa® waterproof tape; MobileAction® iGot-U GT-120, 18 g) and geolocator (using a cable tie around a Darvic leg ring; BAS Mk15, 3.6 g). The total weight of these devices was no more than 3% of the birds' body mass. GPS devices were programmed to record one position every hour for the duration of the battery life or foraging trip, whichever came first. GLS dataloggers recorded light levels (Phillips et al., 2004), and whether the device was wet or dry every 3 s, and stored summarized data (maximum light level and number of wet samples) every 10 min (Mackley et al., 2011). In 2011, attempts were made to re-capture birds during the subsequent visit in July, whilst in 2012 birds were recaptured when they returned after their first foraging trip, when possible.

More detailed investigation of the pre-laying exodus was made using data from GLS deployments on Eynhallow fulmars that had previously been used to study on winter distribution patterns between 2006 and 2012 (Quinn, 2014). These dataloggers had been deployed using the same attachment method described previously.

GPS loggers were downloaded and extracted using '@trip' software (MobileAction™). Geolocator loggers were downloaded, extracted and location estimates generated using the BASTrak software package (British Antarctic Survey). Data processing was carried out in Excel (Microsoft Corporation) and statistical analyses were carried out using R (R Core Development Team 2013) and WinBUGS (Lunn et al., 2000), using the method described in Winship et al. (2012). Data visualisation and mapping was carried out in ESRI Arc GIS 10.0.

Double-tagged data analysis

GPS tracking data were filtered to include only the period when the birds were away from the nest on foraging trips. The filtered data were then used to estimate the total duration of each trip. Time of departure from the nest was identified as the time of first location greater than 500 m from the nest site. Time of return was taken as the time of the first location less than 500 m from the nest site.

GLS data files containing light levels were then analysed to produce twice-daily location estimates for the period of interest, using the BASTrack software suite (Fox, 2010). A light threshold level of 10 and a solar elevation of -3.5° were used to identify sunrises and sunsets (transitions) using TransEdit2 software (following the procedures used by Quinn, (2014)). The solar transitions were used to calculate a maximum of two locations per day, based on day length and the time of noon and midnight, using BirdTracker software. The quality of light data from GLS dataloggers can sometimes be affected by body and feather shading, time sitting at the nest site and weather conditions. These errors resulted in uncertainty around some estimates of sunrise and sunset. Locations based on poor-quality transitions (from visual examination of the light trace, i.e. where estimation of the time of sunrise/sunset was highly uncertain) were therefore removed from the analysis. Where loggers had recorded uninterrupted daylight (due to 24 h daylight at high latitudes) no transitions could be identified and thus no estimated positions could be derived, although the data do confirm that birds were in northern latitudes.

GLS files were thereafter filtered to include only the period when the bird was known to be off the nest (established from GPS data). Times of the start and end of foraging trips (estimated from the GPS logger data) were included in the GLS location data file, and were fixed to the known location of the breeding colony.

For each double-tagged individual in turn, a Bayesian state-space model (SSM; Winship et al., 2012) was fitted to both GLS and GPS datasets simultaneously. GPS data were used within the model with an assumed high precision, to estimate the probability distributions for the geolocator position estimates (states). The process model within the SSM was the first-difference correlated random walk model, as described by Jonsen et al. (2005). Location states at each regularised time step (6 h) were estimated from the GPS data, using movement parameters based upon mean direction of movement and mean turning angle. Speed during any given time step was derived as a vector based on the movement in latitude and longitude between time t and $t+1$, as a function of speed during the previous time step and movement parameters. The model assumes linear movement between two time points.

The observation model related the two data sources to the true animal locations:

$$y_i = \mu_i + \varepsilon_i$$

where y_i *is the* i^{th} pair of GPS/GLS latitude/longitude data, μ_i is the corresponding true latitude and longitude, and ε_i is the random, normally distributed, serially independent observation error. True locations were calculated from estimated states that were regular in time. The process is described in detail by Winship et al. (2012).

The model output generated one location per day. Means of estimated longitude and latitude geolocation errors were calculated for each individual animal from the double-tagged study. These mean errors could then be applied to other tracking data sets where only GLS data were available.

Defining the pre-laying exodus

General patterns of colony attendance through the early breeding period (1 April to 31 May) of 2012 & 2014 were characterised using time-lapse photography. A time-lapse camera (Pentax K200D) was located overlooking approx. 20 regularly used nest sites on a cliff at 59.156° N 3.11° W, on the north coast of Eynhallow. Photographs were first graded to exclude those in which poor light or weather conditions might bias counts. Counts of the total number of both pairs and single birds were then made from each photograph, and the maximum daily count was used to investigate variability through the two-month period.

Individual pre-laying exodus trips were defined by investigating the light and activity trace from GLS loggers. Some of the loggers used in Quinn's (2014) studies had failed by April, whilst others had incomplete activity data due to limited memory capacity. For this study, only birds that had light data for the early breeding period (15 May – 30 June) were selected. Furthermore, only birds that were observed actively breeding (incubating an egg or rearing a chick, whether successfully or not) in the year of study were included in the analysis.

Initial exploratory analyses considered only those cases where both members of the pair were carrying geolocators. Light (and where available, activity) traces were examined simultaneously for each member of the pair, to determine when both birds were at the colony. Where transition from an irregular (due to shading on land) to a clean light trace occurred concurrent with the transition from dry to wet/mixed activity (*Fig. 3.1*), this was taken as indication that the bird had departed to sea after a period on land. Where activity data were not available, only the light data could be used to estimate the start of the pre-laying exodus.

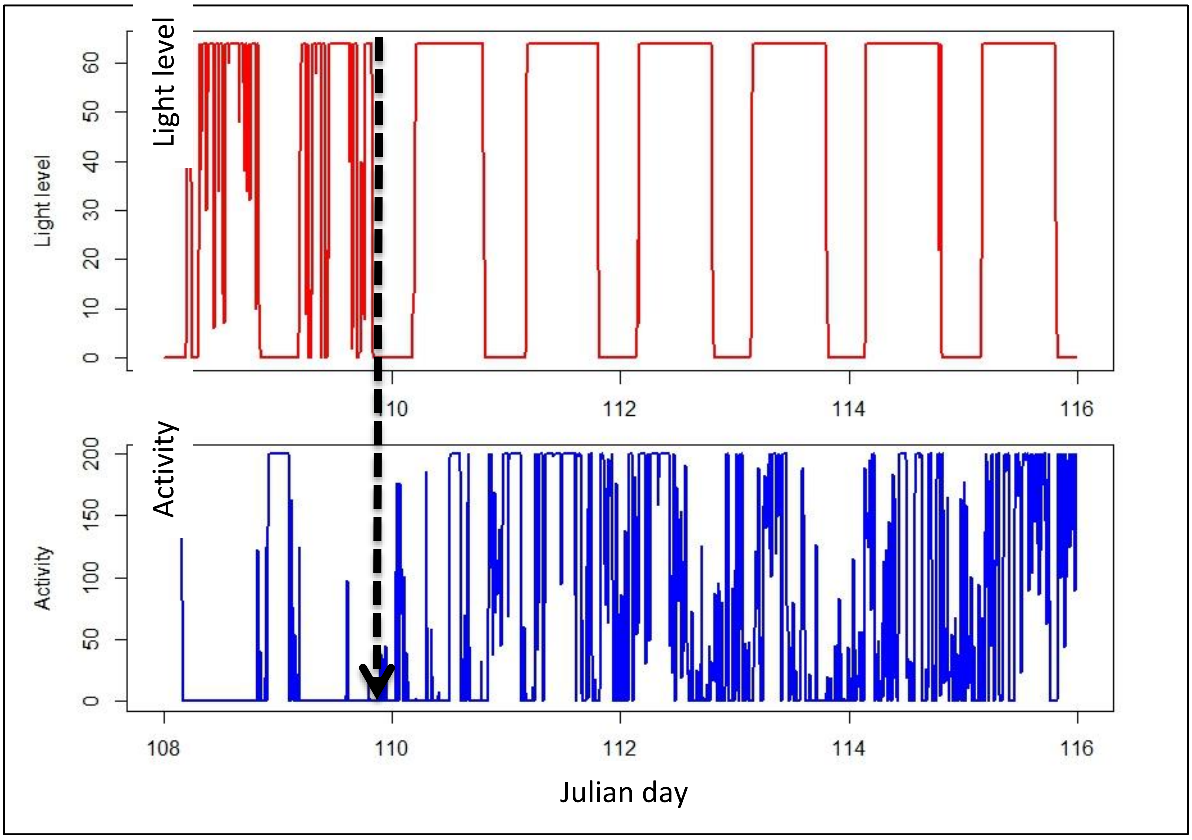


Fig. 3.1. Example of a light and activity trace from a fulmar (female; birdID 1595_2010) at the start of the pre-laying exodus. The dashed arrow indicates the point when the bird was deemed to have departed the nest. It can be seen that the light trace above becomes clean and uninterrupted during days, and the activity trace no longer illustrates extended dry periods.

Return date/time was estimated from the first extended long dry period (> 6 h) after a long period where the logger was periodically wet. Typically, this also corresponded with transition from well-defined days and nights to an irregular light trace, where the logger was hidden under body feathers and thus regularly occluded during the days whilst on the nest. This reinforced the assumption that the bird was at the colony. Trip durations could be estimated from these departure and return date/times.

The analyses of data from tracked pairs indicated that robust estimates of the duration of the pre-laying exodus could generally be derived from the GLS light traces alone. Light traces from all other birds in the data set were then analysed to estimate the dates and times of departure from, and return to, the nest using the same rules. All available GLS light files were subsequently analysed to produce location estimates for each day and night during each birds pre-laying exodus trip. If pre-laying exodus data were available for multiple years, data from only one year was selected. To maximise sample size within one year, 2011 data were preferentially retained. If 2011 data were not available, data from one other year were selected at random. Following previous data filtering, poor quality light data were removed from the analyses. Also, tracking data points during periods when birds were exposed to constant daylight could not be used to determine location so were filtered from the GLS location data sets.

Some birds that flew north were exposed to constant daylight in the Arctic region. Where this occurred, locations were not estimated because no sunsets or sunrises could be defined. All instances of constant daylight were recorded separately as this indicated that these birds were in high latitudes at this time.

State-space modelling of pre-laying exodus trips

For each individual pre-laying exodus trip, the SSM was fitted to the geolocator positions, parameterised with the mean of the geolocation error estimates in latitude and longitude estimated from the double-tagged incubation trips (Table 1). The start and end times of each pre-laying exodus trip were included within the data file to which the SSM was fitted, fixed to the latitude and longitude of the colony.

The resulting modelled daily locations for each trip were then explored in ESRI ArcGIS. The maximum distance from the colony during the pre-laying exodus trips was characterised by identifying the furthest modelled location from the colony, and taking the mean of this location and both the preceding and subsequent locations. This mean of these three most distant locations was then used to estimate foraging range from the colony and categorise each pre-laying exodus trip to an OSPAR biogeographical region (OSPAR 1992). Linear mixed-effects models were used to compare between sexes using ‘lme4’ (Bates et al., 2015) and with ‘lmerTest’ (Kuznetsova et al., 2015) to estimate degrees of freedom and calculate p-values.

Results

Double-tagged analysis

From nine double-tagged deployments in 2011, only one bird was recovered with both loggers still attached. In 2012 from 22 deployments, 10 birds were recaptured with both loggers still attached. In 2012, two birds lost their GLS logger and four birds had lost their GPS. 14 birds (2011, n=8; 2012, n=6) were not recaptured within the year of study. Deployments where recovery was attempted after one foraging trip (2012) were more successful than those where recoveries were attempted after a six-week interval between colony visits (2011).

Fitting the state-space model to data from each individual trip produced a mean geolocation error (in degrees) per trip for the sample (*Table 3.1*). The sample mean error in both latitude and longitude were later used within the GLS-only pre-laying exodus analysis.

Table 3.1. SD of errors in longitude and latitude, in degrees, estimated from state-space model (Winship et al. 2012) fitted to both GLS and GPS data collected from double-tagged individuals during incubation period. Also included are the trip duration (in days) and numbers of locations used to fit the model.

Year_BirdID	**$\widehat{SD}_{\text{lon}}$ error (± °)**	**$\widehat{SD}_{\text{lat}}$ error (± °)**	**Trip duration (d)**	**No. GPS locations**	**No. GLS locations**
2011_1890	0.024	0.310	8.69	213	18
2012_1568	0.114	0.399	14.06	348	30
2012_1153	0.074	0.193	11.90	290	25
2012_1854	0.059	0.173	9.88	176	14
2012_1915	0.315	0.496	2.61	64	7
2012_1911	0.056	0.302	14.20	157	29
2012_1355	0.116	1.212	5.08	126	11
2012_1631	0.735	0.057	3.92	97	8
2012_1641	0.090	0.086	2.91	72	7
2012_1893	0.184	0.260	1.80	45	5
2012_1580	0.572	0.808	3.69	64	8
Mean	**0.212**	**0.391**	7.16	150	14.7

Analysis of photographs from the time-lapse camera study site revealed that the mean peak in attendance of individual birds fell on 19 April. The mean peak in attendance for pairs of birds at nest sites was also 19 April (*Fig. 3.2*). Numbers of individual birds attending the colony had fallen to 25% of the peak numbers by 4 May.

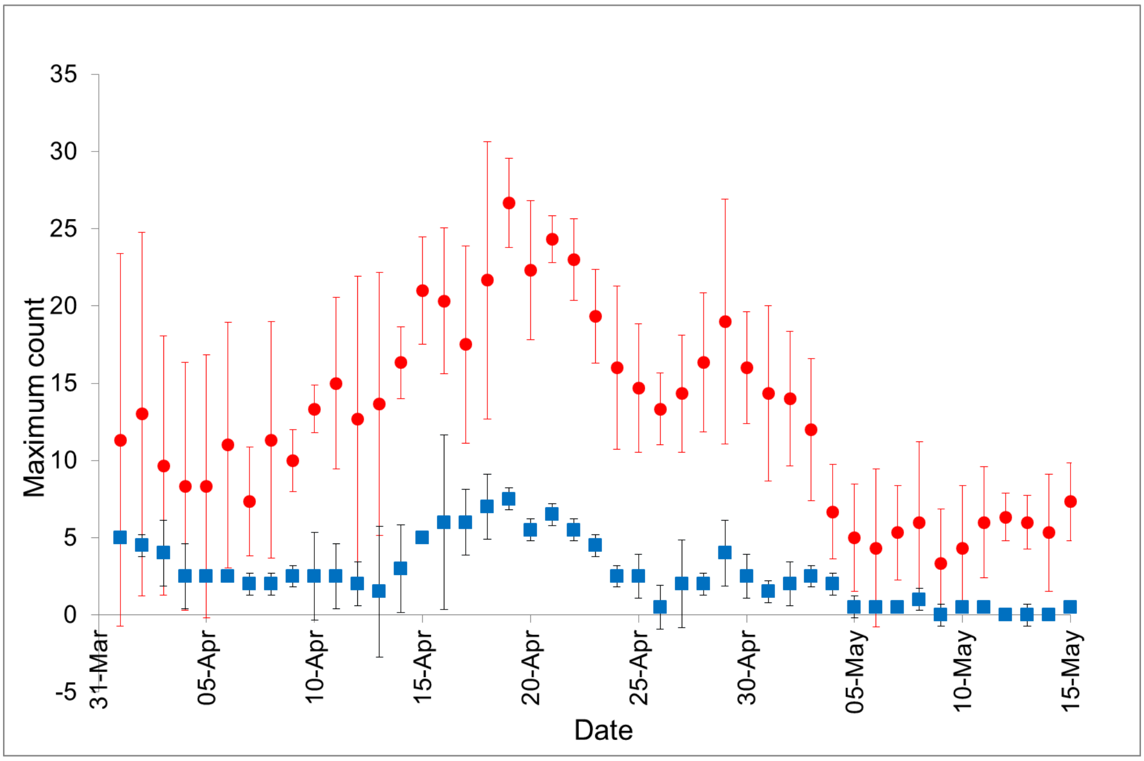


Fig. 3.2. Average attendance at the colony of number of individual birds (mean of two years ± SD; red circles), and pairs of birds at nest sites (mean of two years ± SD; blue squares), for the period 1 April to 31 May 2012 and 2014.

Of 163 geolocators deployed between 2006 and 2012, the pre-laying exoduses of 39 actively breeding fulmars were analysed (20 males; 19 females). GLS light traces for each individual were examined in detail to determine date and time of departure (*Table 3.2*). Generalized linear mixed-effects models were used to investigate the effect of sex on the maximum distance from colony, departure date and pre laying exodus duration. In all three models, year was included as a random effect to account for interannual variability. Sex affected pre laying exodus duration, with trips by males about 7.08 days ± 1.69 (SD) shorter than those of females (t(36.53)= -4.2, p < 0.001; *Fig. 3.3(a)*). There was a sex difference in departure date, with males departing about 6.13 days ± 1.5 (SD) than males (t(36.5) = 4.1, p < 0.001; *Fig. 3.3(b)*). Sex also affected maximum distance from the colony, with males staying about 496.6 km ± 243.1 (SD) closer to the colony (t(37) = -2.04, p = 0.049).

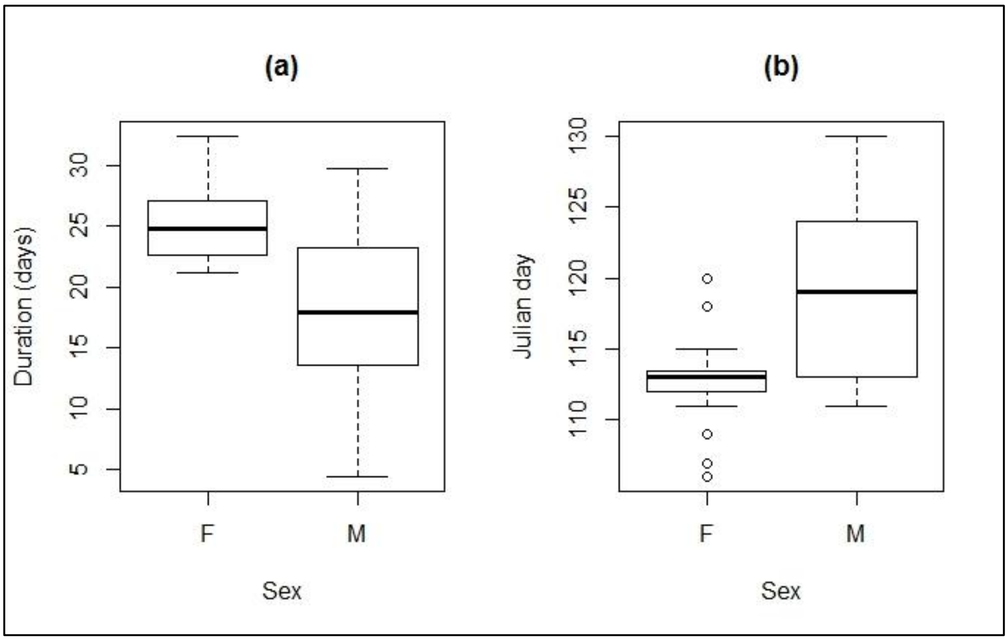


Fig. 3.3. Boxplots showing (a) pre-laying exodus durations for males and females, and (b) pre-laying exodus departure date (in Julian days) for males and females. Data from all years (2008 – 2012).

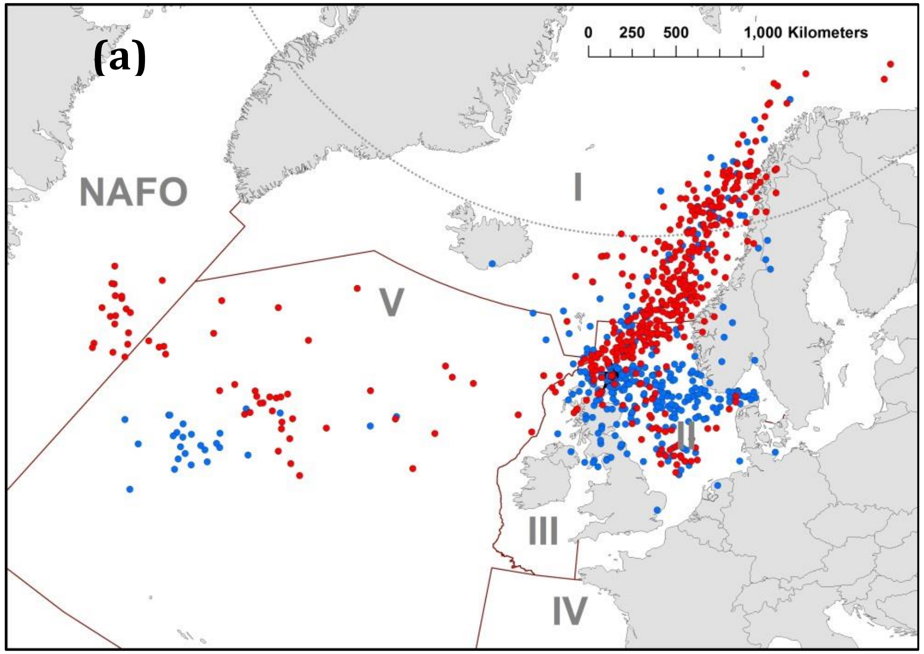
Table 3.2. Summary of pre-laying exodus characteristics for male and female fulmars, tracked using geolocator.

