Drivers of seabird distribution and foraging movements



Jessica Phillips

Merton College

University of Oxford

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Abstract

Recent improvements in biotelemetry and analytical methods have increased our understanding of the at-sea movements and behaviour of elusive pelagic seabirds, many of which are becoming the focus of conservation efforts. In this thesis, I consider several issues related to the environmental correlates of the foraging movements and at-sea distributions of a critically endangered shearwater in UK waters and of two penguin species in Antarctic and sub-Antarctic waters; I also consider the use of the 'dual foraging strategy' (i.e., both short- and long-distance foraging) during chick-rearing of different seabird taxa.

This thesis explores the associations of oceanographic variables and prey abundance with the at-sea distribution of both non-breeding seabirds (Balearic shearwater *Puffinus mauretanicus*, Chapter 2) and of breeding seabirds (macaroni penguins *Eudyptes chrysolophus*, Chapter 4). Chapter 2 combines 5 years of vessel-based surveys of post-breeding Balearic Shearwaters in the western English Channel and southern Celtic Sea with simultaneously collected bio-acoustics data of fish abundances and remote-sensed environmental data. I map Balearic shearwater presence across the area using both Generalized Additive Models (GAMs) and Random Forest (RF) models, providing the first estimate of the distribution of this critically endangered seabird in UK waters, information that is essential for the designation of a Special Protection Area (SPA). Oceanic variables associated with prey distributions were better predictors of seabird movements than direct measures of prey distribution, possibly because snapshots of prey availability cannot capture the dynamic nature of prey distributions.

Using data from GPS and time-depth recorders, this thesis also investigates the presence and dynamic nature of prey depletion around breeding colonies in two penguin species (chinstrap penguins *Pygoscelis antarcticus* in Chapter 3, and macaroni penguins in Chapter 4) and estimates foraging patch quality based on time allocation during foraging dives. Foraging patch quality increased with increasing distance from the colony for both species, suggesting that birds depleted prey near their colony, providing evidence for "Ashmole's halo". However, neither species utilized the dual foraging strategy. Interestingly, habitat quality near the chinstrap penguin colonies *improved* over the breeding season, suggesting that chinstrap penguins, like some other seabirds, time their reproduction so that the period of maximum resource availability in the environment aligns with their period of maximum demand for resources.

Finally, the drivers of dual foraging in different seabird families are identified in a systematic review (Chapter 5) that compiles published literature on the use of dual foraging by seabirds during chick-rearing with concurrent estimates of habitat quality around the colonies. We found the likelihood that seabirds use the dual foraging strategy increases with increasing magnitude of the difference in the quality of the habitat accessible during short- versus long-distance foraging trips. However, there were significant differences in the use of dual foraging across taxa: Albatrosses and Penguins were significantly less likely to dual forage than Procellariidae, while Sulids were significantly more likely to dual forage than Procellariidae. This suggests that other, taxon-specific factors – such as travel costs and the resilience of chicks against starvation – also play a role in determining the use of the dual foraging strategy by different seabird taxa.

Overall, these findings advance our understanding of the environmental drivers of seabirds' foraging distributions and provide valuable information for their conservation.

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Author contributions

All of the work in this thesis is primarily my own.

Eighteen collaborators co-authored one or more of the data chapters. Their contributions are as follows:

Tim Guilford contributed his ideas and feedback for all data chapters from the conception to analysis and manuscript preparation.

Annette Fayet contributed her ideas and feedback for Chapter 3, 4, and 5 from the conception to analysis and manuscript preparation.

Alex Banks contributed his ideas and feedback for Chapter 2, from the conception to analysis and manuscript preparation.

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Phil Trathan participated in the fieldwork and provided data for Chapter 3, and contributed his ideas and feedback on Chapters 3 and 4.

Victoria Warwick-Evans contributed her ideas to the analysis and gave feedback for Chapter 3.

Fabrizio Manco contributed his ideas for the analysis and participated in fieldwork for Chapter 3.

Sophie Feilding provided the data on krill abundances for Chapter 4.

To Michael, Marlys, and Jaden

my parents and sibling

Table of Contents

Chapter 1 General Introduction 11

Chapter 2 Consistent concentrations of critically endangered Balearic shearwaters in UK waters revealed by at-sea surveys..... 53

Chapter 3 Foraging conditions for breeding penguins improve with distance from colony and progression of the breeding season at the South Orkney Islands..... 97

Chapter 4 Foraging behaviour and characteristics of preferred foraging sites of breeding macaroni penguins..... 135

Chapter 5 Systematic review of dual foraging across seabirds: probability of dual foraging varies with habitat quality and taxa..... 165

Chapter 6 General discussion 215

Chapter 1

General Introduction

1. Introduction 12

2. Why study seabirds at sea 13

3. Central-place foraging 14

4. Visual surveys of seabirds at sea 17

5. Tracking seabirds at sea 18

6. Animal care and ethics..... 20

7. Behaviour classification 22

8. Measuring patch quality 25

9. Environmental drivers of seabird distributions 28

10. The Balearic Shearwater 29

11. The Chinstrap Penguin 31

12. The Macaroni Penguin 32

13. Objectives and structure of the thesis 34

14. References 36

1. Introduction

The Chinese word for animal '动物' (dòng wù) translates to 'moving organism'. Animals are characterised by their movement. From salmon leaping upstream to albatross soaring over the ocean or wildebeest migrating across the Serengeti, animal movements have captured our imagination. Given the tangible benefits of knowing where animals are, this fascination with animal movement may be a trait that provided competitive advantages. Whether it was to hunt or avoid being hunted, knowledge of where animals were in the local environment must have played a role in the survival of early human societies.

Despite domestication of plants and terrestrial animals about 12000 years ago (Zeder, 2008), the exploitation of wild marine animals, fish in particular, has continued to this day, requiring knowledge of their distributions. The industrial revolution brought about industrial fishing in the 19th century (Thurstan et al., 2010), marking a turning point in which our ability to extract animals from the ocean exceeded their capacity to recuperate (Myers and Worm, 2003). While we can see when we have clear-cut an entire forest and understand that a lake can only sustain a finite number of fish, what of the ocean? The idea that we could deplete the ocean was preposterous until it actually happened (Pauly et al., 2005). From the collapse of industrial whaling (Springer et al., 2003) to the collapse of the northern cod fishery (Milich, 1999), we have been notoriously cavalier about the sustainability of our exploitation of the ocean.

2. Why study seabirds at sea

Healthy oceans help sustain global ecosystems in several ways, including sustaining water quality, seafood provision, and coastal protection (Lemasson et al., 2017; Drakou et al., 2018; Hall-Spencer and Harvey, 2019). However, ongoing monitoring of ocean health – which requires collecting data on all relevant biological and physical processes – is a massive undertaking (Piatt et al., 2007). One method for making this monumental task more manageable is to use apex predators as indicators of ecosystem health ; for example, researchers' frequent use of seabirds as indicators of ocean health (Reynolds et al., 2019). In an environment where most organisms are constantly submerged, seabirds are highly visible, allowing them to be easily counted as they travel to marine hotspots to forage (Sydeman et al., 2006). Additionally, most seabirds are colonial, gathering annually to reproduce in the same locations, facilitating the study of population trends (Piatt et al., 2007). While other marine animals also regularly return to their breeding grounds, seabirds breed on land, and some species are easy to capture at their colonies, enabling the measurement of a wide range of demographic, behavioural, and physiological traits (Lavers et al., 2008; Wanless et al., 2009; Harris et al., 2013; Mills et al., 2020). Seabirds are also top predators in their ecosystems, and thus changes in lower trophic levels will likely be reflected in their populations (Parsons et al., 2008). As long-lived species which reproduce annually, seabirds have relatively stable population sizes between years, allowing long term changes in environmental conditions to be detected from changes in their population sizes (Anderson et al., 2017). Seabird diets also reflect the prey available to them within their foraging ranges, potentially providing information on the abundance of their prey species (Velarde et al., 2019). Seabirds have been used to monitor fish stocks since the 1980s (Cairns, 1987; Montevecchi, 1993; Depot et al., 2020); more recently, they have been used to monitor

fisheries management (Lorentsen et al., 2018; Scopel et al., 2018) and to assess environmental levels of pollutants (Rutkowska et al., 2018) and micro-plastics (Alvarez et al., 2018).

Besides their value as indicators of ocean health, seabirds are also worthy of study for intrinsic reasons. One of the most threatened group of birds on Earth (Croxall et al., 2012), seabirds face numerous threats both on land and at sea. In decreasing order of importance, these threats include: invasive species at their breeding colonies, fisheries bycatch, climate change and severe weather, overfishing, pollution, hunting and trapping, native predator species, human disturbance, and energy production and mining (Dias et al., 2019a). Major breeding sites of many seabirds are well known and receive some protection, but their habitats at sea are far less well understood and, thus, largely unprotected (Critchley et al., 2018). We must learn more about their distributions and behaviour at-sea to understand their interaction with the marine environment and to improve our ability to protect them.

3. Central-place foraging

As central-place foragers faced with a heterogeneous ocean to forage and constrained by the need to return to the colony, breeding seabirds must make complex decisions, such as whether to forage close to or far from the colony (Weimerskirch, 1998). As iteroparous animals, they also must balance their own needs with the needs of their current offspring to maximize their fitness (Ricklefs, 1977). Faced with these decisions, some seabirds adopt a 'dual foraging' strategy, where parents alternate frequent short foraging trips which make it possible to feed chicks regularly (Cuthill and Kacelnik, 1990) with less frequent long trips to better foraging grounds to restore their own condition (Matsumoto, 2008). When chick

condition is poor, adults shorten their foraging trips (Wischnewski et al., 2019); this keeps the energy cost of capturing and carrying food for the chick low (Cuthill and Kacelnik, 1990) and improves chick growth rate through more frequent feedings (Schaffner, 1990). During short trips, adults are constrained to feed at foraging grounds near the colony where prey may be depleted through competition (Weimerskirch, 1998; Weimerskirch and Cherel, 1998). During long trips parents prioritize their own needs, traveling further where they can exploit better foraging sites (Shoji et al., 2015). There is some evidence that partners coordinate the timing of their long trips to ensure chicks do not go for long periods without feeding (Shoji et al., 2015; Tyson et al., 2017). Using the dual foraging strategy allows parents to maintain their own body condition without compromising chick growth (Ochi et al., 2016).

While dual foraging is not ubiquitous among seabirds (Phillips et al., 2009), it has been reported in several seabird families, including Alcidae (Steen et al., 2007; Welcker et al., 2009; Brown et al., 2012; Jakubas et al., 2014), Diomedeidae (Weimerskirch et al., 1994; Berrow and Croxall, 2001; Pinaud et al., 2005), Fregatidae (Austin et al., 2019), Laridae (Paredes et al., 2012; Christensen-Dalsgaard et al., 2018), Phaethontidae (Sommerfeld and Hennicke, 2010), Procellariidae (Chaurand and Weimerskirch, 1994; Weimerskirch et al., 1994; Weimerskirch, 1998; Congdon et al., 2005; Magalhaes et al., 2008; Paiva et al., 2010; McDuie et al., 2015; Shoji et al., 2015; Ochi et al., 2016), Spheniscidae (Clarke et al., 1998; Luna-Jorquera, 1999; Irvine et al., 2000; Barlow and Croxall, 2002; Taylor et al., 2002; Clarke et al., 2006; Blanchet et al., 2013; Carpenter-Kling et al., 2017), and Sulidae (Adams and Klages, 1999; Zavalaga et al., 2007; Warwick-Evans et al., 2016). Some studies report that the use of the dual foraging strategy can vary between years at the same colony (Besel et al., 2018), and others report that it is employed by males but not by females (Nel et al., 2002; Matsumoto et al., 2017). While dual foraging is assumed to occur only when the quality of foraging grounds near the colony are insufficient to provide for the needs of both adults and

chicks (Chaurand and Weimerskirch, 1994; Granadeiro et al., 1998; Weimerskirch, 1998; Weimerskirch and Cherel, 1998), the drivers of dual foraging are not well understood.

Due to the over-exploitation of local resources, seabirds in large colonies can create a zone of food depletion around the colony, known as "Ashmole's halo" (Ashmole, 1963; Birt et al., 1987). When this occurs, travelling further would be likely to yield a higher reward per unit time because prey availability improves with increased distance from the colony (Ashmole, 1963). Given that travelling further incurs greater energy costs, Central Place Foraging Theory (Orians and Pearson, 1979) predicts that seabirds will only travel further from the colony to forage if more distant foraging patches are better quality (due to higher prey availability or quality) than local patches (Houston and McNamara, 1985; Cuthill and Kacelnik, 1990; Waite and Ydenberg, 1996), assuming they know the distance and quality of accessible prey patches. However, due to the logistical difficulty of identifying successful foraging events in the ocean, this prediction has rarely been tested (Birt et al., 1987; Elliott et al., 2009; Shoji et al., 2014; Oppel et al., 2015). In this thesis I examine whether the Ashmole's halo can be detected around large chinstrap penguin *Pygoscelis antarcticus* and macaroni penguin *Eudyptes chrysolophus* colonies and whether food depletion near the colonies becomes more pronounced over the breeding season.

Central Place Foraging theory is relevant to the studies reported in the current thesis in two separate ways. Firstly, this thesis investigates the way in which the presence of a fixed breeding colony (i.e., the 'central place') impacts the intraspecific competition and foraging decisions of breeding seabirds. Specifically, I investigate the presence and dynamic nature of prey depletion around breeding colonies and how local prey depletion drives seabirds to use the dual foraging strategy. Secondly, by considering the ocean surface – which seabirds must always return to between dives to replenish oxygen – as another type of 'central place'

(Orians and Pearson, 1979; Houston and McNamara, 1985), we are able to estimate foraging patch quality at the site of dives. Patch quality is derived from dive depth profiles based on the assumptions that oxygen depletion is costly and that seabirds should only be willing to pay the cost of additional recovery time at the surface if prey availability is sufficiently high to justify this cost.

In the rest of this chapter I present the field methods, analytical tools, and species selected to address these questions.

4. Visual surveys of seabirds at sea

Scientists have studied the distribution of seabirds at sea for decades. One of the key tools used to conduct such studies is at-sea surveys (Carroll et al., 2019). At-sea visual surveys from boats (Mondreti et al., 2020) or planes (Kelsey et al., 2018; Jessopp et al., 2020) are still in use. These surveys, which follow linear transects, use distance sampling, strip transects (Pettex et al., 2017; Barbraud et al., 2018), photographs (Garcia-Garin et al., 2020), or videos (Zydelis et al., 2019) to estimate the numbers of individual seabirds. Compared to studies that use animal-borne trackers, at-sea surveys usually have larger sample sizes and do not exclude seabirds due to size, breeding status, or colony of origin. Moreover, unlike tracking studies, at-sea surveys identify both areas where seabirds are absent and areas where seabirds are present, facilitating estimates of their local distribution (Carroll et al., 2019). The main limitations of at-sea surveys are that they are expensive to run, tend to cover relatively small areas near the coast, and are usually unable to specify the sex, age, breeding status, or colony of origin of identified individuals (Lascelles et al., 2012). Nevertheless, when combined with large-scale environmental data and simultaneous measurements of prey

abundance, visual surveys of seabirds at sea are powerful tools for identifying their habitat preferences in the marine environment.

5. Tracking seabirds at sea

Animal-borne sensors have revolutionized the study of ecology (Wilmers et al., 2015) by enabling the remote measurement of the movements and activity of animals in the wild (Rutz and Hays, 2009). Half a century ago, ecologists tracked marine animals by visually following balloons attached to their backs (Rutz and Hays, 2009). Three decades ago, researchers estimated the maximum diving depth of marine animals by attaching capillary tubes lined with icing sugar and calculating the compression of air in the tube to estimate the depth of the dive (Burger and Wilson, 1988). Today, we have sensors which can continuously measure a broad range of location (e.g., latitude, longitude, depth), biological (e.g., calorie consumption, heart rate), behavioural (e.g., foraging behaviour, interaction with other species) and environmental (e.g., water temperature) variables (reviewed in Wilmers et al., 2015). Animal-borne sensors are now routinely deployed on a wide range of marine taxa, including mammals, seabirds, turtles, and fish (reviewed in Hazen et al., 2012), and data from these sensors are used to answer questions about animal foraging, habitat selection, sociality, migration, physiology, and energetics (see review in Wilmers et al., 2015).

Trackers for marine animals were first developed 55 years ago for Weddell seals *Leptonychotes weddellii* to measure their dives (Kooyman, 1965). Six years later, bird-borne tags were created and deployed on Emperor penguins *Aptenodytes forsteri*, recording the diving depth of a seabird for the first time (Kooyman et al., 1971). These early depth sensors only recorded the maximum depth reached, but more recent time-depth recorders (TDRs) can

record depth profiles continuously (Naito et al., 1990; Hindell et al., 1991a; Sakamoto et al., 1993; Christensen-Dalsgaard et al., 2017). Satellite tracking devices and Global Positioning System (GPS) loggers were initially limited to larger species (Jouventin and Weimerskirch, 1990); as the size and weight of the devices decreased, it became possible to deploy them on smaller species (Browning et al., 2018; Bennison et al., 2019; Campion et al., 2020). For small migratory birds, geolocators, which use light levels to estimate global position to within a few hundred kilometres (Phillips et al., 2004), and unlike GPS can continuously function for months to years with minimal battery consumption, are a powerful tool to study continental migrations (Guilford et al., 2009; Gaston et al., 2017; Redfern and Bevan, 2020). Accelerometers, trackers which provide detailed measurements of an animal's acceleration, are commonly used to study animals' time-activity budgets (Brown et al., 2013; Berlincourt et al., 2015). These devices have been invaluable in enhancing our understanding of the spatial and temporal distribution of species (reviewed in Cagnacci et al., 2010). However, to allow for the collection of more nuanced information about animal behaviour, more recent research routinely involves simultaneously tagging animals with multiple devices or with single devices that have multiple sensors (e.g., Christensen-Dalsgaard et al., 2017; Bennet et al., 2019; Collins et al., 2020). For instance, current research about the behaviour of marine animals typically involves tagging the animals with both GPS units and TDRs (e.g., Crossin et al., 2015; Christensen-Dalsgaard et al., 2017; Bennet et al., 2019), which simultaneously provide information on the location, depth, and duration of dives (Waggitt and Scott, 2014).

Notwithstanding the valuable data they can collect, animal-borne sensors are not without limitations. First, sensors can negatively impact the tracked animals due to both the stress induced by capturing the animals to attach and retrieve devices (Hawkins, 2004) and due to the increased energetic consumption required to carry the devices (Wilson and McMahon, 2006). Second, in some cases tracking devices may alter the behaviour of the

animal researchers aim to study. For example, a recent study found that GPS tagging of incubating Manx shearwaters did not affect their long-term fitness but did affect their short-term behaviour by reducing foraging gains and doubling their time away from the nest (Gillies et al., 2020). Additionally, despite the decreasing cost of tracking devices, the number of individual animals tracked from each colony tends to be relatively small (Carroll et al., 2019), so the surveyed sample may not be representative of the whole colony (Camphuysen et al., 2012; Lascelles et al., 2012; Soanes et al., 2013).

Animal-borne sensors have come a long way since their development over half a century ago. The multiple functions assessed by the newer devices and their continuously increasing power-to-size ratios make them essential tools for understanding the behaviour of seabirds at sea. However, like all research methods, their potential limitations need to be carefully considered when designing studies of animal behaviour and when assessing the results of such studies.

6. Animal care and ethics

The impacts of tagging on study animals is one of the important considerations. Meta-analyses identified small but significant impacts of tagging on animal survival, activity, and reproduction (Barron et al., 2010; Bodey et al., 2018). Reported behavioural impacts of tagging seabirds include higher energy expenditure (great cormorants *Phalacrocorax carbo* (Vandenabeele et al., 2015)), increased autopreening (African penguins *Spheniscus demersus* (Wilson and Wilson, 1989)), greater foraging effort (Emperor penguins (Kooyman et al., 1992)), and changes in nest attendance (Atlantic Puffins *Fratercula arctica* (Harris et al.,

2012) and Alcids (Wanless et al., 1989)). However, numerous factors can influence the impacts of tagging.

The attachment method can impact survival, reproduction and preening behaviours in seabirds. Barron and colleagues (2010) found that anchored and implanted devices which require anaesthesia had the highest rates of device-induced mortality— followed by harnesses and collars, which can cause birds to become entangled in vegetation. Glue and tail-mounted attachments were associated with the lowest mortality rates. Bodey and colleagues (2018) found that harnesses and tail-mounted devices induced had the highest impacts on survival, followed by neck attachment and leg bands. Barron and colleagues (2010) also found that tags attached with subcutaneous wires had the highest impact on nest success, followed by harness attachments, with no impact from glue attachments. Bodey and colleagues (2018) found that collar attachments negatively impacted reproductive success. Finally, Barron and colleagues (2010) found that breast-mounted devices had the highest rates of device-induced behaviour (e.g. preening), followed by harness mounted devices, with no impact from glued or implanted devices.

While Barron and colleagues (2010) found no evidence that proportionally heavier devices had a greater impact on seabirds, Bodey and colleagues (2018) found that devices below 1% of body mass had no apparent negative impacts on survival or reproduction, while devices above 1% did have impacts, but they tended to be ‘small’. Whereas Phillips and colleagues (2003) found that devices above 3% body mass were particularly likely to cause increase trip durations and higher rates of nest desertions in albatrosses and petrels. Bodey and colleagues (2018) also found that tagging had a greater impact on the survival and reproduction of seabirds using flapping flight than on soaring or flightless species.

The possible knowledge gained from tagging seabirds need to be carefully considered against the potential costs, in particular when studying rare or declining species (Barron et al., 2010; Bodey et al., 2018). Impacts should always be minimised by choosing the appropriate device and attachment method.

7. Behaviour classification

Differentiating foraging behaviour from other types of behaviours in seabirds at sea is essential for identifying the locations and characteristics of preferred foraging habitats and, thus, to designating specific locations for protection (Gonzalez-Solis and Shaffer, 2009). For seabirds at sea, where direct observations are difficult, it is possible to use data from bird-borne tags to infer behaviours (Guilford et al., 2009; Hart et al., 2010; Awkerman et al., 2014; Chimienti et al., 2016; Patterson et al., 2019). Advances in analytical techniques have facilitated these behaviour classifications (Edelhoff et al., 2016).

Animal location data were traditionally analysed as point patterns, which shed light on habitat use and home ranges (Worton, 1987; Moorcroft and Barnett, 2008) but could not distinguish different behaviours. More recently, higher sampling frequencies of minutes (e.g. Weber et al., 2015) to seconds (e.g. Thiebault and Tremblay, 2013) have allowed researchers to analyse the points as movements paths. Path segmentation is now one of the most widely used methods for identifying behaviours from movement paths (Edelhoff et al., 2016).

Path segmentation methods dissect movement paths into segments of distinct behaviours (Gurarie et al., 2016), and generally fall into three groups: pattern description, change point detection or process identification (Edelhoff et al., 2016). *Pattern description*

methods estimate movement parameters (Hurme et al., 2019) – either primary parameters such as speed (Meier et al., 2015) and turning angle (De Pascalis et al., 2020) or secondary parameters calculated from multiple steps. Behaviours are then assigned manually or via supervised (Carroll et al., 2014; Sutton et al., 2020) or unsupervised (Patterson et al., 2009; Breed et al., 2012; Langrock et al., 2012; Gibb et al., 2017) machine learning. In supervised machine learning, the researcher labels a dataset that is used to identify behaviours in a new dataset. In unsupervised machine learning, similar patterns are identified within the dataset without pre-labelling. One widely used secondary parameter is first passage time (Fauchald and Tveraa, 2003), which calculates the time it takes an animal to cross a virtual circle at every point along the track, identifying areas of intensive search (Hurme et al., 2019). *Change point detection* methods use a moving window along movement paths to identify where local means of movement parameters differ from global averages, suggesting a behavioural change (Gurarie et al., 2009; Gurarie et al., 2016). Finally, *process identification* methods model the temporal and spatial change in speed and turning angle to determine behaviours (Morales et al., 2004; Patterson et al., 2008). For example, hidden Markov models (HMMs) assume that the tracking data recorded is driven by a series of underlying behaviours, in which the underlying behaviour at each step depends only on the behaviour of the previous step (Rabiner, 1989). Alternatively, expectation-maximization and binary clustering (EMbC) clusters locations into groups of high and low speed and high and low turning angle, resulting in four groups to be assigned behaviours (Garriga et al., 2016; Soldatini et al., 2019).

A few studies have compared the performance of some of these methods in classifying seabird behaviour. Bennison and colleagues (2018) compared seven methods for identifying search behaviour in northern gannets *Morus bassanus*, and found HMMs performed best. Whereas Browning and colleagues (2018) found supervised deep learning

models outperformed HMMs in predicting dives in European shags *Phalacrocorax aristotelis*, common guillemots *Uria aalge* and razorbills *Alca torda*.

For air-breathing marine animals that must balance their need for oxygen with searching for prey underwater, dives are a natural unit of behaviour (Soto et al., 2008; Hart et al., 2010). The diversity of within-individual dive profiles identified by TDRs suggest that many marine animals have a repertoire of dives that serve different functions (Halsey et al., 2007). This has led researchers to classify dives based on their theorized functions. Early studies identified three distinct dive types based their shape: V-, W-, and U-shaped dives (Leboeuf et al., 1988; Hindell et al., 1991b; Wilson et al., 1995; Schreer and Testa, 1996). V-shaped dives, which consist of a descent and ascent phase but no bottom time, are considered exploratory dives (Wilson, 1995). U-shaped dives consist of a descent phase, a period spent at the bottom of the dive, and an ascent phase. W-shaped dives, are similar to U-shaped dives but include undulations during the bottom phase of the dive which are associated with prey-capturing (Kirkwood and Robertson, 1997; Ropert-Coudert et al., 2000).

This method of classifying dives was employed in many earlier studies of penguins (Williams et al., 1992; Chappell et al., 1993; Wilson et al., 1996; Kirkwood and Robertson, 1997; Putz et al., 1998; Ropert-Coudert et al., 2000; Ropert-Coudert et al., 2002; Lescroel and Bost, 2005; Putz and Cherel, 2005). However, this labour-intensive manual method of classifying dives is somewhat subjective (Ropert-Coudert et al., 2000; Lescroel and Bost, 2005) and, thus, prone to problems of inter-rater reliability (Schreer et al., 2001). This method is considered less appropriate for classifying dive types in the much larger TDR datasets from more recent studies (Thums et al., 2008). Multi-variate statistics, which classify dive types based on characteristics such as the maximum depth and duration of each dive (Hart et al., 2010), provide a faster, more objective alternative (Schreer and Testa, 1996).

8. Proxies of prey availability

Besides identifying foraging locations and behaviour, testing the predictions of the Central Place Foraging Theory also requires quantifying the quality of different foraging patches. However, it is challenging to make concurrent evaluations of prey availability in the patches animals are currently foraging, so it is necessary to identify proxy measures for patch quality.