	Sample size	Median departure date (range)	Median return date (range)	Median trip duration (range)
Male	20	29-April (21-April – 10-May)	17-May (8-May – 23-May)	18.0 (4.4 – 29.8)
Female	19	23-April (16-April – 30-April)	18-May (14-May – 28-May)	24.8 (21.1 – 32.5)

Twelve (60 %) of the 20 males foraged within the greater North Sea (OSPAR regions II/III) during the pre-laying exodus. Six (30 %) foraged in Arctic waters (OSPAR region I) and two (10 %) foraged in the Wider Atlantic region (OSPAR region V), as far west as 42° W. Three male birds were classified as foraging over the west coast of the UK, but it is likely that these locations are artefacts of averaging the three modelled locations, and the birds are likely to have foraged within OSPAR Region II (*Fig. 3.4*).

In contrast only three (16 %) of the 19 females foraged within OSPAR regions II/III, whereas thirteen (68 %) foraged within OSPAR region I. Two (11 %) foraged in the OSPAR region V and one bird foraged west of the OSPAR region, within the NAFO fisheries management area (46° W; *Fig. 3.4*).

From the sample of 39 individuals, 14 birds (36 %) foraged to the north of the Arctic Circle (latitude 66.23° N). Six individuals lost GLS locations due to 24h daylight in the Arctic at this time of year (3 male, 3 female). Of these, the average number of daily GLS locations lost per bird was 10, with a range from 1 – 22 (*Fig. 3.5*).



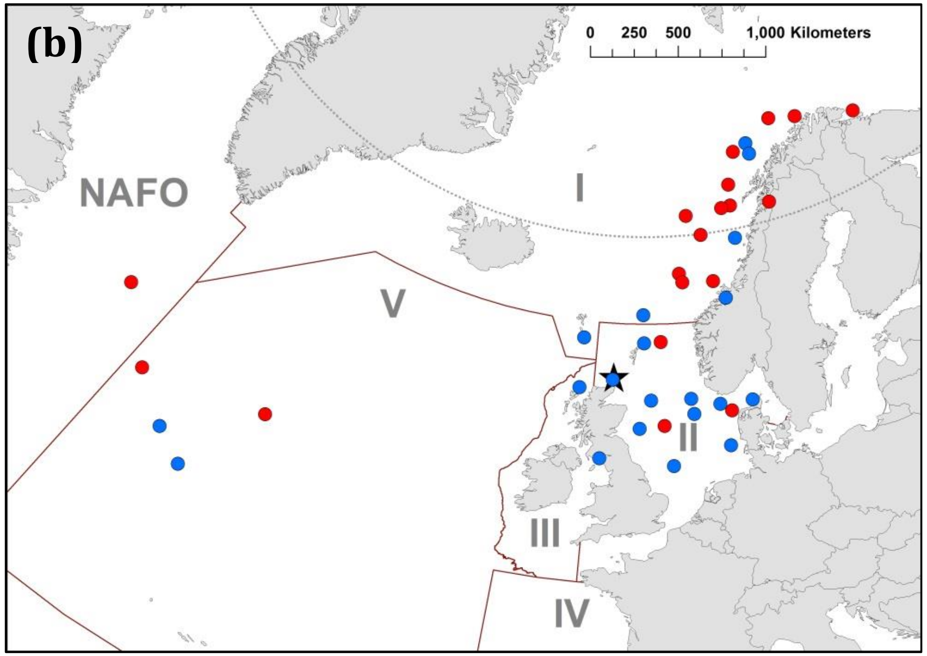


Fig. 3.4(a). Map showing daily modelled locations of each bird tracked during the pre-laying exodus. Males are indicated by blue points, females are indicated by red points. The black star indicates the location of the colony. OSPAR and NAFO management regions are delineated by red lines. The Arctic Circle (66.33° N) is indicated by the dashed grey line.

Fig. 3.4(b). Map showing maximum distance from the colony for each male (blue) and female (red) fulmar. The black star indicates the location of the colony. OSPAR and NAFO management regions are delineated by red lines. The Arctic Circle (66.33° N) is indicated by the dashed grey line.

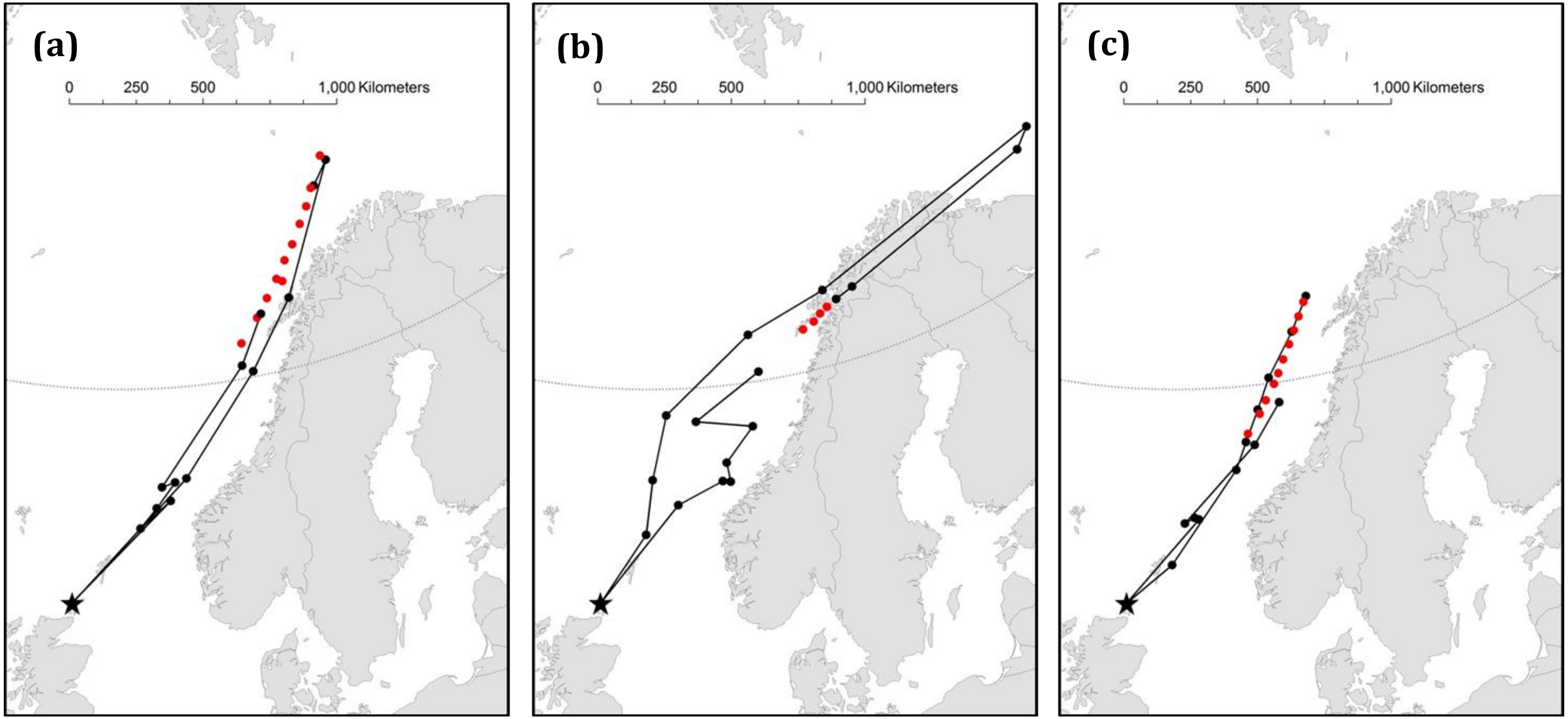


Fig. 3.5. Maps showing track of pre-laying exodus of three individual fulmars. Black circles linked by black lines indicate daily locations from state-space model fitted to GLS data. Red circles indicate locations from the state-space model for days where no GLS location was available because of high-latitude constant daylight. Black stars indicate the location of the study colony (a) bird 1854 (12 days 24 h daylight), (b) bird 1777 (5 days 24 h daylight), (c) bird 1862 (11 days 24 h daylight).

The extent to which birds were found in different OSPAR regions differed between sexes, χ^2(df = 2, n = 39) = 8.16, $p < 0.05$. Most females (68 %) foraged in OSPAR region I, and most males (60 %) remained within the greater North Sea area (regions II/III). Numbers of male and female birds that foraged in the mid/west Atlantic were small (*Table 3.3*).

Table 3.3. Birds tracked using geolocator, classified to a foraging region based on their maximum extent from colony during the pre-laying exodus

	Sample size	Number of birds in OSPAR Region I (%)	Number of birds in OSPAR Region II/III (%)	Number of birds in OSPAR Region V or NAFO region (%)	Mean maximum distance from the colony (km ± SD; (range))
Male	20	6 (30)	12 (60)	2 (10)	942 ± 773; (24 – 2792)
Female	19	13 (68)	3 (16)	3 (16)	1438 ± 743; (385 – 2887)

Birds that foraged in OSPAR Region I carried out significantly longer duration trips than birds that foraged in Region II (Student's t-test, t = 2.62, df = 26.2, p-value = 0.014). Birds that foraged in Region V appeared to carry out longer trips than birds that foraged in Region II, but the small sample size (n = 5) meant they were not compared statistically (*Fig. 3.6*). Pre-laying exodus duration was positively correlated with the square-root-transformed maximum distance from the colony (n = 39, R^2 =0.89, $p < 0.001$; *Fig. 3.7*).

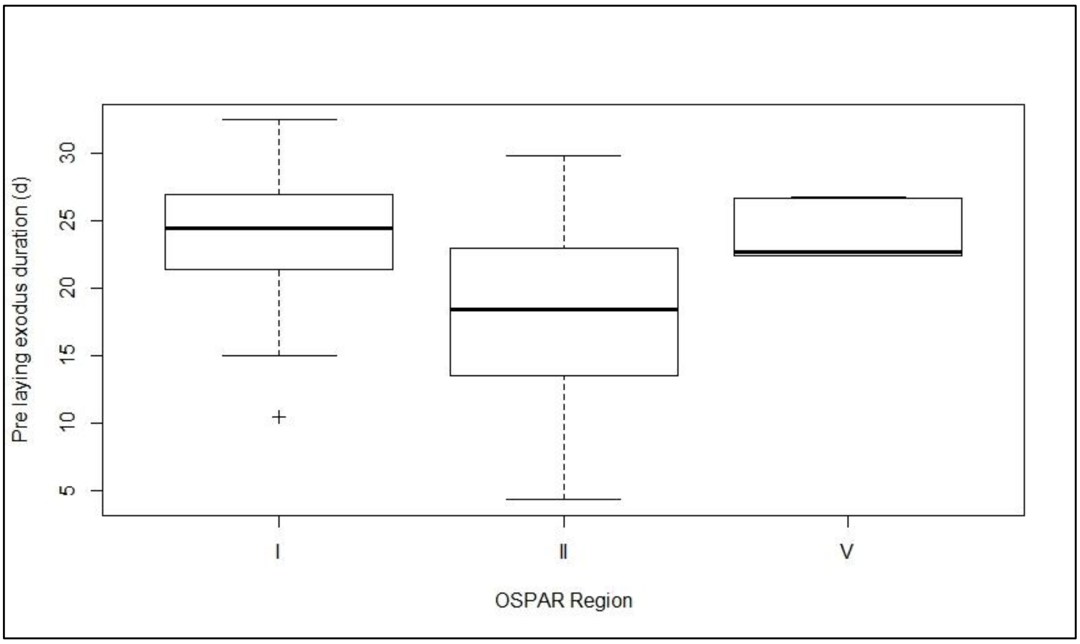


Fig. 3.6. Comparison of trip duration between birds foraging in three OSPAR regions.

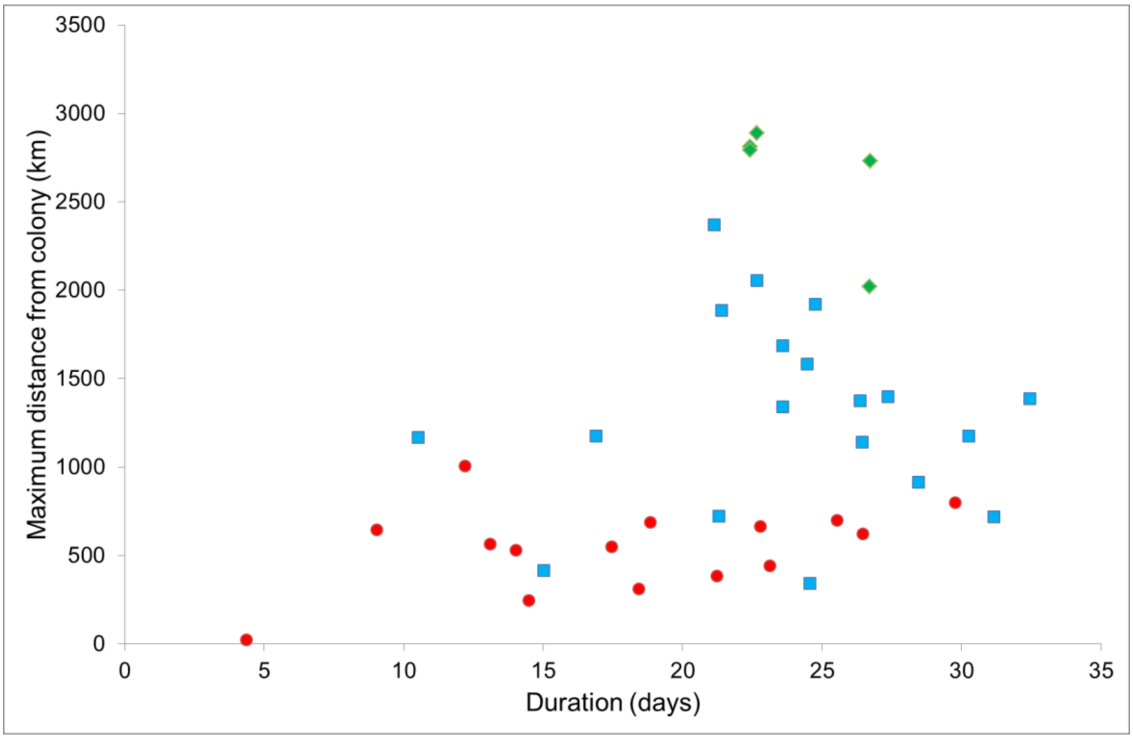


Fig. 3.7. Scatterplot showing relationship between pre-laying exodus duration and maximum distance from the colony. Blue squares represent birds that foraged in OSPAR Region I (Arctic Waters). Red circles represent birds that foraged in OSPAR Region II (Greater North Sea). Green diamonds represent birds that foraged in the Region V (Wider Atlantic).

Discussion

Even though earlier studies revealed that fulmars can make a pre-laying exodus of 3-4 weeks (MacDonald, 1977b, Hatch, 1990b), no study has previously shown where birds foraged during these longer trips. The work presented here has revealed that fulmars from a single Scottish colony can forage across three very different biogeographical regions, over 25° of latitude, and 78° of longitude, during the early breeding season. The data suggest a maximum range of 2890 km from the colony. Whilst acknowledging that this study explored an early stage of the breeding season when birds were known to undertake long excursions from the colony (MacDonald, 1977b), this range far surpasses the previously estimated breeding foraging range of approximately 580 km during the chick rearing period (Thaxter et al., 2012, Hamer et al., 1997).

Determining GLS error

A state-space model was fitted to both GPS and GLS data from double-tagged fulmars during the incubation period. The estimated geolocation errors in latitude and longitude were largely comparable to those found by Winship et al. (2012) as part of a multi-species tagging study, although the mean fulmar error estimates were smaller for both longitude and latitude than those calculated for both black-footed albatross and Laysan albatross in the multi-species study (2-4°). This was the fourth study to attempt to estimate GLS error from seabirds through double tagging (Phillips et al., 2004, Shaffer et al., 2005, Winship et al., 2012), the first on a non-*Diomedeidae* species and the only one in the North Atlantic area. This was only possible due to the concurrent deployment of high-precision GPS data loggers with the light-level geolocators, and the results of this study build confidence in the usefulness of GLS location data in the study of spatial ecology of wide-ranging marine animals.

Fulmars are known to range widely during the overwinter period (Macdonald, 1977c, Quinn, 2014, Wernham, 2002) and there is growing evidence that fulmars can cover long distances during the breeding season (Weimerskirch et al., 2001, Edwards et al., 2013). This study shows that foraging > 2000 km from the breeding colony is not restricted to the post-breeding period. During a critical period in the early breeding season, fulmars of both sexes are traveling thousands of kilometres from their colony, and foraging in three distinct biogeographical regions with very different oceanographic regimes.

Duration of the pre-laying exodus.

The time-lapse camera data suggested a peak number of birds at the colony around 20 April. This is just prior to the median departure date of female birds as estimated from geolocator data (23 April). A previously-established median lay date at Eynhallow of 22 May (Ollason and Dunnet, 1978) also corresponds closely with the end of the pre-laying exodus as judged from the geolocator data in this study. Earlier studies at fulmar colonies in Europe and North America reported pre-laying exodus durations. A study at Eynhallow in the early 1960s reported a mean pre-laying exodus duration of 14 days for males, and 16 days for females (Dunnet et al., 1963), whilst a study in Aberdeenshire in 1972 – 1975 reported that females depart, on average, 21 days before egg laying and that the male pre-laying exodus is 12 days (MacDonald, 1977b). In the Pacific, Hatch (1990) recorded pre-laying exoduses of 12.2 days for males and 17.6 days for females. The pre-laying exodus durations reported in this study are longer (females 25 days, males 18 days). It is uncertain whether this is due to inter-colony variability, differences in the method of determining departure from the colony, or a real increase in the duration of pre-laying exodus trips since this early study is uncertain.

This study was carried out more than 40 years after the previous investigations on the durations of the pre-laying exodus at Scottish colonies, during which time the fulmar population in north western Europe has undergone a large expansion in size (Fisher, 1966, Cramp et al., 1974, Lloyd et al., 1991, Mitchell et al., 2004) and range (Kerbiriou et al., 2012). Trip durations for birds foraging within OSPAR Region II (Greater North Sea) are more closely comparable to those from the earlier study at Eynhallow (Dunnet et al., 1963). The increase in mean foraging trip duration could be related to birds having to travel farther from the colony to find food, owing to greater intraspecific competition, as seen in gannets which have also experienced a dramatic population increase (Lewis et al., 2001).

Together, data from the time-lapse camera and geolocators give confidence that the rules used to define departure from the colony and return to the nest site give a reasonable estimation of trip duration. Whilst defining time on land using dry periods of activity coupled with interrupted light traces is most likely reliable, there is still uncertainty about whether this time on land was at the breeding colony. Nevertheless, *Procellariformes* generally show high site fidelity and monogamy (Thibault, 1994, Mougin, 1996, Bried et al., 2003) and as such it is likely that during this time the birds are at nest sites at which they intend to breed.

Using the clean light trace to define the start and end of the pre-laying exodus, time of departure from the colony is unlikely to be mis-specified by greater than 7 h: the approximate night duration (i.e. between sunset and sunrise) at Eynhallow during the period considered in this study. In future, a combination of geolocator and time-lapse photography (Gaston et al., 2014), or passive integrated transponder (PIT) tagging of individuals (Mallory et al, 2008) could provide more precise definition of a rule for departure and return time.