Seabirds often concentrate their foraging efforts at specific areas within their range (Weimerskirch, 2007). Their movements at sea are presumably driven by the availability of prey, but this assumption has been surprisingly hard to prove (but see Fauchald et al., 2000; reviewed by Cox et al., 2018). However, there is good evidence that seabird behaviours at sea are influenced by oceanographic processes associated with prey availability (Cox et al., 2013; Bertrand et al., 2014; Woodson and Litvin, 2015; McInnes et al., 2017). Wind can drive cold, nutrient-rich water to the ocean surface in a coastal upwelling, where a front separates the cold water from warmer water offshore (Meunier et al., 2012). Phytoplankton respond to these high concentrations of nutrients inshore of the front by expediting growth and reproduction, which increases primary production near the surface (Huete-Ortega et al., 2011). Dips in the depth of the seafloor, such as shelf edges, also create upwellings of nutrient-rich cold water (Eichler et al., 2019), which stimulate primary production through the same process. This sets off a cascade of relationships: nutrient-rich water encourages phytoplankton population growth (Abreu et al., 1995), zooplankton prey on phytoplankton (Noges, 1997), fish feed on zooplankton (Ware and Thomson, 2005), and seabirds target locations of high fish abundance. Thus at-sea seabirds often forage near oceanographic features that produce nutrient-rich water (such as upwellings) where their prey are likely to be congregating (van Franeker et al., 2002). The increasing availability of oceanographic data

from satellite remote sensing (Miller, 2009) has made it possible to include these features in models of seabird distributions.

A variety of environmental variables which serve as proxies of prey availability have been used to predict seabird distributions and abundances (reviewed in Cox et al., 2018): large scale marine features (Ainley et al., 2009; Wakefield et al., 2012; Araujo et al., 2017), chlorophyll levels (Louzao et al., 2006a; Araujo et al., 2017; Perez-Roda et al., 2017; Kane et al., 2020), sea surface temperature (Wakefield et al., 2015; Karris et al., 2018), and depth (Chivers et al., 2013). However, they can have low predictive power (e.g. Winiarski et al., 2014). While these variables can indicate phytoplankton abundance, seabirds do not feed on phytoplankton. They feed one to four trophic levels above phytoplankton (Barnes and Hughes, 1988). Thus these environmental variables will be better predictors of prey availability for seabirds that feed at lower trophic levels that those that feed at higher tropic levels. Nevertheless, these environmental predictors have been useful in predicting seabird distributions, and until we find an inexpensive way to sample prey availability across large distances they will likely remain useful.

Proxies of prey availability can also be derived from the foraging behaviour of animals—e.g. as collected through biologging devices. For example, the diving rate of foraging time spent in a given patch by an animal may reveal some information about the quality of this patch. Diving behaviour in particular can provide information about the surrounding prey availability. Considering dives as the unit of behaviour (Soto et al., 2008; Hart et al., 2010) and the surface as the central place (Houston and McNamara, 1985) air-breathing predators must offset the higher energy cost of travelling to deeper prey patches by increasing energy acquisition at the chosen prey patch (Houston and McNamara, 1985; Cuthill and Kacelnik, 1990; Waite and Ydenberg, 1996). Diving animals can accomplish this

by spending more time at the depth prey congregate in the chosen prey patches (Mori, 1998), increasing prey encounters and captures (Thompson and Fedak, 2001).

Mori and colleagues (2002) developed an 'index of patch quality' (IPQ) based on the assumptions that (1) both the time taken to dive to a prey patch at a certain depth and the abundance of prey in that patch will determine how long an animal spends at depth in the prey patch (Stephens and Krebs, 1986); and (2) that foraging dives are optimized to maximize prey intake (the principle of inverse optimality (McFarland, 1977)). The IPQ is the rate of change in energy gain in relation to time spent in the bottom phase of the dive (i.e., foraging) and is calculated for each dive (Mori et al., 2002) as:

$$x = \frac{(1 + bce^{cu})(u - \tau)}{bce^{cu} + u}$$

Where x is the IPQ, b and c are constants derived from the relationship between dive duration and the post-dive surface pause duration, u is dive duration, and τ is the time taken to travel to the depth of the prey patch (sum of descent time and ascent time). How these parameters and this equation were derived is described in detail in Chapter 3 on page 102. IPQ has been employed as a proxy for prey availability in several marine predators (Mori and Boyd, 2004; Mori et al., 2005; Elliott and Gaston, 2014; Shoji et al., 2014) and was validated by comparing the results with direct observations using cameras deployed on Weddell seals (Mori et al., 2005) and with hydro-acoustic surveys of krill abundance in a study of fur seals (Mori and Boyd, 2004).

9. Environmental drivers of seabird distributions

The processes driving species distributions have enthralled researchers since the origin of ecological research (Sclater, 1858; Wallace, 1876; Merriam, 1894; Griggs, 1914). For over a century, the characterization of species distributions remained descriptive (Terborgh and Weske, 1975; Root, 1988), but with advances in tracking, remote-sensing, and habitat modelling, we can begin to unravel the underlying mechanisms driving these distributions.

Generating 'Habitat Models' to clarify the relationships between species distributions and environmental processes (Virgili et al., 2017b) is an essential part of ongoing analytic efforts to (1) identify key areas for the protection of at-risk species (Guisan et al., 2013); (2) estimate and manage anthropogenic impacts (Redfern et al., 2013); and (3) predict continued habitat suitability as climate change progresses (Robinson et al., 2015; Willis-Norton et al., 2015). For example, habitat models have been employed to assess associations between habitat characteristics and seabird distributions (Clay et al., 2017; Perez-Ortega and Isfendiyaroglu, 2017; Thiers et al., 2017; Virgili et al., 2017a; Dias et al., 2019b; Orgeret et al., 2019; Wilkinson et al., 2020). The traditional method for creating habitat models is to use Generalized Additive Models (GAMs) (Hastie and Tibshirani, 1986; Hastie and Tibshirani, 1990) that link the mean of the response variable (seabird distribution) to smoothed functions of the explanatory variables (environmental characteristics). GAMs assume that included variables are continuous but not necessarily normally distributed and, thus, permit non-linear and non-parametric relationships between species presence and predictive environmental variables (Wood, 2017). GAMs are currently widely used in studies of seabird distributions at sea (Peron et al., 2013; Scales et al., 2014; Virgili et al., 2017a). However, newer machine learning approaches such as Random Forest (RF) can identify relationships beyond the scope

of traditional GAM approaches. RF analyses consider complex interactions spanning numerous dimensions and, thus, potentially provide more accurate predictions of species distributions than the traditional GAM approaches (Evans et al., 2011). RF is increasingly recognized as a promising method of predicting species distributions (Oppel et al., 2012; Fox et al., 2017; Reisinger et al., 2018) that is competitive with the best available traditional modelling methods (Lawler et al., 2006; Prasad et al., 2006).

10. The Balearic Shearwater

The first species discussed in this thesis is the Balearic Shearwater (Lowe, 1921). Balearic shearwaters were initially considered a subspecies of the Manx shearwater *Puffinus puffinus* (Lowe, 1921) then thought to be a subspecies of the Yelkouan shearwater *Puffinus yelkouan* (Bourne et al., 1988) before finally gaining species status based on emerging palaeontological and molecular evidence (Mayol et al., 2000). Balearic shearwaters are the only critically endangered seabird in Europe (BirdLife International, 2018), with global population estimates ranging from 10,000 to 30,600 individuals (Ruíz and Martín, 2004; Arcos, 2011a; Arroyo et al., 2016). Based on this small and rapidly declining population (Meier, 2015), restricted breeding range, and low survival rates (Genovart et al., 2016), demographically informed population viability models suggest that Balearic shearwaters will go extinct in the next few decades (Oro et al., 2004; Genovart et al., 2016). Balearic shearwaters are threatened by a lack of habitat for breeding, predation by invasive species, pollution (Costa et al., 2016), and decreasing prey populations (Boué et al., 2013). Fisheries bycatch is one of the most important contributors to their decline (Oro et al., 2004; Louzao et al., 2006b; Genovart et al., 2016; Cortes et al., 2017), so reducing bycatch is an essential

component of efforts to prevent their extinction (Cooper et al., 2003; Oro et al., 2004; Louzao et al., 2006b; Louzao et al., 2011; Abelló and Esteban, 2012; Genovart et al., 2016).

Balearic shearwaters breed on the Balearic Islands in the western Mediterranean (Louzao et al., 2012) from February to May (Ruíz and Martín, 2004; Louzao et al., 2006a; Arcos, 2011b; Guilford et al., 2012) and leave the Mediterranean in late May to June to migrate into the Atlantic (Guilford et al., 2012). They spend their post-breeding period in Atlantic waters off the coasts of Portugal (Ramírez et al., 2008; Guilford et al., 2012; Oppel et al., 2012; ICNF, 2014), Spain (Mouriño et al., 2003), France (Yesou, 2003; Février et al., 2011), and the UK (Jones et al., 2014). They then return to the Mediterranean in late September to early October (Meier et al., 2015) through the Strait of Gibraltar. While studies have shown that Balearic shearwaters utilize shallow shelf and near-shore areas with thermohaline fronts close to the colony during the breeding season (Louzao et al., 2006a), little is known about their habitat preferences during the non-breeding season (Louzao et al., 2006a).

The number of Balearic shearwaters in northwest Europe during the post-breeding period has been increasing since the 1990s (Wynn and Yésou, 2007; Wynn and Brereton, 2009; Jones et al., 2014), particularly in northwest France (Jones et al., 2014) and southwest UK (Wynn and Yésou, 2007; Darlaston and Wynn, 2012; Jones et al., 2014). This may be associated with increasing sea surface temperatures (Wynn et al., 2007; Luczak et al., 2011) and corresponding changes in prey distributions (Wynn et al., 2007; Wynn et al., 2008; Luczak et al., 2011; Jones et al., 2014), particularly the growth in anchovy and sardine abundances (Beare et al., 2004; Alheit et al., 2012). Tracking data from breeding birds have not yet revealed movements further north than Brittany (Guilford et al., 2012; Meier et al., 2017). There is no published estimate of Balearic shearwater abundance in UK waters, so our

knowledge of their spatial distribution in UK waters is incomplete. This thesis aims to improve the understanding of Balearic shearwater distributions and habitat preferences in the UK.

11. The Chinstrap Penguin

The second species discussed in this thesis is the Chinstrap Penguin. As described in *The penguins: Spheniscidae* (Williams, 1995), Chinstrap penguins have a circumpolar distribution, breeding on the Antarctic Peninsula and sub-Antarctic islands in the South Atlantic. During breeding, they nest in dense colonies on circular platforms of small stones located on ice-free sections of coasts. They are monogamous and almost always return to the same nest site in successive years. While it may not be apparent to BBC viewers who see romanticized films about the species, these colonies, and the penguins in them, tend to be saturated in guano (Phillips, personal observation).

Chinstrap penguins arrive in their breeding colonies in late September to early November and lay their clutch (typically of two eggs) in November or December. Parents alternate 5- to 10-day incubation shifts until the eggs hatch. After hatching one or two chicks, both parents make daily trips to forage while their partner guards the chick(s) at the nest. After 20 to 30 days, chicks enter the crèche stage, forming loose aggregations with other chicks, which frees parents to leave them unattended. During this period, chicks are fed daily by both parents until they fledge, when they are 50 to 60 days old. After chicks fledge, they go to sea for the pre-moult period, return to land for a 13-day moult in March to April, and then over-winter at sea.

Chinstrap penguins mainly prey on Antarctic krill (Woehler and Croxall, 1997) – they are one of the major consumers of Antarctic krill in the Southern Ocean (Wilson et al., 1995) – though they also consume smaller amounts of myctophid fish (Rombola et al., 2006). They catch prey by pursuit-diving, mostly at depths of less than 40 meters. Their breeding success can fluctuate widely between years and can be adversely affected by extensive sea-ice around their colonies (which restricts their ability to forage at sea). At the colonies, Skuas and Snowy sheathbills *Chionis albus* prey on their eggs and chicks, and at sea they can be captured and consumed by Leopard seals *Hydrurga leptonyx*.

Chinstrap penguins breed sympatrically with Adélie penguins *Pygoscelis adeliae* across the Scotia arc, from the southern South Sandwich Islands to the Antarctic Peninsula; the Adélie penguins typically breed 3 to 4 weeks earlier than Chinstraps (Lynnes et al., 2002). Chinstraps also breed sympatrically with Gentoo penguins *Pygoscelis papua* on the Antarctic Peninsula; the two species occupy similar ecological niches (Kokubun et al., 2010) with minor differences in foraging behaviour (Miller and Trivelpiece, 2007) and breeding chronology (Trivelpiece et al., 1987). Although their foraging movements during breeding have been tracked on several occasions (e.g., Kokubun et al., 2010; Kokubun et al., 2015), the interaction between breeding stage, prey availability, and intraspecific competition of chinstrap penguins is not well understood.

12. The Macaroni Penguin

The last species discussed in this thesis is the macaroni penguin. Macaroni penguins arrive at their colonies between October and November and lay a 2-egg clutch in November, where the first egg laid is smaller than the second. Incubation is divided into three shifts, with

both parents taking the first shift, the female taking the second shift, and the male taking the third shift (Williams and Croxall, 1991). The male then remains at the nest throughout brood, while the female takes foraging trips that tend to follow a diurnal pattern, departing at dawn and returning before dusk. Then chicks enter the crèche stage and are fed every 1 to 2 days, at first by the female alone, then by both parents until fledging in February, by which time the chicks are 60 to 70 days old. At most one chick per nest survives to fledging. The smaller egg rarely survives and females may refuse to incubate it. After two weeks at sea following fledging, adults moult in March to April at the colony.

The global population of macaroni penguins is declining (Crossin et al., 2013), but they remain the most numerous penguin species in the world and the largest consumer of marine resources amongst all seabirds (with an annual consumption estimated at 9.2 million tonnes (Brooke, 2004)). Macaroni penguins catch prey by pursuit diving to a mean depth of 50 meters (maximum recorded depth, 163m (Green et al., 1998)). Krill is their main food source (Barlow et al., 2002), though in years of limited Antarctic krill (*Euphausia superba*) availability, amphipods and fish can make up a significant portion of their diets (Waluda et al., 2010).

Macaroni penguin colonies are usually located on steep rocky slopes or level ground with no vegetation. Their nests consist of shallow scrapes in the mud lined with a few small rocks. They are monogamous and have high fidelity to their breeding sites. At the colony, their eggs, particularly deserted eggs, are vulnerable to predation from Skuas, sheathbills, and Kelp gulls *Larus dominicanus*. Chicks, particularly chicks that are weak or separated from their crèche, are vulnerable to predation from Skuas and Giant Petrels. At sea, adults are preyed upon by sub-Antarctic fur seals *Arctocephalus tropicalis* and Leopard seals.

Macaroni penguins have a circumpolar distribution; they breed on sub-Antarctic islands in the South Atlantic and South Indian Oceans and have one colony on the Antarctic Peninsula. One of the largest breeding colonies of macaroni penguins in the world is at Bird Island on the north-western tip of South Georgia in the Scotia Sea, containing about 46,500 breeding pairs (Trathan et al., 2006; Trathan et al., 2012). The environmental characteristics of the foraging locations used by macaroni penguins and the quality of prey patches at these locations have not been well characterised.

13. Objectives and structure of the thesis

This thesis addresses knowledge gaps in the at-sea behaviour and distribution in apex marine predators that are intrinsically hard to study. Specifically, this thesis (1) tests Ashmole's hypothesis of prey depletion around seabird colonies, (2) investigates drivers of dual foraging strategies in seabirds, and (3) tests whether remote-sensed environmental variables are better predictors of seabird distributions than prey distributions. It also investigates questions which haven't been addressed in specific species, providing new knowledge of the UK distribution of Balearic shearwaters, and testing whether habitat quality can be estimated from penguin dive profiles.

In addition to this introductory chapter, the thesis includes four research chapters written as separate manuscripts that can be read independently.

Chapter 2 investigates the UK at-sea distribution of the Balearic shearwater – the most endangered seabird in Europe. While the species has extended its post-breeding range into the UK, its distribution in UK waters is not well understood. Using both Generalized Additive Models and Random Forest models, I combine three sources of data to identify the

environmental factors associated with Balearic shearwater presence in UK waters: (1) 5 years of strip transect data of Balearic shearwaters locations at sea collected from vessel-based surveys in the western English Channel and southern Celtic Sea during the shearwater's post-breeding period in 2013 to 2017; (2) fish abundance data collected from an acoustics device on-board the survey vessel; and (3) environmental data from remote sensors. Using these models, I map the distribution of Balearic shearwater individuals across the western English Channel and southern Celtic Sea, identifying areas with consistently high probabilities of Balearic shearwater occurrence in UK waters.

Chapter 3 aims to determine the association between breeding stage and foraging strategy in chinstrap penguins. Specifically, I test whether birds foraging far from the colony visit higher quality patches than those available near the colony and whether prey depletion near the colony during the breeding season is associated with increased foraging at greater distances from the colony. To address these questions, I use GPS and TDR data from 232 chinstrap penguins from 4 colonies across the South Orkney Islands.

Chapter 4 aims to identify the environmental characteristics of locations where macaroni penguins forage and the quality of prey patches at these locations. Specifically, I investigate (1) whether prey patch quality improves with increasing distance from the colony; (2) whether parents forage at different quality patches when foraging for themselves compared to when foraging for chicks; and (3) whether the prey patch quality varied with time of day in parallel with the diel migration of krill – the macaroni penguins' main prey. To address these questions, I use GPS and TDR data from 32 chick-rearing macaroni penguins breeding on Bird Island, South Georgia, and data on krill abundances from a simultaneous krill acoustic survey near Bird Island.

Chapter 5 integrates research data provided in published reports on dual foraging in seabirds with remote-sensed chlorophyll concentrations surrounding each study colony. The aim is to determine whether larger differences in the habitat quality accessible during short- and long-distance foraging trips are associated with an increased likelihood that chick-rearing seabirds adopt a dual foraging strategy, and how this relationship varies between taxa. I conduct a systematic review of all studies published to date that provide definitive data on whether seabirds in a colony used the dual foraging strategy and cross-reference results from these studies with globally available data on chlorophyll levels at short- and long-distances from the colonies at the time the corresponding studies were conducted.

Finally, **Chapter 6** summarizes and discusses the main findings of the thesis, provides recommendations for establishing a Special Protection Area (SPA) for Balearic shearwaters in UK waters (based on the results of Chapter 2), and suggests directions for future research.

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Chapter 2

Consistent concentrations of critically endangered Balearic shearwaters in UK waters revealed by at-sea surveys

Jessica Ann Phillips[a], Alex N. Banks[b], Mark Bolton[c], Tom Brereton[d], Pierre Cazenave[e], Natasha Gillies[a], Oliver Padget[a], Jeroen van der Kooij[f], James Waggitt[g], Tim Guilford[a]

[a] Department of Zoology, University of Oxford, UK
[b] Natural England, Exeter, UK
[c] RSPB Centre for Conservation Science, Beds, UK
[d] MARINElife, Hampshire, UK
[e] Plymouth Marine Laboratory, Plymouth, UK
[f] Centre for Environment, Fisheries & Aquatic Science (Cefas), Lowestoft, UK
[g] School of Ocean Sciences, Bangor University, UK

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1. Abstract 54
2. Introduction 55
3. Methods 58
4. Results 67
5. Discussion 73
6. Acknowledgements 76
7. Author contributions 77
8. Data availability statement 78
9. References 78
10. Supplementary materials 85

1. Abstract

Europe's only globally critically endangered seabird, the Balearic shearwater *Puffinus mauretanicus*, is thought to have expanded its post-breeding range northwards into UK waters, although its at-sea distribution is not yet well understood. This study identifies environmental factors associated with the species' presence, maps the probability of presence of the species across the western English Channel and southern Celtic Sea, and estimates the number of individuals in this area. This study analyses strip transect data collected between 2013 and 2017 from vessel-based surveys in the western English Channel and southern Celtic Sea during the Balearic shearwater's post-breeding period. Using environmental data collected directly and from remote sensors, both Generalized Additive Models and Random Forest models were used to determine shearwater presence at different locations. Abundance was estimated separately using a density multiplication approach. Seafloor aspect, sea surface temperature, depth, salinity, and maximum current speed were the most important predictors. The estimated number of Balearic shearwaters in the prediction area ranged from 652 birds in 2017 to 6,904 birds in 2014. Areas with consistently high probabilities of shearwater presence were identified at the Celtic Sea front. Our estimates suggest that the study area in southwest Britain supports between 2% and 23% of the global population of Balearic shearwaters. Based on the timing of the surveys (mainly in October), it is probable that most of the sighted shearwaters were immatures. This study provides the most complete understanding of Balearic shearwater distribution in UK waters available to date, information that will help inform any future conservation actions concerning this endangered species.

2. Introduction

With global population estimates ranging from 10,000 to 30,600 individuals (Ruíz and Martín, 2004; Arcos, 2011a; Arroyo et al., 2016), demographically informed population viability models suggest that without action Balearic shearwaters *Puffinus mauretanicus* (Lowe, 1921) are likely to face global extinction in the next few decades (Oro et al., 2004; Genovart et al., 2016). Their relatively small and apparently rapidly declining population (Meier, 2015), restricted breeding range, and very low survival rates compared to similar species (Genovart et al., 2016) make them the only critically endangered seabird in Europe (BirdLife International, 2018).

Balearic shearwaters face a number of threats, including insufficient habitat for breeding, predation by introduced species, pollution (Costa et al., 2016), and decreasing prey populations (Boué et al., 2013). Notwithstanding the publication of the Action Plan to protect Balearic shearwaters by the EU in 2011 (Arcos, 2011b), few threats to the species have been comprehensively addressed, and the global population continues to decline (Genovart et al., 2016; Oro and Guilford, 2017). Bycatch is a leading cause of loss (Oro et al., 2004; Louzao et al., 2006b; Genovart et al., 2016; Cortes et al., 2017), so reducing fisheries bycatch is a vital part of comprehensive plans to stop losses and start recovery (Cooper et al., 2003; Oro et al., 2004; Louzao et al., 2006b; Louzao et al., 2011; Abelló and Esteban, 2012; Genovart et al., 2016). Reducing bycatch could increase immature survival rates from 0.4 to 0.6, resulting in an increase in the population growth rate from 0.856 to 0.972 (Genovart et al., 2016). However, the distribution of immature shearwaters is not well understood, so conservation measures have not been specifically targeted at immatures anywhere across their range.

Balearic shearwaters breed on the Balearic Islands (Louzao et al., 2012) between February and May (Ruíz and Martín, 2004; Louzao et al., 2006a; Arcos, 2011b; Guilford et al., 2012) and spend the post-breeding months in Atlantic waters off the coasts of Portugal (Ramírez et al., 2008; Guilford et al., 2012; Oppel et al., 2012; ICNF, 2014), Spain (Mouriño et al., 2003), France (Yesou, 2003; Février et al., 2011) and, more recently, the UK (Darlaston and Wynn, 2012). Breeding birds leave the

Mediterranean in late May to June to migrate into the Atlantic (Guilford et al., 2012) and return in late September to early October (Meier et al., 2015) through the Strait of Gibraltar. Occasional sightings of putative Balearic shearwaters off the English coastline have been reported since 1868 (as 'Levantine shearwaters' *Puffinus puffinus mauretanicus* (Wynn, 2013)), but starting in the 1990s there has been an apparent increase in the number of Balearic shearwaters in northwest European coastal areas during their post-breeding period (Wynn and Yésou, 2007; Wynn and Brereton, 2009; Jones et al., 2014), particularly in northwest France (Jones et al., 2014) and southwest UK (Wynn and Yésou, 2007; Darlaston and Wynn, 2012; Jones et al., 2014), with hundreds seen off Portland (Wynn and Yésou, 2007) and occasional sightings of hundreds off Brittany (Yesou, 2003). While this apparent increase could be due to improvements in identification and increased observer awareness (Votier et al., 2008), it could also be a consequence of increasing sea surface temperatures (Wynn et al., 2007; Luczak et al., 2011) and associated changes in prey distributions (Wynn et al., 2007; Wynn et al., 2008; Luczak et al., 2011; Jones et al., 2014), in particular, increases in anchovy and sardine populations (Beare et al., 2004; Alheit et al., 2012) – species previously limited to the Iberian and Mediterranean regions.

During the breeding season, Balearic shearwaters favour shallow shelf and near-shore areas with thermohaline fronts close to the colony (Louzao et al., 2006a), but little is known about their preferred habitat during non-breeding seasons (Louzao et al., 2006a). Tracking data from breeding birds have not yet revealed movements further north than Brittany (Guilford et al., 2012; Meier et al., 2017), so our knowledge of their spatial distribution in UK waters is incomplete. There is, as yet, no published estimate of Balearic shearwater abundance in UK waters.

While the movements of seabirds at sea are driven by prey (Fauchald et al., 2000; Fauchald and Erikstad, 2002; Ainley et al., 2009), a wide range of environmental factors have been found to predict seabird distributions (Cox et al., 2018), including oceanographic features, bathymetric features, primary productivity, sea surface temperature, and distance to colony. Habitat models that integrate these environmental characteristics to predict seabird distribution have facilitated the

identification of areas critical to seabird protection (Nur et al., 2011; Lascelles et al., 2012; Oppel et al., 2012; Waggitt et al., 2020a). Generalized Additive Models (GAMs) – which allow the estimation and use of non-linear and non-parametric relationships between species presence and predictive environmental variables (Hastie and Tibshirani, 1990; Wood, 2017) – are widely used to explain the distribution of seabirds at sea (Peron et al., 2013; Scales et al., 2014a; Virgili et al., 2017). However, predictive analyses using machine learning methods such as Random Forest (RF) can handle complex interactions across many dimensions to uncover relationships beyond the reach of traditional GAM approaches and, thus, potentially provide more accurate predictions of species distributions (Evans et al., 2011). RF is emerging as a promising method for the prediction of species distributions (Oppel et al., 2012; Fox et al., 2017; Reisinger et al., 2018) that is proving competitive with the best available traditional modelling approaches (Lawler et al., 2006; Prasad et al., 2006).

This study analyses five years of Balearic shearwater sightings data from annual at-sea surveys around the southwest UK, where previous studies suggest that the species is most prevalent (Wynn and Yésou, 2007; Jones et al., 2014). We aim to 1) use both explanatory RF and GAMs to determine the relationship between the distribution of Balearic shearwaters and potential predictive variables including fish distributions and environmental variables; 2) use predictive RF-based and GAM-based species distribution models to predict the annual and average distribution of Balearic shearwaters to identify areas of relatively higher probability of occurance; and 3) estimate abundance of Balearic shearwaters in the prediction area.