Using geolocator data to investigate distribution during the pre-laying exodus

The state-space model was fitted to the GLS location data collected during the pre-laying exodus, from 39 fulmars known to be breeding during the year of tracking. This required using the error estimates from the double-tagged incubation data to parameterise the model and GLS activity and light data to estimate departure and return times. For female birds, the duration of the pre-laying exodus was clearly identified from patterns in the geolocator light data. Based on examination of the geolocator data, female fulmars were not thought to attend the colony at all during their pre-laying exodus. However, male fulmars are known to make shorter pre-laying exoduses than females (Dunnet et al., 1963, MacDonald, 1977b, Hatch, 1990b), and some never leave the vicinity of the colony. It is obvious from patterns in the geolocator data that males often spent longer around the colony after the departure of the female, and some male birds showed intermittent dry periods longer than would be expected of birds on a long foraging trip, indicative of time on land. For this reason it is reasonable to assume that departure and return dates/times based on geolocator data from females is of a higher reliability than that of males. The fact that even female pre-laying exodus durations are substantially longer than those found in previous studies, suggests that the increased durations of absence from the colony reported in this study are a true increase in trip duration, rather than an artefact of poor definition of start and end times of trips.

This study illustrates that fulmars use similar areas during the pre-laying exodus as they do during post-breeding dispersal/migration (Quinn 2014). More data would be required to examine whether an individual's pre-laying exodus distribution was related to its overwintering or incubation-period distribution. It would be of additional interest in the future to compare winter and pre-laying exodus consistency, and to assess whether pre-laying exodus characteristics have an impact on breeding success.

The locations generated by the state-space modelling of GLS data are by no means error-free. Nevertheless the relatively few number of locations appearing over land, even where birds have flown to coastal regions such as the Norwegian Shelf and the Skagerrak, adds confidence to the modelled outputs of the SSM being of higher accuracy than raw geolocator locations, which have a mean error of around 186 km (Philips et al. 2004). One caveat of geolocator data at this time of year is that the birds can encounter constant daylight at very high latitudes. As geolocators use sunrises/sunsets to estimate location, the constant daylight means that location data are lost. One bird lost 22 consecutive locations due to being exposed to constant light, and six birds lost ≥ one location, due to foraging in Arctic waters.

At latitudes north of the Arctic Circle (66° 33′ N), the sun does not set during midsummer. At approx. 70° N, constant daylight (with no sunrises or sunsets) is experienced continuously from mid-May until late July. North of 78° N the sun does not set between mid-April and late August. It is therefore apparent that when no sunrise/sunsets are recorded by the geolocator, the birds are north of the latitude at which the sun does not set on any given day.

When no consecutive sunrise and sunset is recorded, no location can be estimated from geolocation data. When no daily estimated location was provided to the state-space model, locations are interpolated linearly between the preceding and successive estimated daily locations (as estimated from sunrise/sunset time). As a result it is highly probable that interpolated locations from the state-space model (e.g. the locations in red, *Fig. 3.5*) are underestimations of latitude, and thus maximum distances from the colony for birds foraging in these northern latitudes are also underestimated. If the logger was not recording solar transitions the birds are likely to be further north than these estimated locations. This problem is especially prominent for females, the majority of which foraged in OSPAR region I. One possible way of overcoming this would be to force the state space model to consider the lowest possible latitude in these instances would be the latitude at which the sun does not set on a given day. Developments in geolocator technology, using more sensitive light sensors, may allow more accurate estimation of locations even at latitudes when the sun does not set at certain times of year.

Ecological and management implications

By dispersing over such a wide area, fulmars can forage in regions with more predictable prey patches (Weimerskirch, 2007). Fulmars spend much of the early part of their life (i.e. pre-breeding) at sea, and no doubt explore much of the North Atlantic. It is possible that these experiences in early life dictate where they forage as adults. Deployment of geolocators on fledglings may reveal information about distribution during the early years. This will come with the cost of a low device recovery rate as recruitment of known-age individuals to the Eynhallow study colony is low, whilst geolocator battery life is at present restricted to ca. 2 years, and fulmars do not breed until ca. 7 years of age (Dunnet et al., 1979).

This wide-ranging behaviour can expose birds to different risks. Tens of thousands of fulmars are killed every year in demersal longline fisheries in Scandinavian waters (Anderson et al. 2011) and birds are also entangled in drift nets fishing for tuna west of Ireland (Rogan and Mackey, 2007). Whilst EU states have an obligation to protect birds within territorial waters (EC, 2009), birds do not recognise national boundaries. This study suggests that Scottish fulmars may not be subject to similar protection within international waters or other national jurisdictions that they visit, such as the Faroe Islands, Norway and Canada. More females than males foraged in Scandinavian waters, and thus it is possible that the risk of longline bycatch is greater to a particular sex, as has been seen in other species (Ryan and Boix-Hinzen, 1999). At the same time, stomach contents from fulmars collected in Icelandic waters showed lower plastic loading than birds found in the North Sea region (Kühn and van Franeker, 2012), with evidence that levels of plastic decline with increasing latitude within the North Atlantic. By foraging in OSPAR Region I, it is possible that some fulmars (mostly females) are exposed to less marine litter and its associated contaminants. Nevertheless, the central-place constraint later in the breeding season restricts the range of fulmars to the vicinity of the colony (ca. 1000 km radius), thus foraging within the more polluted North Sea region is necessary during chick-rearing (Chapter 1).

The oil and gas industry has also been identified as a threat to seabirds (Montevecchi et al., 2012, Ronconi et al., 2015, Fort et al., 2013). The prevalence of exploration and drilling installations along the Norwegian shelf is one potential threat which fulmars that use this region are exposed to. Indeed, many of the birds from this study overlap in range with a region of intensive fossil fuel exploitation. Threats come from pollution in the form of oil spills but also from risk of collision with flares and infrastructure (Wiese et al., 2001).

In conclusion, this study has shown that geolocator data can be used to investigate distribution of a wide-ranging seabird during the breeding season. Fulmars from this single Scottish colony foraged across three distinct biogeographical regions (OSPAR, 1992) during the early breeding season. Through a state-space model framework it has been possible to estimate geolocator location error using fulmars, double-tagged during incubation. This has been used to improve knowledge of foraging region using tracking data with low precision in its native form.

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Chapter 4: Tracking a northern fulmar from a Scottish nesting site to the Charlie Gibbs Fracture Zone: evidence of linkage between coastal breeding seabirds and Mid-Atlantic Ridge feeding sites

This chapter is included here as published: Edwards, E. W. J., Quinn, L. R., Wakefield, E. D., Miller, P. I. & Thompson, P. M. 2013. *Tracking a northern fulmar from a Scottish nesting site to the Charlie Gibbs Fracture Zone: evidence of linkage between coastal breeding seabirds and Mid-Atlantic Ridge feeding sites.* Deep Sea Research Part II: Topical Studies in Oceanography. Vol. 98, Part B, 15 December 2013, Pages 438–444

Abstract

The seas above mid-ocean ridges are biodiversity hotspots in an otherwise largely oligotrophic environment, but the nature and extent of linkage between these offshore regimes and coastal ecosystems remains uncertain. Using a combination of GPS and geolocation tracking data, we show that a male fulmar, breeding on the Scottish coast, foraged over areas of persistent thermal fronts along the Charlie-Gibbs Fracture Zone (CGFZ) of the Mid Atlantic Ridge during the incubation period. The bird travelled over 6200 km in 14.9 days. First-passage time analysis identified seven areas of restricted search, four on the shelf and three in the vicinity of the Mid Atlantic Ridge. Previous studies of incubation foraging trip durations at this site suggest that a trip of this duration is unusual, and further work is required to assess the extent to which different individuals use these offshore resources. Nevertheless, these data highlight the potential importance of high sea areas beyond the limits of national jurisdiction when considering the management and conservation of seabirds breeding in NW Europe, and raises the potential for even greater linkage between the CGFZ and seabirds breeding colonies in other regions.

Introduction

In recent years, the sea above the Charlie-Gibbs Fracture Zone (CGFZ) has become recognized as a region of rich biodiversity (Letessier et al., 2011, Letessier et al., 2012), providing an important foraging area for a broad suite of marine predators, including fishes (Fossen et al., 2008), seabirds (Bogdanova et al., 2011, Egevang et al., 2010, Frederiksen et al., 2012) and mammals (Doksæter et al., 2008, Skov et al., 2008). As a result, the region has been designated as a large High Seas Marine Protected Area by the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Commission) and the North East Atlantic Fisheries Commission (NEAFC) (Ospar, 2010). However, the nature and extent of linkage between these offshore areas and coastal ecosystems remains uncertain. Some of the animals (e.g. cetaceans, fishes) feeding in these areas remain in the pelagic environment throughout their life. But seabirds must return to land to breed, and an understanding of the relationship between these high seas regions and seabird breeding sites is essential to support efforts to conserve their populations. For example, European legislation calls for specific action to protect birds and their habitats (EC, 2009) with a particular focus on reduction of incidental bycatch of seabirds in fishing gears within European Union waters (FAO, 2008). However outwith territorial waters the legislation is more difficult to enforce.

Previous surveys of seabirds at sea (e.g. Boertmann, 2011) have been unable to determine the breeding origin, fidelity or frequency of use of individuals observed in high seas areas such as the CGFZ. Furthermore, seabirds do not recruit until they are several years old, and may skip breeding in some years. Consequently, even when seabirds have been observed in the CGFZ during the breeding season, these individuals may represent birds from the non-breeding component of the population that spend extended periods foraging at sea.

Tracking technologies have recently revealed that seabirds from Icelandic, Scottish and Canadian breeding colonies may spend some of their time over the Mid-Atlantic Ridge (MAR) area (Bogdanova et al., 2011, Egevang et al., 2010, Mallory et al., 2008b). Most published studies provide examples of seabirds foraging in this region during the winter, when individuals do not need to return regularly to coastal breeding colonies. To date, the only example of actively breeding adult birds that foraged over the CGFZ has been a study of Cory's shearwaters (*Calonectris diomedea*), which breed approx. 1200 km away on the Azores archipelago (Magalhães et al., 2008).

In this paper, we present tracking data from an adult male northern fulmar (*Fulmarus glacialis*) breeding on a Scottish island, which demonstrate that seabirds breeding at colonies on the European continental shelf can actively forage in the MAR area during the breeding season. This finding emphasises the trophic importance of high seas beyond the limits of national jurisdiction when considering the management and conservation of seabirds, and highlights the potential for even greater linkage between the CGFZ and seabird breeding colonies in other regions.

Study species

Northern fulmars, a circumpolar boreal species, are the most widespread and abundant seabird in the North Atlantic, breeding on coastal cliffs and grassy slopes from Arctic islands to the coast of Brittany, France (Mitchell et al., 2004). As generalist predators and scavengers, they consume a variety of fish, squid, crustaceans and offal (Phillips et al., 1999). Typical of other Procellariids, they are long-lived (Grosbois and Thompson, 2005), with a breeding period that extends, at Scottish colonies, from laying a single egg in mid-May, to fledging in late August (Dunnet, 1991). Foraging trips during the breeding season are considered to be constrained in range and duration because both partners share incubation (Mallory et al., 2008a), and then continue to take turns brooding and feeding the chick until fledging (Hamer and Thompson, 1997, Phillips and Hamer, 2000). Foraging trips during the breeding season have been reported to have a maximum duration of 18 d (Mallory et al., 2008a), and assumed to be limited to a maximum range of 580 km (Thaxter et al., 2012) based upon published information on foraging trip durations during chick rearing (Furness and Todd, 1984).

Materials and methods

The study was conducted at a fulmar breeding colony on Eynhallow, an uninhabited island in Orkney, off the north coast of Scotland (59.14° N, 3.12° W). This colony has been the subject of detailed demographic studies since 1950 (Dunnet, 1991). On-going tracking studies at Eynhallow seek to define the range of foraging by adults during the breeding season, and broad-scale winter distribution patterns. This paper presents data from tracking records that shows how far and for how long one fulmar forages.

Datalogger deployment and recovery

To attach and recover dataloggers, fulmars were caught under licence on the nest using a net or noose. In May 2012, 22 birds were fitted with a GPS logger (attached to mantle feathers using strips of Tesa® waterproof tape; MobileAction® iGot-U GT-120, weight 18g after modification) and geolocator (using a cable tie around a Darvic leg ring; BAS Mk15, 3.6g). Together the devices weigh ~3% of the birds' body mass. The GPS was set to record position every hour for the duration of the battery life or foraging trip, whichever came first. Geolocators (GLS) logged light levels (Phillips et al., 2004), and whether the device was wet or dry (see Mackley et al., 2011), every 3 s, and stored summary data (maximum light level and number of wet samples) every 10 min. Although these devices were used on deployments over single foraging trips in May 2012, they had previously been fitted to over 100 birds between 2008 and 2011, allowing daily data collection until recovery in subsequent breeding seasons.

The data presented in this paper were collected from an adult male (sexed using morphometric measurements; Dunnet and Anderson, 1961), fulmar #1568, which had bred at the same nest site and with the same partner since 2001. This bird was captured on the nest at 12:06 BST on May 23, 2012, while its female partner was on a foraging trip. Following capture, we removed a GLS logger that had previously been fitted to this male in July 2010, and a new GLS logger and GPS tag were then applied before he was resettled onto the nest. Both the new GLS logger and GPS tag were then recovered at 10.00 BST on June 10, 2012, after the male bird had completed one foraging trip and returned to relieve the incubating female. Following recovery, the male bird was resettled on the nest.

Analyses

GPS data were downloaded using the manufacturer's software, and tracks plotted using ESRI® Arc GIS 10. Great circle distances between each at-sea location and the nest site were calculated. Flight speeds between successive GPS locations were also calculated using great circle distances. We identified core foraging or resting areas using first-passage time (FPT) analysis (Fauchald and Tveraa, 2003, Pinaud and Weimerskirch, 2007), using the 'adehabitatLT' package (Calenge, 2006) in R 2.12.2 (R Core Development Team, 2013).

Data on light levels and activity were downloaded from the GLS logger, extracted and filtered using the BASTrak software suite (Fox, 2010). Sunsets and sunrises were manually identified using the programme TransEdit; the solar angle of elevation was set as -3.5°. All data from the equinoxes were excluded to avoid periods when latitude estimation was not possible, and noon and midnight positions were then visualized in ArcGIS. Activity data, available as the number of wet samples within each 10-min period through the deployment, were then used to classify the activity within each 10 min sample as completely dry, completely wet or mixed. Subsequently, sequences of these records were analysed to define the duration of extended bouts of each of these activity category.

Remote sensing data from microwave (AMSR-E, TMI, WindSAT) and infrared sea surface temperature (SST; AVHRR, MODIS) sensors were used to locate persistent oceanic fronts. Merging these data, seven-day composite front maps (Miller, 2009) were derived. More detailed descriptions of these methods are presented by Miller et al., 2013).

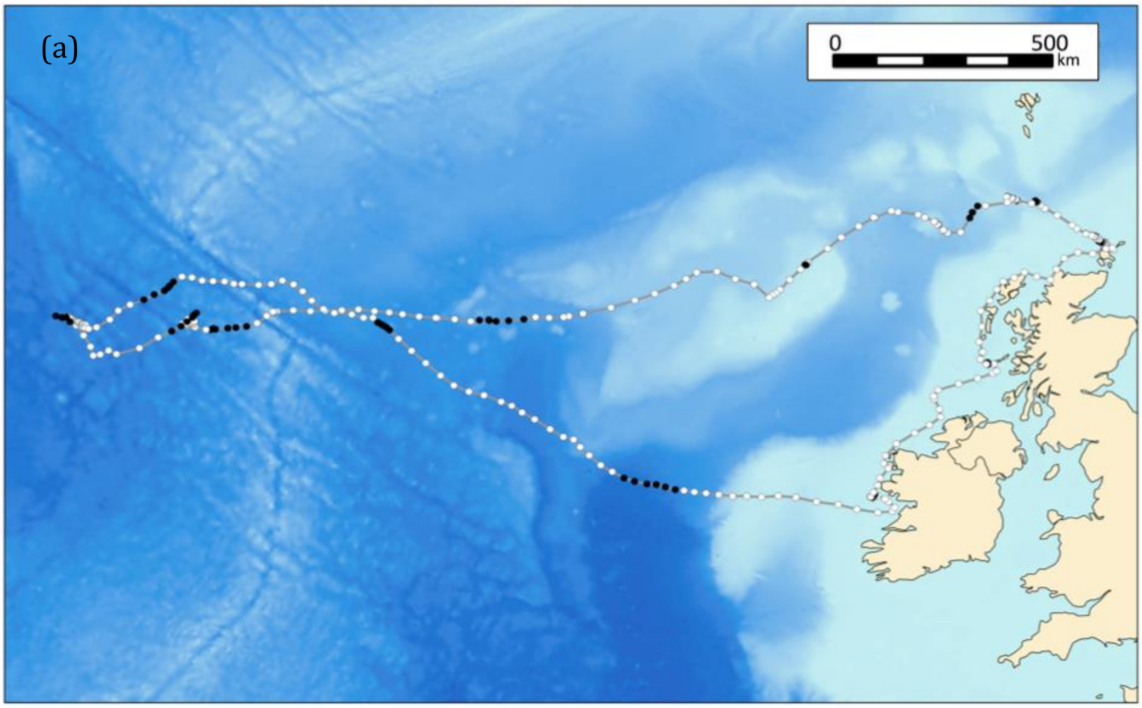
Results

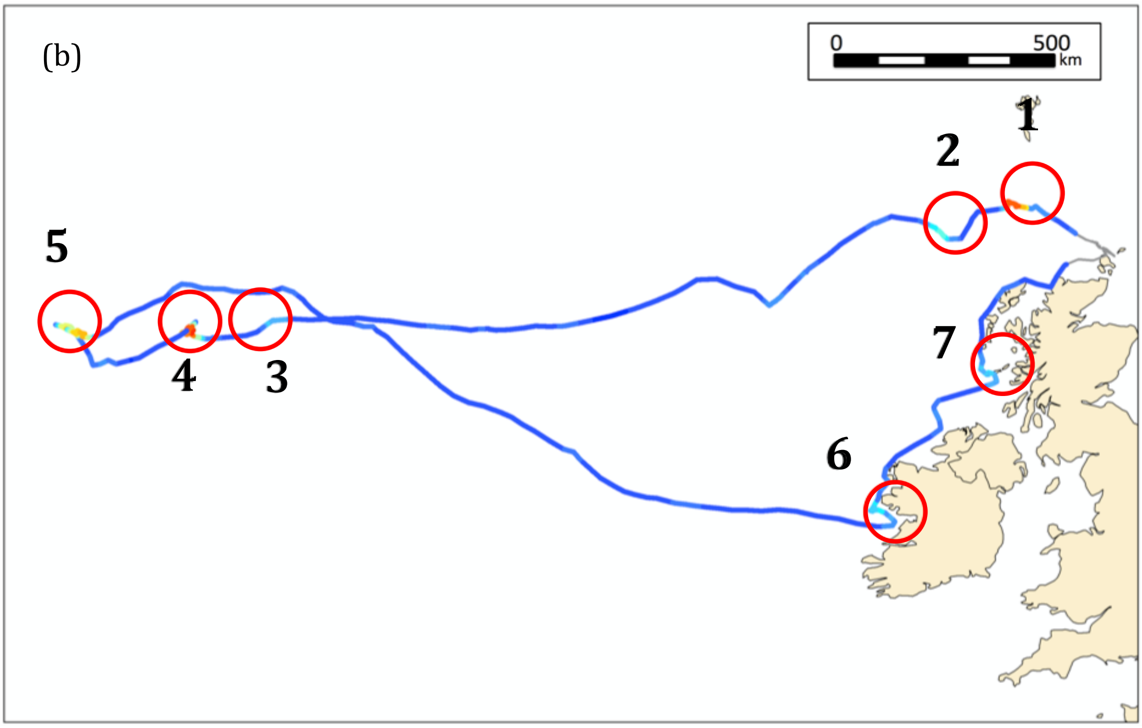
General foraging trip pattern and areas of restricted search

GPS loggers were recovered from 12 out of 22 tagged birds. In May and June 2012, GPS tracks indicated that 10 male and 2 female birds made foraging trips ranging from 4 to 15 d during incubation. Most trips were within 100 km of the breeding colony, one male travelled to the eastern North Sea (approx. 800 km). Of particular interest was one male fulmar, #1568, who flew 2500km west to the MAR as described in detail below. The foraging characteristics of the remaining 11 birds are reported in Chapter 2.