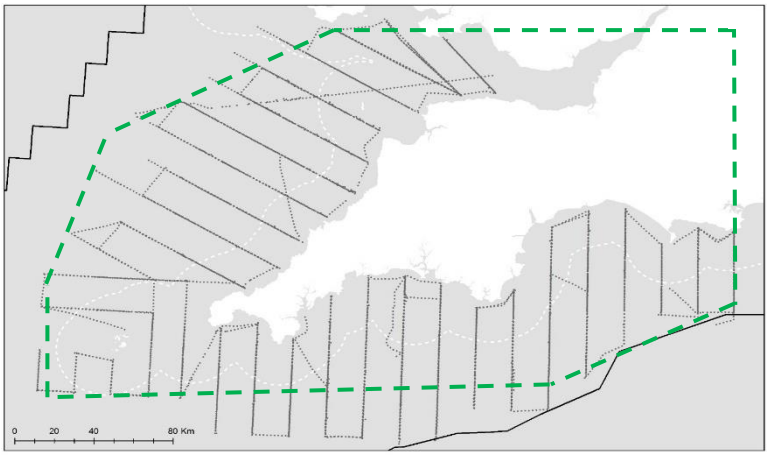
3. Methods

3.1 Data collection

3.1.1 Survey details

Informal sightings suggest that the waters off southwest UK (England and Wales) may be important for Balearic shearwaters (Wynn and Yésou, 2007). To investigate this, annual vessel-based surveys of Balearic shearwater abundance were conducted between 2013 and 2017. Surveys mainly took place during October in tandem with the Pelagic Ecosystem Survey in the western English Channel and Celtic Sea, which primarily aims to map and quantify the small pelagic fish community (ICES, 2015). Most sightings of Balearic shearwaters in UK waters occur from July through October (Wynn and Yésou, 2007). The vessel followed a typical acoustic survey design along a series of parallel transects perpendicular to the coast, spaced such that spatial coverage was even (Rivoirard et al., 2000). The survey design changed in 2017 to cover slightly different transects (Figure 1a and 1b), but the broader area studied did not change.

a)



b)

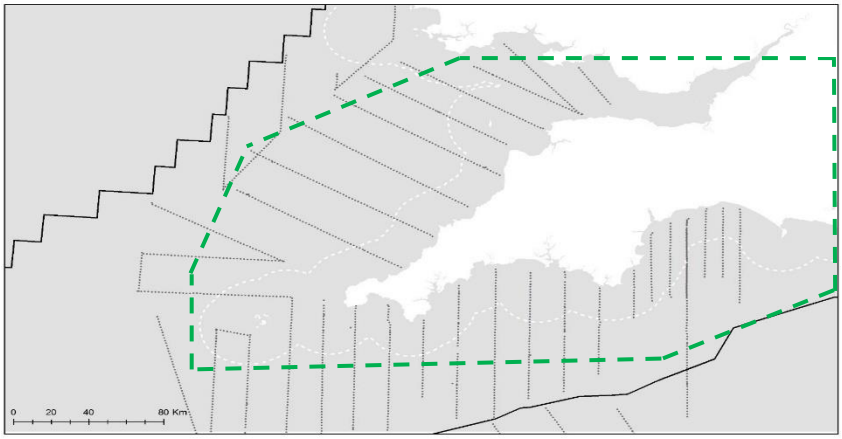


Figure 1. Transect lines surveyed in a) 2013 – 2016 and b) 2017 superimposed onto the area of interest where we predict Balearic shearwater presence. White dotted line indicates 12 nautical mile limit (territorial limit of England / Wales); unbroken black line indicates UK Exclusive Economic Zone limit; the green dashed line encloses the marine area in which we predict distribution and abundance.

3.1.2 Search effort and sightings

Two methods of search were employed across the five-year period. In all years, bespoke methods (Jones et al., 2014) were used. These methods required one observer on one side of the boat to continuously search a box 1,000 m wide, extending 300 m in front of the vessel, with 90° coverage during 'effort' periods (defined as daylight hours when the vessel was not stationary or steaming between transects) grouped into one minute intervals. Between 2015 and 2017, additional European Seabirds At Sea (ESAS) procedures (Camphuysen et al., 2004) with 90° coverage were added to the opposite side of the transect line, resulting in 180° coverage of the sea. Binoculars were used to aid identification of more distant birds. Although ESAS protocol allocates bird sightings on the water into distance bands to derive detection functions for abundance estimates within 300 m of the vessel, additional observations of Balearic shearwaters out to 1,000 m were included, both to be consistent with the bespoke method and to include observations in the 'band E' in ESAS methodology (i.e., greater than 300 m from the transect). The snapshot method (Tasker, Jones, Dixon, & Blake, 1984) used by the ESAS surveyor was used to provide instantaneous counts of birds within 300 m ahead and 1,000 m to the side of the vessel approximately every minute (dependent on vessel speed). In years

with observers on both sides of the vessel, communication between observers by radio ensured birds were not double-counted. The bird survey was suspended during trawls.

Recorded information included the vessel's latitude and longitude, the time of observation, and the number of individuals seen. Because sightings of Balearic shearwaters were scarce, all birds on the water or in flight within 1,000m of the transect were included in the analysis. Individuals that changed location while being observed were assigned to the first location identified. To assess whether the detection of birds decreased with increasing distance from the transect line, both the distance of identified Balearic shearwaters from the observer and their angle from the observer were estimated.

Because of its potential influence on the detectability of seabirds (Camphuysen et al., 2004), sea state was recorded continuously; sea state ratings varied between 0 and 8 on the Beaufort scale, 55% of which were less than 4. Vessel speed during observations used in the analysis ranged between 0.14 knots and 16.45 knots (mean = 9.90 knots, see Supplementary materials, Figure S.1). The vessel, *Cefas Endeavour*, supported observers working from a platform of 12.6 m above sea level.

3.1.3 Prey variables

During bird sightings, continuous simultaneous information was collected on fish in the water-column using fisheries acoustics. Prey data were identified using a calibrated multifrequency Simrad EK60 split-beam echosounder (38, 120 and 200 kHz) deployed on a dropkeel 8 m below the sea surface. The backscatter associated with small pelagic fish (ICES, 2015) was identified and proportionally attributed to species using the catch composition of the nearest trawl. A pelagic (mid-water) trawl was deployed opportunistically – when fish schools were observed on the echogram – to confirm species composition. The acoustic transect was interrupted for trawling (ICES, 2015) and resumed after completion of the trawl. A species-specific algorithm was applied to extract the backscatter of mackerel, which has a unique acoustic signature (van der Kooij et al., 2016). Prey

presence and density (estimated from the Nautical Area Scattering Coefficient [NASC]) were used in the analyses.

3.1.4 Environmental variables

Data on salinity, sea surface temperature, and chlorophyll levels for the area of interest (latitude: 49.491 to 51.622, longitude: -6.888 to -2.003) in each of the five years (2013-2017) were downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS). Temperature data (CMEMS, 2019b) produced with a numeric ocean model were available for each day on a geographic resolution of 0.25 degrees; salinity data (CMEMS, 2019a) were available in weekly averages on a 0.25-degree grid; and chlorophyll data (CMEMS, 2019c) were available for each day on a resolution of 1km longitude by 2km latitude. We averaged the values across each survey period. Data on sea floor depth covering the area of interest with a resolution of 0.0142 degrees longitude and 0.00899 degrees latitude were downloaded from the European Marine Observation and Data Network (EMODnet, 2019). Seafloor roughness, aspect, and anomalies were derived from depth data. Sea floor roughness, calculated using a terrain ruggedness index (TRI) (Wilson et al., 2007), identified bathymetric features associated with abrupt changes in depth. Sea floor aspect identified bathymetry features associated with persistent depth changes in a particular direction. Both seafloor roughness and aspect were calculated using the "raster" (version 2.8-4, (Hijmans, 2018)) package in R 3.5.3 (R core team, 2019). Sea floor anomalies identified bathymetric features associated with unusually shallow or deep depths for their location, that is, areas that deviated from the typical depth within a particular location. We modelled depth as a continuous response variable and coordinates as a continuous two dimensional smooth explanatory variable in a GAM with Gaussian distribution and unconstrained knots, using the "mgcv" (version 1.8-27, (Wood, 2017)) and "raster" packages in R. Positive and negative residuals indicate a cell was shallower or deeper than expected for its location. Maximum current speed was the maximum depth-averaged current speed (m s^{-1}) over a spring neap cycle extracted from an existing Finite Volume Community Ocean Model (Cazenave et al., 2016). It identifies areas of particularly strong currents, which are known to attract foraging seabirds in some

circumstances (Waggitt et al., 2016). A stratification index (Hunter–Simpson parameter, $\log_{10}(h/u^3)$, where h is the water depth and u is the maximum depth-averaged current speed) was used to identify tidal fronts ($\log_{10}$ m^{-2} s^3 = 1.9), mixed water ($\log_{10}$ m^{-2} s^3 < 1.9), and stratified water ($\log_{10}$ m^{-2} s^3 > 1.9) (Simpson and Sharples, 2012).

3.2 Analytical methods

The area of interest was divided into a grid of 1 km^2 cells to provide predictions of bird presence at a suitably fine spatial scale whilst allowing variation between cells. Given that 1 km^2 is a relatively small area when considering the observation methods, it was assumed that observers effectively surveyed the entire grid cell. Environmental data were extracted for each 1 km^2 cell for each of the five years. Salinity, sea surface temperature, and chlorophyll data were estimated for each cell from its nearest neighbours, using bilinear interpolation. Sightings were attributed to cells based on the birds' location. To reduce falsely classifying cells as 'absence' (Oppel et al., 2012), cells were assigned absence only if the survey vessel spent a minimum of three minutes in the cell and no Balearic shearwaters were sighted. This requirement resulted in removing 29% of the cells with zero sightings from the analyses, but it reduced the potential negative effects of false absence cells on the performance of the models (Martin, 2005; Lobo et al., 2010; Oppel et al., 2012). All processing was done in the "raster" package in R.

Three sightings were excluded because the vessel was traveling above 17 knots or spent over 15 minutes in the cell. Vessel speed during the remaining sightings ranged from 0.14 knots to 16.45 knots (mean = 9.90 knots). 'Effort' was defined as the number of seconds the vessel spent in each grid cell. Sea state, the estimated wave height caused by swell and wind, was assigned to cells from observer records. Latitude, longitude and distance to coast were calculated for the centre of each cell.

3.2.1 Explanatory GAM

We set the presence or absence of Balearic shearwaters as the response variable and used a binomial distribution. We assigned sea state as a variable to account for variations in detectability and

log-transformed fish abundances to decrease the influence of extremely high values. To reduce overfitting and improve the model's extrapolative abilities, GAM smoothers were constrained to four knots for each variable using REML (restricted maximum likelihood); this ensured that plausible and ecologically-interpretable relationships between Balearic shearwaters and explanatory variables were produced (Lambert et al., 2017). We built GAMs for all combinations of oceanographic variables and identified the model with the lowest AIC. Maximum current speed and stratification index correlate with each other, and aspect, anomalies, and roughness also correlate with each other, so only one variable from each of these two groups of variables could occur in the same GAM. Latitude and longitude were two separate variables that were only considered in models that did not include 'distance to coast' due to the high correlation of these characteristics. We built GAMs for all combinations of fish variables and compared the AIC of the fish and oceanographic models with the lowest AIC to determine which model best described Balearic shearwater presence. GAMs were constructed using the 'mgcv' package (version 1.8-27, (Wood, 2017)) in R 3.5.3.

3.2.2 Predictive GAM

Because measurements of prey were not available beyond boat transects, separate predictive models based entirely on environmental variables were constructed. To avoid making extrapolations of Balearic shearwater presence beyond the surveyed area, we restricted our prediction area to the intersection of the area of interest, the area in which we had environmental data, and the minimum convex polygon of all cells travelled to between 2013 and 2016. The transect followed in 2017 differed from previous years (Figure 1), so we did not include 2017 data when determining the area of prediction.

We used presence or absence as the response variable, so a binomial distribution was used. We only included variables for which data covered the entire prediction area in the analysis (Table 1). We were modelling presence rather than abundance, so we accounted for effort by excluding absent cells where the boat spent less than 3 minutes (described above). We then created GAMs from all

combinations of this more limited selection of variables and identified the model with the lowest AIC. We used this model to create annual maps of the probability of the presence of Balearic shearwaters across the prediction area. We evaluated the accuracy of predictive GAMs by their Area-Under-Curve (AUC) where 0.5 indicates no predictive ability, 0.7 to 0.8 is acceptable, 0.8 to 0.9 is excellent, and higher than 0.9 is outstanding (Hosmer and Lemeshow, 2000). We also mapped the 95% confidence intervals of the prediction. GAMs were constructed using the "mgcv" package in R 3.5.3.

Table 1. Variables evaluated for each of four models (grey shading indicates variables evaluated for each model).

Group	Variables	Explanatory GAM[Π]	Predictive GAM	Explanatory RF	Predictive RF
Static oceanographic features	maximum current speed	■	■	■	■
	stratification index	■	■	■	■
	depth	■	■	■	■
	seafloor roughness	■	■	■	■
	seafloor anomalies	■	■	■	■
	seafloor aspect[Ŧ]	■	■	■	■
Dynamic oceanographic features	sea surface temperature	■	■	■	■
	chlorophyll	■	■	■	■
	salinity	■	■	■	■
Fish abundance	mackerel	■		■	
	sprat	■		■	
	anchovy	■		■	
	sardine	■		■	
	horse mackerel	■		■	
	herring	■		■	
	boarfish	■		■	
Location	longitude		■		
	latitude		■		
	distance to coast	■		■	■
Survey specifics	sea state	■			

[Π] Fish abundance variables and oceanographic variables were not included in the same models; they were considered in separate sets of models as shown in Table 3.

[Ŧ] Orientation of the slope of the seafloor

3.2.3 Explanatory RF

RF bootstrap samples the dataset, fitting a regression tree to each random subset of the data (Breiman, 2001). At each split in the tree, the data are divided in two by the value of a predictor variable, chosen from a random subset of all predictor variables. Each tree then predicts the out-of-

bag (OOB) observations (i.e., data not used in the construction of that tree) with the errors in these predictions called OOB error. Breiman (1996) showed that OOB error is as good as the error estimate calculated from setting aside a test-dataset equal in size to the training dataset (Breiman, 2001). All OOB predictions are averaged to generate predictions for each observation (Cutler et al., 2007). As RF models are non-parametric and do not assume independence, they are not affected by spatial auto-correlation (Evans et al., 2011). RF ranks variable importance by the drop in the accuracy of the predictions when that variable is randomized (Prasad et al., 2006), a method that can identify the most ecologically meaningful variables more effectively than other methods (Cutler et al., 2007).

With the nine oceanographic variables, distance to coast, and the abundance of seven fish species as the predictor variables, we ran a RF on our dataset using the 'RandomForest' package (version 4.6-14 (Liaw and Wiener, 2002)). Unlike in the GAM analyses, in this RF analysis fish abundances were not transformed because RF does not require data to be normally distributed (Evans et al., 2011), and correlated variables were not removed because RF spreads the importance of the collinear variables (Cutler et al., 2007). We grew 500 regression trees, each on a random subset of 66% of the cells. Each node in each tree split the data with a variable from a random sample of four of the 17 predictor variables. We then ranked the importance of the variables (Figure 3).

3.2.4 Predictive RF

We first excluded fish abundance variables when creating the predictive model, as no data were available outside the boat transects. In order to have an unseen dataset to test the predictive accuracy of our RF model, we set aside the 2013 data and used the 2014 to 2017 data as the training dataset. As there are only 179 'present' cells amongst the 8,107 cells with known presence or absence across the five years, to reduce the class imbalance in the training dataset we randomly sampled absences so that there would be the same number of absences and presences in the models (Sun et al., 2009). In RF models, by default the number of randomly selected predictive variables to split each node in a tree is the square root (rounded down to the nearest integer) of the total number of predictive variables. Using the 'SuperLearner' package (version 2.0-25 (Polley et al., 2019)), we built RF

models with three multiples of this default (0.5, 1 and 2), compared their performance, and produced an optimal weighted average, an 'ensemble'.

This process was repeated with each of the remaining years held out in turn. We then used each of the five ensembles to predict Balearic shearwater presence and absence on the held-out year, and calculated the area-under-curve (AUC) as a metric of the models' ability to accurately predict the unseen year. We then used all five years of data to create a model ensemble that mapped the probability of presence of Balearic shearwaters in each year. The area of prediction considered is the same as that described in section 3.2.2.

3.2.5 Abundance estimate

Oppel and colleagues (2012) attempted to predict Balearic shearwater abundance using five methods, including RF and GAMs; they concluded that all five models had limited predictive power. Given this prior finding and the relatively low number of sightings in our dataset, we were unable to reliably map the spatial variation of Balearic shearwater abundance across our survey area. However, we were able to estimate the overall (mean) abundance in the entire survey area.

For this analysis we only included birds sighted within 300m of the vessel transect. There appears to be little decline in detectability to this distance because most birds detected to this distance are in flight (see Supplementary materials Figure S.2). We assume all birds present within 300 m of the vessel transect were detected, allowing us to use a strip width of 300m in 2013 and 2014, and 600m in 2015 to 2017 to estimate density, without correction for detectability. We estimated density by dividing the numbers of Balearic shearwaters seen within 300m of the boat transect by the total area searched per year (i.e., the distance of the transect multiplied by 300m in 2013 and 2014, and by 600m in 2015, 2016, and 2017). We assumed that surveys covered a broad range of habitats, supporting both low and high densities of birds. Based on this assumption, the densities calculated should be representative of the density across the region, so we estimate the annual number of individuals in our prediction area by multiplying the calculated annual density by the size of the

prediction area (41,771 km^2) – that same polygon on which we predicted distribution. We derived variance of bird density by calculating the variance in bird density across days, weighted by transect distance covered each day. Multiplying the variance in density for each year by the size of the prediction area produced the variance in abundance.

4. Results

The vessel covered transects totalling 12,366 km in 100 days of surveying across the five years. The final analysis included data on 393 birds sighted in 179 of the 1 km^2 grid cells (Table 2).

Table 2. Details of vessel survey in UK waters and Balearic shearwaters sighted per year

Year	Survey method	Dates	Duration (days)	Number of birds	Number of 1km^2 cells with birds (% of cells with birds)
2013	BM	15-30 October	16	66	42 (3.2%)
2014	BM	4-17 October	14	168	61 (3.2%)
2015	ESAS	4-21 October	18	62	33 (2.0%)
2016	ESAS	4-19 October	16	84	34 (2.3%)
2017	ESAS	29 September - 3 November	36	13	9 (0.5%)
Total	.	.	100	393	179 (2.2%)

BM= bespoke methods ESAS = European Seabirds at Sea

The explanatory oceanographic GAM with the lowest AIC contained chlorophyll, salinity, sea surface temperature, depth, seafloor aspect, distance to coast, and stratification index (Table 3. Figure 2). The explanatory fish GAM with the lowest AIC contained mackerel, sprat, anchovy, horse mackerel, herring, and boarfish. The oceanographic model had a substantially lower AIC (ΔAIC=161.0) (Table 3).

Table 3. Top five fish models and top five oceanographic models that explain Balearic shearwater presence based on the explanatory GAMs with the lowest AIC (grey shading indicates variables included in each model)

Variable group	Variables[ℓ]	Oceanographic models					Fish models				
		env.1	env.2	env.3	env.4	env.5	fish.1	fish.2	fish.3	fish.4	fish.5
Oceanographic variables	maximum current speed[∏]					■					
	stratification index[∏]	■	■	■	■						
	seafloor roughness[ጠ]										
	seafloor anomalies[ጠ]			■	■						
	seafloor aspect[ጠ,Ŧ]	■	■			■					
	sea surface temperature	■		■		■					
	chlorophyll	■	■	■	■	■					
	salinity	■	■	■	■	■					
	depth	■	■	■	■	■					
	distance to coast	■	■	■	■	■					
Fish variables	mackerel						■	■	■	■	■
	sprat							■			■
	anchovy						■	■	■	■	■
	sardine								■		■
	horse mackerel						■	■	■	■	■
	herring						■	■	■	■	■
	boarfish						■	■	■		■
Δ AIC	-	0.0	2.8	5.8	7.2	11.0	161.0	161.8	162.1	162.9	163.1

[ℓ] All models include sea state as a variable.

[∏] Maximum current speed and stratification index are correlated, so they cannot both be included in the same model

[ጠ] Seafloor roughness, seafloor anomalies, and seafloor aspect are correlated, so they cannot both be included in the same model

[Ŧ] Orientation of the slope of the seafloor

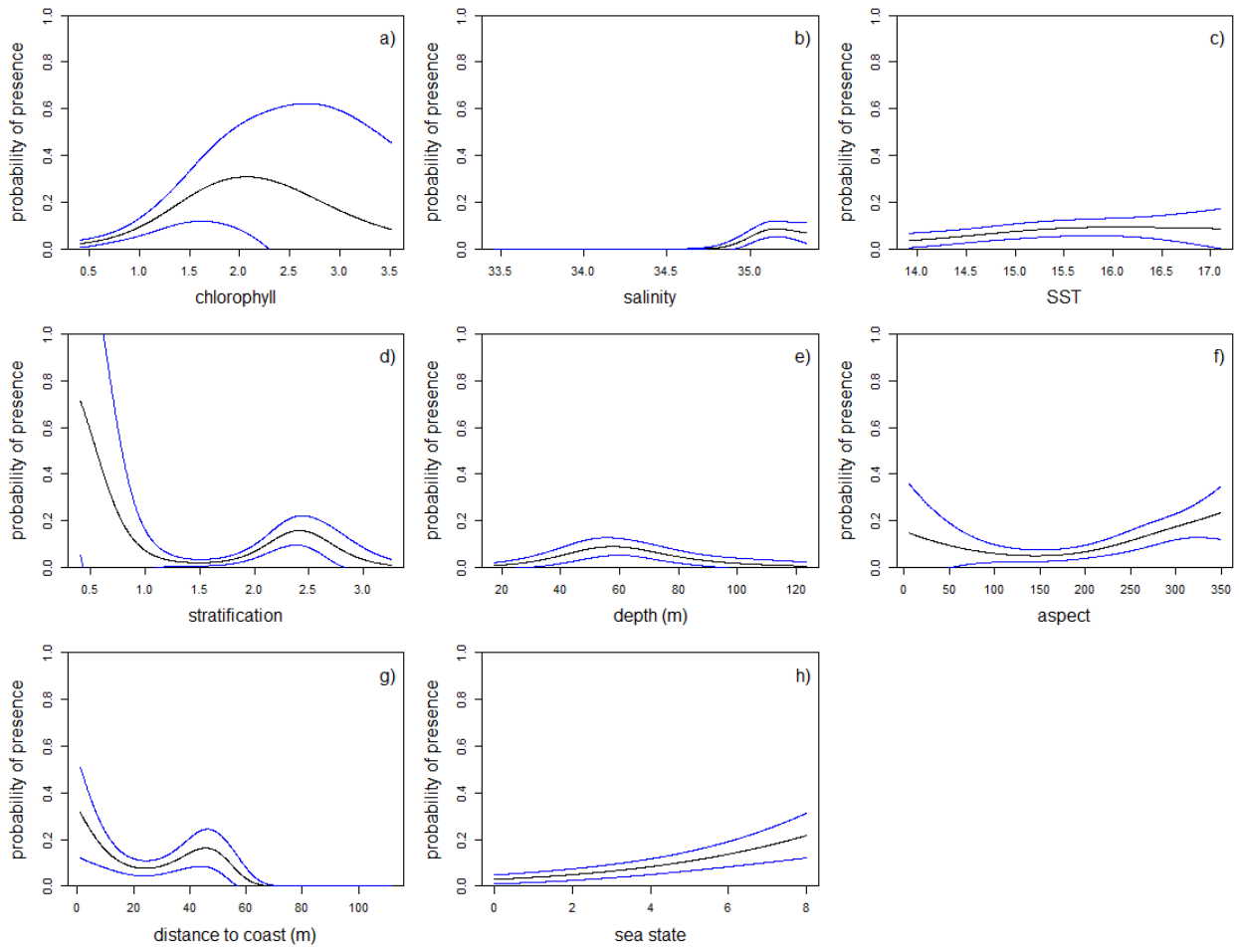


Figure 2. Relationship between variables retained in explanatory GAM with lowest AIC and probability of Balearic shearwater presence (with 95% confidence intervals) when all other variables are set at their mean. For a) chlorophyll; b) salinity; c) sea surface temperature; d) stratification index; e) depth; f) aspect; g) distance to coast; and h) sea state.

The ranking of the importance of different variables in the explanatory RF (Figure 3) supports the conclusion of the explanatory GAMs: oceanographic variables are better at predicting Balearic shearwater presence than surveyed abundance of individual fish species. In the RF variable ranking, all oceanographic variables ranked higher than any fish species abundance, except for seafloor roughness which ranked below horse mackerel. Sea floor aspect emerged as the most significant variable followed by depth and salinity. The explanatory RF has an OOB error rate of 0.06, indicating the model has high accuracy.

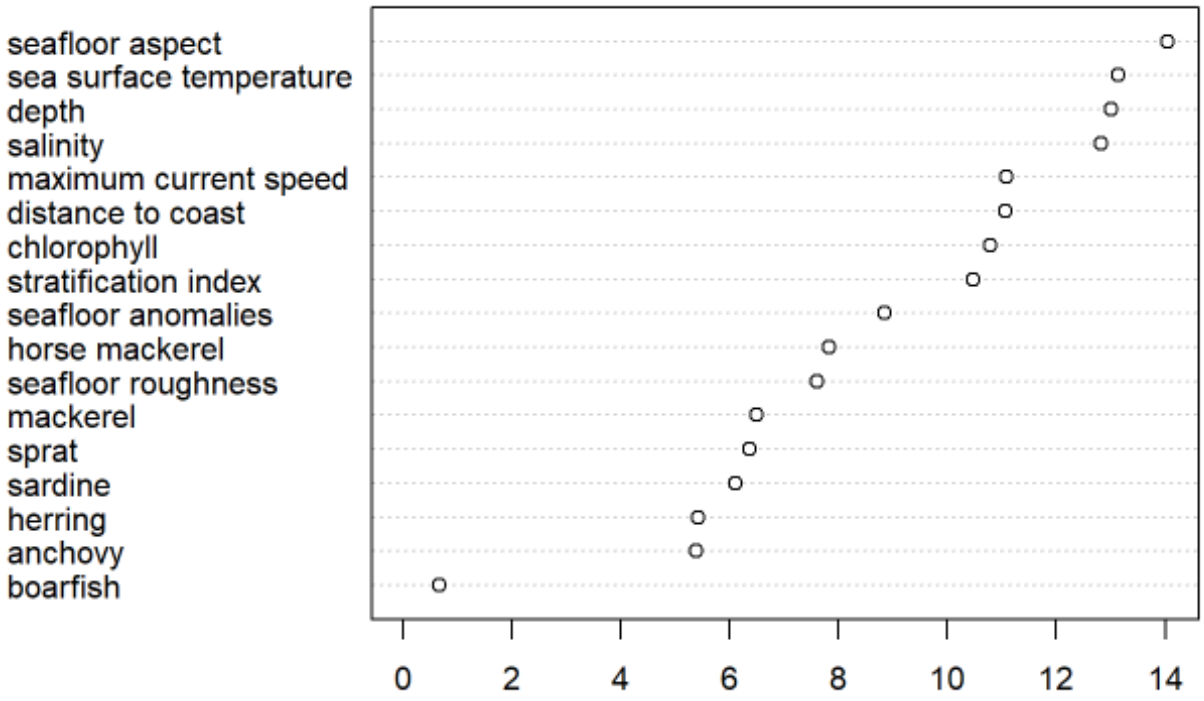


Figure 3. Importance of variables in the explanatory random forest model, calculated from the drop in prediction accuracy when each variable is randomized. The values on the x-axis have no intrinsic meaning, they represent the relative importance of the 17 variables included in the model.

The predictive GAM retained depth, sea surface temperature, salinity, chlorophyll, latitude, longitude, seafloor anomalies, and stratification index. As shown in supplementary Figure S.3, there is no evidence of residual spatial auto-correlation. The predictive GAM has an AUC of 0.869 for 2013, 0.839 for 2014, 0.848 for 2015, 0.837 for 2016, and 0.669 for 2017; the AUC was 0.849 in a model that combined all 5 years of data. The AUC for the model ensembles with each of 2013 to 2017 data held out were: 0.78, 0.68, 0.80, 0.75, and 0.48. We used a model ensemble built on all five years of data to make predictive maps of Balearic shearwater distributions for each of the 5 years. The predictive maps of the GAM and RF identified similar areas of highest shearwater density (Figure 4, 5, and see Figure S.4 and S.5 in Supporting Information).

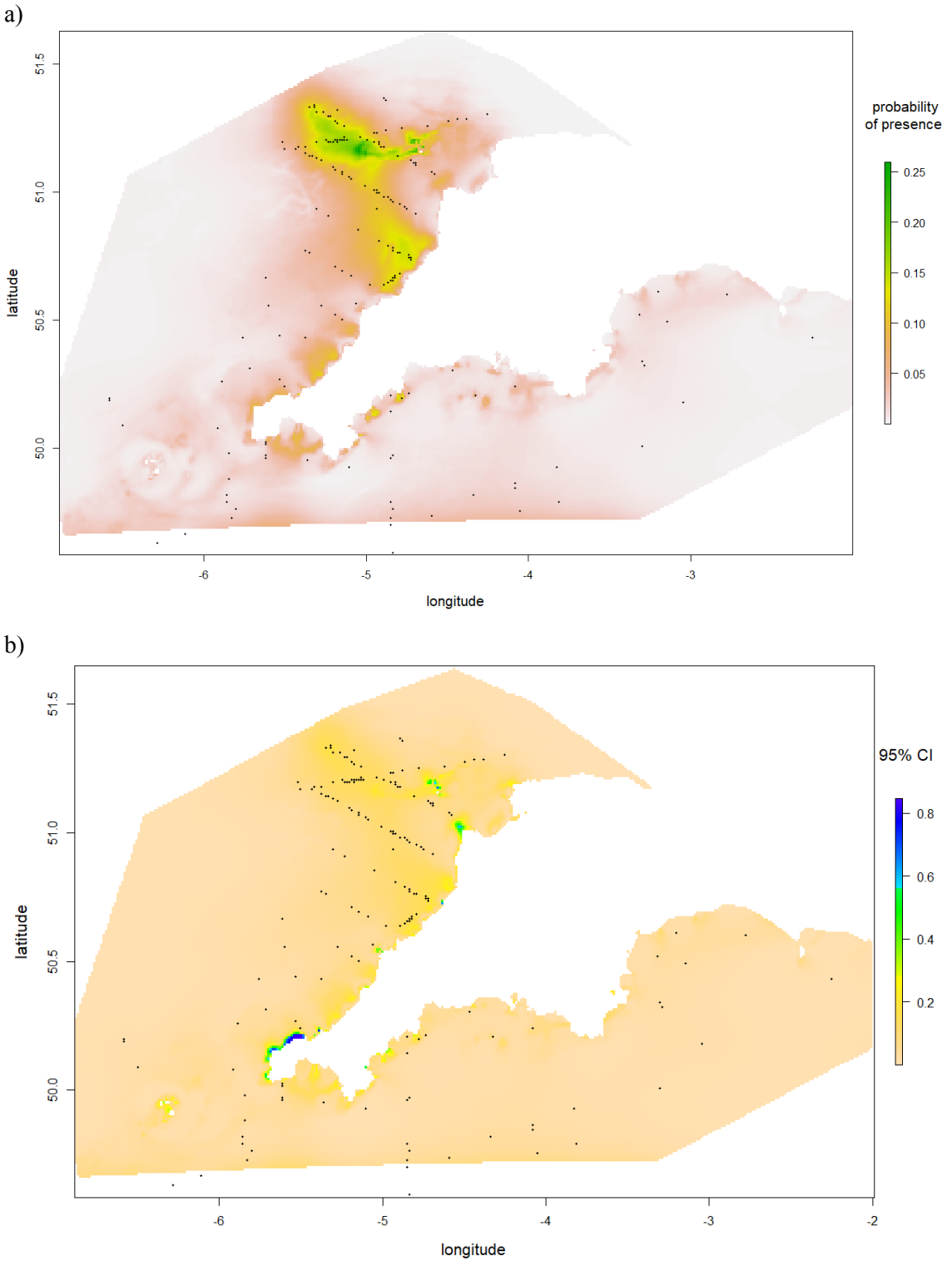


Figure 4. a) Probability of Balearic shearwater presence predicted by the Generalized Additive Model averaged across five years, and b) the 95% confidence intervals of the probability of presence (i.e. the difference between the upper and lower bound), with sightings superimposed on the maps (black dots).

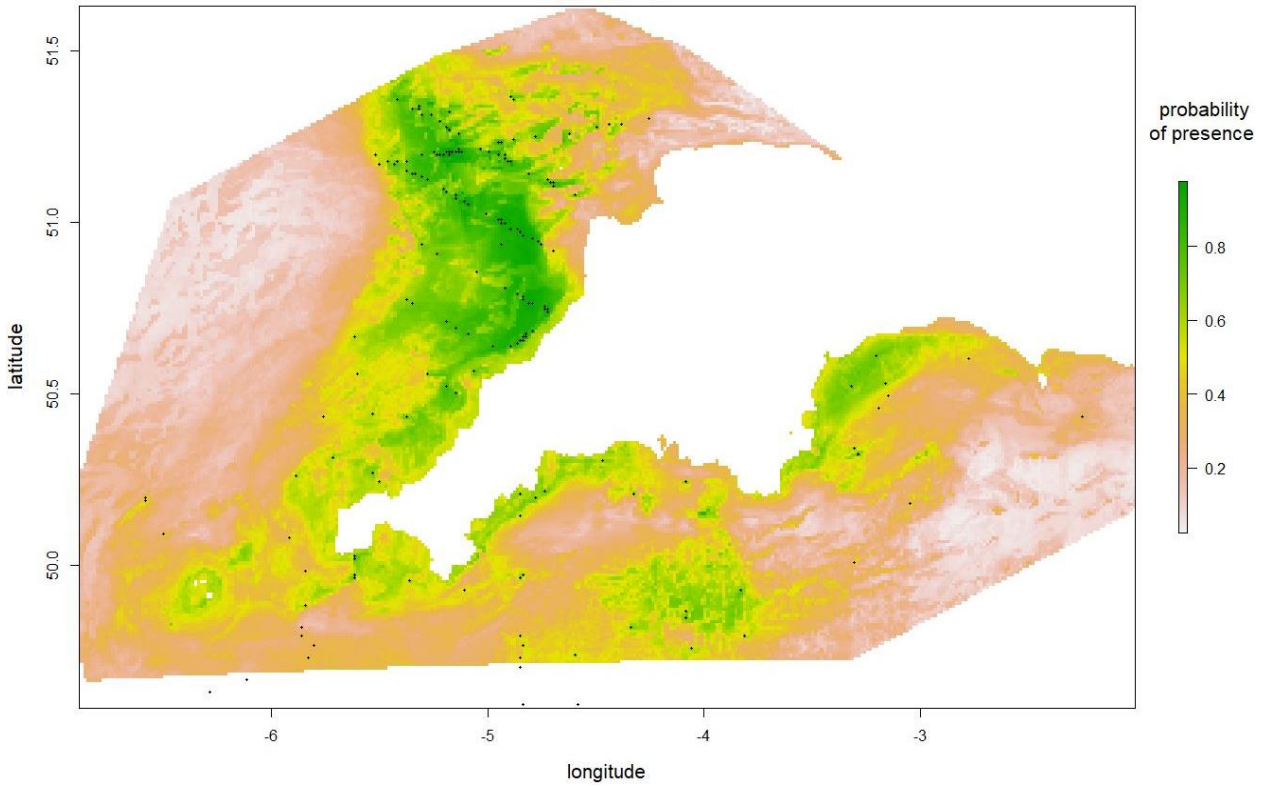


Figure 5. Probability of Balearic shearwater presence predicted by Random Forest model ensembles averaged across five years with sightings superimposed on the map as black dots.

The estimated number of Balearic shearwaters in the prediction area ranged from 652 birds in 2017 to 6,904 birds in 2014 (Table 4).

Table 4. Estimated abundance of Balearic shearwaters in the prediction area in each year during the survey period

Year	transect distance (km)	birds within 300m of transect*	density (variance) (birds/km^2)	abundance (variance)
2013	2,232	43 [43]	0.064 (0.012)	2,682 (521)
2014	2,621	130 [80]	0.17 (0.12)	6,904 (4,925)
2015	2,414	73 [64]	0.050 (0.012)	2,106 (506)
2016	1,896	36 [33]	0.032 (0.0055)	1,322 (230)
2017	3,203	30 [26]	0.016 (0.0019)	652 (79)

* Numbers in square brackets are the number of birds which were flying

5. Discussion

Our findings suggest that there is a high probability of occurrence of non-breeding Balearic shearwaters at the Celtic Sea front (Simpson, 1976), which had a relatively stable inter-year structure from 2013 to 2017. Both our explanatory GAM and RF models indicate oceanographic variables are better predictors of Balearic shearwater presence than surveyed abundance of individual fish species. The bio-acoustics surveys did not measure the main foraging depths of Balearic shearwaters, which likely limited their predictive power. This high probability of occurrence at the Celtic Sea Front is in line with previous work on breeding Balearic shearwaters in the western Mediterranean, which highlights the importance of frontal-features (Arcos and Oro, 2002; Louzao et al., 2011; Louzao et al., 2012). This discussion initially focusses on these findings and then discusses the relevance of the results for conservation.

The distribution of seabirds should broadly overlap with the distribution of their prey (Fauchald et al., 2000). However, prey abundance did not emerge as the most important predictor of Balearic shearwater presence in our analysis (Figure 3). There are four potential explanations. First, the fisheries acoustic equipment used to assess prey abundance was mounted on a dropkeel below the hull, which did not capture fish abundance in the top 12 m of water, excluding the main foraging depth of Balearic shearwaters (Meier et al., 2015). Thus the prey measured could be abundant at depths less preferred or inaccessible to seabirds (Waggitt et al., 2018; Boyd et al., 2017). Second, fisheries discards are a substantial part of the Balearic shearwater's diet (Arcos and Oro, 2002), and Balearic shearwaters are known to follow trawlers. However they are less likely to do so after the breeding season (Arcos and Oro, 2002), and trawler presence does not predict shearwater distribution on large spatial scales (Louzao et al., 2006a). While we did not have data on fishing activities, it would be useful for future predictive analyses to account for the potential impact of fishing activities, particularly given that bycatch is a leading cause of their decline (Oro et al., 2004; Louzao et al., 2006b; Genovart et al., 2016; Cortes et al., 2017). Third, predator and prey distributions may be mismatched at the fine-scales (<1 km) used in our analyses because seabirds do not have complete

knowledge of prey distribution (Gremillet et al., 2008) and prey can engage in anti-predator responses (Crook and Davoren, 2014). Fourth, Balearic shearwaters have a mixed diet (Navarro and Gonzalez-Solis, 2009). Thus the overall abundance of fish may be more important for their movements at sea than the abundance of specific individual species. While we could not calculate overall fish abundance from our dataset as the backscatter for mackerel were extracted using a different algorithm than that of the other species due to its unique acoustic signature (van der Kooij et al., 2016), it is an important question for future research. This study reaffirms the difficulty of capturing spatiotemporal relationships between mobile marine top-predators and prey (Fauchald, 2009). Nevertheless, the study supports suggestions that oceanographic variables indicative of enhanced prey availability are better predictors of marine top-predator distributions than direct measurements of prey abundance (Torres et al., 2008).

Knowledge on Balearic shearwater phenology and migration suggests that most shearwaters sighted were non-breeders. In 2013 and 2014, the mean date breeding Balearic shearwaters tracked from Mallorca returned through the Strait of Gibraltar was September 26th and September 22nd, respectively (Meier et al., 2015). Therefore, breeding birds would have predominantly been back in the Mediterranean before the annual surveys described here were conducted in October, which suggests that birds sighted during the surveys were not breeding birds. Sighting data from SeaWatch SW supports this hypothesis, showing that Balearic shearwaters are found in the southwest UK throughout the breeding period (Jones et al., 2014), with the highest number of sightings occurring when breeding birds were at their colonies in the Mediterranean (Guilford et al., 2012). Additionally, breeding birds tracked on Mallorca (Meier et al., 2015) and Ibiza (Perez-Roda et al., 2017) did not travel as far north as UK waters, making it unlikely that birds sighted during the survey were breeding birds from other colonies displaying migratory segregation (Louzao et al., 2011; Guilford et al., 2012). Sighted birds are also unlikely to be failed breeders as failed breeders tracked on Mallorca were predominantly back before our surveys started (Meier et al., 2015). To date, the only Balearic shearwater of known provenance that has been seen as far north as our surveys were conducted was

an immature (Wynn, 2013). Thus, most of the birds sighted in our surveys were probably immatures, though our sightings may also include some adults taking sabbaticals.

We identified the Celtic Sea front as an important habitat for Balearic shearwaters across years (Figure S.4 and S.5), mirroring findings from previous studies on Manx shearwaters *Puffinus puffinus* in the region (Waggitt et al., 2018). Tidal fronts are linked to high primary and secondary productivity, attracting large numbers of marine predators (Scales et al., 2014b). The interface between mixed and stratified waters at tidal fronts could also provide suitable combinations of prey density, depth and prevalence; maximising prey availability and providing good foraging opportunities for diving seabirds (Waggitt et al., 2018). Moreover, tidal fronts are persistent in time and space, allowing seabirds to efficiently locate these foraging opportunities from memory (Scales et al., 2014b).

Finally, we found that Balearic shearwater presence increased at higher sea states. Flying shearwaters are probably more visible in higher winds because they are more likely to be shear soaring, intermittently presenting the observer with a large surface area as well as an alternating light-dark coloration. Therefore, the association between Balearic shearwaters and high sea-state may indicate enhanced detectability of flying birds (Waggitt et al., 2020b) rather than larger abundances of birds during stormier conditions.

We found considerable inter-annual variation in abundance of Balearic shearwaters in southwest UK over the five years of the survey (2013-2017). As all static oceanographic features remained constant across years, changes in model predictions must be related to changes in dynamic oceanographic features such as sea surface temperature, salinity, and chlorophyll. Investigating inter-annual differences in the abundance of Balearic shearwaters requires additional studies considering oceanographic processes and the associated movement of prey. However, when assessing this inter-annual variation from a conservation perspective, our estimates suggest that the study area in southwest UK annually supports between 2% and 23% of the global population of Balearic

shearwaters (based on a global population estimate of 30,600 (Arcos, 2011a)). Although the survey was explicitly designed to be systematic, there were small deviations from the planned route, which could introduce some bias to our calculations. The abundance value presented is inevitably an estimate, and is susceptible to factors we could quantify variance in, as well as factors in which it was were much harder to quantify variance. Despite the variation in our estimate, even the minimum abundance estimate (2% of world population of Balearic shearwaters) is still of global importance.

Further studies are needed to determine the threats facing the species in this area. For example, current knowledge of bycatch across this area is very limited. This study will help identify the areas of greatest interest.

5.1 Conclusion

We have presented the most comprehensive description of Balearic shearwater distribution in UK waters currently available. We found a higher probability of occurrence of Balearic shearwater around the Celtic Sea front with relatively stable inter-year structure. If, as evidence here suggests, this location is a key foraging ground for immature Balearic shearwaters, the area could be the primary focus should any conservation measures separately be identified. The widespread predicted distribution of Balearic shearwaters at lower probability (especially with the RF model) suggest that mitigation efforts may also be necessary in other parts of the species' range within UK waters where pressures such as fisheries bycatch threaten their survival.

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7. Author contributions

Jessica A. Phillips: Formal analysis (lead); Writing-original draft (lead); Writing-review & editing (equal). **Alex Banks:** Conceptualization (lead); Formal analysis (supporting); Project administration (lead);Supervision (supporting); Writing-original draft (supporting); Writing-review & editing (equal). **Mark Bolton:** Data curation (equal); Formal analysis (supporting); Writing-review & editing (equal). **Tom Brereton:** Data curation (equal); Formal analysis (supporting); Writing-review & editing (equal). **Pierre Cazenave:** Data curation (equal); Writing-review & editing (equal). **Natasha Gillies:** Formal analysis (supporting); Methodology (equal); Writing-review & editing (equal). **Ollie Padget:** Formal analysis (supporting); Project administration (supporting); Writing-review & editing (equal). **Jeroen van der Kooij:** Data curation (equal); Formal analysis (supporting); Methodology (equal); Writing-original draft (supporting); Writingreview & editing (equal). **James Waggitt:** Data curation (equal); Formal analysis (lead); Validation (lead); Writing-review & editing

(equal). **Tim Guilford:** Formal analysis (supporting); Supervision (lead); Writing-original draft (supporting); Writing-review & editing (equal).

8. Data availability statement

Data on salinity, sea surface temperature and chlorophyll levels were downloaded from the Copernicus Marine Environment Monitoring Service, at: http://marine.coper nicus.eu/servi ces-portfolio/acces s-to-produ cts/. Data on seafloor depth, seafloor aspect, seafloor anomalies, and seafloor roughness were downloaded from the European Marine Observation and Data Network, at: https://www.emodn et-bathy metry.eu/data-products. Data on small pelagic fish distribution and abundance are available for some species at https://acous tic.ices.dk/submi ssions. Other data are available on request from Jeroen Van Der Kooij. 2015–2017 ESAS bird sightings data under contract to Natural England, all other bird sightings data collected by MARINELife, available on request. The raster layers of the maximum current speed and stratification index used to create the models, as well as the R code, are available on Dryad at https://doi.org/10.5061/dryad.9p8cz 8wdz.

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10. Supplementary materials

10.1 Accuracy of data

We are confident that identification of Balearic shearwaters was accurate for several reasons. Firstly, most (96%) Balearic shearwaters sightings were in flight, when identification is much easier due to their underwing plumage and body shape (Gil-Velasco et al., 2015). Secondly, the classic decline in detectability with distance was seen for all Balearic shearwaters recorded in these surveys: 48% of sightings were within 300 m of the vessel, 71% within 500 m, and 93% within 800 m. Thirdly, all observers were trained, experienced marine surveyors who rated their sightings as 'definite' or 'probable'. In 2017, when other shearwater species (Manx, sooty and great) were also recorded, 94% of Balearic shearwater identifications were classified as 'definite'.

10.2 Continuous recording of birds in flight

Relatively low densities of Balearic shearwaters were detected during the five survey years, and only 393 could be included in our analysis. To improve detection of at-sea aggregations, it was necessary to include all observations recorded out to 1 km whilst the vessel was not stationary (defined as spending over 15 minutes in a 1km^2 cell) or steaming above 17 knots. To prevent inflation of bird abundance estimates, conventional ESAS methods recommend restricting the analysis of birds in flight to those recorded in 300 m square 'snapshots'. However, in this case the very low density of Balearic shearwaters made the danger of inflation of Balearic shearwater abundance estimates small (primarily because we used bespoke methods to continuously record observed birds in flight) compared to the benefit of including birds observed out to 1000m in snapshot counts. Additionally, because we only used these data for observations up to 1000m from the vessel in models to predict probability of Balearic shearwater *presence* (not abundance) and to identify key environmental predictors of Balearic shearwater occurrence, we believe it appropriate to use all available sightings of the species in the models.

10.3 Supplementary figures

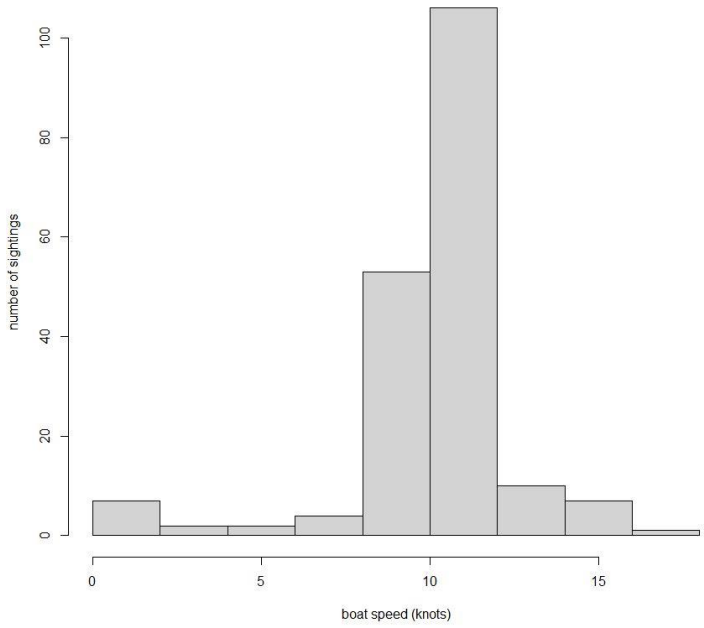


Figure S.1 Boat speed of all Balearic shearwater sightings included in the analysis