Following tagging on May 23, bird #1568 remained on the egg until the return of his partner. At around 10:30 BST on May 26, 2012, he left the nest site and spent the next 48 h to the northwest of Orkney, before embarking on a sustained flight (11 h) to the middle of the Shetland-Faeroes Channel (*Fig. 4.1(a)*). After spending approximately 18 h around the Wyville Thompson Ridge, he headed WSW into the central Atlantic Ocean, remained around the CGFZ region for 2-3 d and then headed due east. After 19 h his route deviated to the ESE towards Ireland, reaching Galway Bay where he spent 8 h before turning north along the Irish coast. After 18 h he flew to the west of Tiree and the Outer Hebrides, headed east at the northern tip of the Isle of Lewis, and followed the coast around the NW tip of Scotland to return to Eynhallow at ca. 21:00 on June 9, 2012.

Based upon great-circle distances between the hourly GPS locations, the total foraging trip length was 6219 km, which the bird completed in 14.9 days. Data from the GLS logger provided information on local dawn and dusk (*Fig. 4.2*), and show how the bird's distance from the colony varied through this period during different light and dark periods. FPT analysis identified seven apparent regions of area-restricted search (ARS) during the trip (*Fig. 4.1(b)*): one on the Wyville Thompson Ridge in the Faeroes-Shetland channel (60°N, 7°W); one on the Rosemary Bank, off the NW of Scotland; three within the CGFZ/SPF region; one in outer Galway Bay, Ireland; and one W of the island of Tiree, Scotland. Comparing these areas of ARS with oceanic fronts present at this time (*Fig. 4.1(c)*) revealed that the bird's activity around the CGFZ was concentrated near the SPF.





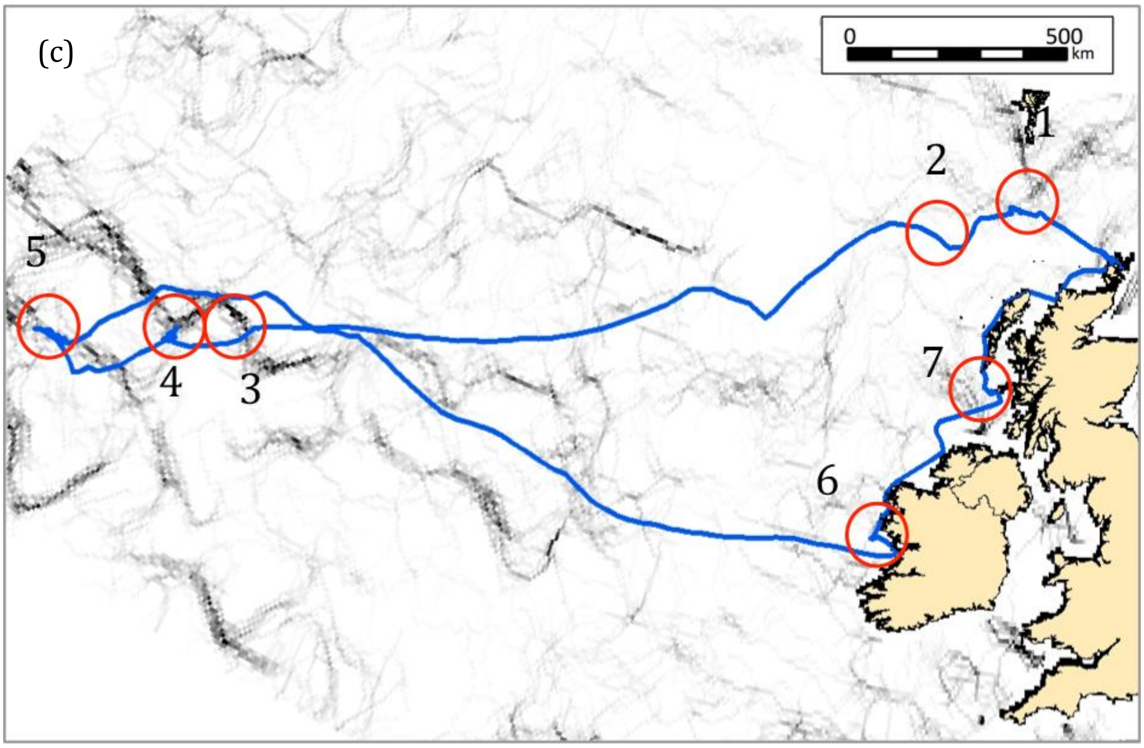


Fig. 4.1. Maps showing the foraging trip GPS track of bird #1568 from Eynhallow to the Mid Atlantic Ridge and back. (a) shows periods of night (dark circles) and light (white circles) on a bathymetric chart (darker colours indicate deeper water). (b) shows the regions of ARS as identified by first-passage time (warmer colours indicate higher FPT). ARS regions are circled and numbered. (c) shows the GPS track overlaid on a composite front map showing the position and strength of thermal fronts, averaged between 31 May 2012 and 06 June 2012 (darker greys indicate stronger fronts in terms of gradient and persistence). ARS regions are circled and numbered.

Year-round distribution

The geolocator deployed on this bird in July 2010 indicated that, whilst dispersing widely across the North Atlantic, including time in the Labrador Strait and Norwegian Sea, the bird had clearly visited the CGFZ during the previous 24 months (*Fig. 4.3*). Also of note is that relatively few geolocator positions occur between the MAR and the UK, suggesting (as with this study) rapid transits between the MAR and European shelf waters.

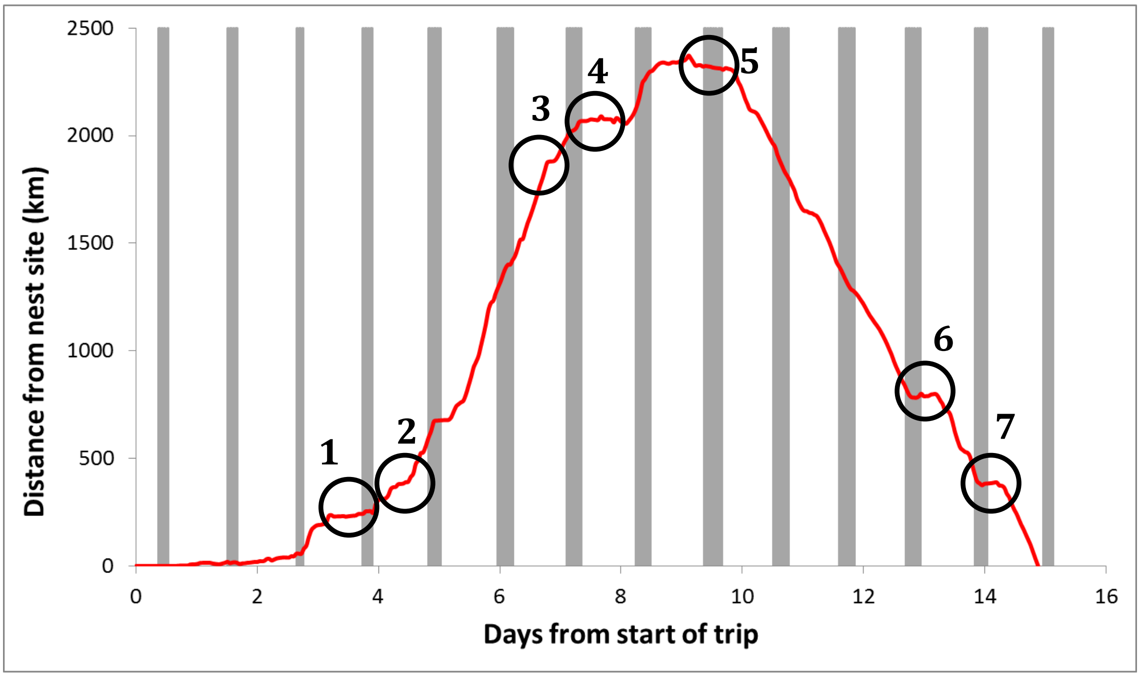


Fig. 4.2. Graph showing distance from nest site on Eynhallow through time. Black circles indicate the location of ARS regions, as identified by FPT analysis. Numbers correspond to numbers in Fig. 4.1(b) and 4.1(c). Local daylight and darkness indicated by light and dark bars.

Activity and Flying speed

There were two periods of ARS at the beginning and end of the trip, and three whilst the bird was around the MAR (*Fig. 4.1(b)*; *Fig. 4.2*). We explored wet/dry patterns and flight speed within each of these ARS, and during the major transits across the Atlantic. Flying speeds during the transits were similar on both outward and return journeys. The distance between ARS 2 on the Porcupine Bank and ARS 3 at the CGFZ was 1610 km, and was flown in 55 h, giving an overall travel speed of 28.6 km h^{-1}. The maximum hourly speed was 63.3 km h$^{-1.}$ This outward journey was associated with strong E/SE winds associated with a deep depression (971mb at 0000 UTC, 31 May 2012) in the central North Atlantic. On the return trip, the distance between ARS 5 at the CGFZ and ARS 6 in Galway Bay was 2055 km, and was flown in ~73 h, giving an overall travel speed of 27.7 km h^{-1} and a maximum hourly speed of 48.7 km h^{-1}. This return journey was undertaken in largely headwind conditions, with a deepening low-pressure area to the SW of the UK resulting in a north easterly airflow.

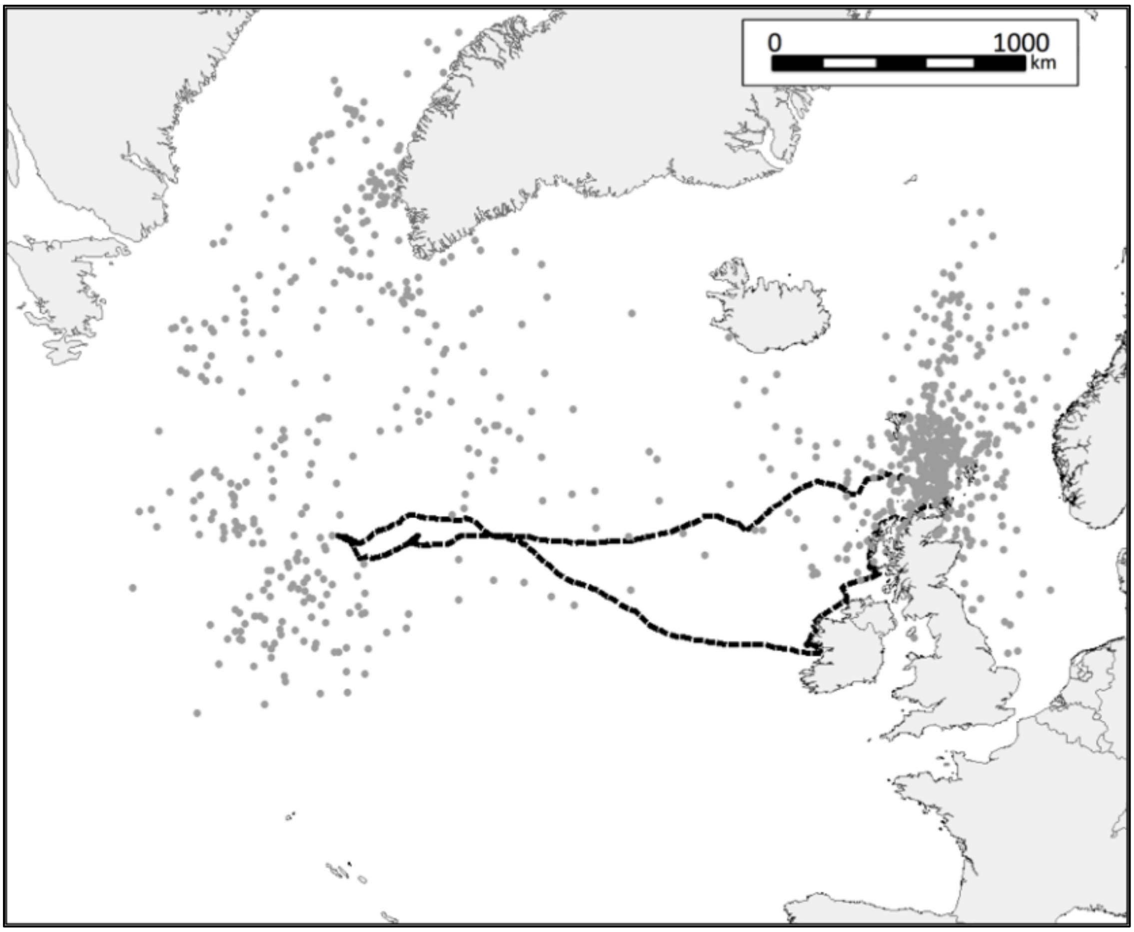


Fig. 4.3. Map showing North Atlantic region, with foraging trip from this study (dashed line) presented alongside twice-daily locations from preceding two years of geolocator tracking (double-smoothed; Phillips et al., 2004)

Flight speeds were faster during these transits (median = 30.1, range = 0.57-63.3, n = 134) than during periods of ARS (median = 4.43, range = 0.42-24.9, n = 99; Wilcoxon Rank Sum test, W=1362, p<0.001, df=1). During transits, flight speeds were faster during the day (median = 33.8, range = 3.41-63.3, n = 105) than at night (median = 16.7, range = 0.57-34.1, n = 29; Wilcoxon Rank Sum test, W=522, p<0.001, df=1), but there was no significant difference between flight speeds by day (median = 4.08, range = 0.81-24.9, n = 78) or night (median = 7.33, range = 0.42-23.5, n = 21) during periods of ARS (Wilcoxon Rank Sum test, W=1008, p=0.1067, df=1; *Fig. 4.4*).

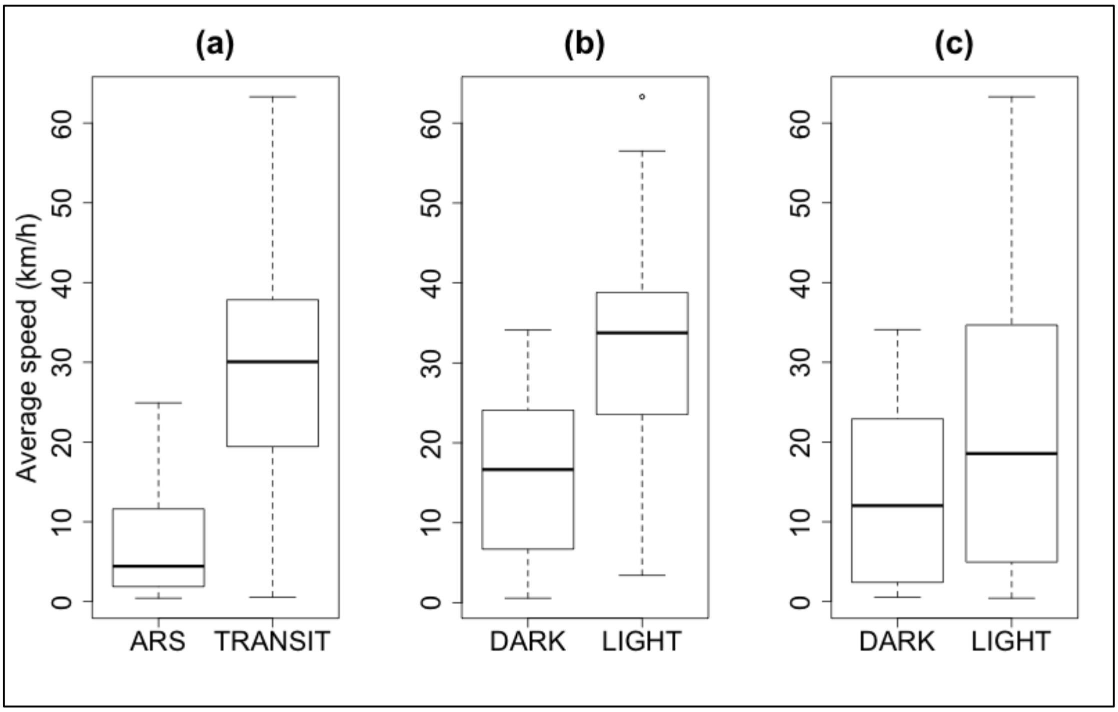


Fig. 4.4. Boxplots showing (a) the difference in flight speed between transits and regions of ARS; (b) the difference in flight speed between periods of light and dark during transits; and (c) the difference in flight speed between periods of light and dark during ARS.

Periods of ARS varied from <3 to >30 h, with three occurring completely in local daylight, two in complete or pre-dominant darkness, and the two longest being primarily in daylight (*Table 4.1*). The shortest of these periods was the last ARS, to the west of Tiree (*Fig. 4.1(b)*), when the bird spent almost all of its time on the water in the dark. In all other cases, activity in the ARS regions showed a prevalence of both mixed and wet behaviours (median 94% (range 83-100%)), with very little time spent dry (median 5.5% (range 0-17%) (*Table 4.1*). Conversely, during the long transits to the east/west, the majority of time was spent dry (median 43%, range 42-44%) or engaged in mixed wet/dry behaviour (median 43%, range 38-47%), with minimal time spent on the water (median 14%, range 8-20%). Within ARS areas, hourly GPS positions indicated that the bird still searched extensively, with average distance covered per h ranging between 3.5 and 9.5 km. The longest periods of mixed activity occurred during the two long ARS over the CGFZ (*Table 4.2*). Data from the long transits suggest that sustained periods of flight typically lasted about 30 min, interspersed with periods of mixed activity or total immersion on the water.

Table 4.1. Details of activity in ARS regions and two major transits.

	Start date and time	**End date and time**	**Duration (hours)**	**Duration (days)**	**% time in local darkness**	**Mean speed (km/h)**	**Max speed (km/h)**	**% 3-sec samples wet**	**Proportion of 10min periods**		
									Dry	**Mixed**	**Wet**
ARS 1	29/05/2012 03:18	29/05/2012 19:55	16.62	0.69	0.0	3.52	-	78.13	0.10	0.33	0.57
ARS 2	30/05/2012 03:54	30/05/2012 10:46	6.87	0.29	0.0	8.26	-	79.15	0.02	0.45	0.52
ARS 3	01/06/2012 17:45	01/06/2012 20:44	2.98	0.12	0.0	7.10	-	87.94	0.00	0.39	0.61
ARS 4	02/06/2012 06:20	03/06/2012 03:32	21.20	0.88	22.7	9.52	-	59.47	0.06	0.53	0.41
ARS 5	03/06/2012 13:14	04/06/2012 19:24	30.16	1.26	22.0	6.93	-	59.17	0.05	0.62	0.33
ARS 6	07/06/2012 20:47	08/06/2012 04:27	7.68	0.32	80.4	9.05	-	59.45	0.17	0.50	0.33
ARS 7	08/06/2012 22:48	09/06/2012 01:46	2.96	0.12	100.0	2.22	-	97.06	0.00	0.08	0.92
Westbound	30/05/2012 10:46	01/06/2012 17:45	54.99	2.29	20.8	28.58	63.30	33.03	0.42	0.38	0.20
Eastbound	04/06/2012 19:24	07/06/2012 20:47	73.38	3.06	25.2	27.66	48.66	21.84	0.44	0.47	0.08

Table 4.2. Descriptive statistics of activity bouts during ARS and transits

	Dry Bout Durations (mins)				Mixed Bout Durations (mins)				Wet Bout Durations (mins)			
	Mean	**SE**	**Max**	**n**	**Mean**	**SE**	**Max**	**n**	**Mean**	**SE**	**Max**	**n**
ARS 1	37	27	90	3	23	5	70	14	54	22	190	11
ARS 2	10	-	10	1	30	9	70	6	37	10	70	6
ARS 3		-		0	60	20	80	2	110		110	1
ARS 4	27	17	60	3	88	32	300	9	104	30	190	5
ARS 5	18	6	40	5	81	24	290	14	75	25	190	8
ARS 6	62	43	190	4	23	4	40	10	25	6	50	6
ARS 7			-	0		-		0	210	-	210	1
Westbound	34	4	130	57	31	4	160	67	34	8	90	11
Eastbound	38	7	240	37	25	3	110	49	54	21	280	12

Discussion

Seabirds often forage in high seas regions distant from their breeding colonies during post-breeding dispersal or the winter (Mallory et al., 2008b, Frederiksen et al., 2012). However, our study highlights the potential linkage between coastal and mid-ocean ecosystems within the fulmar breeding season. Information on the duration of foraging trips during incubation is available from only a small number of individual fulmars (Mallory et al., 2008b), suggesting that, whilst such a long trip may be unusual, it was probably not exceptional. For example, incubation trip durations of 16 days and 18 days have been recorded for fulmars breeding at sites in Alaska and arctic Canada (Mallory et al., 2008b).

No previously published tracking data during the incubation period exist to compare foraging ranges of fulmars at this or other sites, but we recorded such an extensive range in only one of the 12 individuals tracked using GPS loggers during our study. Previous satellite tracking studies of fulmars in northern Europe and North America have shown that birds may travel long distances on foraging trips, the furthest recorded being 32,000 km in 239 days over the winter period (Mallory et al., 2008b), however most of these data were collected during the post-breeding period or from failed breeders (Falk and Møller, 1995, Hatch et al., 2010, Mallory et al., 2008b). Longer-term GLS data collected from bird #1568 indicates that he returned to the CGFZ region in other seasons and in other years (*Fig. 4.3*). Whilst these GLS data lack the accuracy of GPS tracks, they do provide excellent opportunities for broader scale and longer term studies that can in future be used to assess the extent to which different individuals use the MAR and similar offshore areas over extended periods of time. Fulmars tracked using satellite tags from the Canadian high Arctic (Devon Island) were found to migrate into the NW Atlantic between Canada and Iceland, and East to the CGFZ during the winter (Mallory et al., 2008b). Together, these studies highlight that fulmars from both North American and European colonies may overlap in their usage of the MAR during the non-breeding season.

First-passage time analysis demonstrated that the bird in this study exhibited area-restricted searching behaviour at seven stages during its trip, both on the shelf and in the mid-Atlantic. The occurrence of oceanic thermal fronts over this period suggested that the bird associated with areas known to be productivity hotspots (Letessier et al., 2012). Furthermore, this bird appeared to concentrate its foraging in the region of the SPF. Little is known of the diet of fulmars outside the chick-rearing period (Owen et al., 2013). However, it is clear that fulmars are primarily surface-feeding visual predators or scavengers (Garthe and Furness, 2001). In this study, the small percentage of flight time and the high proportion of mixed activity during the longer periods of ARS suggest that foraging probably involves short searching flights within prey patches, followed by brief periods on the water to capture and consume prey (*Table 4.2*). The majority of these episodes occurred during daylight hours, which is consistent with the visual nature of the fulmars' foraging, but these activity patterns could also be influenced by the diurnal vertical migration of prey in the region (Sutton et al., 2008).

Activity data from the GLS loggers indicate that the bird also engaged in mixed activity during the long transits, where short flights were interspersed with regular contact with sea water. This mixed activity may be indicative of foraging whilst travelling. Flight speed during these phases of the trip was similar during the westbound and eastbound transits, despite different environmental conditions and wind strengths. Given the regular bouts of wet or mixed activity (*Table 4.2*), and the assumption that speed is uniform in a straight line between hourly position fixes, these are likely minimum estimates of flying speeds. Furthermore the meandering path of *Procellariformes* engaged in dynamic soaring (Tickell, 2000, Pennycuick, 2002) is likely to result in much faster instantaneous travel speeds than those speeds calculated from distance between hourly positions.

GPS data highlight that the bird did not embark on the westbound transit of this foraging trip immediately after leaving the nest, instead, spending several days to the NW of Orkney (*Fig. 4.1(a)*). Whilst the decision to remain in this area may have been due to favourable local foraging conditions, this period coincided with a large and stable anticyclone in the region. Previous research has highlighted the high energetic cost that this species incurs when flying in low wind speeds, and it is possible that the delayed departure to foraging grounds on the MAR was a response to insufficient winds for energetically efficient flight (Furness and Bryant, 1996). On the return leg, the fastest flight speeds were attained ca. 100km to the west of the Irish coast, as the bird flew close to an area of low pressure centred over the British Isles, where wind speeds were probably the highest encountered during the foraging trip. Inspection of the activity patterns and locations within the trip suggest that in the absence of such adverse wind conditions, this bird could have completed the foraging trip in just 11 or 12 days.

The observations detailed within this paper highlight how GPS and GLS tracking can now be used to explore the extent to which other breeders from this colony use distant offshore resources. Previous work at this colony provided evidence that reproductive rates (Thompson and Ollason, 2001) and adult survival (Grosbois and Thompson, 2005) were influenced by the North Atlantic Oscillation (NAO). At the time, it was suggested that effects on reproduction and survival could result from known relationships between the NAO and potential prey stocks. However, the discovery that birds make long foraging trips during the incubation period highlights that changes in wind speed related to the NAO (Pirazzoli et al., 2010) could affect the cost of flying to different foraging grounds (Furness and Bryant, 1996). In the Southern Ocean, wandering albatrosses breeding on Crozet Island have shifted their at-sea distribution southwards and shown higher breeding success, corresponding with an increase in intensity and polewards shift in prevailing winds (Weimerskirch et al., 2012). Future tracking studies should examine how variation in wind fields may influence fulmar foraging trip characteristics in different parts of their foraging range.

In Pacific fulmar colonies (Hatch et al., 2010), one negative consequence of using distant foraging areas during the breeding season is the risk of mortality from being caught on hooks in a wide range of different longline fisheries. In this study, the single fulmar travelled through areas where the Spanish demersal longline fishery catches over 50,000 birds per year, mostly great shearwaters *Puffinus gravis* and fulmars (Anderson et al., 2011). On the same trip, the bird traversed areas where Faroese demersal longliners regularly record fulmars as bycatch. The possibility of bycatch also exists from pelagic fisheries over the MAR (OSPAR, 2010). This study shows that even birds breeding several thousand kilometres from such areas may be at risk of bycatch. Many breeding colonies are situated outwith regions where longline fishing occurs, but evidence is mounting that these birds are still at risk from fisheries bycatch. Consequently, conservation programs that focus entirely on territorial waters adjacent to breeding sites are likely to underestimate the management practices that are necessary to wide-ranging species such as fulmars.

Acknowledgements

We thank Orkney Islands Council for access to Eynhallow and Talisman Energy (UK) Ltd and Marine Scotland for fieldwork and equipment support. Handling and tagging of fulmars was conducted under licences from the British Trust for Ornithology and the UK Home Office. Microwave SST data were provided by RSS (Remote Sensing Systems, http://www.ssmi.com), and processed by the NERC Earth Observation Data Acquisition and Analysis Centre, Plymouth. Ewan Edwards was supported by a Marine Alliance for Science and Technology Scotland studentship, and Lucy Quinn was supported by a NERC Studentship. Thanks also to the many colleagues who assisted with fieldwork during the project, and two anonymous reviewers for their comments on the manuscript.

Supplementary Material

A video clip showing the route of the foraging trip, annotated to illustrate wet/dry activity along the route, and with detail of ARS regions at the Charlie-Gibbs Fracture Zone, is available online:
http://www.sciencedirect.com/science/article/pii/S0967064513001501

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Chapter 5: Physical, biological and anthropogenic drivers influencing the habitat preference of northern fulmars during the chick rearing period

Abstract

There is a growing need both to understand the relative importance of factors that affect the distribution of seabirds, and to predict the impact that changes in fisheries management may have on populations. The northern fulmar (*Fulmarus glacialis*) is a widespread and abundant northern hemisphere species, and lengthy debate has surrounded drivers of its historic population change. The population explosion witnessed in the fulmar has been in part attributed to provision of fisheries discards as a food source. Until recently, however, links between fulmar distribution and foraging on discards have been drawn from diet samples taken from birds at colonies and observations at sea. The importance of discards to regional populations remains relatively unknown. In recent years certain fulmar populations have shown signs of decline, and the relative role of fisheries and oceanography to the success of fulmars remains unclear. I used habitat preference modelling to compare the relative influence of fisheries and natural environmental variables upon the foraging distribution of fulmars during the chick rearing period, to characterise important foraging habitat in Scottish territorial waters. Fulmars were tracked during the chick rearing period with GPS data loggers in four breeding seasons, at three Scottish colonies. A binomial GEE-GAM modelling framework was formulated using foraging locations, randomly generated pseudoabsences and explanatory covariates including remotely-sensed oceanographic and fisheries data, to model the occurrence of foraging activity at each location. The results suggest a combination of factors interplay to influence the movement patterns of fulmars, and suggest that a combination of energetic (distance from colony), abiotic (seabed depth and gradient, sea surface temperature, thermal fronts), biological (chlorophyll-A concentration) and anthropological (fishing activity) factors all influence distribution. The model can be used to predict relative abundance of fulmars from three breeding colonies, which could be used to inform marine spatial planning or to focus conservation efforts.

Introduction

Identification of key animal foraging areas is vital for the conservation of threatened marine species. It can inform various aspects of marine spatial planning, such as the designation of Marine Protected Areas (MPAs; Thaxter et al., 2012) and potential interactions within regions of offshore industrial development. This requires information on where individual animals forage. However, conservation measures will be more effective if an understanding of species-environment relationships can be used to extend our predictive capacity (Aarts et al., 2008). Seabirds are wide-ranging marine predators, potentially making them a useful indicator of ecosystem health (Furness and Camphuysen, 1997). At the same time, they are also one of the taxa most likely to be impacted by changing marine industrial regimes (Schwemmer et al., 2011, Furness et al., 2013, Ronconi et al., 2015).

In European waters, various management measures require a better understanding of the relative importance of different factors that may affect the distribution of protected seabirds. Member states of the European Union (EU) have a duty to designate Special Protection Areas (SPAs) for seabirds under the Wild Birds Directive (EC, 2009). Additionally, the management of offshore renewable energy developments must consider potential threats to seabirds through collision with turbines (wind and tidal energy devices; (Desholm and Kahlert, 2005, Furness et al., 2013) or modification of habitat (wind, wave and tidal devices; Witt et al., 2012). Commercial fisheries are also recognised to have complex influences on seabirds. These may involve the direct provision of a food source through discarding (Hudson and Furness, 1988, Garthe and Camphuysen, 1996), direct or indirect impacts on prey availability through fishing (Furness and Tasker, 2000, Furness, 2002, Furness, 2003), and mortality risk as a result of by-catch (Dunn and Steel, 2001, Anderson et al., 2011). Previous research has described how several bird species alter their foraging behavior in the presence of fishing vessels (Bartumeus et al., 2010, Votier et al., 2010, Granadeiro et al., 2011, Torres et al., 2011). The EU Common Fisheries Policy (CFP) has resulted in substantial changes in fishing practices in NW European waters since implementation in 1970. Reform in 2013 has proposed further measures to reduce fish mortality and discarding of non-target fish (Damalas, 2015). Many seabirds are known to feed on these discharges from commercial fisheries (Bicknell et al., 2013).

There is therefore a growing need both to understand the extent to which fisheries may influence seabird distribution, and to predict the impact that changes in fisheries management may have on protected seabird populations (Croxall et al., 2012, Torres et al., 2013). However, it has been argued that distribution patterns are likely to be more closely linked to natural habitat features (Camphuysen and Garthe, 1997, Skov and Durinck, 2001, Votier et al., 2010). Previous research has shown that regions of heterogeneity in the marine environment, where high primary production attracts zooplankton grazers are often the most biodiverse (Wingfield et al., 2011, Letessier et al., 2011). Heterogeneous oceanic regions such as continental shelf edges (Holligan, 1981), mid-ocean ridges (Letessier et al., 2011) and persistent strong thermal fronts (Miller and Christodoulou, 2014), contrast with the largely oligotrophic environment of the high seas. This heterogeneity often leads to nutrient cycling through upwelling and eddies. These areas provide productive foraging habitats for many species of marine predator, e.g. seabirds (Scott et al., 2010, Wakefield et al., 2011), marine mammals (Skov et al., 2008) and fish (Sabatés and Masó, 1990). The development of remote sensing of oceanographic variables such as sea surface temperature, rates of primary production in the upper water column (Chlorophyll-A) and location and persistence of thermal fronts has enabled near-real-time monitoring of the biotic and abiotic environment at high spatial resolutions and fine time-scales (Pinaud and Weimerskirch, 2007, Wakefield et al., 2011, Scales et al., 2014). Combining biological and physical oceanographic variables with information on static environmental parameters such as bathymetry can provide the potential to explore complex relationships between spatial patterns in the distribution of animals and their associated environmental preferences.

The *Procellariformes* (albatrosses and petrels), are known to range widely during breeding (Guilford et al., 2008, Wakefield et al., 2011, Thiers et al., 2014) and migrate over large distances during the post-breeding winter period (Mallory et al., 2008b, Quinn, 2014, Mackley et al., 2010). Fulmars, the most widespread and numerous northern hemisphere procellarid (petrel) species, are an interesting taxon for exploring the relative roles of natural environmental variables and fisheries, given a long history of debate about drivers of their historic population change. The expansion of commercial fisheries around Scotland has been shown to coincide with an extensive expansion in fulmar numbers in the region. Fisher (1952) proposed that the provision of fisheries-related food may have been the major driver of the success of the species, as the birds feasted on net overspill, offal discharge and, especially more recently, undersized and over-quota fish discarded by commercial vessels at sea (Camphuysen and Garthe, 1997).

At Scottish colonies, fulmars show large individual generality and inter-colony variation in diet (Furness and Todd, 1984, Hamer and Thompson, 1997, Phillips et al., 1999). The precise role of fishery waste in sustaining the population is unclear although in some regions discharge from vessels does comprise a large component of fulmar diet, whilst being unable to fully support the species (Camphuysen and Garthe, 1997, Phillips et al., 1999). Intra-annual variability in prey and spatial patterns in fishing effort may lead to increased seasonal and regional dependence on fishery waste. Fulmars in the Bering Sea and North Pacific showed a decline in abundance and a northwards shift in distribution concurrent with a spatial change in fish catches and regional ocean warming (Renner et al., 2013). At the same time, certain fisheries pose a threat to fulmar survival, especially in Nordic demersal longline fisheries (Løkkeborg and Robertson, 2002, Anderson et al., 2011).

Over the past 15 years, there have been useful developments in the statistical tools available to explore these relationships (Guisan and Zimmermann, 2000, Matthiopoulos, 2003, Aarts et al., 2008, Aarts et al., 2013). Recent advances in statistical techniques using extensions of linear modelling, such as generalized linear and additive models (GLM and GAM) have enabled habitat preference modelling frameworks to relate wildlife telemetry data to environmental covariates.

Typically, animal location data come with associated complications such as small sample sizes, and inherent intra-individual serial and temporal autocorrelation.

Generalized estimating equations (GEE; Hardin and Hilbe, 2003) can be used to relate animal presence to environmental covariates, whilst accounting for this autocorrelation within individuals. Animal location data and contemporaneous information of the environmental conditions have been used in studies to assess habitat preference of marine predators from visual observations (Pirotta et al., 2011, Scott et al., 2013) and temporal patterns in marine predator occurrence (Bailey et al., 2013).

Lately GEEs have also been used to model habitat preference of seabirds. One study analysed at-sea survey data using GEE-GLMs to predict the foraging occurrence of northern gannets *Morus bassanus* and European storm petrels with respect to oceanographic features and tidal cycles. This revealed differences in the predictability of presence of each species with respect to varying oceanographic features and tidal effects (Scott et al., 2013). Meanwhile, the habitat preference of northern gannets, tracked using GPS and quantified using GEE-GAMs explored relationships between the location of persistent mesoscale oceanic fronts and seabird foraging behavior (Scales et al., 2014). Integrating an index of fisheries effort in a habitat preference study such as these can indicate the role of fishing vessel presence in seabird foraging habitat. However, boat-based survey data, frequently used in past habitat preference studies (Garthe, 2006, Skov et al., 2008), are likely to be less suitable for exploring potential associations between piscivorous, scavenging seabirds and commercial fisheries, since species such as seabirds can be attracted to vessels at large spatial scales (Votier et al., 2010, Renner et al., 2013). Consequently, tracking data potentially provide a less biased method of assessing distribution at sea, and can be used within models to examine the relationship with environmental variables.

In previous chapters of this thesis the foraging range of fulmars during the breeding season has been discussed in great detail. However there are still questions regarding what dictates birds to forage in certain regions. By determining the preferred habitat, and characterizing the association between fulmars and fisheries, this can inform marine spatial planning and policy decisions relating to this species. In this study, habitat preference modelling was used to compare the relative influence of fisheries and natural environmental variables upon the at-sea distribution of fulmars during the chick rearing period. Static physical variables, remotely sensed environmental data, an index of commercial fisheries effort and GPS tracking data from birds from three colonies were used to assess the important factors influencing the distribution of fulmars. This modelling will allow identification and characterisation of important foraging habitat for fulmars in Scottish territorial waters and assess the influence of fisheries on their distribution.

Materials and methods

Study area

Fieldwork was carried out during June and July between 2009 and 2012 at three fulmar colonies around the Scottish coast: near Berriedale, Caithness (58.18° N, 3.49° W) in 2011, Eynhallow in Orkney (59.14° N, 3.12° W) in the years 2009 – 2011, and St Kilda, W of the Outer Hebrides (57.81° N, 8.57° W) in the years 2011 – 2012 . Berriedale is situated on the north east coast of Scotland, on the Moray Firth, a generally shallow (< 200m depth), sandy region of the North Sea. Eynhallow lies in the western Orkney Islands, on the continental shelf but roughly equidistant between the shallow North Sea and deep (> 2000m) North Atlantic waters beyond the shelf break. St Kilda lies 150 km west of the Scottish mainland, close to the edge of the continental shelf (*Fig. 5.1.*).

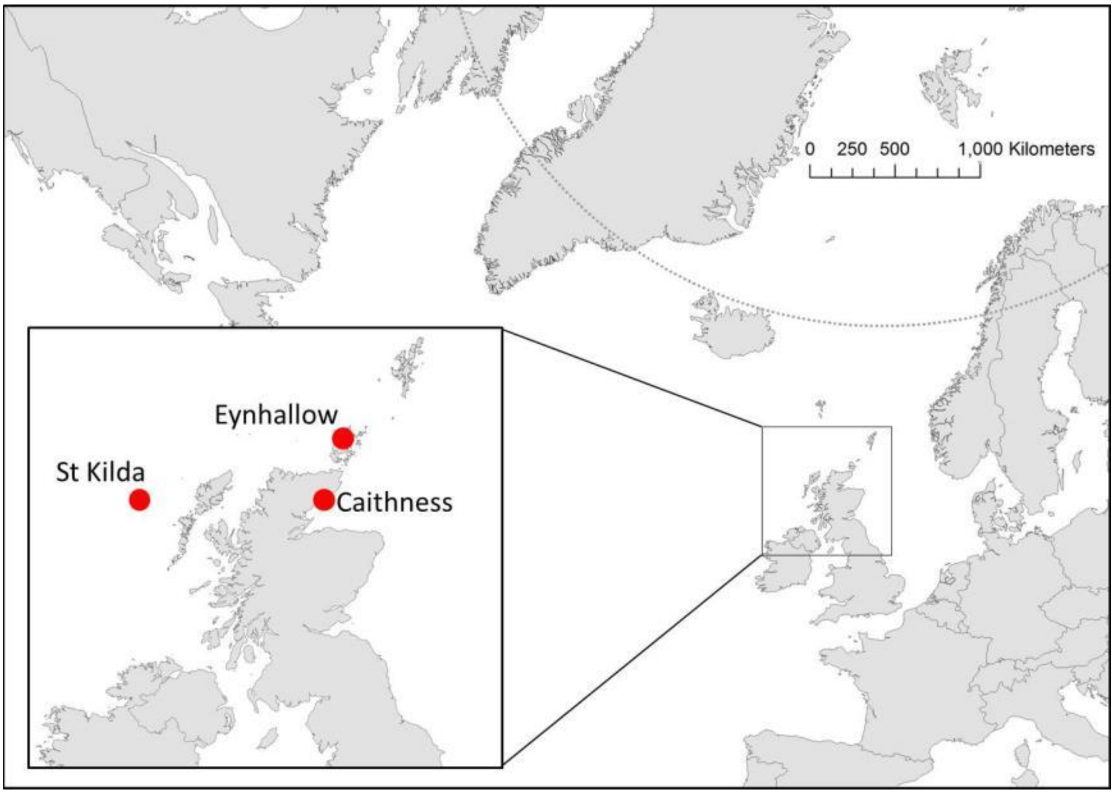


Fig. 5.1. Map of Scotland showing the locations of the three fulmar colonies included in this study. Grey dotted line illustrates the Arctic Circle, 66.56° N.