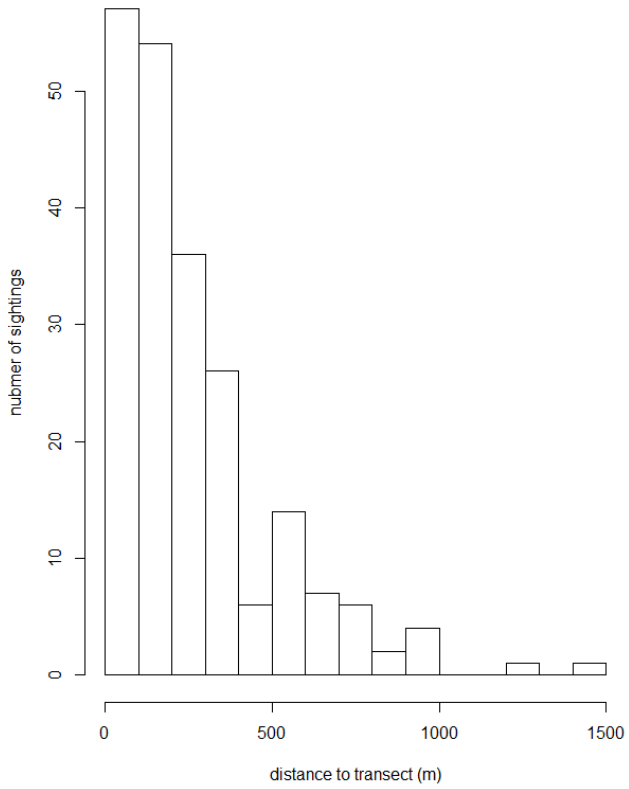


Figure S.2 Triangulated distance to boat transects of all raw sightings

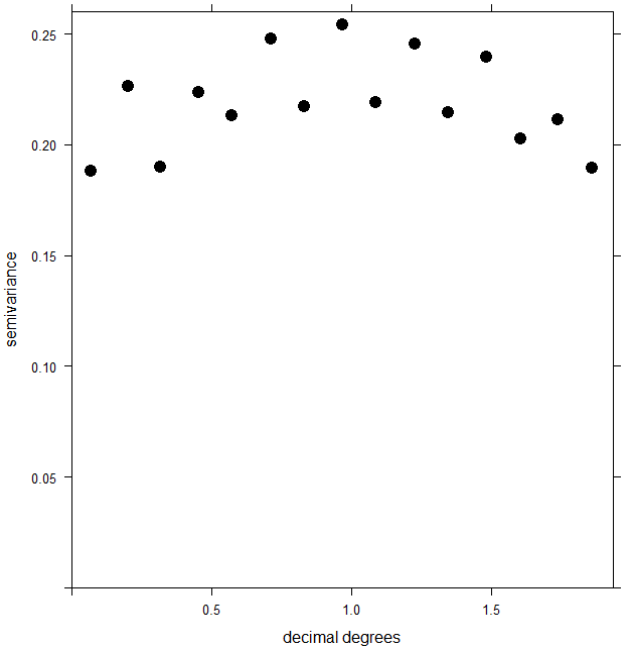
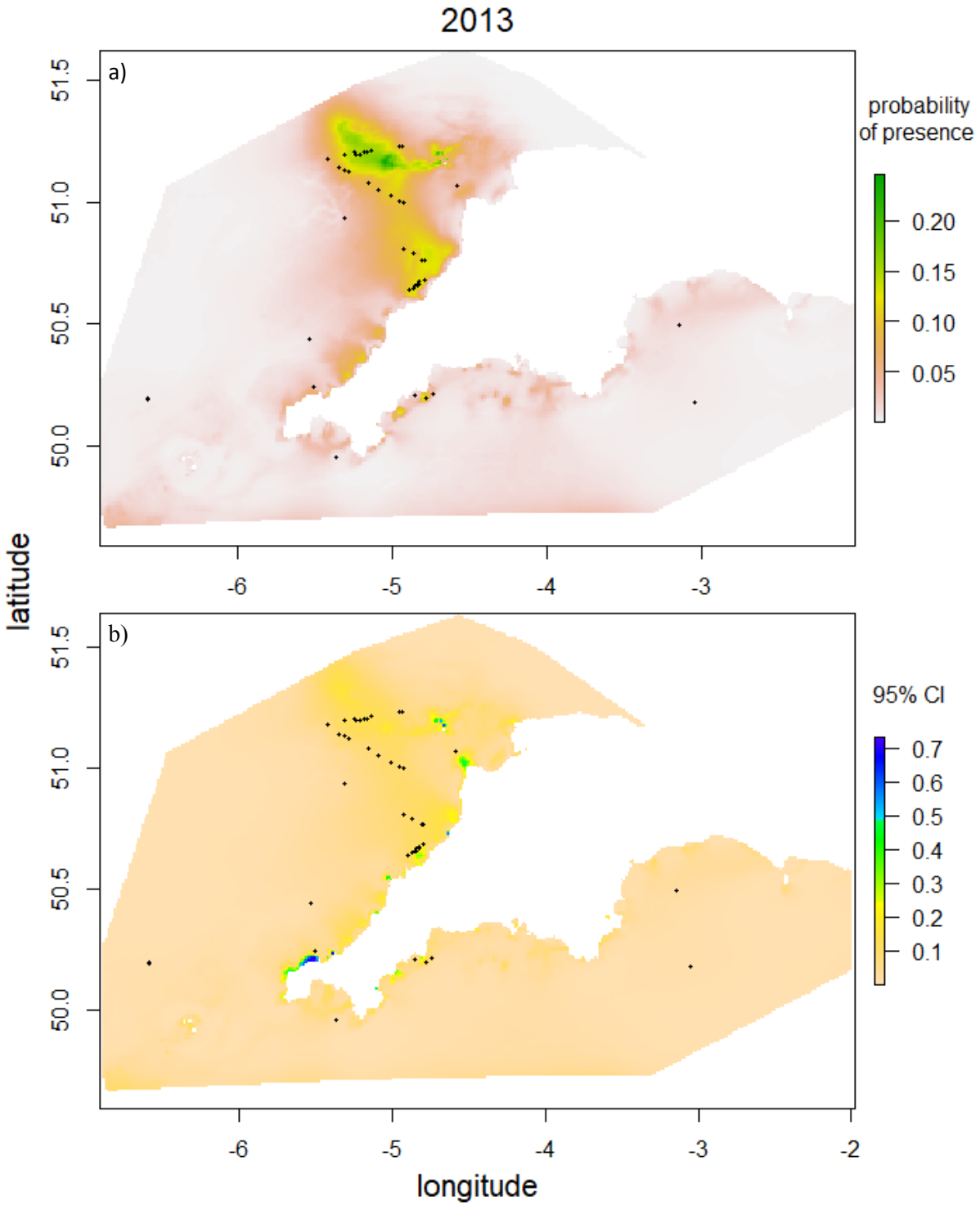
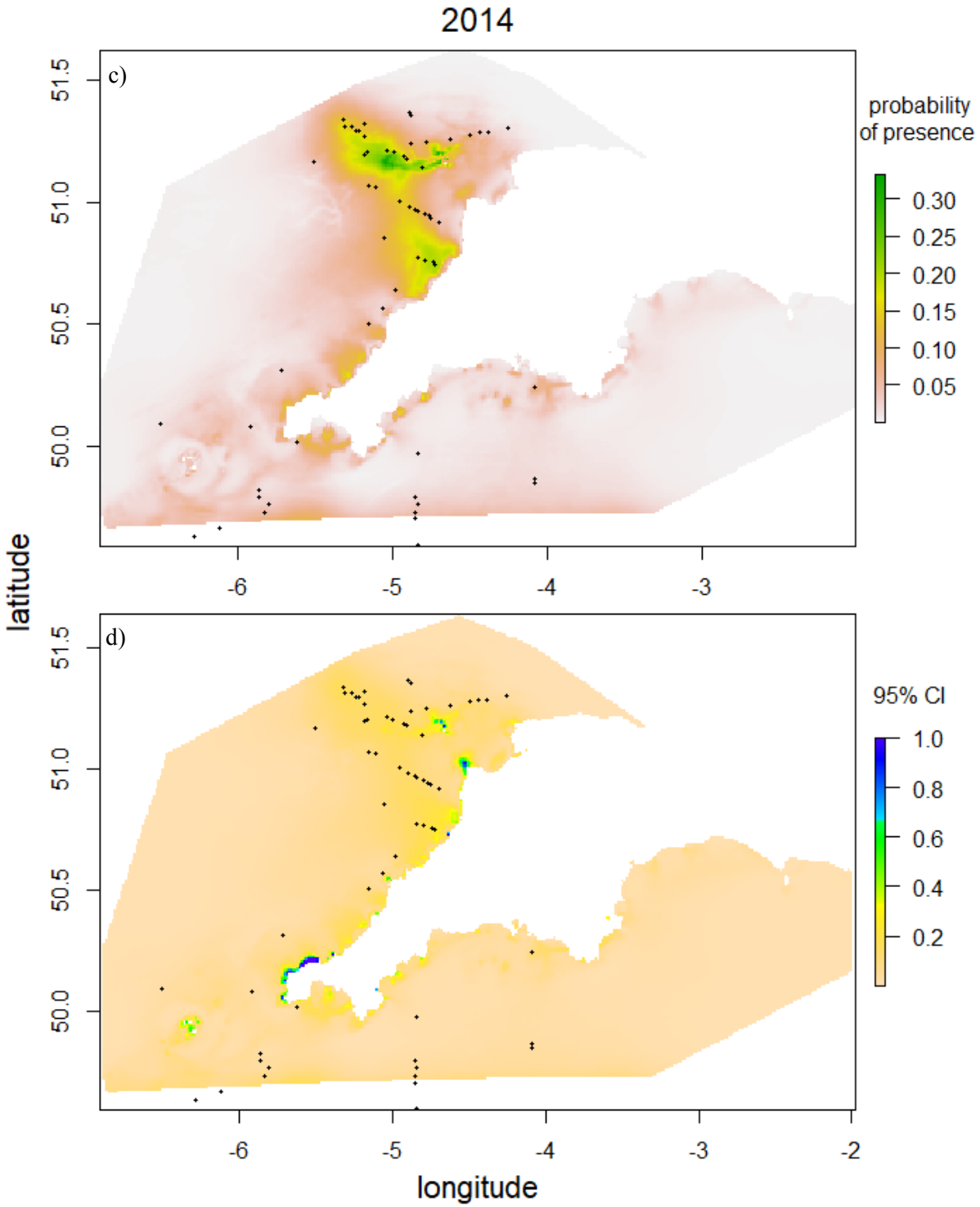
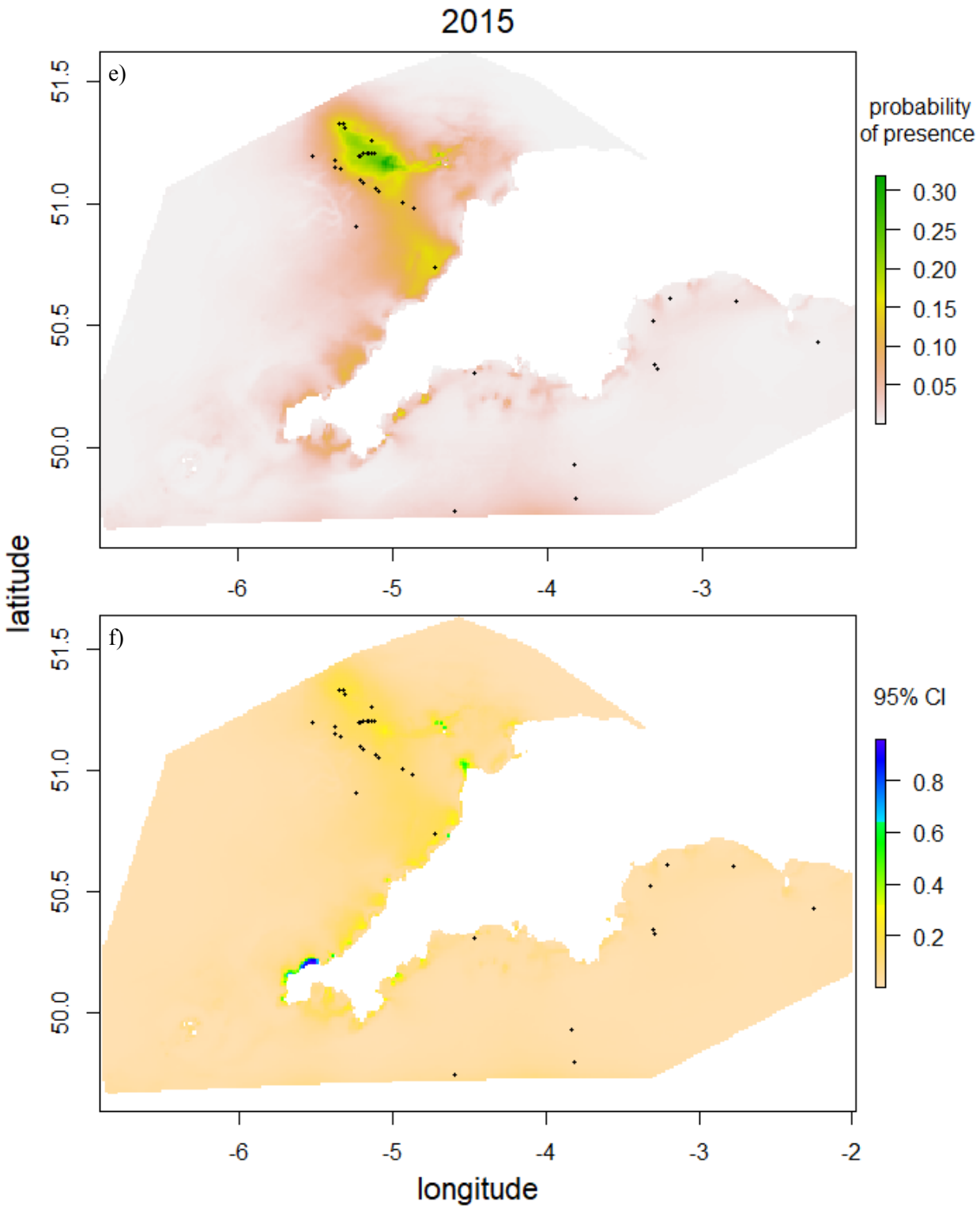
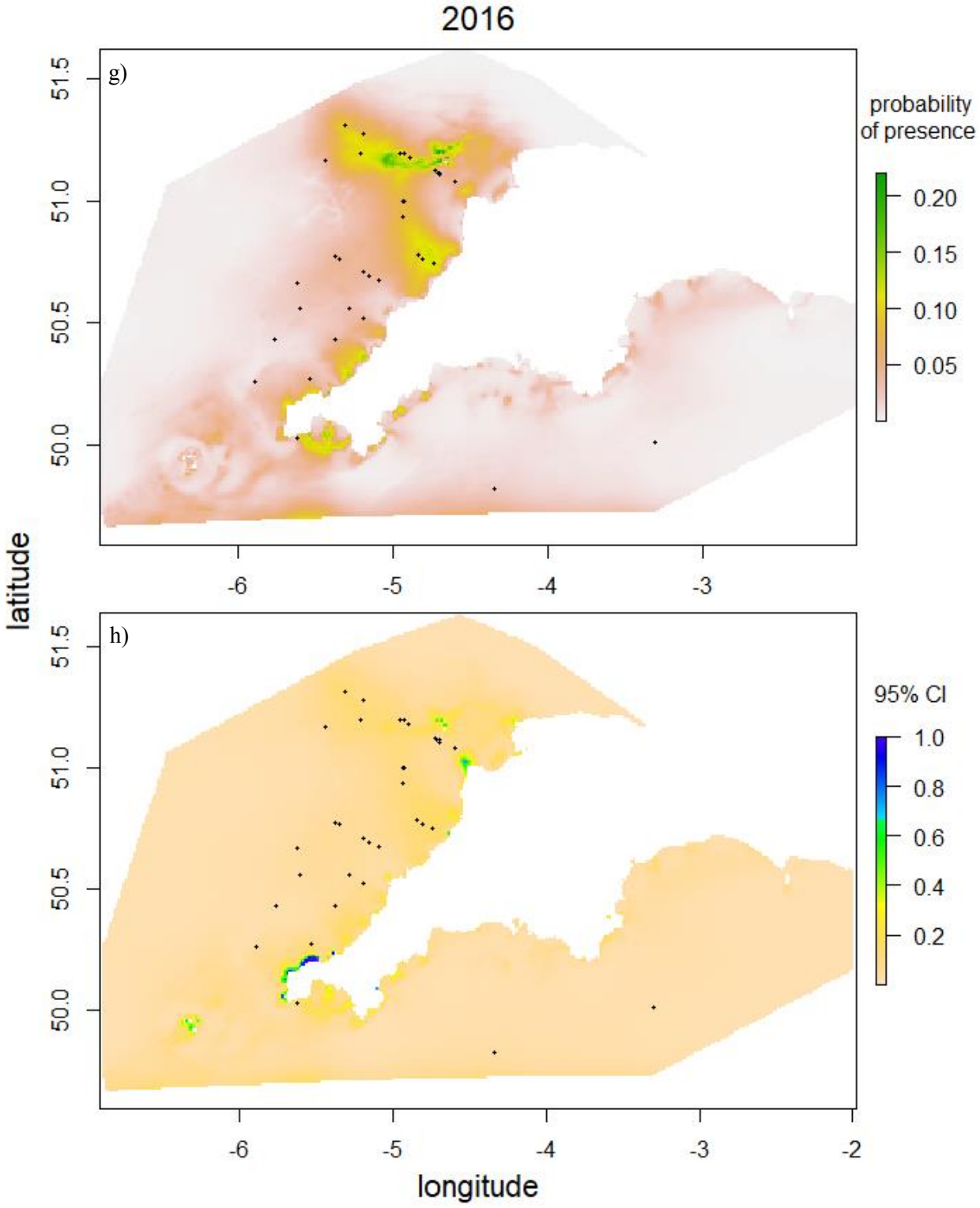


Figure S.3 Residuals of predictive GAM


2013
a)
b)
probability of presence
0.20
0.15
0.10
0.05
95% CI
0.7
0.6
0.5
0.4
0.3
0.2
0.1
latitude
longitude
50.0
50.5
51.0
51.5
-6
-5
-4
-3
-2


2014
c)
d)
probability
of presence
0.30
0.25
0.20
0.15
0.10
0.05
95% CI
1.0
0.8
0.6
0.4
0.2
latitude
longitude
51.5
51.0
50.5
50.0
-6
-5
-4
-3
-2


2015
e)
f)
probability
of presence
0.30
0.25
0.20
0.15
0.10
0.05
95% CI
0.8
0.6
0.4
0.2
latitude
longitude
51.5
51.0
50.5
50.0
-6
-5
-4
-3
-2


2016
g)
probability
of presence
0.20
0.15
0.10
0.05
51.5
51.0
50.5
50.0
-6
-5
-4
-3
latitude
h)
95% CI
1.0
0.8
0.6
0.4
0.2
-2
longitude

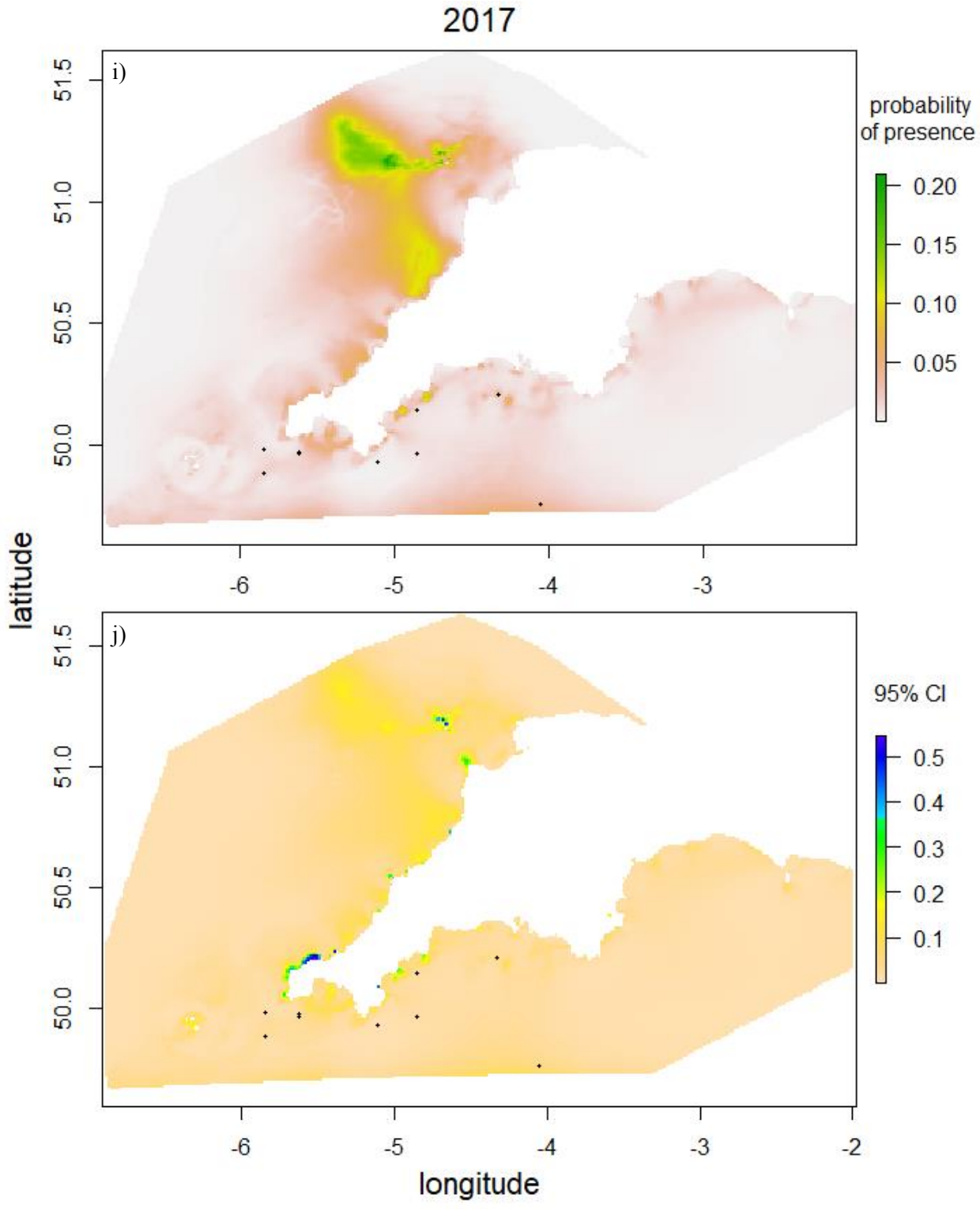
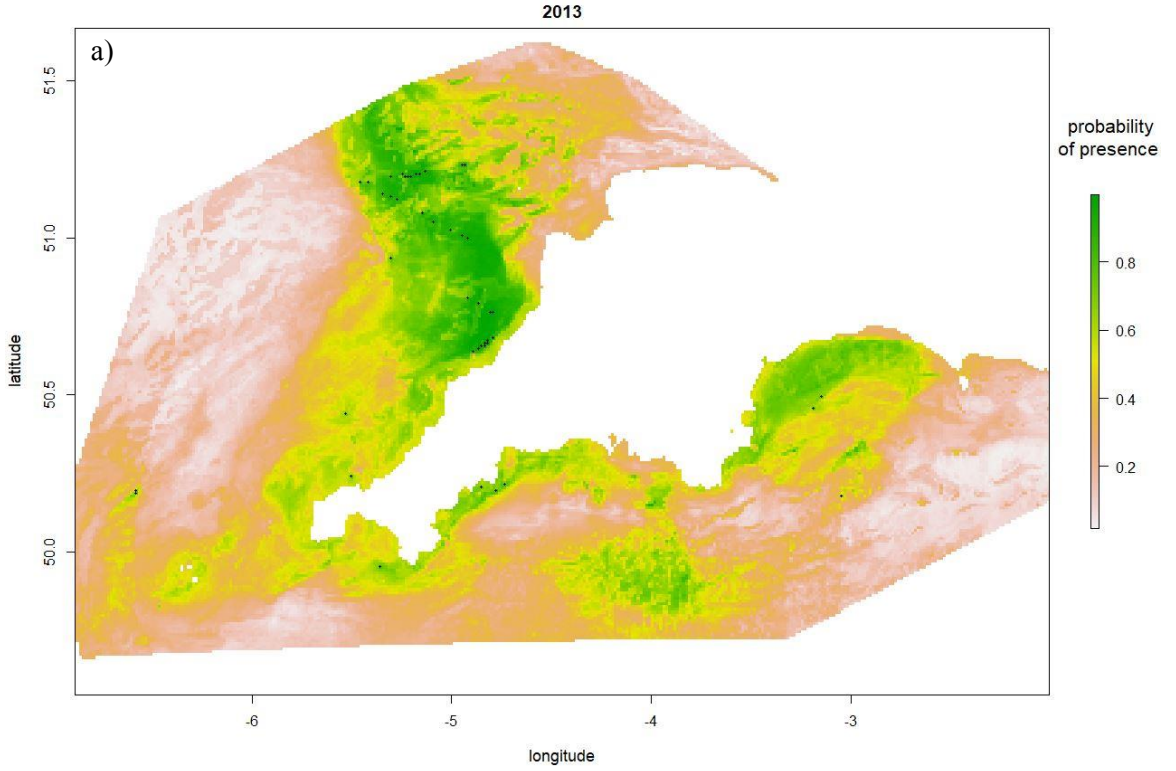
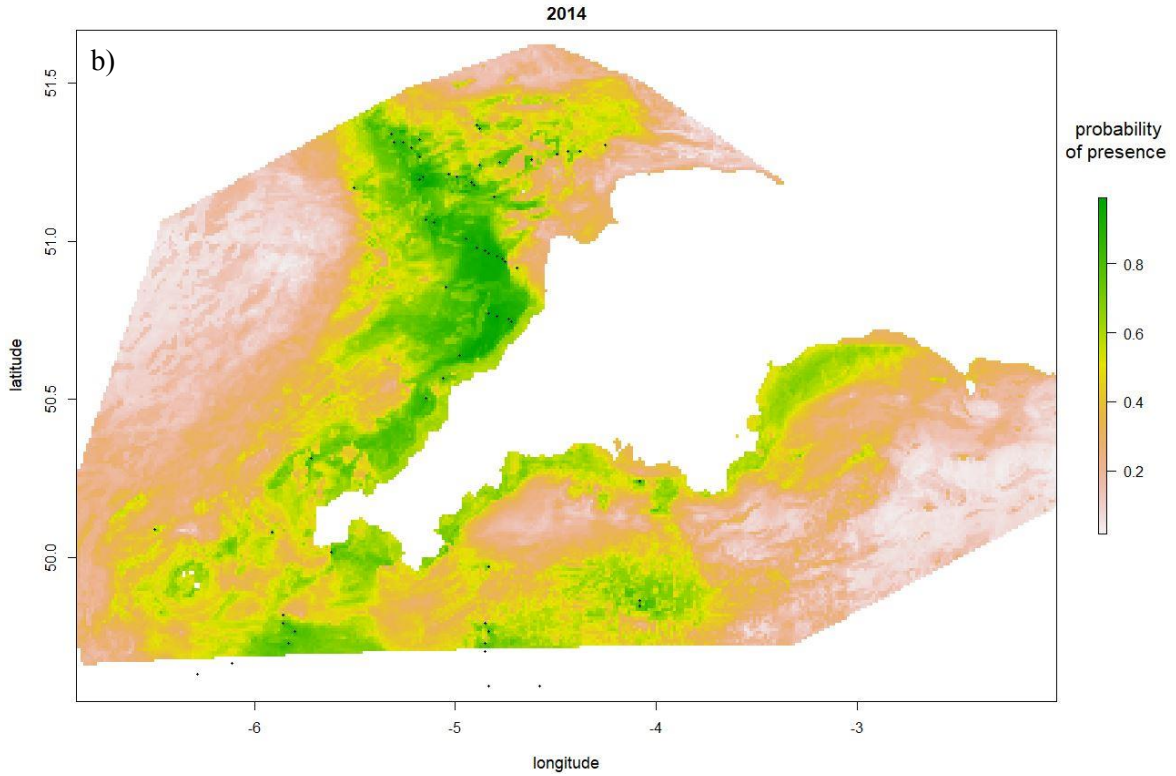
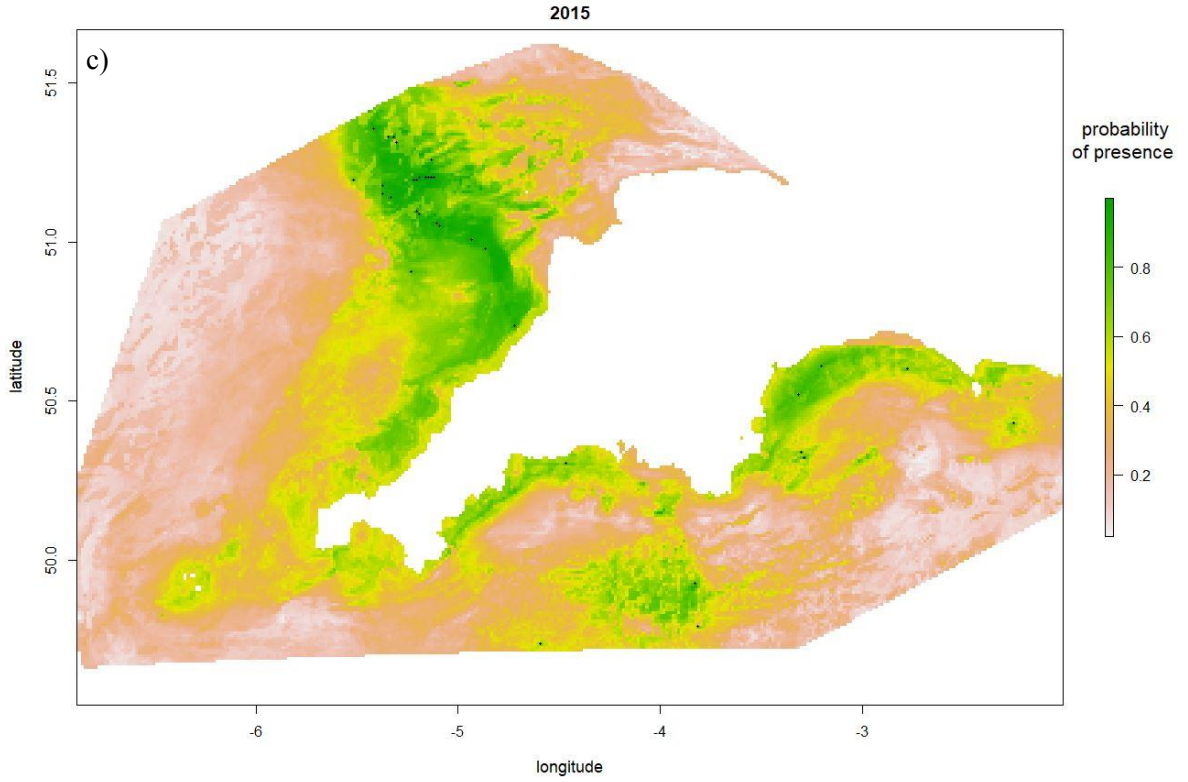
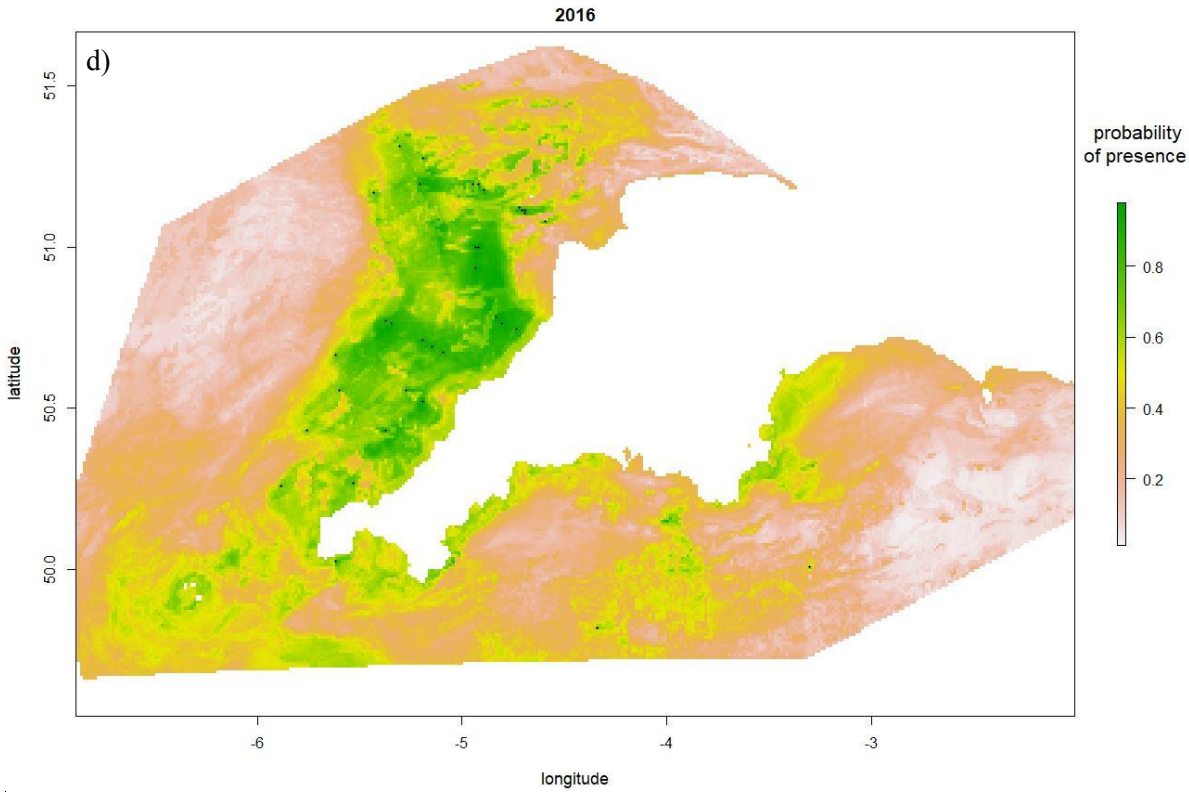


Figure S.4 Probability of Balearic shearwater presence predicted by the Generalized Additive Model in a) 2013, c) 2014, e) 2015, g) 2016, and i) 2017; and 95% confidence intervals of these predictions in b) 2013, d) 2014, f) 2015, h) 2016, and j) 2017.