Data collection

Adult fulmars were caught under British Trust for Ornithology (BTO) license on the nest during early chick rearing (1-5d post-hatching, whilst the chicks were still being guarded) using a net or noose. GPS data loggers (MobileAction® iGot-U GT-120; weight 18 g), recording position every 2 – 10 min, were attached to mantle feathers using 5 – 7 strips of Tesa® tape which could be removed post-deployment. Birds were recaptured after 1 – 5 foraging trips, before the end of the brood/guard period. GPS loggers were removed upon recapture. Neither capture nor deployment of tracking devices caused any signs of injury, distress or changes in the birds' behavior. Some birds were tracked again in subsequent seasons.

Modelling approach

We adopted a case-control approach whereby each fulmar GPS location was complimented with temporally matched, randomly generated pseudo-absence (control) locations (Wakefield et al., 2011). Control points were selected from within a biologically realistic null model i.e. an envelope within which a fulmar might be if it had movement constraints but not preferences. The statistics software R 3.0.0 was used (R Core Development Team, 2013) for all statistical modelling and calculations. Data were manipulated in Microsoft Excel. ESRI® Arc GIS 10, in conjunction with Geostatistical Modeling Environment (Spatial Ecology), was used for GIS operations.

Unit of analysis

Sampling frequency ranged from 2 – 10 locations per minute. Where necessary, these tracking data were subsampled to provide only one location every 10 minutes, to a) reduce the number of data points for computational ease and to b) limit serial autocorrelation. For birds where the data logger remained active during two or more consecutive foraging trips, only the first trip was included in the model-fitting dataset (i.e. only one trip, per individual, per year were used). This allowed us to retain an additional small dataset for testing model credibility (Guisan and Zimmermann, 2000).

Since the primary interest was in fulmar foraging habitat, it was necessary to distinguish foraging from transiting phases of each trip. Firstly a buffer with a radius of 10km was placed around each colony, for four main reasons: 1) to exclude locations where the bird had gone to sea to wash and recover following GPS deployment i.e. non-foraging excursions to sea; 2) to eliminate periods of social behavior in the vicinity of the colony, where seabirds commonly rest on the water in large aggregations, which could otherwise be interpreted as foraging, 3) to exclude locations in coastal regions where remotely sensed environmental covariates are inaccurate or unavailable, and 4) to eliminate bias in coastal regions where fishing vessel presence is inflated by the location of commercial harbours (e.g. Scrabster, Peterhead). With this buffer excluding a portion of each foraging trip, the remaining data included more than 75% of the GPS locations for each trip in every case (median 95.3%, range 76.6 – 99.4 %).

First-passage time (FPT), the time taken to depart a circle of a given radius (Fauchald and Tveraa, 2003, Pinaud and Weimerskirch, 2005) was used to identify regions of area-restricted search (ARS) throughout each foraging trip, using the ‘adehabitatLT’ package in R (Calenge, 2006). Each foraging trip was converted to a trajectory, and interpolated with a point every 500 m (rather than raw GPS locations every 10 min). FPT was calculated at each interpolated position for a series of radii from 1 - 100 km. The peak of the variance of log(FPT) was identified for each trip independently, as this indicates the scale at which ARS is being conducted by each individual bird. The mean of these individual search scales was calculated to give an ARS search scale for the population.

To define a critical FPT threshold to distinguish between foraging and travelling, median flight speed was calculated for each foraging trip, based on the distance and time between GPS locations. A FPT threshold t (s) was calculated, using the formula:

$$t = d/v,$$

where d is the radius of the mean search scale in m, and v is the median speed per trip for the entire dataset in m s^{-1}. If FPT for each foraging location was greater than the FTP threshold t, the bird was assumed to be foraging rather than travelling. Foraging locations, as extracted from the complete dataset using FPT analysis, represented the presence locations in the model.

Generating control points

Control points were selected from within an envelope of radius equal to the maximum recorded foraging range from this tracking study (1016 km). This assumed that fulmars were constrained in range to the maximum recorded biological distance from the study colony, but had the ability to forage anywhere within the envelope.

Methods of selecting pseudo-absence (control) points can significantly impact the predictive power of a model. It has been suggested that, for regression-type models such as those employed in this study, the best results are obtained by generating a large number of pseudo-absences within the entire study area (Barbet-Massin et al., 2012). It was necessary in this study to choose an appropriate number of control locations. The ratio (r) of randomly selected control points to observed bird locations was selected by running GEE models with an increasing number of control points. We tried models with ratios r ranging from 2 to 14. The model's regression coefficients were inspected visually at increasing values of *r* and we selected the smallest value of *r* at which coefficients attained a stable value.

Environmental covariates

We selected variables *a priori* that we considered likely be related to fulmar habitat preference. These included some that may have been of direct importance to fulmars themselves, and others that may influence the distribution and availability of prey. Data that directly describe spatial and temporal prey distribution are sparse, so environmental variables are chosen which may act as a proxy for prey availability. The variables used to predict fulmar relative abundance, were distance from colony (km), seabed depth (m), seabed slope gradient (°), Chlorophyll-*A* (ChlA) surface concentration, sea surface temperature (SST; °C), an index of strength/persistence of oceanic thermal fronts and an index of fishing vessel presence (number of vessel locations in a grid square).

Biological (as opposed to straight-line Euclidean) distance from every bird location to the colony of origin, i.e. the distance between the bird location and colony without passing over land, was calculated using the Spatial Analyst package in Arc GIS 10 (to the nearest km). Depth data were obtained from the US National Oceanic and Atmospheric Administration (NOAA; www.ngdc.noaa.gov), and expressed as a positive value in metres. Steep seabed slopes are known to be associated with areas of upwelling of nutrients and prey (Bailey and Thompson, 2010). Slope gradient was defined as the average rate of change in depth per grid cell, and expressed in degrees. Remotely–sensed SST (AVHRR satellite-derived composites) and ChlA (MODIS/MERIS satellite-derived composites) data were provided by Natural Environment Research Council (NERC) Earth Observation Data Acquisition and Analysis Service (NEODAAS, Plymouth Marine Laboratory, UK). The July composite values for SST and ChlA were used for the study. An index of oceanic thermal front strength, persistence and proximity to other fronts (F_{comp}) was processed as an average for the period of interest (28 June – 19 July) for the years 2009 – 2012 .

Every EU fishing vessel larger than 12 m must carry a Vessel Monitoring System (VMS) transmitter, which provides a location record every 2h to the Fisheries Monitoring Centre of the country under whose jurisdiction they are fishing (Witt and Godley, 2007). Fisheries data were provided by Marine Scotland as a count of number of recorded UK vessel VMS locations, per International Council for the Exploration of the Seas (ICES) sub-rectangle (0.1° latitude x 0.1° longitude; 1/50th of an ICES statistical rectangle) for the month of July in the years 2009 – 2012. Data were provided for all mobile gear types together (pelagic trawl, demersal trawl, beam trawl, benthic trawl), for (a) all vessels and (b) for only vessels travelling slower than 5 knots, as a proxy for when engaged in fishing. Since fisheries discards could be available at almost any time of a fishing vessel's excursion from port (due to processing and discarding of fish offal whilst in transit) as opposed to only being available when actively engaged in fishing, the dataset encompassing all VMS locations (no speed filter) was used in the analysis. These data represented a proxy for total presence of fishing vessels within the area of interest, rather than an absolute value of fishing intensity. Non-UK vessels and smaller boats (< 12 m) that could be present in the studied regions were not included because fisheries managers do not collect this information.

A data frame was compiled whereby values of explanatory covariates were extracted to presence and pseudo-absence points using ESRI Arc GIS 10. Both presence and control locations were associated with a colony, whereby the distance covariate always related to Eynhallow, Caithness or St Kilda. Data points were omitted where one or more explanatory values were missing, as these would prevent the models from running. A systematic pattern associated with these missing data points would affect the validity of the null model; however, the number of data points omitted was low (n = 115 of 5919 data points; < 2 %) and there appeared to be no obvious pattern to where they were located.

Modelling approach

A GEE-GAM modelling framework was used to model the occurrence of foraging activity at each data point as a function of the available covariates. Used with longitudinal data, GEEs have advantages over other models as they can successfully correct for autocorrelation in the response variable. As well as being considerably faster, their parameter estimates and empirical standard errors are robust to misspecification of the correlation structure of the dataset (Liang and Zeger, 1986). A GAM approach was chosen due to the inherent complex, non-linear relationships linking animals with their habitat preference.

GEE-GAM models with a binomial error structure and logistic link function were implemented using the ‘geepack’ package in R (Yan et al., 2012). Collinearity of explanatory variables was checked using the variance inflation factors, and no variables were found to vary collinearly. Bird locations were grouped into trips by individual, whereby in the model, serial autocorrelation within trips was accounted for, but locations from two different individuals were assumed to be independent. Each pseudo-absence point was given a unique blocking ID, because these locations were generated randomly within an envelope, with no correlation structure and this allowed the models to run faster with no difference in outcome. Quasi-likelihood under Independence model Criterion (QIC; Pan, 2001) was used to select a working independence correlation structure for model residuals, in preference over a first-order autoregressive (AR1) or exchangeable correlation structure.

Model selection was carried out by running models sequentially and comparing QIC_u values (i.e. an approximated version of the QIC; Pan, 2001). Firstly, a model was run where all seven environmental covariates were included, and each covariate had a linear relationship to the response. Models were then implemented sequentially, where the relationships between the response and explanatory variables were smoothed (using beta-splines with 4 degrees of freedom, and a knot positioned at the mean) and QIC_u values were compared. Covariates were then removed one by one in backwards step-wise selection, and the final, most parsimonious model was identified based on lowest QIC_u score. Interactions of the available covariates with colony were also tested using QIC_u, to assess inter-colony differences in such relationships. If an interaction with colony resulted in a lower QIC_u score, this suggested that the relationship with that environmental variable varied with colony of origin. Where the distribution of the explanatory covariate was left-skewed, the $\log_{10}$ of the covariate was calculated to improve normality of the data.

Model validation

A confusion matrix was used to assess the goodness-of-fit of the model (Fielding and Bell, 1997), comparing binary predictions with the observed numbers of bird locations and pseudo-absences in the original data set. Using the model the probability that each data point was a bird presence or control location was determined, based on the values of the covariates at that location. A cut-off threshold probability was specified based on a Receiver Operating Characteristic (ROC) curve (Sing et al., 2005), above which a location was considered a presence.

We also tested the predictive performance of the model using the additional data from tracked individuals that had not been included in the model fitting described above. Where one bird had made more than one foraging trips, the data points from these subsequent trips were compiled into a validation dataset, completed with an additional suite of control locations, using the same ratio of pseudo-absences to bird locations.

A grid of cells (0.1° latitude x 0.1° longitude) was generated and used for prediction. To avoid extrapolation, the prediction points included only those that fell within the margins of the study, i.e. the maximum recorded foraging range of a fulmar. For time-varying covariates, i.e. fishing effort, ChlA, front density and SST, average values for the years 2009 – 2012 were calculated to give a multi-year mean. GIS tools calculated the mean of each covariate in each grid cell and assigned the mean covariate value to each centroid point. The probability of fulmar relative abundance for each cell centroid was predicted (on the response scale) using the final model. Gridded maps of fulmar relative abundance for each colony were generated.

Results

Distribution

Birds were tracked during four years (2009 – 2012) at three colonies around Scotland, resulting in 71 tracks from 63 individuals (8 individuals were tracked during two years, and these data were included). The maximum foraging range was 1016 km (10.1 – 1016 km) and the maximum foraging trip duration was 4.74 days (0.23 – 4.74 days). From visual observation of the tracks plotted on a map, there was a distinct difference in distribution in relation to the colony of origin, with generally little overlap. St Kilda birds foraged mostly to the South and West of the St Kilda archipelago; Eynhallow birds foraged largely to the NW of Orkney, with several making trips into the central North Sea. Meanwhile, Caithness birds foraged mostly within the Moray Firth (*Fig. 5.2(a)*). Several Caithness birds flew SE into the central North Sea, but these generally demonstrated little overlap with Eynhallow birds.

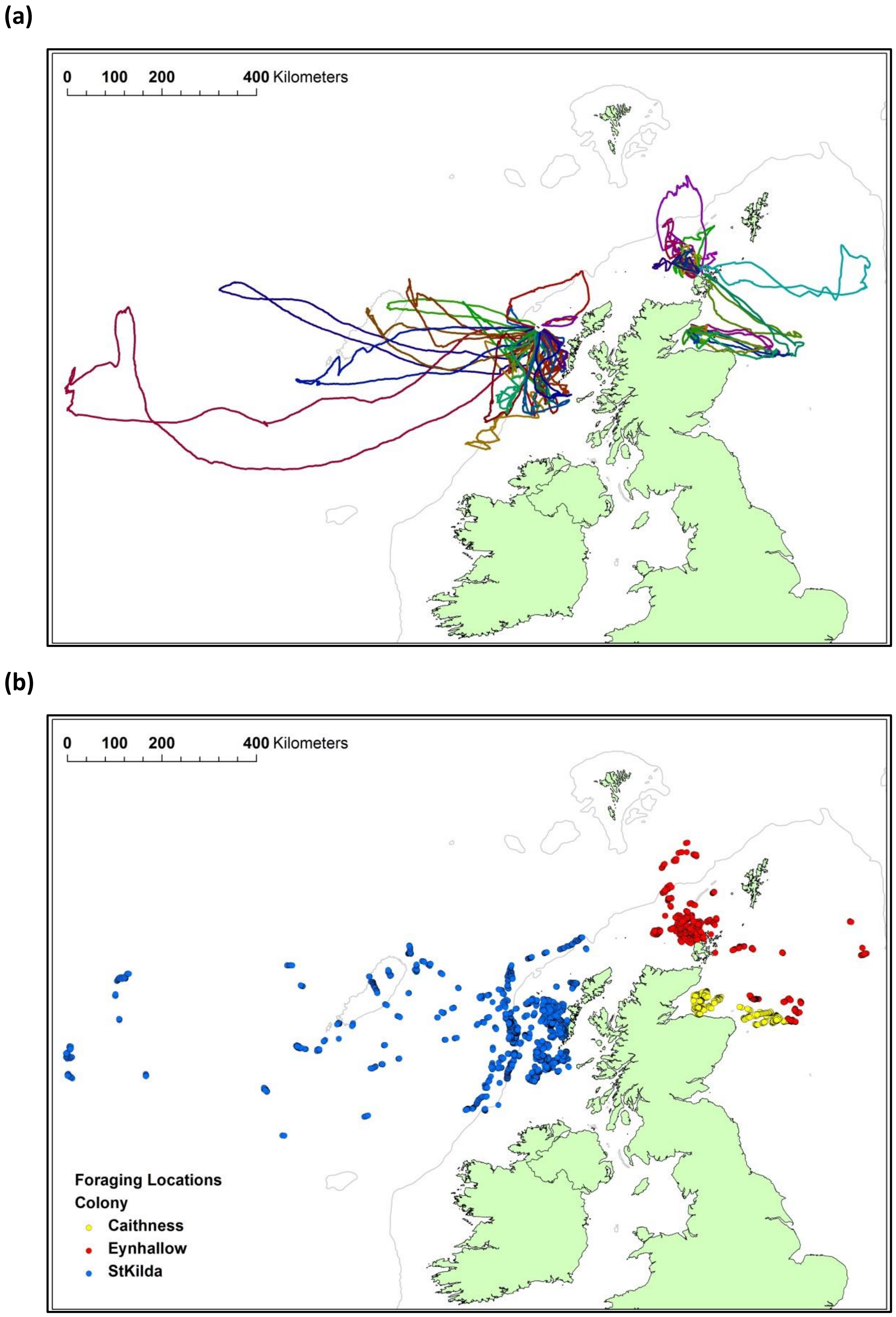


Fig. 5.2 (a) Map illustrating every foraging trip used in this study; (b) the foraging locations, extracted using FPT, used in the model. Grey line represents the 200 m seabed contour.

Identifying foraging locations

The mean of var(log(FPT)) from the whole dataset of 71 foraging trips was 4.5 km. Therefore 4.5 km was used as the most appropriate scale of restricted search for the fulmars within this study. This is comparable to the scale of ARS of 9.1 ± 1.9 km found for gannets (Hamer et al., 2009). Median flight speed for every foraging trip was calculated. The median of the whole dataset was calculated to be 16.7 m s^{-1}. The FPT threshold was calculated as 2412 s (roughly 40 min). This means that if a fulmar at location *i* took longer than 40 min to leave a circle of r = 4.5km, and was thus travelling at below the median speed of the sample, the location *i+1* was identified as a foraging location.

Visual examination of the changing FPT at each interpolated location for the chosen scale (radius 4.5 km) for each trajectory confirmed that a FPT of 40 min (as calculated from median speed and chosen radius) was an appropriate time period to capture most ARS regions. Thus, bird locations were classified as being either points in an ARS segment, or as non-ARS travelling points. Only the ARS locations were used in the model (*Fig. 5.2(b)*).

Model selection

After visually identifying the point at which the estimated model coefficients stabilized with an increasing ratio *r* of control points, pseudo-absence locations were generated at a ratio of six control points to every bird location.

Following stepwise model selection using QIC_u values, the final model that best described the foraging distribution of fulmars tracked in this study contained front density, seabed depth, sea surface temperature, the $\log_{10}$ of chlorophyll-A, seabed slope gradient, the $\log_{10}$ of fishing effort, and biological distance from colony; all as smooth terms.

Table 5.1. Model output ANOVA table with Wald's statistics and p-values for the seven covariates used in the GEE model to assess fulmar habitat preference.

Covariate	Df	Wald's chi-sq statistic	P-value
Front density	4	16.9	0.002
Depth	4	31.7	< 0.0001
SST	4	86.8	< 0.0001
Log_{10} ChlA	4	49.6	< 0.0001
Log_{10} seabed slope	4	87.9	< 0.0001
Log_{10} fishing	4	105.2	< 0.0001
Distance from colony	4	222.5	< 0.0001

All seven covariates included in this study *a priori* were retained following step-wise model selection. The strongest relationship was with distance from colony, whereby the probability of fulmar presence is higher closer to the colony. The weakest relationship between fulmar presence and the environment was for oceanic fronts (*Table 5.1*), with a preference for moderate F_{comp} values but a rapidly declining preference at very high values (*Fig. 5.3*). Fulmars in this study demonstrated a preference for sea surface temperatures between 5 – 15 °C, declining sharply above this range. Fulmars preferred to forage on the continental shelf and slope, but also over very deep waters. The probability of finding fulmars increased with $\log_{10}$ chlorophyll-A concentration, but decreased at very high concentrations. Fulmars had a preference for regions with a sloping seabed. The probability of fulmar presence also increased in relation to $\log_{10}$-transformed counts of fishing vessel locations per month (*Fig. 5.3*).