2013
a)
latitude
51.5
51.0
50.5
50.0
-6
-5
-4
-3
longitude
probability
of presence
0.8
0.6
0.4
0.2


2014
b)
latitude
51.5
51.0
50.5
50.0
-6
-5
-4
-3
longitude
probability
of presence
0.8
0.6
0.4
0.2


2015
c)
latitude
51.5
51.0
50.5
50.0
-6
-5
-4
-3
longitude
probability
of presence
0.8
0.6
0.4
0.2


2016
d)
latitude
51.5
51.0
50.5
50.0
-6
-5
-4
-3
longitude
probability
of presence
0.8
0.6
0.4
0.2

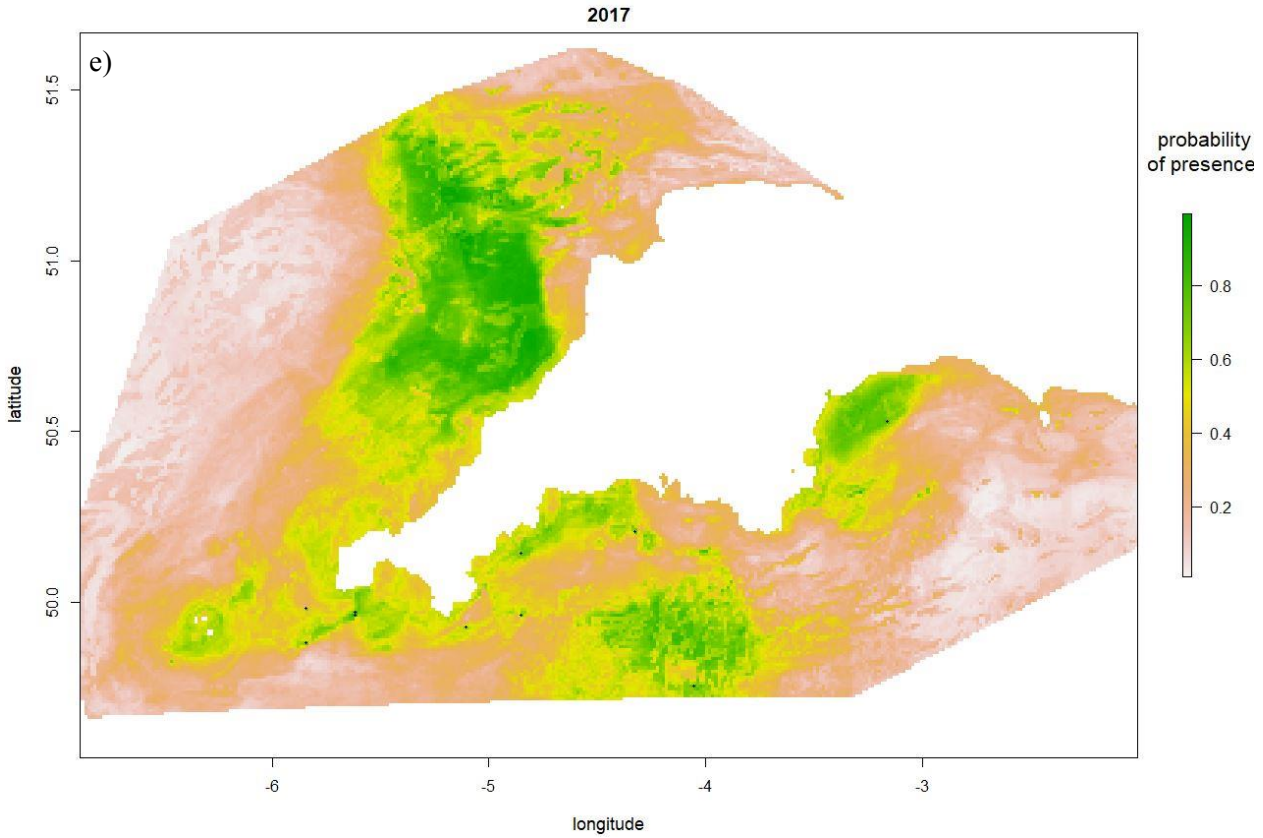


Figure S.5 Probability of Balearic shearwater presence predicted by a Random Forest model ensemble for a) 2013, b) 2014, c) 2015, d) 2016, and e) 2017

Chapter 3

Foraging conditions for breeding penguins improve with distance from colony and progression of the breeding season at the South Orkney Islands

Jessica Ann Phillips [a], Annette L. Fayet [a], Tim Guilford [a], Fabrizio Manco [b], Victoria Warwick-Evans [c] & Phil Trathan [c]

[a] Department of Zoology, University of Oxford, UK

[b] Anglia Ruskin University, Cambridge, UK

[c] British Antarctic Survey, Cambridge, UK

Now published in Movement Ecology

1. Abstract 98

2. Introduction 99

3. Methods 102

4. Results 112

5. Discussion 117

6. Acknowledgements 123

7. Author contributions 123

8. Data availability statement 123

9. References 124

10. Supplementary materials 132

1. Abstract

According to central place foraging theory, animals will only increase the distance of their foraging trips if more distant prey patches offer better foraging opportunities. This theory predicts that breeding seabirds living in large colonies potentially create a zone of food depletion around the colony, known as "Ashmole's halo". However, seabirds' decisions to forage at a particular distance are also likely to be complicated by their breeding stage. After chicks hatch, parents must return frequently to feed their offspring, so they may be less likely to visit more distant, higher-quality foraging patches. However, the interaction between prey availability, intraspecific competition, and breeding stage on the foraging decisions of seabirds is not well understood. The aim of this study was to address this question in chinstrap penguins *Pygoscelis antarcticus* breeding in a large population. In particular, we aimed to investigate 1) how breeding stage affects foraging strategy; 2) whether birds foraging far from the colony visit higher quality patches than available locally; and 3) whether there is evidence for intraspecific competition, indicated by increasing prey depletion near the colony over time and corresponding increases in the length of foraging trips. We used GPS and time-depth recorders to track the foraging movements of 221 chinstrap penguins from 4 sites at the South Orkney Islands during incubation and brood. We identified foraging dives and calculated the index of patch quality based on time allocation during the dive to assess the quality of the foraging patch. We found that chinstrap penguin foraging distance varied between stages, and that trips became shorter as incubation progressed. Although patch quality was lower near the colony than at more distant foraging patches, patch quality near the colony improved over the breeding season. These results suggest that chinstrap penguin foraging strategies are influenced by both breeding stage and prey distribution, and that the low patch quality near the colony may be due to a combination of depletion by intraspecific competition which is partially compensated for by natural variation in prey availability. Reduced trip duration towards the end of incubation may be associated with meeting the needs of newly hatched chicks to be fed frequently. It could also be associated with an increase in food availability, as seabirds time their reproduction so that the period of maximum energy demand in late chick-rearing coincides with maximum resource availability in the environment. This may also

explain why patch quality around the colony improved over the breeding season. Overall, our study helps identify the drivers of foraging decisions in colonial seabirds, an important question in foraging ecology.

2. Introduction

Many animals repeatedly return to a central place following foraging trips (Orians and Pearson, 1979). This includes all animals feeding young in the nest (Kaspari, 1991; McClintic et al., 2014; Oppel et al., 2015), animals that use burrows as shelter from predators (Kramer and Nowell, 1980; Lima et al., 1985; Bowers and Ellis, 1993), social insects foraging for the colony (Kacelnik et al., 1986; Bovet et al., 1989), and incubating birds not fed by their partners (Kato et al., 2008; Patenaude-Monette et al., 2014). This constraint of repeatedly returning to a central place has implications for the foraging sites animals select and, thus, for the degree of prey depletion close to the central place (Stephens and Krebs, 1986). However, the drivers of foraging strategies of central place foragers facing dynamic and heterogeneous environments are not fully understood. In particular, how different factors such as breeding stage and prey availability interact to affect foraging strategy remains unclear. Here, we explore these questions in seabirds, which during breeding act as central place foragers but also need to commute long distances to forage for patchy and ephemeral prey (Lack, 1968; Ashmole, 1971).

Central place foraging theory is a special case of optimal foraging theory (Emlen, 1966; MacArthur and Pianka, 1966), in which the forager is tied to a specific location and must return to this location after each foraging bout. Central place foraging theory predicts that animals will only increase the distance of their foraging trips if more distant prey patches offer better foraging opportunities (i.e., better prey quality and/or availability) than local prey patches (Houston and McNamara, 1985; Cuthill and Kacelnik, 1990; Waite and Ydenberg, 1996), and longer trips do no compromise offspring survival. The theory predicts that they would return to offspring in a minimal

amount of time while acquiring the maximum amount of resources by exploiting the nearest prey patch or exploiting a more-distant high-quality prey patch (Ydenberg et al., 1994; Ropert-Coudert et al., 2004). In seabirds, a consequence of preferential feeding close to the colony during breeding is that in large colonies this could create a zone of food depletion around the colony, known as "Ashmole's halo" (Ashmole, 1963), which widens as the season progress (Ashmole, 1963; Gaston et al., 2007). When this occurs, the theory predicts that traveling further would likely yield higher reward per unit time, as prey availability would be higher outside of the halo (another mechanism to reduce intraspecific competition is sex-specific niche partitioning (Ratcliffe et al., 2013)). However, due to the logistical challenge of quantifying successful foraging events in the open ocean, this prediction has rarely been tested. Ashmole (1963) also postulated that this prey depletion around colonies would be less likely at higher latitudes where seabirds can time their reproduction to coincide with seasonal abundance of prey availability. Despite this prediction, evidence of "Ashmole's halo" has been found at higher latitudes as well as in the tropics. In the tropics, Oppel et al. (2015) found that masked boobies *Sula dactylatra* from a smaller colony went on shorter duration foraging trips, foraged closer to the colony, had lower energy expenditure, and higher nest survival than birds from a larger colony. In the UK, Shoji et al. (2014) found that patch quality improved with distance from the colony in razorbills *Alca torda*. In Canada, Birt et al. (1987) found that the density of bottom fish increased with distance from a double-crested cormorant *Phalacrocorax auritus* colony, providing direct evidence for local prey depletion. In northern Canada, Elliott et al. (2009) found that the mass of prey retrieved increased with travel distance from a Brünnich's guillemot *Uria lomvia* colony, suggesting the birds depleted large prey near the colony. However, the interaction between natural variation in prey availability and intraspecific competition in driving seabird foraging decisions are not well understood. For instance, how seabirds change their foraging behaviour when prey depletion near the colony is compensated or aggravated by natural variation in prey availability has not been investigated previously.

Another potential key driver of foraging strategy is breeding stage. Adults need to adjust their foraging strategy based on the changing needs of their eggs and chicks (Goodman, 1974; Drent and

Daan, 1980; Ydenberg et al., 1994). During the incubation phase, one parent must fast while the other feeds and then they need to switch roles. This is necessary to keep their eggs warm and to protect them from predation and bad weather. The chick-rearing phase is much more energetically demanding for parents (Ricklefs, 1983). They must feed chicks frequently, both to prevent the chicks from starving and because young chicks often cannot ingest large quantities of food in a single feeding (Phillips and Hamer, 2000). Compared to incubating seabirds, chick-rearing seabirds have been shown to 1) have higher foraging costs (Salamolard and Weimerskirch, 1993; Shaffer et al., 2003); 2) have higher field metabolic rates (e.g., Gales and Green, 1990; Montevecchi et al., 1992); 3) have increased activity at night (Charrassin et al., 1998); 4) make deeper foraging dives (e.g., Charrassin et al., 1998; Ito et al., 2010); 5) reduce their foraging range (e.g., Stahl and Sagar, 2000; Poupart et al., 2017); and 6) make foraging trips that are shorter in both distance and duration (e.g., Shaffer et al., 2003; Ichii et al., 2007). However, how breeding stage interacts with prey availability to affect seabird foraging strategies are not fully understood.

We investigate this interaction using chinstrap penguins breeding at the South Orkney Islands in a very large population (Strycker et al., 2020). While the number of chinstrap penguins in Antarctica increased in the decades proceeding the 1970s (Croxall and Furse, 1980; Trivelpiece et al., 2011), numbers have declined since (Strycker et al., 2020), with certain areas recording declines over 50% (Sander et al., 2007; Trivelpiece et al., 2011; Lynch et al., 2012; Naveen et al., 2012; Lynch et al., 2016; Strycker et al., 2021), including Signy Island (Dunn et al., 2016) in the South Orkney Islands. One hypothesis is that penguin population sizes are limited by krill abundance, which is increasingly constraining due to declines with the reduction in sea ice, krill fishing and competition from recovering whale and seal population, (Fraser et al., 1992; Trivelpiece et al., 2011; Hinke et al., 2017; Hill et al., 2020). With a population of ~0.96 million breeding pairs, the South Orkney islands contain nearly a third of the world's 3.42 million breeding pairs of chinstrap penguins (Strycker et al., 2020), making it an excellent location to study the impacts of prey depletion. The region is also home to Gentoo penguins *Pygoscelis papua* and Adélie penguins *Pygoscelis adeliae* (Dunn et al., 2016), which like chinstrap penguins, mainly consume Antarctic krill *Euphausia superba* during the summer

months (Forcada et al., 2006), and likely contribute to prey depletion near colonies. Chinstrap penguins mainly consume Antarctic krill (Volkman et al., 1980; Lishman, 1985; Woehler and Croxall, 1997) and smaller amounts of myctophid fish (Jansen et al., 1998; Rombola et al., 2006). After laying in early November (Jansen, 1996), parents alternate on long incubation shifts between 5 and 10 days (Williams, 1995) until eggs hatch in late December, when parents take turns brooding the chick and making daily foraging trips. We studied penguins between the months of December and February, covering the incubation and brood periods.

We fitted 221 chinstrap penguins with Global Positioning System (GPS) devices and time-depth recorders (TDRs). We use these data to investigate the drivers of variation in foraging strategies of breeding chinstrap penguins, focusing on the potential roles of intraspecific competition, prey availability, and breeding stage on foraging distance. More specifically, we wanted to determine 1) how breeding stage affects foraging strategy in chinstrap penguins; 2) whether, as predicted by Ashmole's theory of intraspecific competition, birds foraging far from the colony visit higher quality patches than those available locally; and 3) whether prey depletion near the colony increases over the breeding season, which may cause foraging distances to extend and which would indicate an effect of intraspecific competition on foraging strategies.

3. Methods

3.1 Field methods

All tracking data were collected by scientists and collaborators of the British Antarctic Survey at four of the South Orkney Islands in the Southern Ocean (Figure 1) between 2011 and 2016: at Cape Geddes (60°41' S, 44°34' W) on Laurie island from December 2011 to January 2012, at Powell Island (60°41' S, 45°02' W) from December 2013 to January 2014, at Monroe Island (60°36' S, 46°03' W) from December 2015 to February 2016, and at Signy Island (60°42' S, 45°35' W) from January to February 2016. The population size of breeding chinstrap penguins on the South Orkney Islands is

estimated at ~960,000 pairs (Strycker et al., 2020). Signy Island contains~19,500 nests (Dunn et al., 2016), Laurie island contains at least 143,800 breeding pairs (Coria et al., 2011), however the populations of Monroe and Powell Island are unknown (Strycker et al., 2020).

Breeding chinstrap penguins were captured at the nest during the incubation and brood periods, and fitted with a fast acquisition GPS and a TDR device. The TDRs recorded depth every second and the GPS loggers recorded location every 4 minutes – though time intervals were sometimes longer when the GPS could not connect to satellites (e.g., when birds were underwater (Tomkiewicz et al., 2010)). The TDRs used were either Lotek LAT 1810 (6 g in air, 38 x 11 mm) or CEFAS G5s (either 2.7g in air, 31 x 8 mm; or 6.5 g in air, 35 x 12 mm). The GPS loggers used were

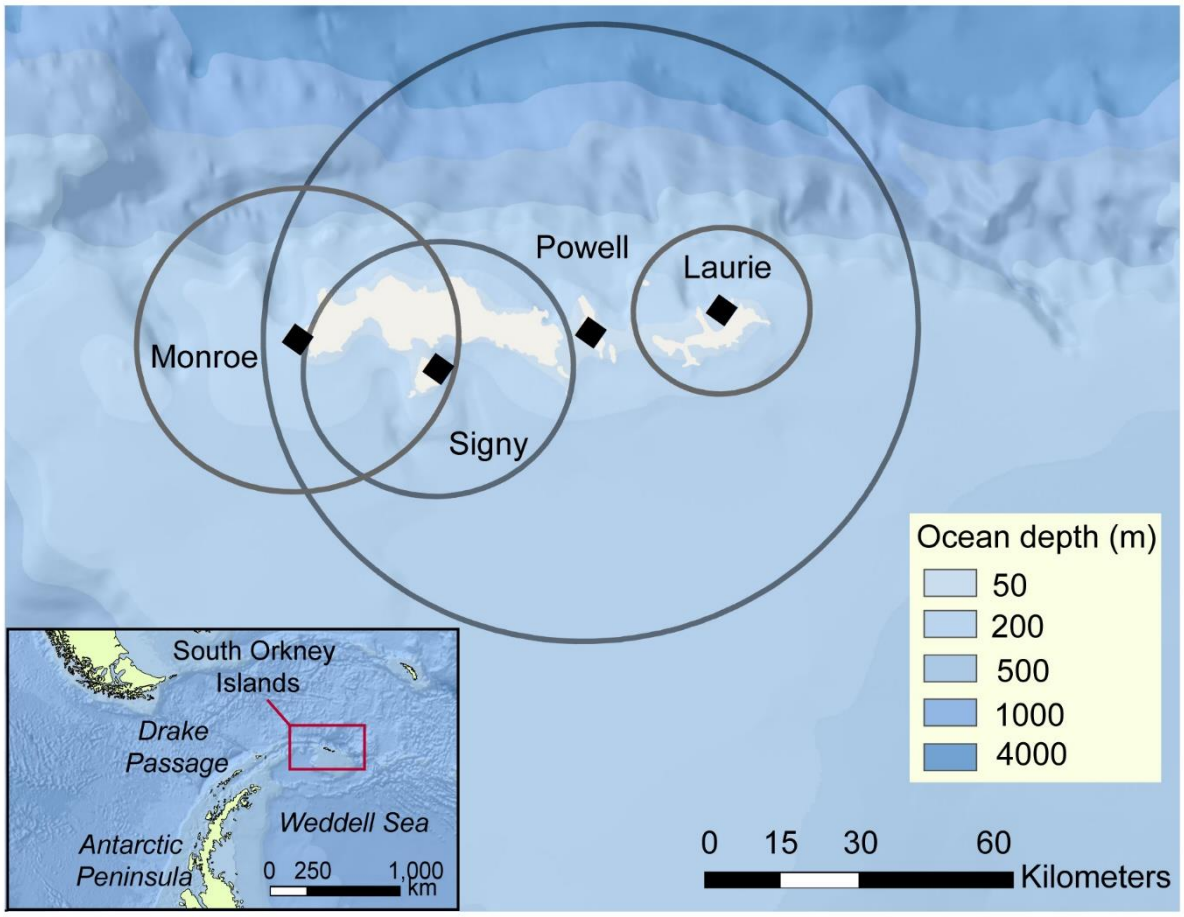


Figure 1. Map of South Orkney Islands. Study colonies are labelled and marked with black diamonds. The circles around each colony have a radius of the median distance of foraging trips up to a day in duration: 17km at Laurie, 63km at Powell, 31km at Monroe, and 26km at Signy. The base map is from ESRI, Garmin, GEBCO, NOAA and other contributors.

either Sirtrack™ Fastloc™ 33 F2G133A (38.4 g in air, 65 x 28 x 22 mm with 40 mm whip antenna) or Sirtrack™ Fastloc™ 33 F3G133A (31.0 g in air, 63 x 24 x 22 mm with 40 mm whip antenna). The TDR and GPS loggers were attached with Tesa© tape and 2-part quick-setting glue, as described by Warwick-Evans and colleagues (2018). Whether chicks were in brood or crèche was recorded at device deployment at all sites and at retrieval in all sites other than Signy. Handling time did not exceed 10 minutes for deployment and 5 minutes for retrieval. Tagged penguins included 60 at Laurie Island, 65 at Powell Island, 73 at Monroe Island, and 23 at Signy Island. Devices were retrieved on average after 4.7 ± 0.2 days and the data were subsequently downloaded. Potential impacts of logger deployments were not measured directly, but the combined mass of device deployments was always <1% of the bird's body mass. In a study investigating tagging impacts on little penguins, the authors found no effect of GPS or TDR attachment on adult body weight change or survival, hatch, fledging or chick growth (Agnew et al., 2013). Another study on Adélie penguins found no impact of TDR and radio-transmitter attachment on foraging trip duration or nesting success (Ballard et al., 2001).

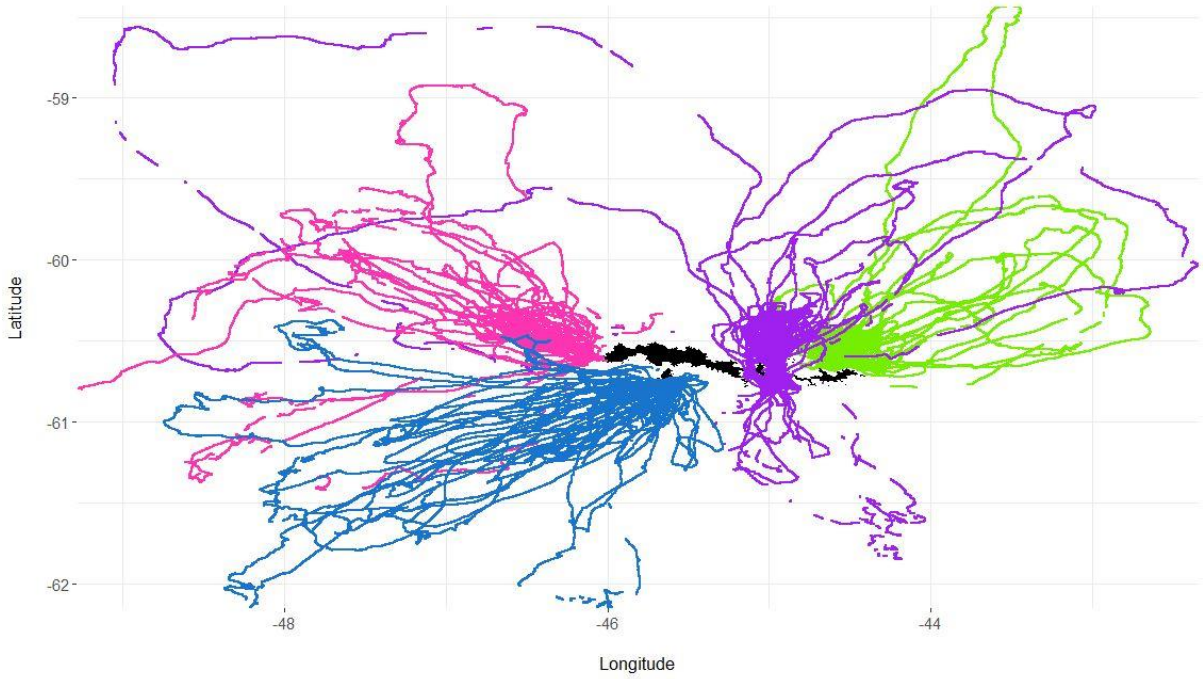


Figure 2. GPS tracks of breeding chinstrap penguins on Monroe (December 2013- January 1014; pink), Signy (January – February 2016; blue), Powell (December 2013 – January 2014; purple) and Laurie (December 2011- January 2012; green),

All fieldwork was approved by the joint British Antarctic Survey and University of Cambridge Animal Welfare and Ethical Review process. It was performed under permits granted under sections 7 (permit No. 26/2015), 12 and 13 (permit No. S7-09/2011; No. S9-02/2012; No. S7-05/2015 and No. S7-07/2015) of the Antarctic Act 1994. All methods conformed to the Scientific Committee of Antarctic Research (SCAR) Code of Conduct for Use of Animals for Scientific Purposes in Antarctica (2011).

3.2 Analytical methods

All analyses were undertaken in R 3.5.3 (R core team, 2019).

First, the GPS output from each penguin was mapped onto the coastline of the South Orkney Islands, obtained from the Scientific Committee for Antarctic Research (2017) to identify when the penguin was at sea; all data points while on land were excluded. We defined a foraging trip as a sequence of 10 or more consecutive GPS locations at sea that covered a time span of at least one hour. Trip duration was defined as the interval between the last GPS point on land before the trip and the first GPS point back on land after the trip (see Table 1 for sample sizes, see Figure 2 for GPS tracks).

Table 1. Summary of the numbers of chinstrap penguins in each breeding stage which we collected GPS and TDR data from, across four sites at the South Orkney Islands, and the numbers and types of dives performed at each site.

	Laurie	**Powell**	**Monroe**	**Signy**	**ALL SITES**
NUMBER OF BIRDS, n	58	52	57	23	190
BREEDING STAGE	----	----	----	----	----
incubation, n (%[Ŧ])	22 (38%)	6 (12%)	13 (23%)	9 (39%)	50 (26%)
incubation to brood*, n (%)	13 (22%)	9 (17%)	1 (2%)	0 (0%)	23 (12%)
brood, n (%)	23 (40%)	37 (71%)	43 (75%)	14 (61%)	117 (62%)
NUMBER OF FORAGING TRIPS, n	155	166	57	51	453
NUMBER OF DIVES, n	65,170	64,352	36,479	48,244	214,245
TYPES OF DIVES	----	----	----	----	----
foraging, n (%[Π])	14,790 (23%)	15,054(23%)	6,293 (17%)	10,550 (22%)	46,687 (22%)
explore, n (%)	24,515 (38%)	21,695(34%)	15,842 (43%)	23,634 (49%)	85,686 (40%)
travel, n (%)	25,865(40%)	27,603 (43%)	14,344 (39%)	14,060 (29%)	81,872 (38%)
NUMBER OF DIVING BOUTS, n	2,294	2,385	980	1,180	6,839
NUMBER OF NON-BOUT DIVES, n	1,908	2,417	1,190	1,330	6,845

*These penguins only had eggs at the nest at deployment and had at least one chick at the nest at retrieval, so the incubation vs brood category could not be assigned.

[Ŧ]Percentage of birds in this stage at each colony

[Π]Percentage of dives which are this type at each colony

3.2.1 Identification of Dives

TDR readings from each penguin were truncated to correspond to the start and end times of each foraging trip as determined by the GPS data. To adjust for the drift in TDR pressure readings associated with temperature changes, the depth data were zero-offset corrected (Luque and Fried, 2011) using the 'DiveMove' package (Luque, 2007). For each separate dive in the foraging trip, we recorded start time, duration, maximum depth, descent time, ascent time, time spent on the surface before the subsequent dive, time spent in the bottom phase of the dive (bottom time), and distance moved up and down during the bottom phase (bottom vertical distance). Bottom vertical distance is a measure of the amount of 'wiggles' in the dive that reflects penguins pursuing prey (Kirkwood and Robertson, 1997; Rodary et al., 2000; Simeone and Wilson, 2003; Bost et al., 2007; Zimmer et al., 2010), and we use it to validate our measure of foraging patch quality (section 4.1). We detected 237,814 dives ; 9 dives were excluded because they were far beyond the diving abilities of chinstrap penguins in terms of duration or depth (Takahashi et al., 2003) and, thus, presumably the result of TDR malfunction.