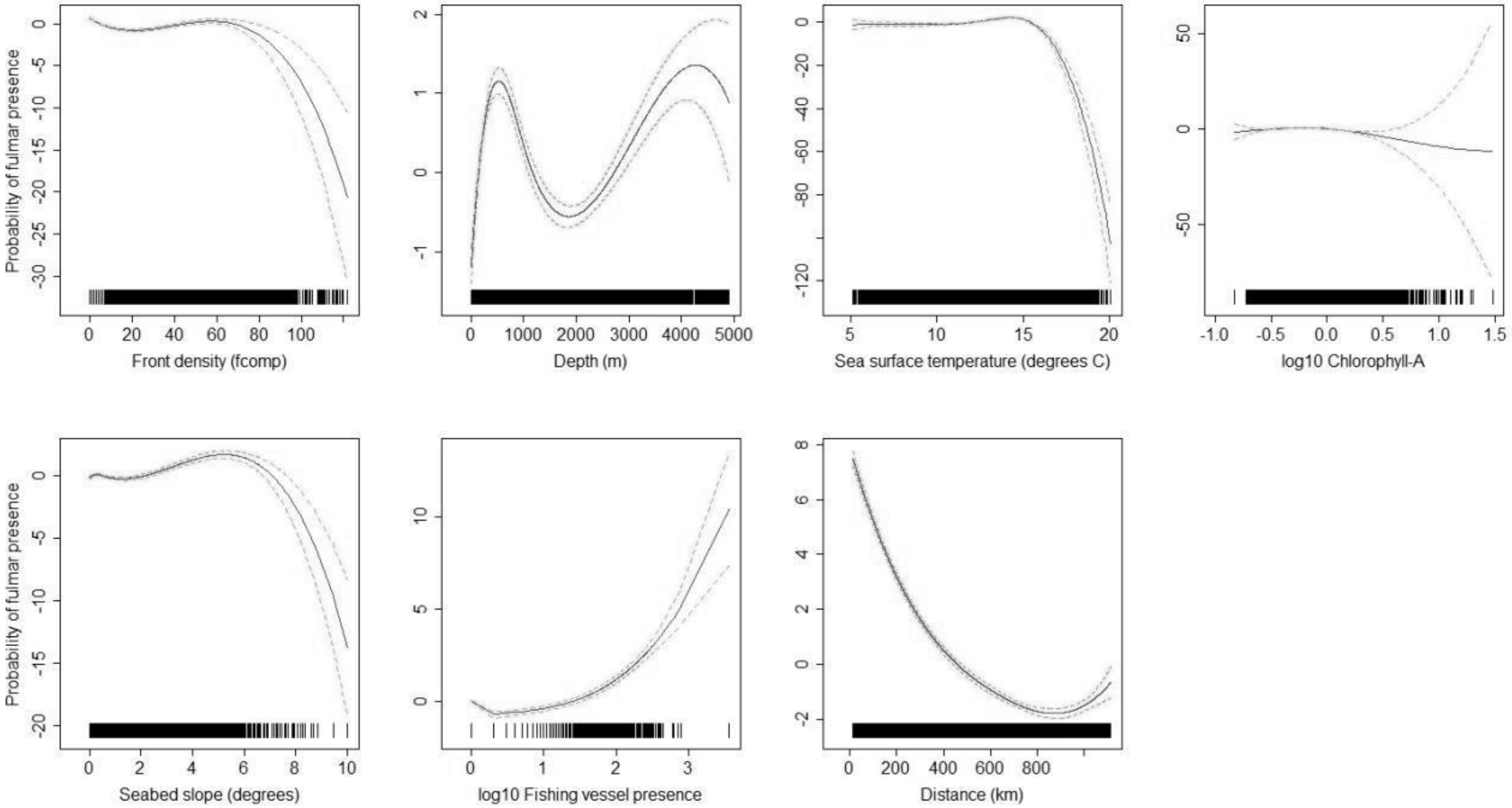


Fig. 5.3. Plots showing the relationship between probability of fulmar presence and seven environmental covariates included in the model: clockwise from top-left: front density, seabed depth, sea-surface temperature, log_{10} ChlA concentration, biological distance from colony, log_{10} fishing vessel presence and seabed slope gradient. 95 % confidence intervals shown as dashed lines.

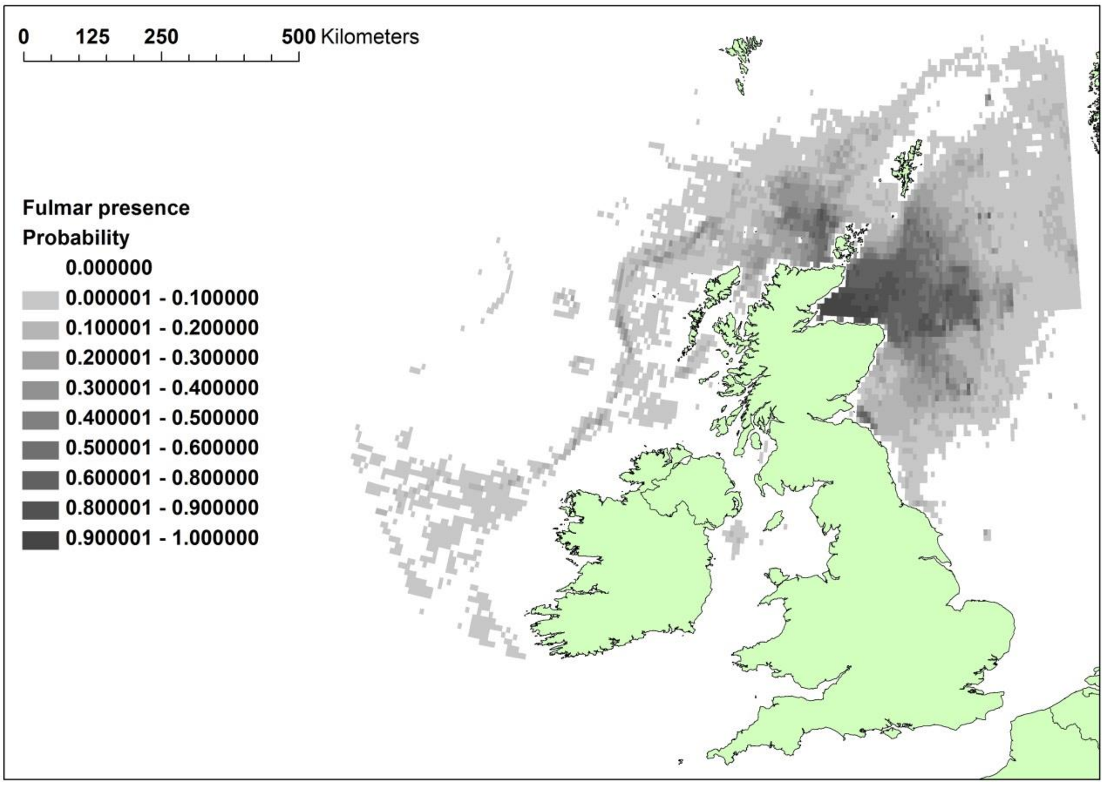
Model validation confirmed goodness-of-fit for the final model. The cut-off probability, as generated by the ROC curve, was 0.139. The model was applied to a confusion matrix to predict, based upon covariate values, whether each location was a bird presence or control point. The model correctly identified 91.5 % of presence locations as bird presences, and 93.0 % of control locations as bird pseudo-absences. The model was also used to predict the likelihood of each point being a presence or absence from a confusion matrix generated from the validation data set. The model correctly identified 75.2 % of the presence points as presences, and identified 94.6 % of the pseudo-absences as control points.

Models using colony interactions with covariates were also tested. Interactions with $\log_{10}$ ChlA and colony, as well as fishing vessel activity and colony, resulted in improved model performance according to QIC_u. However testing model goodness-of-fit using the confusion matrix resulted in only a marginal improvement in model performance (ca. 1%). Thus, the model without colony interactions was retained as this was the most parsimonious model.

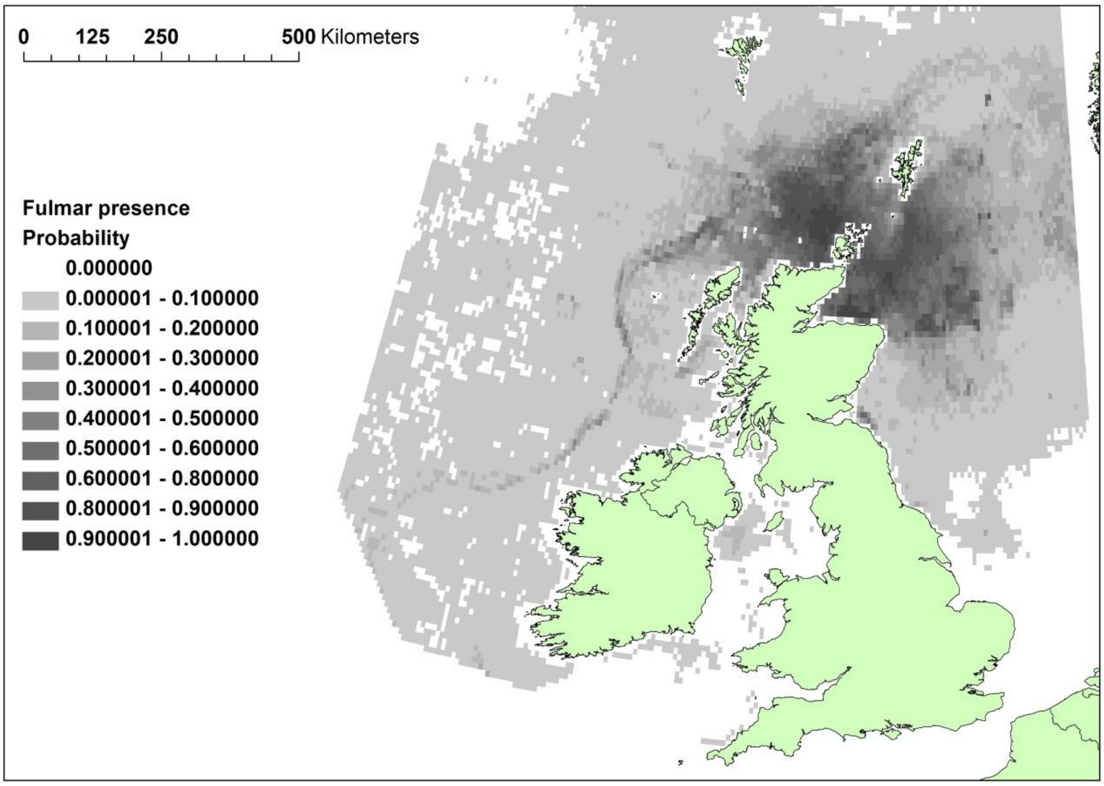
Modelled fulmar habitat

Relative abundance as predicted by the model showed a large degree of overlap with the distribution seen in the tracking data (*Fig. 5.2(a)*), with higher probabilities of finding fulmars closer to colonies, in regions with high fishing vessel activity and in regions where the slope of the seabed is greater (*Fig. 5.4*). The highest likelihood of abundance of Caithness birds was predicted to be within the Moray Firth and central North Sea (*Fig. 5.4(a)*). Abundance of Caithness fulmars to the west of the British Isles is expected to be low, despite being within potential range of these birds. Eynhallow fulmars were predicted to use the region to the north west of Orkney, and the central North Sea. They also show high preference for the shelf edge within the Faroes-Shetland Channel (*Fig. 5.4(b)*). St Kilda fulmars are predicted to use the region around the Outer Hebrides especially the Sea of the Hebrides and to the west of the archipelago, and including the edge of the continental shelf, the Rockall and Porcupine Banks and Anton Dohrn Seamount (*Fig. 5.4(c)*).

(a)



(b)



(c)

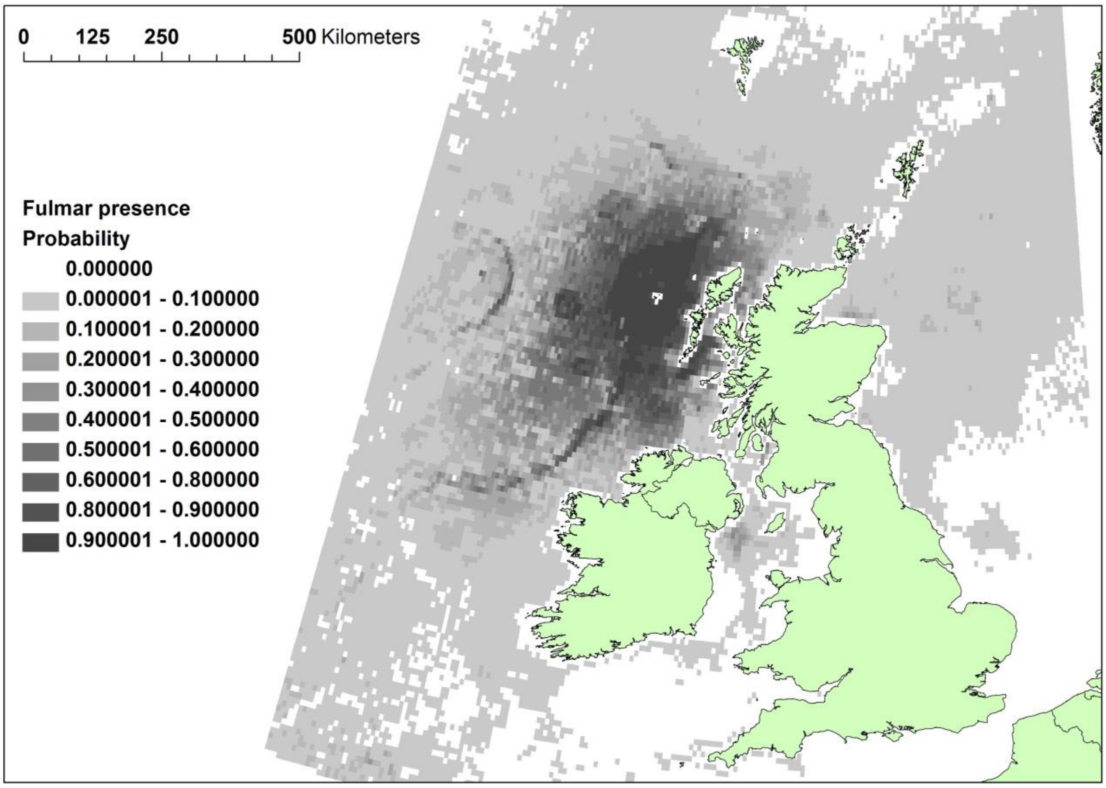


Fig. 5.4. Predicted relative abundance of fulmars from (a) Caithness, (b) Eynhallow, and (c) St Kilda, predicted from the model generated in this study.

Discussion

We have used a combination of GPS tracking, remotely-sensed oceanographic and fisheries data to model the spatial usage of fulmars as a function of habitat preference, accounting for autocorrelation in the tracking data through the use of GEE models. These modelling approaches have revealed patterns in the habitat preference of fulmars that were tracked from three colonies during the breeding season. Our results suggest fulmar foraging distribution is influenced by a combination of biotic (primary productivity), physical/oceanographic (distance from the colony, sea surface temperature, the location of thermal fronts, and seabed depth/slope), and the activity of commercial fisheries around the UK.

Before this study little was known about the foraging habitat of fulmars that were breeding at known colony locations. Existing data on foraging distribution has been based upon surveys that provided no information on the source colonies of birds that were observed at sea (Garthe, 1997, Camphuysen and Garthe, 1997, Renner et al., 2013). Our model was able to predict with very high (92%) accuracy whether a point in space with known environmental characteristics was likely or not to be a foraging location of a fulmar from one of the colonies in the study. Not only was it good at characterising bird locations as presences, it also identified randomly generated control locations as pseudo-absences with a high rate of success. Based on visual examination of the predicted distribution map (*Fig. 5.4*), the model appears to effectively characterise the habitat preference of birds from St Kilda, Eynhallow and the Caithness coast.

Colony interactions were tested and these did improve the model according to QIC_u. However, this made very little difference in the quality-of-fit based on the confusion matrix. For this reason, we worked with the simpler model, without colony interactions. Any colony interactions could possibly have been due to differences in sample sizes between colonies (i.e. 3236 locations from 40 individuals at St Kilda; 1639 locations from 25 individuals from Eynhallow; and 926 locations from 12 individuals from Caithness), rather than true differences in preference per colony.

Several dietary studies have found that the importance of fisheries discards varies between colonies (Furness and Todd, 1984, Hamer and Thompson, 1997, Phillips et al., 1999), and that diet at St Kilda was less fisheries based. However, this study suggests that all three colonies were influenced by the presence of fishing vessels. The probability of fulmar presence increased in regions where the number of VMS recordings during the period of study was higher. The presence of fishing vessels and thus the availability of fishery discharge may provide a predictable food source for fulmars, whereby birds regularly visit areas known to have intense fishing activity. Alternatively, birds are known to be able to detect fishing vessels operating from a great distance and target these for scavenging opportunities (Verheyden and Jouventin, 1994, Nevitt, 1999, Nevitt, 2008, Small et al., 2013).

Quantifying the importance of fishery waste to fulmars, however, is complex for several reasons. Firstly it is uncertain whether fulmars are feeding on whole fish discards, bycatch or on fish offal following processing on-board. These different products vary greatly in their energy content and thus in their importance to fulmars (Phillips et al., 1999). It has been noted following observations at birds attending fishing vessels that fulmars rarely consume whole discarded fish, preferring offal such as livers (Camphuysen and Garthe, 1997). Secondly, it is challenging to infer from data such as these whether the birds are foraging in regions with high fishery activity because they are targeting the vessels as sources of food or because birds and vessels independently target productive oceanic regions. Without access to real-time fishing vessel locations, to compare with known bird locations, and knowledge of activity on board fishing vessels at any time (e.g. net hauling, catch processing, offal discarding) it is hard to tease apart this complex relationship. However, the study presented here reveals detail regarding the relationship between fishing vessel activity and habitat preference of fulmars, and is a starting point for future studies investigating the influence of fishing vessels on fine-scale fulmar behaviour, which would be possible given access to time-linked VMS data.

A useful way to test the model further would be to compare predicted distributions from this study with at-sea survey data (e.g. European Seabirds At Sea; Tasker et al., 1984). This may yield different results for the primary reason that the model detailed in this study predicts foraging distribution for birds from only three colonies. Commuting between colonies and foraging regions accounts for a large proportion of the duration of each foraging trip in this study, and as at-sea sightings often do not distinguish between travelling and foraging behavior, this may lead to inflation of sightings in regions where very little foraging takes place. Vessels also may act as an aggregator of seabirds at sea (Hyrenbach, 2001), substantially biasing counts during surveys at sea, and for this reason it is believed that data collected using GPS devices presents a more realistic description of the distribution of fulmars. The type of analysis presented here also allows for the relationship between birds from different colonies to be distinguished, which is not possible using only at-sea observations. A combination of two survey methods may in future enable more detailed studies (Louzao et al., 2009).

The data excluded from the model fitting to test the model performance showed a good quality of fit, suggesting that our model performed well for other trips made by individuals included in the study. However, this does not test performance of the model using tracking data from other individuals. The higher predictive performance using the model-fitting dataset (91%, cf. 75% for the validation dataset) results from the fact that these data were indeed used to parameterise the model, so the model should be expected to fit better. Testing the model using a larger chick-rearing fulmar tracking data set from these colonies would in future provide a better test of the predictive performance of the model and could potentially improve the characterisation of fulmar habitat.

Predicting the distribution of fulmars from other colonies (extrapolation) using the model presented here makes one major assumption, i.e. that individuals from other large colonies (for example, Shetland or the east Aberdeenshire coast) show similar habitat preference to the birds tracked in this study. Whilst species distribution models have revealed pitfalls when used to extrapolate and predict distribution across ocean basins (Torres et al., 2014), a prediction within the north east Atlantic/North Sea region may perform with higher reliability. A development of the final model from this study within a Generalized Functional Response (Matthiopoulos et al., 2011, Aarts et al., 2013) framework would be a logical and useful follow-up to this study. This framework aims to characterise the environment around other colonies to predict distribution based on the functional response of fulmars to the habitat covariates that we have identified as important.

The data analysed in this study reflect habitat choice during a period of the breeding cycle when the birds are most constrained by the necessity to regularly provision chicks. GPS and light-level geolocator tracking data were also collected at the Eynhallow colony during the incubation period, where previous work has shown that birds are less restricted in duration of foraging trips (Mallory et al., 2008a; Chapter 2). During this earlier phase of the breeding season, fulmars have the ability to cover large distances (> 6000 km) during foraging excursions of up to two weeks (Chapter 4). Characterizing habitat preference during these other phases of the breeding season may reveal differing patterns in where fulmars forage, given the ability to fly further and for longer. Future work should seek to identify important foraging areas from the geolocator data set, potentially complemented by further targeted GPS deployments, thereby allowing a more detailed assessment of differences in habitat use between breeding stages (Chapters 2 & 3).

This study was conducted using variables on as fine a scale (temporal and spatial) as were obtainable at this time. In some cases, certainly for remotely sensed SST and ChlA, cloud cover and satellite unavailability result in restricted availability of values. Some biological relationships may be present between fulmars and very fine-scale environmental features e.g. ephemeral fronts and eddies that concentrate prey at a coarse scale or short-lived algal blooms that result in locally high prey concentrations for a short time (Wakefield et al., 2009). These features may not be predictable between days, nor identifiable from smoothed data sets. When smoothed over a month, these features are not clearly identifiable and longer-term trends are not appropriate. In this study covariates were often monthly averages, which aim to identify seasonal trends rather than fine scale anomalies. Local processes driving fulmar foraging locations may have a greater impact on their distribution in the short term.