In order to determine the number of different dive types performed by chinstrap penguins, we used a machine learning method that employs the Calinski-Harabasz criterion (Caliński and Harabasz, 1974) to group dives into relatively distinct clusters using the 'vegan'(Oksanen et al., 2019) package. We were particularly interested in identifying foraging dives. So given that prey pursuit (Chappell et al., 1993) and prey capture (Ropert-Coudert et al., 2006; Bost et al., 2007) mainly occurs during the bottom phase of penguins' dives, we chose bottom time, dive duration, and maximum depth as the criteria for clustering different types of dives (Malcolm and Duffus, 2000). This procedure identified 3 as the optimal number of dive types (i.e., 'clusters'). We then used k-means clustering to group all dives (Schreer et al., 1998) into one of these three groups. We attributed the main cluster of dives with the shallowest depth, shortest duration, and shortest bottom time to 'travelling dives', dives in which penguins 'porpoise' on the surface to commute to and from foraging areas. We attributed the smallest cluster of dives, with the deepest depth, longest duration, and longest bottom time to 'exploratory

dives', dives in which penguins pursue and manipulate prey at depth. We attributed the medium sized cluster of dives with intermediate depth, intermediate duration and intermediate bottom time as 'prey searching dives', dives in which penguins search for prey in the water column but do not successfully capture prey, or capture only small amounts of prey (Table 2). As chinstrap penguins breeding in the South Orkney Islands mainly consume Antarctic krill (Lishman, 1985; Rombola et al., 2006), it is unlikely that this cluster, representing 39% of their dives would be associated with preying on a different type of prey.

Table 2. K-mean clustering results (mean (se)) of chinstrap penguins diving data collected with temperature-depth recorders (TDRs) at the South Orkney islands

Dive type	Dive duration (s)	Maximum depth (m)	Bottom time (s)	Number of dives
Travel	23.9 (0.04)	5.6 (0.01)	2.3 (0.01)	94,781 (40%)
Explore	69.8 (0.04)	22.3 (0.04)	9.3 (0.03)	93,202 (39%)
Forage	112.4 (0.08)	61.6(0.09)	16.0 (0.07)	49,822 (21%)

3.2.2 Matching GPS and dive data

For each GPS recording, we calculated the distance to the colony and the time, distance, and speed of travel to the next recording. We excluded data from all points where travelling speeds from the previous point and to the following point were both over 10 m/s; such rapid speeds are not realistic (Culik et al., 1991) so they indicate GPS device error. We visually inspected the remaining GPS points in each trip to remove other obvious GPS errors, such as single points which were unrealistically distant from the remainder of the track. To further ensure accuracy of the GPS assigned to dives, we also excluded dives that occurred during periods in trips where there was over an hour without GPS data. These three steps resulted in removing 204 of the 98,569 (0.2%) GPS points during foraging trips, and 23,560 of the 237,805 (9.9%) dives during foraging trips. Dives in the remaining time intervals were assigned GPS coordinates by interpolating the GPS data to the start time of each dive, using the Piecewise Cubic Hermite Interpolation 'pchip' function in the 'signal' (Signal developers, 2013) package. For each dive, we used the GPS coordinates to determine the distance to the colony.

3.2.3 Index of Patch Quality

Mori and colleagues (2002) developed an 'index of patch quality' (IPQ) based on two assumptions: 1) a time-allocation model, that is, where time spent at depth in a prey patch is a function of both time taken to travel to the prey depth and prey abundance in that patch (Stephens and Krebs, 1986); and 2) the principle of inverse optimality (McFarland, 1977) which assumes that foraging dives are optimized to maximize prey intake. IPQ is calculated for each foraging dive as the rate of change in energy gain in relation to the time spent at the bottom phase of the dive (Mori et al., 2002):

$$g(t) = a \cdot t^x \quad [1]$$

Where g is energy gain, a is a constant which does not affect the calculation, t is the time spent foraging (i.e., in the bottom phase of the dive), and x is the IPQ. The time spent on the surface after the dive, s, also called surface-pause duration, is a function of dive duration, u (Elliott et al., 2008):

$$s(u) = be^{cu} \quad [2]$$

Where b and c are constants derived from the relationship between u and s. Based on equation [1] and [2] we can derive (Elliott et al., 2008):

$$x = \frac{(1 + bce^{cu})(u - \tau)}{bce^{cu} + u} \quad [3]$$

Where τ is the time taken to travel to the depth of the prey patch (sum of descent time and ascent time).

The IPQ has been used as a metric of prey abundance for several marine predators (Mori and Boyd, 2004; Mori et al., 2005; Elliott and Gaston, 2014; Shoji et al., 2014) and has been shown to be correlated with various proxies of prey abundance, including prey mass brought back to the colony in seabirds (Elliott et al., 2008), prey abundance measured by on-board cameras in Weddell seals (Mori

et al., 2005), and krill abundance measured by hydro-acoustic surveys in a study of fur seals (Mori and Boyd, 2004).

We calculated the IPQ for each foraging dive, except those with a subsequent surface pause greater than 325 seconds (the inflection point in the frequency of post-dive surface pause graph (Gentry and Kooyman, 1986; Zimmer et al., 2010)) because longer pauses were unlikely to indicate the time taken for penguins to recover from the dive. While Elliot and colleagues (2008) estimated the sum of ascent and descent time in the function to calculate IPQ as a linear function of bottom depth, we were able to use the actual ascent and descent time for each dive, which improves accuracy of the estimation of IPQ. We also excluded 7 dives with IPQ greater than 5, as it is not realistic for energy gain at depth to increase with a function of bottom time to the power of five (Mori et al., 2002; Elliott et al., 2008). We calculated the value for the constants b and c using equation [2] by running the equation on the dive duration (u) and surface pause duration (s) for all foraging dives and taking the median values for b and c. We identified 'diving bouts' as clusters of foraging dives occurring within less than 325 seconds of surface time between each dive. For each diving bout, we recorded the number of dives in the bout, the mean distance to the colony, and mean IPQ. To validate our use of IPQ as an indicator of patch quality, we tested whether IPQ increased as expected in concert with increases in the number of dives in a bout (Mori et al., 2002) and with the vertical distance covered at the bottom of the dive, which reflects penguins pursuing prey (Zimmer et al., 2010) .

3.2.4 Statistical Analysis

We used linear mixed models (LMM) to validate the IPQ by testing for 1) correlations between dive IPQ and bottom vertical distance; 2) correlations between bout IPQ (i.e., mean IPQ for all dives in a bout) and the number of dives in the bout; and 3) whether dive IPQ differed between dives which were or were not part of a diving bout. We then used LMMs to test for evidence of an Ashmole's halo close to the colony by testing if 4) bout IPQ differed with the distance from the colony. We also used LMMs to investigate prey depletion near the colony over the whole season by 5) testing whether bout IPQ near colonies varied with the date of occurrence. For each colony, we

took the median of the maximum distance to the colony of all foraging trips that were less than a day in duration and classified diving bouts that occurred within this distance as 'bouts near colony'. We used LMMs to test for differences in foraging behaviour of birds in different breeding stages by testing 6) if foraging dive depth differed between breeding stages; and 7) if maximum trip distance differed with breeding stage. Finally we used LMMs to test for evidence of prey depletion over time by testing 8) if maximum trip distance of foraging trips during the incubation and brood phases changed over time. We converted all dates into the Julian day and added 365 to dates in January and February so the numbers indicating day would be continuous from December to January. Twenty-three penguins were excluded from the last three models because they had eggs at the time of deployment but had at least one chick at the time of retrieval and, thus, it was not possible to assign a specific breeding stage.

For each model we set penguin identity as a random effect because our dataset contained multiple dives and trips per bird, colony as a fixed effect to account for potential differences across colonies, although colony and year are confounded so differences could be attributed to either. To obtain significance values, we used likelihood ratio tests comparing the model of interest with the null model (the same model but without the variable of interest). For models 4 to 8, we used likelihood ratio test to compare the selected model with a model without colony, to determine whether the effect of colony was significant. If the effect of colony was significant, we ran a separate model for each colony. As each penguin only performed one trip at Monroe Island, we did not need to include penguin identity as a random effect for this island, and used a linear model (LM) for this island in model 8. We square-root transformed IPQ in all models to normalize its distribution. All estimates presented in the results section are mean ± standard error (se) unless indicated otherwise.

4. Results

Chinstrap penguin foraging trips were predominantly performed in northeast, northwest, and southwest directions from the South Orkney Islands. The at-sea distribution of the birds is described in Warwick-Evans and colleagues (2018). Here we focus solely on the birds' foraging behaviour.

4.1 Validation of IPQ

Three separate findings validated our use of IPQ as a measure of patch quality. First, we found that IPQ significantly increased with bottom vertical distance (LMM: slope = 0.0259 ± 0.0001, χ^2_1 = 26876, p<0.0001, Figure 3a). Second, we found that mean IPQ of a dive bout increased significantly with the number of dives in the bout (LMM: slope = 0.0055 ± 0.0004, χ^2_1 = 227.97, p<0.0001, Figure 3b). Diving bouts lasted on average 16.38 ± 0.42 minutes and contained an average of 5.83 ± 0.09 dives. Third, as expected, diving bouts indicate higher prey abundance: mean IPQ of dives in bouts (0.459 ± 0.002) was significantly higher than the IPQ of single dives (0.335 ±0.005) (LMM: χ^2_1 = 352.97, p<0.0001) validating IPQ.

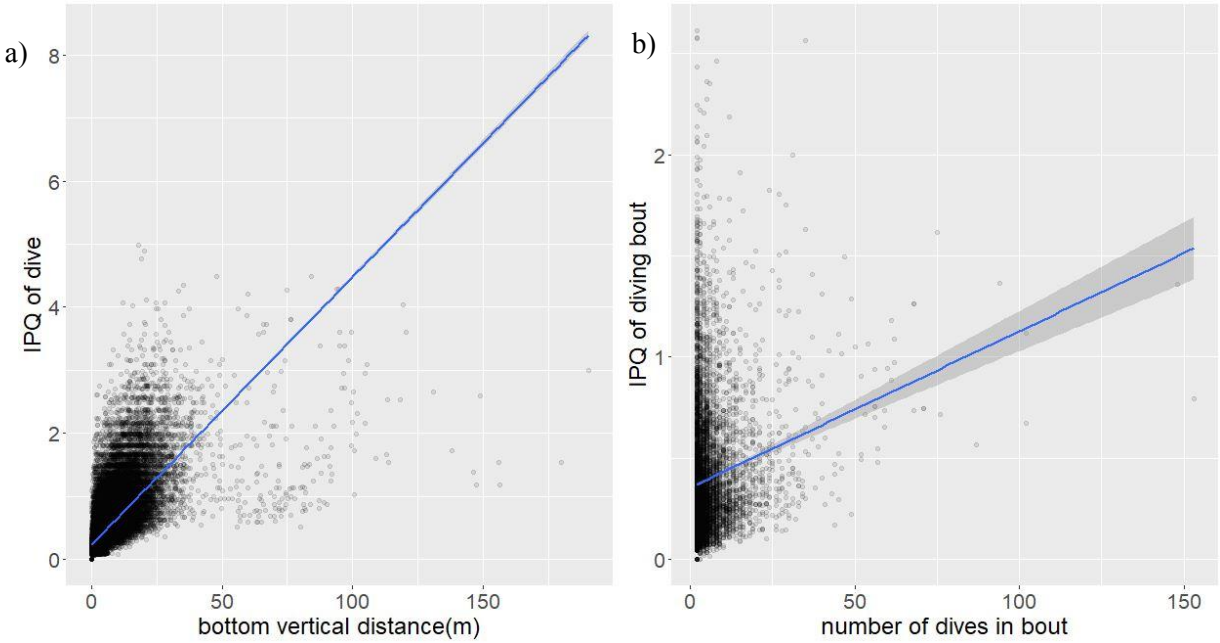


Figure. 3 The a) bottom vertical distance and IPQ of foraging dives, and b) number of dives in foraging bouts versus mean bout IPQ, for chinstrap penguins breeding on the South Orkney Islands. Grey shaded areas indicate standard error.

4.2 Differences between breeding stages

Overall, foraging dives during incubation were significantly shallower than foraging dives during brood (incubation: 50.67±0.12 m, brood: 68.80±0.13 m, LMM: χ^2_1=84.44, p<0.0001), with a significant effect of colony (χ^2_3=28.24, p<0.0001). The effect was significant at every colony (Laurie: incubation: 54.38±0.21 m, brood: 70.20±0.22 m, LMM: χ^2_1=25.58, p<0.0001; Powell: incubation: 54.26±0.29 m, brood: 73.18±0.22 m, LMM: χ^2_1=10.84, p<0.0001; Monroe: incubation: 47.35±0.22, brood: 67.75±0.30 m, LMM: χ^2_1=38.98, p<0.0001; Signy: incubation: 45.13±0.15 m, 60.98±0.25 m, LMM: χ^2_1=13.75, p=0.00021, Figure 5). Overall, foraging trips during the incubation phase were significantly longer than those during the brood phase (incubation: 94.06±8.21 km, brood: 46.54±1.58 km, LMM: χ^2_1=105.66, p<0.0001), with a significant effect of colony (χ^2_3=70.64, p<0.0001). The effect was significant at every colony (Laurie: incubation: 54.62±10.58 km, brood: 18.28±0.94 km, LMM: χ^2_1=12.15, p=0.00049; Powell: incubation: 124.58±22.69 km, brood: 66.45±0.96 km, LMM: χ^2_1=32.40, p<0.0001; Monroe: incubation: 129.94±11.58 km, brood: 35.73±3.14 km, LM: t=11.11, p<0.0001 ; Signy: incubation: 134.26±12.89 km, brood: 52.01±6.69 km, LMM: χ^2_1=17.13, P<0.0001).

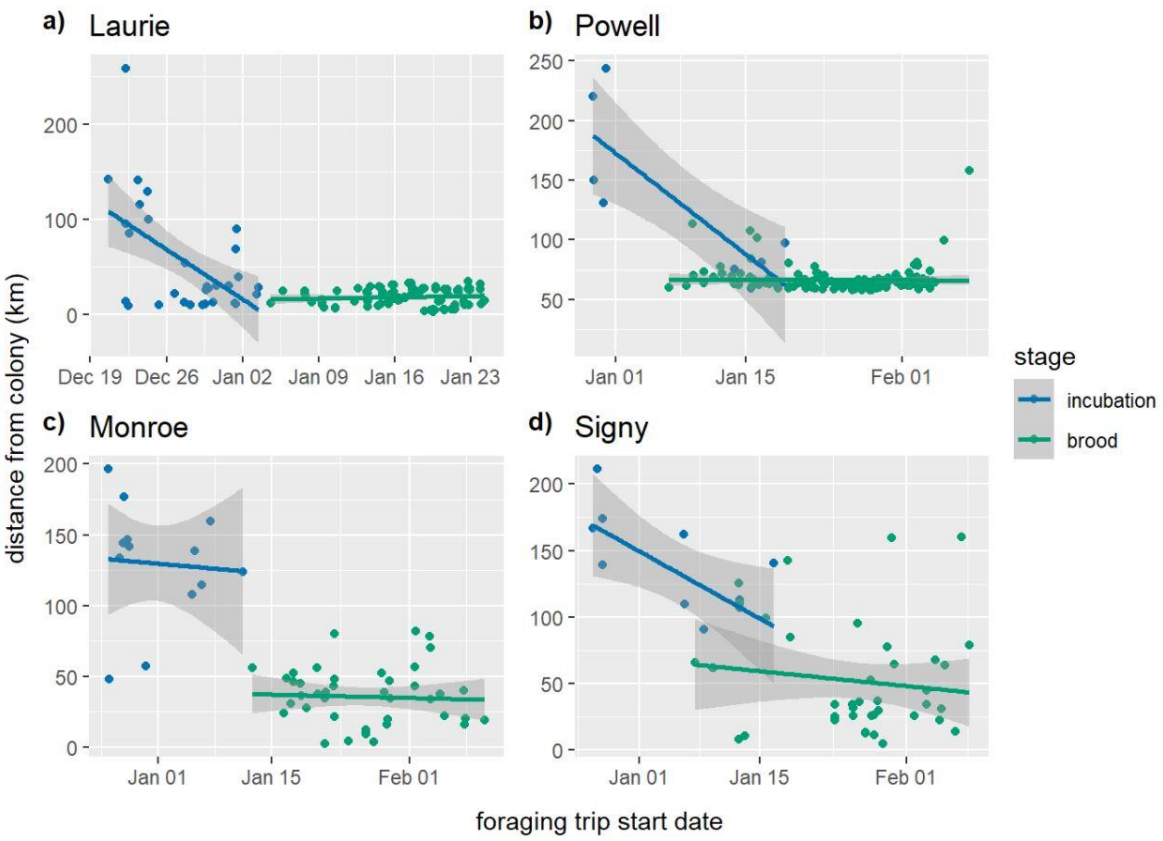


Figure. 4 Maximum distance from the colony of foraging trips by start date during incubation and brood at a) Laurie Island, b) Powell Island, c) Monroe Island, and d) Signy Island. The shaded areas represent slope standard error.

Overall, trip distance during incubation declined significantly with trip start date (LMM: slope=-0.14±1.30, χ^2_1=13.89, p=0.00019), but there was a significant effect of colony (χ^2_3=33.63, P<0.0001). When the colonies were analysed separately, the relationship was significant for Laurie and Signy (Laurie: LMM: slope=-7.45±2.22, χ^2_1=7.82, p=0.0052; Signy: LMM: slope=-3.67±1.49, χ^2_1=5.63, p=0.018, Figure 4) but not the other colonies (Powell: LMM: slope=-5.2±2.14, χ^2_1=3.68, p=0.055; Monroe: LM: slope=-0.72±2.22, t=-0.32, p=0.75, Figure 4). Overall, trip distance during brood declined significantly with trip start date (LMM: slope=-0.039±0.012, χ^2_1=7.29, p=0.0069), with a significant effect of colony (χ^2_3=91.20, P<0.0001). However, when colonies were analysed separately, there was no significant effect at any colony (Laurie: LMM: slope=0.15±0.24, χ^2_1=0.43, p=0.51; Powell: LMM: slope=-0.0094±0.0072, χ^2_1=1.76, p=0.18; Monroe: LM: slope=-0.031±0.020, t=-1.57, p=0.12; Signy: LMM: slope=0.069±0.047, χ^2_1=2.12, p=0.15, Figure 4).

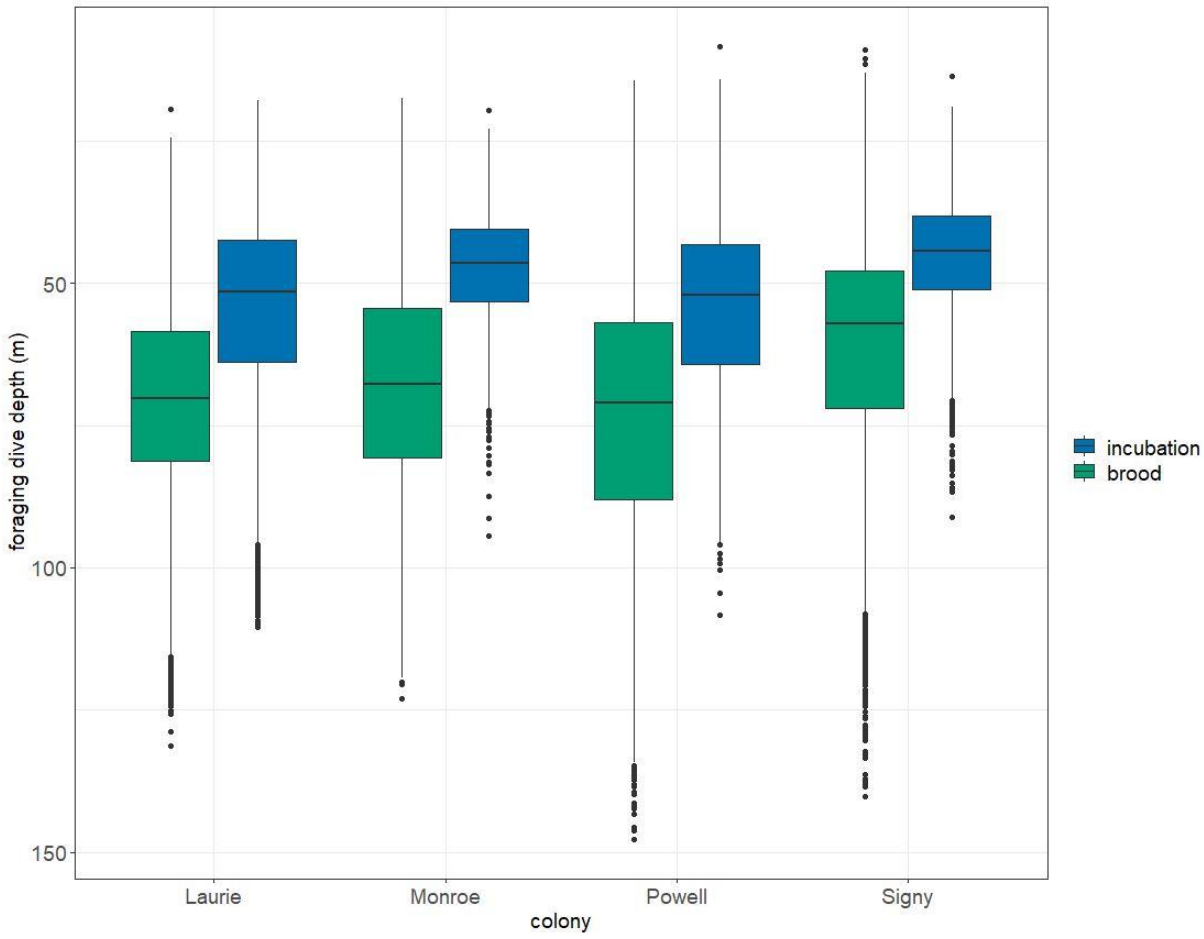


Figure. 5 Depth of chinstrap penguin foraging dives during incubation and brood at four colonies in the South Orkney Islands

4.3 Prey availability as a determinant of foraging distance

Overall, bout IPQ increased significantly with the distance to colony regardless of breeding stage (LMM: slope =0.00071 ±0.000099, χ^2_1 = 43.85, p<0.0001, Figure 6a), with no significant effect of colony (χ^2_3= 7.32, p=0.062) (see Figure S.2 for a kernel density plot of IPQ where penguins foraged). However, this effect was mainly driven by the brood period where IPQ increases significantly with distance to colony (LMM: slope =0.0015 ±0.00028, χ^2_1 = 28.21, p<0.0001), with no significant effect of colony (χ^2_3 = 0.45, p=0.93). During incubation, while IPQ increased significantly with distance to colony (LMM: slope=0.00081±0.00012, χ^2_1 =35.82, p<0.0001), there was a significant effect of colony (χ^2_3=8.71, p=0.033). When the colonies were analysed separately, the relationship was significant for Laurie (LMM: Laurie: slope =0.0013 ±0.00019, χ^2_1 = 42.54,

p<0.0001), but not the other colonies (Powell: slope =0.00032±0.00025, χ^2_1 = 1.81, p=0.18; Monroe: slope=0.00030±0.00039, χ^2_1=0.62, p=0.43; Signy: slope=0.00055±0.00029, χ^2_1 =3.53, p=0.060).

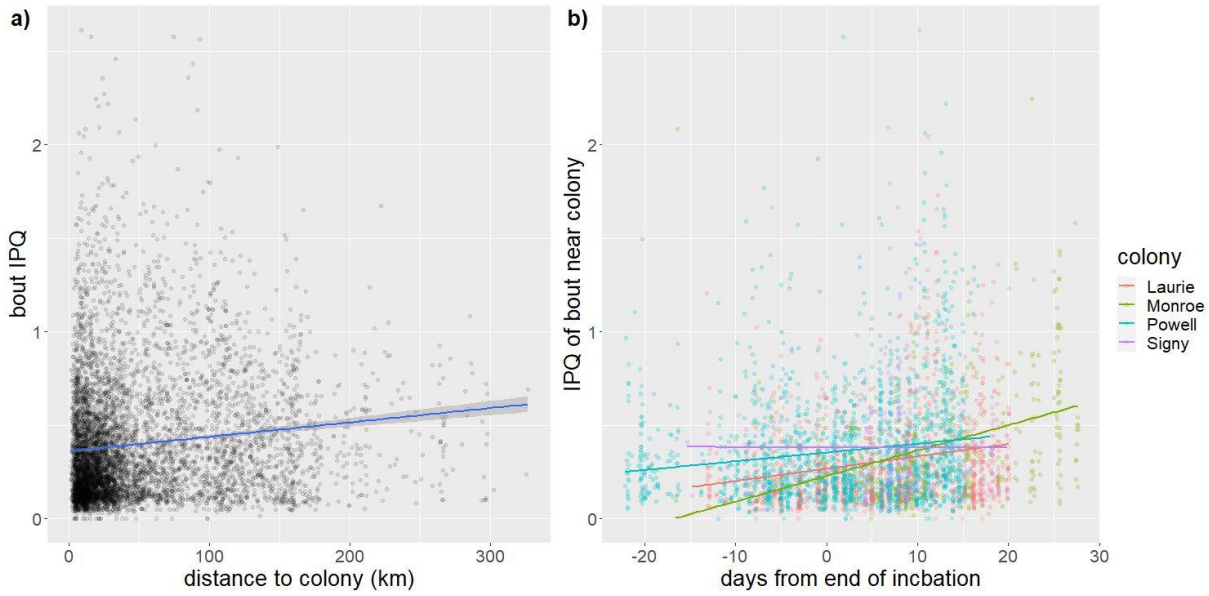


Figure. 6 a) IPQ of diving bouts against the distance from the colony, where grey shaded areas indicate standard error; b) IPQ of bouts near the colony (i.e. within the median distance of trips up to a day in duration: 17km at Laurie, 63km at Powell, 31km at Monroe, and 26km at Signy) over the breeding season. Where "0" on the x-axis denotes the day the last tracked incubation trip ended. Trips that started before the end of the final incubation trip have negative values, and trips that started after that have positive values. The lines represent a linear model fit to the data from each colony.

4.4 Prey availability near the colony throughout the breeding season

To investigate whether patch quality near the colony declined over the breeding season, we tested the relationship between bout IPQ with the date of occurrence of diving bouts near the colony (i.e., within the median distance of trips up to a day in duration: 17km at Laurie, 63km at Powell, 31km at Monroe, and 26km at Signy). We found bout IPQ near the colony increased significantly through the breeding season (LMM: slope=0.0041 ±0.00065, χ^2_1 = 22.33, p<0.0001, Figure 6b) with no significant difference between colonies (χ^2_3 =1.68, p=0.64).

5. Discussion

We used a large population tracking dataset to test how breeding stage, prey abundance, and intraspecific competition influenced foraging strategies of breeding chinstrap penguins. We found strong evidence that breeding stage influenced foraging strategies in chinstrap penguins. Foraging trips became shorter in distance with the progression of incubation at Laurie and Signy Island. We also found that foraging patch quality increased with increasing distance from the colony at all colonies during brood, and at Laurie during incubation. Finally, we found that patch quality near the colony improved over the breeding season at all colonies.