Some fronts in the NE Atlantic region, such as those associated with the continental shelf break, appear to be highly predictable from year to year (Miller, 2009). However oceanic thermal fronts can also be driven by meteorological conditions on shorter time scales. Likewise, changing wind patterns between years (Pirazzoli et al., 2010) have the potential to impact the foraging locations of *Procellariformes* because their movements are finely tuned to utilise the wind (Furness and Bryant, 1996, Weimerskirch et al., 2012). Further investigations of inter-annual differences in foraging location of fulmars, especially with respect to local or regional wind fields may elucidate whether additional factors such as meteorology impact fulmar foraging habitat accessibility and preference.

In conclusion, a complex mixture of factors interplay to influence the movement patterns of fulmars, and it appears that a combination of energetic (distance from colony), abiotic (seabed depth and gradient, sea surface temperature, thermal fronts), biological (chlorophyll-A concentration) and anthropologic (presence of fishing vessels) factors dictate preferred foraging habitat. Using a model that examines the relationship between environmental conditions at fulmar foraging locations and associated control locations, this study has identified a suite of environmental characteristics that describe fulmar foraging habitat, and show that distance from the colony and fishing vessel presence are the two strongest predictors of abundance. The model can be used to predict relative abundance of fulmars from three breeding colonies, which could be used to inform marine spatial planning or to focus conservation efforts. Changes in fisheries management such as a reduction in the availability of discarded fish may have implications for the food supply of fulmars in the north east Atlantic region.

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Chapter 6: General discussion

There is increasing evidence that the marine environment has been altered and continues to change as a result of anthropogenic influences, following the rapid growth of human population throughout the last two centuries and the associated impacts on our seas (Halpern et al., 2008). The study of behavioural and spatial ecology of marine predator populations can elucidate the impacts of human exploitation, pollution and climate change (Boyd et al., 2006, Thaxter et al., 2012, Montevecchi et al., 2012). Monitoring attendance and breeding success of seabirds at nest sites can reveal information linking foraging trip characteristics to reproductive rates (Monaghan, 1996). Meanwhile, surveys from ships and aircraft and recovery or observation of marked individuals provide information on distribution away from breeding colonies (Wernham, 2002, Garthe, 2006). However, without knowledge of where birds are foraging these methods are limited in their potential to relate individual variation behaviour and ecology with breeding success.

Tracking technology has recently revolutionised the study of spatial ecology (Burger and Shaffer, 2008). This thesis has used two methods of tracking to investigate the breeding season distribution of northern fulmars from three breeding colonies on the coast of Scotland. Three limited studies had previously tracked fulmars during the breeding season (Falk and Møller, 1995, Weimerskirch et al., 2001, Hatch et al., 2010) and a recent thesis has revealed detail of the foraging movements of European fulmars during overwintering migration (Quinn, 2014). However, the study presented here was the first to obtain a sample size of more than three tracked individuals during breeding, and the first to be conducted at boreal European colonies. A larger sample size increases the reliability of findings and can allow population-level inferences to be made from individual data (Hebblewhite and Haydon, 2010). The data presented in this thesis have shown that fulmars from Scottish breeding colonies routinely forage within three distinct ecosystems (OSPAR, 1992) during the breeding season, across 70° of longitude and 30° of latitude.

The remarkable foraging trip of a breeding adult male fulmar on a 6200 km round-trip to the Charlie-Gibbs Fracture Zone (CGFZ) during incubation (Chapter 4) has for the first time revealed linkage between a UK colony and pelagic prey communities around the Mid Atlantic Ridge during the breeding season. The CGFZ has recently been shown to illustrate increased seabird abundance and species richness when compared with nearby regions away from the oceanic ridge (Bennison and Jessopp, 2015), whilst other tracking studies have shown that the central Atlantic is regularly used by many seabird species during post-breeding migration such as Manx shearwaters *Puffinus puffinus* (Guilford et al., 2009), kittiwakes *Rissa tridactyla* (Frederiksen et al., 2012) and Atlantic puffins *Fratercula arctica* (Jessopp et al., 2013). Sooty shearwaters *Puffinus griseus* from South Atlantic colonies commonly spend time foraging around the CGFZ during their transequatorial winter migrations (Hedd et al., 2012), and whilst Cory's shearwaters *Calonectris diomedea* are known to forage on the Mid Atlantic Ridge during breeding, these individuals were tracked from the Azores archipelago, itself much closer to the Mid Atlantic Ridge (Magalhães et al., 2008). Whilst only one bird was tracked to the CGFZ using GPS, analysis of the wider suite of GLS data reveals that this region may be routinely used by some birds during breeding (Chapter 2), as it is during migration (Quinn, 2014).

This wide ranging behaviour is made possible through the efficient flight mode employed by procellarids. Fulmars are known to achieve speeds in excess of 60 km per hour (Chapter 4) using dynamic gliding flight (Pennycuick, 1960) and it has been suggested that low wind speeds may limit their foraging range (Furness and Bryant, 1996). There is evidence that anthropogenic climate change is intensifying and changing the track of storm systems (Woollings et al., 2012, Sydeman et al., 2014), whilst a generally increasing trend in the North Atlantic Oscillation (NAO) index, as seen in recent decades (Hurrell, 1995) may continue to have further impacts on the climate of north western Europe. Meanwhile, fulmar breeding success at Eynhallow has been shown to decline since the 1950s, and shows a negative relationship with winter NAO (Lewis et al., 2009). Not only can climate change impact the availability of prey to seabirds, it is possible that changes in the physical environment exploited by *Procellariformes* could influence their habitat accessibility and life history traits

(Wakefield et al., 2009, Weimerskirch et al., 2012). Additionally, whilst a stormier North Atlantic during the summer may offer opportunities for breeding fulmars to access distant prey resources, these long flights from the colony may result in birds becoming becalmed far from their nest site, with potential implications for breeding. Whilst this study has highlighted the potential range of breeding fulmars to remote foraging grounds (Chapters 2, 3 and 4), further analysis of activity patterns and movements from GLS devices in conjunction with wind data will assist in exploring the role of large scale weather systems in the distribution of fulmars.

This study hypothesised that fulmar #1568 did not embark on a transit flight to the Mid Atlantic Ridge immediately, because a large area of high pressure meant that wind conditions at that time were unsuitable (Chapter 4). Further geolocator tracking during the early breeding season (pre-laying exodus and incubation), when birds are making foraging trips of ca. two weeks from the colony, would facilitate investigation into the response of fulmars to Atlantic weather systems. Using the GPS tracking data collected during two seasons at St Kilda (2011 and 2012) alongside meteorological data, it would be possible to explore the fine scale impacts of wind on the distribution and foraging trip range and duration of chick rearing fulmars. The St Kilda example will be particularly useful, as the colony is located on an isolated island with > 40 km of unrestrictedly accessible habitat in all directions.

The duration of the pre-laying exodus in fulmars has received considerable attention at North Atlantic (Dunnet et al., 1963, MacDonald, 1977), high Arctic (Mallory and Forbes, 2008) and Pacific (Hatch, 1990) colonies; however, to date spatial distribution during this period has never been explored. This study found that female fulmars from Eynhallow, Orkney Islands, regularly make long excursions to the central North Atlantic Ocean and the Barents Sea whilst the majority of males remain closer to the colony in the northern North Sea (Chapter 3). A study on the post-breeding distribution of fulmars from Eynhallow found individual differences in winter foraging strategy, with birds foraging in the Arctic and central Atlantic (Quinn, 2014). However the results presented in this thesis find that this wide-ranging behaviour occurs even within the relative constraints imposed by breeding.

By foraging in areas distant from colonies, it is reasonable to believe that fulmars are accessing more predictable prey resources, whilst avoiding intense competition with sympatric predators in the vicinity of breeding sites. However these long excursions may come with associated risks. Whilst measures to avoid seabird bycatch in longline fisheries have long been established (Klaer and Polacheck, 1998, Weimerskirch et al., 2000) and have been shown to be effective in mitigating fulmar bycatch in the North Atlantic longline fishery (Løkkeborg and Robertson, 2002, Løkkeborg, 2003), their uptake in the region has been limited. Whilst there is no longline fishery operated by the UK fishing fleet, long excursions by breeding fulmars into the waters of Nordic countries, as well as to the west of the British Isles, may bring them into association with other fisheries. Whilst data reliability is poor, an estimated mortality of 50000 – 100000 birds annually has been reported from the Norwegian, Faroese and Icelandic longline fishing fleets combined (Dunn and Steel, 2001) with additional bycatch in other regions accessible to Scottish fulmars such as the Gran Sol fishing grounds south west of Ireland (Anderson et al., 2011). If the broad distribution of fulmars as reported in this thesis is a recent consequence of competition avoidance owing to a population that has dramatically expanded, then this wide dispersal, especially of females, comes with considerable implications (e.g. sex-specific survival rates) which could in future be addressed in further studies including demographic data from multiple long term study sites (Cordes et al., 2015).

Nearly every beached fulmar collected within the North Sea region has plastic within its gastrointestinal tract (van Franeker et al., 2011), and amounts of plastic decline with increasing latitude (Kühn and van Franeker, 2012). Although this ingested plastic can be fatal, causing injury or starvation, sub-lethal effects of plastic ingestion are unclear. By foraging in more remote and less polluted regions such as the mid-Atlantic or Barents Sea/Arctic Ocean, it is possible that fulmars breeding in the North Sea region will be subjected to lower levels of ingested plastic. It is conceivable that within the Eynhallow colony, different individuals or sexes may have marked differences in plastic load, based on foraging area during the pre-laying exodus, and this could be tested by examination of diet samples or contaminants in preen oil (Barrett et al., 2007, Hardesty et al., 2015).

A recent study observed higher than expected levels of plastic from fulmars sampled at Svalbard (Trevail et al., 2015). Whilst a latitudinal gradient is generally observed with regard to plastic in stomach contents in the North Atlantic (Kühn and van Franeker, 2012), it has been suggested that an oceanic gyre in the Barents Sea may act as an aggregator of plastic fragments even in this remote region. Levels of contaminants in feathers have been observed to vary with winter foraging distribution (Quinn, 2014). A combination of breeding-season tracking as used in this thesis, stomach content analysis (Phillips et al., 1999) and of chemical contaminants in body tissue (Furness and Camphuysen, 1997, Hardesty et al., 2015) may reveal further complications associated with human activity.

Modelling the habitat preference of fulmars tracked during chick rearing suggested there is complexity in the physical, biological and anthropogenic environmental factors influencing distribution (Chapter 5), but that distance from the colony and fishing vessel activity were the two greatest influences. Fulmars have long been recognised to use fisheries discards (Fisher, 1952, Camphuysen and Garthe, 1997, Phillips et al., 1999), and the habitat preference modelling presented in this thesis demonstrates a high degree of overlap with commercial fisheries. This will provide a useful starting point in teasing apart the complex relationship between fulmars and fishing vessels, for example, behavioural responses of these birds to fishing vessels, as has been shown with gannets (Votier et al., 2010) and black browed albatrosses (Granadeiro et al., 2011). This study was unable to pursue these fine scale fulmar-fishery interactions further, due to confidentiality surrounding fisheries Vessel Monitoring System data.

Whilst it has been shown that fisheries discards in the North Sea could not wholly sustain the fulmar population, it is conceivable that regionally, or seasonally, discards can form an important dietary component (Garthe and Camphuysen, 1996, Phillips et al., 1999). It remains to be tested whether fulmar distribution will change as a result of reforms of the Common Fisheries Policy (CFP). A ban on discarding within the EU pelagic fishery was implemented in 2015 and a demersal discard ban to be introduced in due course (Damalas, 2015). Fulmars reputedly consume more discharged fish offal than whole fish discards like other species (Camphuysen and Garthe, 1997, Votier et al., 2013) so it may be the case that changing practices in discarding will have little or no impact on fulmars (Bicknell et al., 2013). However a dependence on fisheries waste may alter the habitat preference, as fishing fleet size reduces and vessels spend less time at sea, owing to CFP restrictions. With the discard ban being introduced gradually, ongoing studies using geolocators to track fulmars throughout this process can explore the consequences of reductions in this formerly predictable food source to scavenging seabirds. Concurrently comparing diet through analysis of stomach content (Barrett et al., 2007) or blood or other tissues for fatty acids or stable isotopes (Owen et al., 2010, Stowasser et al., 2012, Owen et al., 2013) may also expose shifting prey preferences as availability varies.

Other environmental variables were shown to be important to fulmar distribution. For example, concentration of chlorophyll-A (ChlA) was included in the model as a proxy for prey availability. A high ChlA concentration indicates regions of phytoplankton growth, which is in turn grazed upon by animals comprising an important part of fulmar diet, e.g. *Pandalus borealis* (Phillips et al., 1999). Furthermore, seabirds are known to respond to the olfactory cue provided by dimethylsulphide produced by phytoplankton (Dell'Ariccia et al., 2014). Higher sea surface temperatures and increasingly windy conditions during the summer in the north east Atlantic have been shown to drive changes in abundance of some phytoplankton species, with some taxa declining (commonly dinoflagellates) and some increasing (diatoms) (Hinder et al., 2012). It is plausible that changes in primary production may impact the higher trophic levels upon which marine predators feed, leading to declines in prey availability (Heath et al., 2012).

One additional consequence of increased temperatures may be an increase in harmful algal blooms (HAB) in the region. It has been suggested that the presence of biotoxins from HAB species may have had a role in the population declines witnessed in harbour seals *Phoca vitulina* in Scotland (Jensen et al., 2015) and could potentially impact fulmars, feeding in similar regions at the same trophic level. Analysis of stomach content for the presence of biotoxins from HAB species could indicate whether this is likely to pose a threat to fulmars, as has been observed in Pacific species (Shumway et al., 2003, Phillips et al., 2011).

Extrapolations from the habitat preference model presented here (Chapter 5) to other colonies would be possible through the implementation of a Generalized Functional Response (GFR) model (Matthiopoulos et al., 2011). The GFR facilitates predictions for other colonies, by including the average environmental conditions for the envelope of accessibility surrounding each colony as a covariate within the model to add a colony specific weighting. This would facilitate a more complete estimation of the distribution of fulmars in the north east Atlantic region (Aarts et al., 2013). Future directions should compare predicted habitat with European Seabirds at Sea (ESAS) survey data on fulmar distribution, whilst bearing in mind the caveats of these data. The model could also be used to predict the response in distribution of fulmars to changes in the environment, for example declining fishing activity or an increasing sea surface temperature.

This thesis has presented detailed analysis of the breeding distribution of one species. The rapidly growing field of seabird tracking is beginning to present the opportunity to compare distribution of multiple species, to investigate how competition affects their distribution (Wakefield et al., 2013) and how many sympatric species breeding in a dynamic and changing marine region utilise different aspects of the environment (Daunt, 2012).

Biases in the study

Because both GPS and GLS data loggers had to be recovered for the data to be obtained, birds that were more likely to be recaptured were targeted. These included large birds that were deemed less likely to be impacted by the additional weight of tracking devices (Phillips et al., 2003), and individuals that could be caught easily when approached, without fleeing the nest site. In the case of the GPS tracking during incubation, this bias could be seen in the preponderance of males in the sample (Chapter 2). The study of personality is a rapidly growing area of behavioural ecology, and personality has been shown to be heritable (Taylor et al., 2012, Patrick et al., 2013). A study on black browed albatrosses found foraging behaviour to be highly repeatable within individuals, and thus could be considered a personality trait that was also linked to breeding success (Patrick and Weimerskirch, 2014). Meanwhile gannets also show high individual consistency in foraging behaviour, which may represent a level of specialisation which could be linked to responses to a changing environment (Patrick et al., 2014). As larger, bolder fulmars were targeted for GPS tracking in this study then it is conceivable that traits, including potentially habitat preference, demonstrated by poorly represented shy birds have not been identified through the analyses presented here. Tracking of a larger sample of individuals, for example using remotely downloadable GPS devices to reduce necessity to recapture (Wade et al., 2014), would increase the generality in the data.

Catching and recapturing birds to deploy and recover devices puts considerable stress on the individuals (Phillips et al., 2003) as well as potential disturbance in more dense parts of the colony (Carey, 2009). Removing birds from their nest site twice in one season doubles the risk of predation of their egg/chick. The use of GLS devices, affixed for a longer period, could reduce the disturbance of individuals and the small size of the device reduces the impact of logger attachment. Having demonstrated the use of a state-space model to reconstruct most likely tracks from GLS locations, this technique could be used to explore finer scale associations with habitat features, especially during longer trips and during periods when GPS tracking continues to pose logistical problems. The data presented in Chapter 2 suggest that foraging trips during late chick rearing are longer than the period of GPS tracking during brood/guard. Again, analysing GLS data in conjunction with knowledge of when birds were at the nest (e.g. from attendance monitoring using Passive Integrated Transponder tags (Mallory et al., 2008) or cameras (Gladbach et al., 2009)) may provide information on an expanding foraging range during this period.

During the pre-laying exodus and incubation, some birds forage in Arctic waters (Chapters 2 & 3) where they encounter constant daylight. Whilst geolocator tracking has proved useful when investigating broad scale distribution, its dependence on defined sunsets and sunrises for location estimates renders geolocation impossible when birds are subjected to constant daylight. The state-space model employed in

Chapter 3 interpolated between locations estimated from day length, possibly underestimating the range of birds at this time. Targeted use of GPS to track incubating individuals known from GLS data to forage in OSPAR Region I will allow investigation of northerly movements of individuals into the Arctic during the breeding season. This may reveal precisely how far north these individuals are foraging at this time of year, and may permit inference of prey types in these distant waters.

Summary

This thesis set out to address questions related to distribution of northern fulmars during different stages of the breeding season. Tracking using GLS has revolutionised our knowledge of fulmar distribution during the early breeding season. Meanwhile, tracking using GPS has enabled exploration of foraging behaviour and analysis of the habitat preferences of Scottish fulmars from three colonies. The two methods used together have enabled a detailed analysis of the foraging trip characteristics and spatial distribution of fulmars from three Scottish colonies. Following two extensive studies on the foraging movements of fulmars from north west European colonies during both migration (Quinn, 2014) and now the breeding season (this thesis), there is an opportunity to assess linkage between summer and winter distribution, and the implications of such strategies on breeding success and survival.

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Appendix 1. Summary of northern fulmar foraging trip characteristics from previous studies at NE Atlantic colonies.

Study	Location	Breeding period	Trip durations	Foraging range (km)	N	Method
(Mougin, 1967)	Forvie, UK	Incubation	Mean = 3.7 ± 0.2 d	-	71	Observations of attendance at nests
(Falk and Møller, 1995)	Mallemukfjeld, Greenland	Incubation	Mean = 6.1 d	-	81	PTT tracking
(Ojowski et al., 2001)	Foula/Unst, UK	Incubation	Mean = 32.5 h	-	24	Observations of attendance at nests
(Mallory et al., 2008)	Eynhallow, UK	Incubation	Mean = 6.8 ± 0.4 d	-	69	Observations of attendance at nests/ automatic logging of birds at nests
(Dunnet and Ollason, 1982)	Eynhallow, UK	Chick rearing	-	466	1	Recapture of ringed bird
(Furness and Todd, 1984)	Foula, UK	Chick rearing	Median = 6 h	-	67	Observation of attendance at nests
		Chick rearing	-	Median = 35	10	Observations of marked birds at sea
	St Kilda, UK	Chick rearing	Mean = 29 h (estimated)	580 (estimated)		Observations of feeding interval at nests
(Hamer et al., 1997)	Foula, UK	Chick rearing	Mean = 12 h (estimated)	122 (estimated)		Observations of feeding interval at nests
	St Kilda, UK	Chick rearing	Mean = 24 h (estimated)	245 (estimated)		Observations of feeding interval at nests
(Phillips and Hamer, 2000)	Fair Isle, UK	Chick rearing	Mean = 31 h (estimated)	-		Observations of feeding interval at nests
(Ojowski et al., 2001)	Foula/Unst, UK	Early chick rearing	Mean = 11.2 h	-	25	Observations of attendance at nests
		Mid chick rearing	Mean = 20.4 h	-	25	Observations of attendance at nests
(Weimerskirch et al., 2001)	Bjornøya, Norway	Chick rearing (brooding)	Mean = 8.0 ± 4.5 h	-	146	Automatic logging of birds at nests
		Chick rearing (brooding)	Mean = 10.2 ± 4.0 h	Mean = 60.8 ± 48.7	164	PTT tracking of two birds
		Chick rearing (post-brooding)	2 – 3 d	> 500		PTT tracking of two birds

Appendix 1: References

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