Breeding stage had a strong impact on foraging tactics. First, penguins travelled further from the colony during incubation than chick-rearing at all colonies, a result that is in line with numerous other tracking studies of seabirds, including penguins (Weimerskirch et al., 1993; Charrassin et al., 1998; Barlow and Croxall, 2002; Shaffer et al., 2003; Ichii et al., 2007; Ito et al., 2010; Warwick-Evans et al., 2018). During incubation, penguins prioritize maximizing energy gain (Ichii et al., 2007), so they targeted more distant foraging grounds, which had a higher IPQ and were probably more profitable. Conversely, during chick-rearing, penguins prioritize minimizing time at sea (Ichii et al., 2007), so they targeted closer foraging grounds that had a lower IPQ and were probably less profitable (Ichii et al., 2007). We also found differences in the birds' diving behaviour during different breeding stages. Foraging dives were significantly deeper during chick-rearing compared to foraging dives during incubation at all colonies. Similar findings have been established in Adélie penguins (Kato et al., 2009), and king penguins *Aptenodytes patagonicus* (Charrassin et al., 1998). Deeper dives are more energetically costly to birds than shallow dives because they incur higher metabolic costs (Enstipp et al., 2006). This suggests that chinstrap penguins – like other seabirds (Charrassin et al., 1998; Benvenuti et al., 2002; Ito et al., 2010) – reduce foraging effort during incubation when their time at sea is less restricted, and increase foraging effort during chick-rearing when their time at sea is more restricted (Shaffer et al., 2003). Foraging at shallower depths during incubation may also permit chinstrap penguins more time to search for high quality prey patches (Bost et al., 1997; Guinet et al.,

1997; Charrassin et al., 1998). Alternatively, foraging effort may have to increase during chick-rearing due to lower prey availability near the colony; since survival of penguin chicks is associated with feeding frequency (Clarke et al., 2002; Chiaradia and Nisbet, 2006), during chick-rearing parents must forage close to the nest to ensure they are fed frequently.

We also observed differences in foraging tactics within a breeding stage. As incubation progressed, birds at Laurie and Signy Island made increasingly shorter trips. Their trips also shortened with the progression of the chick-rearing phase, though at a slower rate. This shortening of foraging trips toward the end of incubation leading up to hatching has also been found in albatrosses (Jouventin and Weimerskirch, 1990; Weimerskirch et al., 1993), petrels (Johnstone and Davis, 1990; Weidinger, 1998), fulmars (Hatch, 1990), Manx shearwaters *Puffinus puffinus* (Brooke, 1978), and king penguins (Jouventin et al., 1994). Two hypotheses have been proposed to explain this behaviour (Gonzalez-Solis, 2004): 1) parents predict hatch date based on cues from the egg or from an internal clock, 2) shorter trips are due to seasonal increase in prey availability. The first hypothesis suggests the birds are preparing for a change in parental duties (young chicks need to be fed soon after hatching, therefore parents may want to avoid being on a long trip when the egg hatches); the second hypothesis suggests that the changing foraging behaviour is a simple reaction to changing environmental conditions. In a manipulative experiment that supports the first hypothesis, Gonzalez-Solis (2004) found that petrels use an internal clock to predict hatch date, which they fine-tune with signals from the egg. By shortening trips near to hatch, parents ensure chicks are fed soon after hatching, as the incubating parent may be unable to feed the recently hatched chick after days of fasting whilst sitting (Gonzalez-Solis, 2004). In support of the second hypothesis, we found that the patch quality near the colony increased over the breeding season at all islands, which suggests that the reduction in trip length near hatching may be due to a seasonal upsurge in local prey availability. However, it remains possible that both factors are in play; we cannot rule out the possibility that local prey availability increase *and* birds shortened their foraging trips in time for chick hatching (Gonzalez-Solis, 2004).

Ashmole (1963) suggested that food availability may ultimately limit seabird population size. The intraspecific competition at colonies with high densities of birds would deplete prey around the colony and reduce provisioning rates to chicks, which would then impact reproductive success, recruitment rates, and ultimately, colony size. Our finding of lower IPQ closer to the colony at all colonies provides some evidence for a "halo" of lower prey availability near the colony. However, we did not find any evidence of increasing prey depletion around the South Orkney Islands as the breeding season progressed; in fact, we found the patch quality increased over time. Ashmole (1963) postulated that seasonal abundance of prey availability in higher-latitudes would make prey depletion around higher-latitude seabird colonies less likely. However evidence of "Ashmole's halo" has been found in a number of higher-latitude seabird colonies, including razorbills at Skomer Island, UK (Shoji et al., 2014), double-crested cormorant at Prince Edward Island, Canada (Birt et al., 1987), and Brünnich's guillemot in Nunavut, northern Canada (Elliott et al., 2009). This study adds to the evidence of "Ashmole's halo" existing alongside seasonal upsurge in prey availability. Kokubun and colleagues (2010) found that during brood chinstrap penguins at Barton Peninsula on King George Island foraged further from the colony over time, and attributed this to prey depletion. King George Island and the neighbouring Nelson Island have a breeding chinstrap penguin population estimated at 625,800 pairs (Trivelpiece et al., 1987) , smaller than our population of ~960,000 pairs (Strycker et al., 2020) . However, both King George Island and the South Orkney Islands are also home to many other species of krill-predators, including breeding Gentoo and Adélie penguins (Korczak-Abshire et al., 2013; Dunn et al., 2016), and non-breeding male fur seals (Favero-Longo et al., 2011; Grebieniow et al., 2020). If King George Island has higher densities of krill-predators than the South Orkney island, this could explain the difference in the two studies regarding local prey depletion over time. Another possible explanation is that the South Orkney Islands may be in an area with particularly abundant prey, so a similar number of chinstrap penguins would be unable to deplete the prey abundance in this area, whereas they would be able to deplete prey around King George Island. This is supported by the results of krill surveys over five summers that found that the shelf break northwest of the South Orkney Islands is a hotspot for krill concentration and retention (Krafft et al., 2018).

Another explanation could be that the highly dynamic krill distribution near the South Orkney Islands (Krafft et al., 2018) results in the movement and replenishment of Antarctic krill, through flux with the ocean currents and reproduction (Trathan et al., 2018). This may compensate for prey depletion by intraspecific competition near the colony during breeding, an argument supported by our finding that patch quality increases near the colony as the season progressed.

Seabirds are thought to time their reproduction so that the time of maximum energy demand in late chick-rearing coincides with the period of maximum resource availability in the environment (Lack, 1968). This is probably why we found that IPQ near the colony increased later in the breeding season. This may also be why adults at Laurie and Signy made shorter trips later on in Incubation, as their energy demands could be met more quickly (Gonzalez-Solis, 2004). Changing foraging ranges throughout breeding may also reduce competition with Adélie penguins where the two species breed sympatrically, such as on Signy Island (Clewlow et al., 2019) and Laurie Island (Coria et al., 2011). There are ~19,500 chinstrap penguin nests and ~18,300 Adélie penguin nests on Signy Island (Dunn et al., 2016), and at least ~143,800 pairs of chinstrap penguins and ~81,000 Adélie penguin nests with eggs on Laurie Island (Coria et al., 2011). Clewlow et al. (Clewlow et al., 2019) found an allochory of 28 days between chinstrap and Adélie penguins breeding sympatrically on Signy Island caused them to leapfrog each other's foraging locations and reduced the overlap of their habitat use by 54% over the breeding season. The shortening of foraging trips towards the end of incubation at Signy and Laurie Island may help to reduce overlap in habitat use with sympatric Adélie penguins. While the population sizes of chinstrap penguins at Monroe and Powell Island are unknown (Strycker et al., 2020), penguins travel on average twice as far during trips less than a day in duration at Powell Island compared to any other island, indicating more competition for resources, and/or lower prey availability near Powell Island or during the 2013-2014 season. Trip distances over brood had a lower standard error at Laurie and Powell than Monroe and Signy. This may be partly caused by the smaller sample size of brooding penguin at Signy compared to the other colonies. This could also be associated with the colonies' proximity to the shelf edge. At Laurie and Powell, located on the east of the South Orkney Islands, most birds used the shelf edge north of the colony. In contrast, birds from

Monroe and Powell had further distances to travel to reach the shelf edge to the west of the South Orkney Plateau, which could have led to a greater variation in foraging distance as not all birds travelled to the edge.

However, there may also be benefits to foraging in proximity to other penguins. Sutton et al. (Sutton et al., 2020) found that African penguins *Spheniscus demersus* often forage in proximity to a variety of other predators, and foraging in proximity to other seabirds improved individual foraging success. However, while *Eudyptula minor* little penguins often associated with conspecifics while hunting schooling prey, their foraging gains were similar or smaller compared to solitary foraging on schooling prey, indicating penguins may have to trade off reduced energetic gains from prey against increased likelihood of locating prey items (Sutton et al., 2015). Furthermore, Sutton et al.(Sutton et al., 2021) found that macaroni penguins did not associate with conspecifics during foraging, and attributed this to the low maneuverability and high prevalence of krill. It is not known whether chinstrap penguins associate with other conspecifics or sympatric penguin species during foraging attempts. Future research shedding light on this question could provide information on whether chinstrap penguins can also benefit from foraging in areas with high concentrations of penguins. We found that bout IPQ increased with the distance from the colony, providing evidence for Ashmole's halo, and suggesting that chinstrap penguins' foraging strategies are partly influenced by prey distributions. Our findings support previous studies by Shoji and colleagues (2014), who found that IPQ increased with the distance from the colony in razorbills. Our result also aligns with other studies that found evidence of Ashmole's halo, including Birt and colleagues (1987), who found that the density of benthic fish increased with distance from a double-crested cormorant colony, and Elliot and colleagues (2009), who found that the mass of prey items brought back increased with foraging distance in chick-rearing Brünnich's guillemots. One limitation of our study is that we did not consider potential sex differences. However, previous studies found no intersex differences in chinstrap penguin maximum trip distances (Lynnes et al., 2002; Miller et al., 2010), time spent on the shelf (Miller et al., 2010), or the proportion of fish in the diet (Miller et al., 2010; Polito et al., 2015). Another limitation of our study is that we did not directly measure patch quality, but instead used IPQ

as a proxy. However, several studies have found correlations between IPQ and measures of prey abundance (Mori and Boyd, 2004; Mori et al., 2005), and we found that IPQ correlates with several variables that are linked to prey abundance. Taken together, these previous studies and the findings from our own study suggest that IPQ is an appropriate proxy of patch quality (Mori et al., 2007).

Another finding which highlights how chinstrap penguins respond to local habitat quality is that the number of dives in a bout was positively correlated with the mean IPQ of the bout, which indicates that birds spent longer in higher quality patches. This supports optimal diving models, which predict that divers should perform more dives in high-quality patches, though this hypothesis has seldom been tested due to the challenges of measuring patch quality (Mori et al., 2002). Similar to our findings, Mori and colleagues (2002) found that the number of dives in a bout was positively correlated with the IPQ of the bout in Brünnich's guillemots. We also found that the mean IPQ of diving bouts was higher than that of individual dives, which is similar to the finding of studies by Elliott and colleagues (2008) and Mori and colleagues (2002) of Brünnich's guillemots.

5.1 Conclusions

We have demonstrated that breeding stage, the timing within the breeding stage, and prey distributions are drivers of foraging strategies in chinstrap penguins. We found that patch quality improves with distance to the colony, but there was no evidence that prey depletion near the colony increased over time. This sheds light on how predators select foraging strategies based on the changing requirements of breeding and the spatial and temporal variability in prey distributions. While analysing the effect of population size was beyond the scope of this study, the role of population size on foraging strategies during breeding, and in particular how spatial and temporal prey availability and intraspecific competition may interact is an important avenue for future research.

6. Acknowledgements

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7. Author contributions

Jessica A. Phillips: Formal analysis (lead), Writing-original draft (lead), Writing-review & editing (equal); **Annette L. Fayet**: Methodology (lead), Formal analysis (supporting), Writing-original draft (supporting), Writing-review & editing (equal); **Tim Guilford**: Methodology (supporting), Formal analysis (supporting), Writing-original draft (supporting), Writing-review & editing (equal); **Fabrizio Manco**: Fieldwork (supporting), Formal analysis (supporting), Writing-review & editing (equal); **Victoria Warwick-Evans**: Formal analysis (supporting), Writing-review & editing (equal); **Phil Trathan**: Project design (lead), Fieldwork (lead), Ecological context (lead), Writing-review & editing (equal).

8. Data availability statement

All GPS tracking data and all TDR dive data analysed in this manuscript are available from the UK Polar Data Centre (www.bas.ac.uk/data/uk-pdc/). The code used in this analysis is available on GitHub (https://github.com/JAP2018/Chinstrap-penguin-analysis).

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10. Supplementary materials

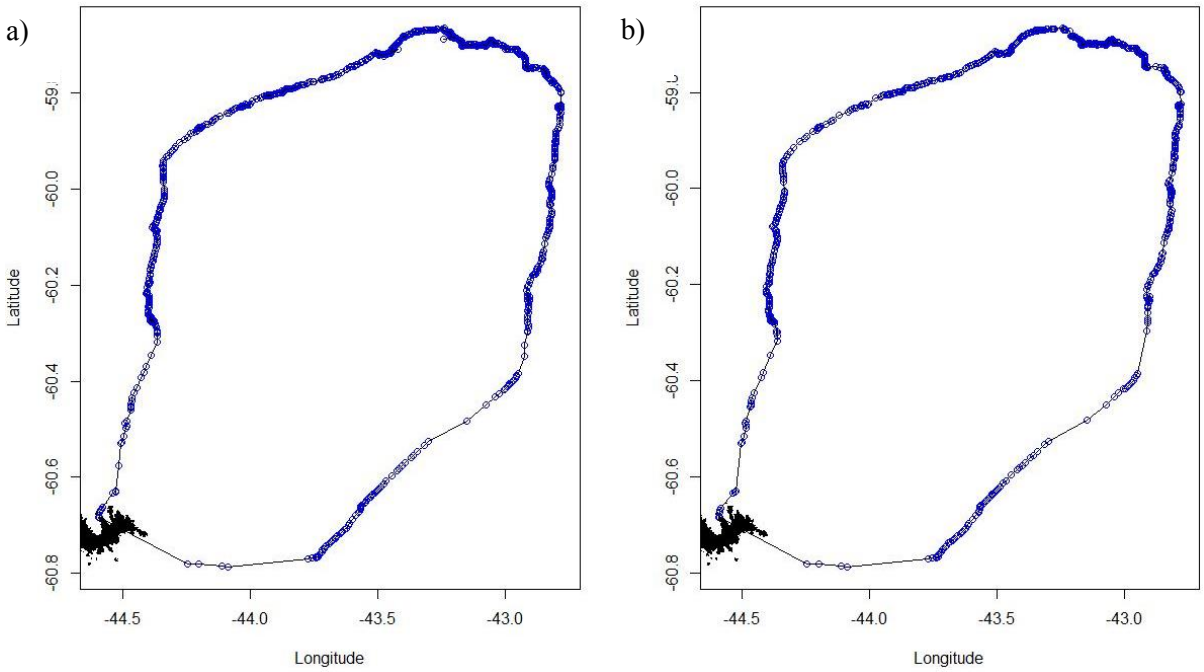
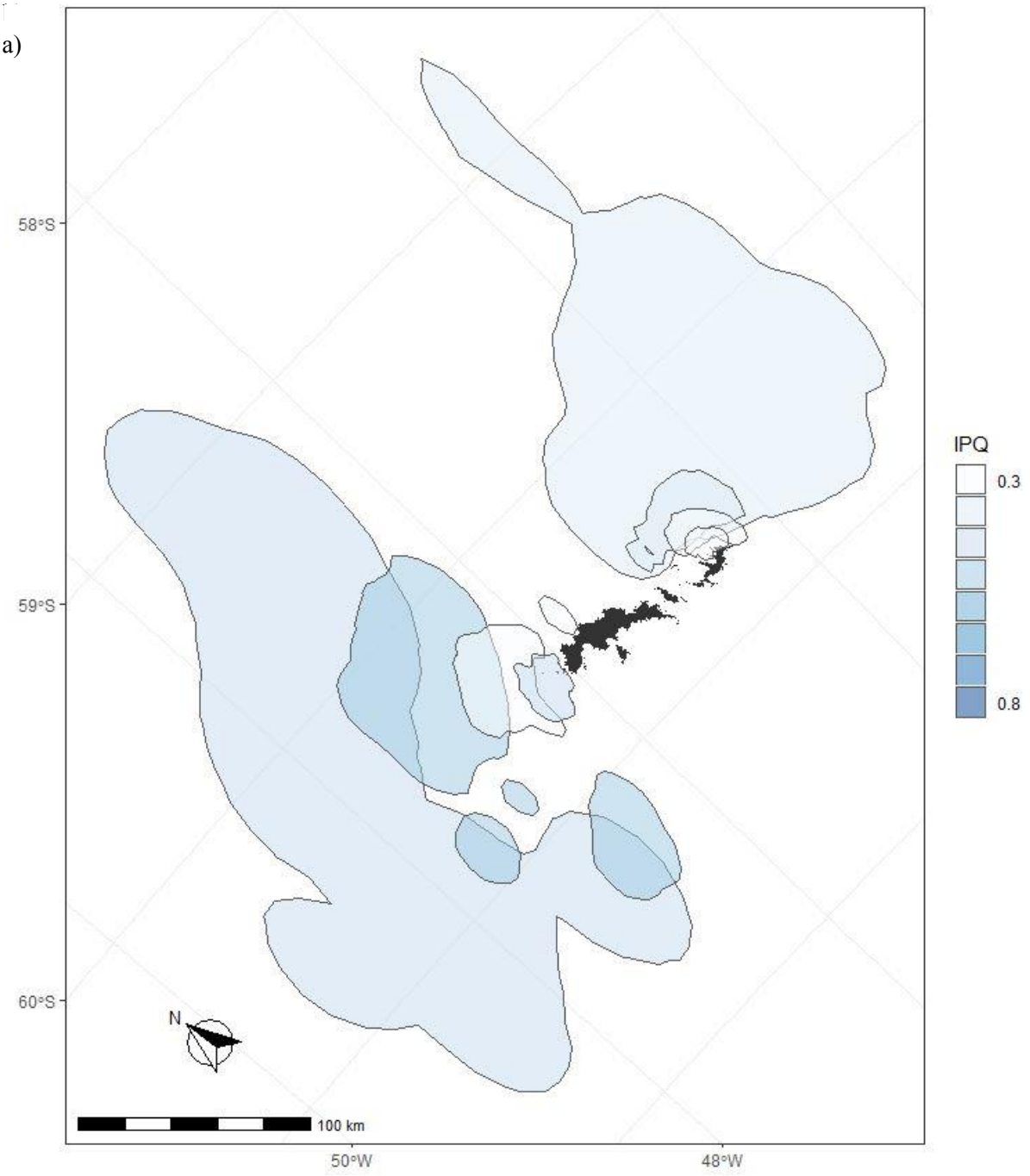


Figure S.1 Comparison of two methods of filtering GPS points using a foraging trip from Laurie Island as an example. Panel a) shows the GPS points remaining after filtering using the method outlined in this chapter, and panel b) shows GPS points remaining after additional filtering by excluding points that were fixed with less than five satellites.

Filtering the GPS points based on the number of satellites connected excluded 206 of the 1083 GPS points retained for the GPS trip plotted in Figure S.1. This additional step of filtering would likely improve the accuracy of the GPS points retained; however, it also reduces the sample size of GPS points by about 19% in this example. As dive locations were interpolated based on the nearest GPS locations, the improved accuracy of retained GPS points should be weighed against the reduced sample size when deciding whether to exclude GPS points with less than five satellite connections from the analysis.

a)



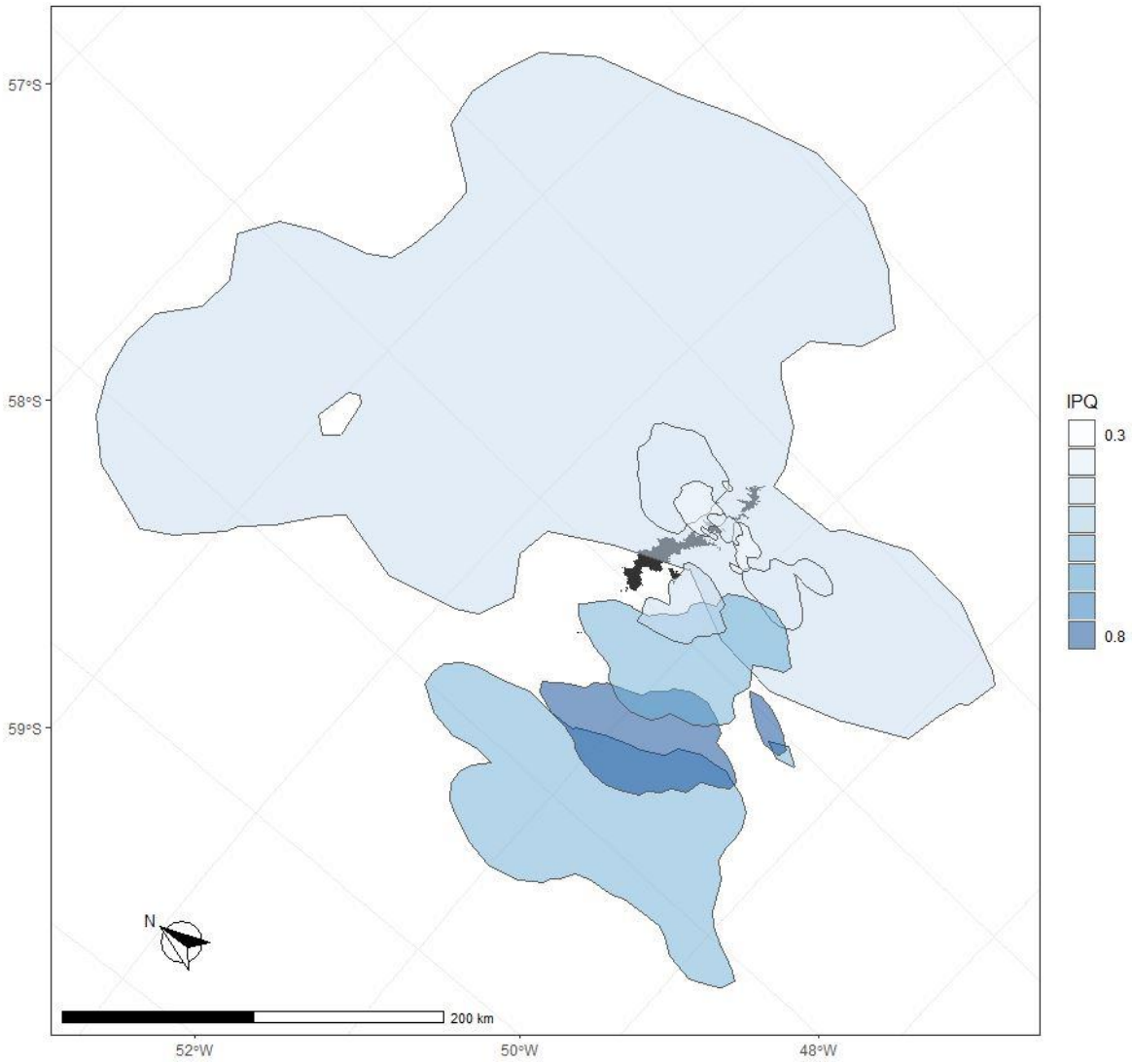


Figure S.2 Kernel density plots of dive IPQ at a) Monroe and Laurie, and b) Powell and Signy. Dives are split into four quantiles based on distance to colony for each colony. Shapes represent 95% contour kernels, and are coloured based on the average IPQ within that quantile, where darker blues indicate higher IPQ.

Chapter 4

Foraging behaviour and characteristics of preferred foraging sites of breeding macaroni penguins

Jessica Ann Phillips[a], Annette L. Fayet[a], Tim Guilford[a], Sophie Feilding[b] & Phil Trathan[b]

[a] Department of Zoology, University of Oxford, UK

[b] British Antarctic Survey, Cambridge, UK

1. Abstract 136
2. Introduction 136
3. Methods 139
4. Results 148
5. Discussion 153
6. Acknowledgements 158
7. Author contributions 159
8. Data availability statement 159
9. References 159

1. Abstract

Understanding the relationship between environmental characteristics and the preferred foraging locations of seabirds is vital for predicting their current and future distributions. However, the environmental characteristics of the foraging locations used by penguins and the quality of prey patches at these locations are not well characterised. We obtained GPS and time-depth recorder tracking data from 32 chick-rearing macaroni penguins on Bird Island, South Georgia, and data on krill abundances from a simultaneous krill acoustic survey near Bird Island. Using an algorithm based on the characteristics of penguin dives to estimate krill patch quality, we found that patch quality improved with increased distance from the colony and that the quality of foraging patches was highest at 5pm to 8pm. Penguins also fed at higher quality patches further from the colony when foraging for themselves than when foraging for their chicks. Based on these data, we developed a model that predicts krill distributions and penguin foraging locations based on environmental characteristics.

2. Introduction

Marine predators must capture sufficient prey in environments where prey distribution is often patchy and scarce (Ricklefs, 1990; Weimerskirch, 2002; Sala et al., 2012). During breeding, marine predators such as seabirds act as central place foragers, commuting between their colony and prey patches. To reduce time between meals fed to offspring and to maximize energy acquisition, they must forage efficiently by choosing prey patches based on distance, prey abundance, prey quality, and competing animals (Ashmole, 1963; Baird, 1991; Ydenberg et al., 1994; Saunders and Ydenberg, 1995; Trathan et al., 1998; Ropert-Coudert et al., 2004; Trathan et al., 2006). Most seabirds depart colonies in specific directions to reach foraging grounds with high productivity such as shelf edges, fronts, and upwellings, suggesting that seabirds can predict the location of prey patches at the mesoscale (Trathan et al., 2006; Weimerskirch, 2007). In these preferred foraging locations, ocean currents, bathymetry, and other biological and physical factors interact to create conditions favourable

to the growth and retention of the phytoplankton (Haury et al., 1978) that are preyed on by the zooplankton (Noges, 1997) that attract the fish (Ware and Thomson, 2005) that, in turn, create favourable foraging conditions for seabirds.

Seabird distributions are ultimately driven by prey availability (Fauchald et al., 2000; Fauchald and Erikstad, 2002; Ainley et al., 2009), but environmental variables associated with foraging locations have been used as proxies to predict seabird distributions. These factors include: distance to colony (Chivers et al., 2013; Karris et al., 2018), bathymetric features (Chivers et al., 2013), primary productivity (Louzao et al., 2006; Araujo et al., 2017; Perez-Roda et al., 2017), sea surface temperature (Wakefield et al., 2015; Karris et al., 2018), and oceanographic features (Ainley et al., 2009; Wakefield et al., 2012; Araujo et al., 2017). However, how these environmental variables affect habitat quality is not well understood (Ballard et al., 2019).

According to optimal foraging theory, animals should forage in a way that maximizes their fitness (Emlen, 1966; MacArthur and Pianka, 1966). For long-lived species, this requires balancing their own long-term needs with those of their offspring (Ricklefs, 1977). A challenge for central place foragers is that prey patches further from their colony are often more abundant or of better quality than those nearer to the colony because of competition or prey depletion occurring around colonies (Birt et al., 1987; Elliott et al., 2009). To maximise fitness under these conditions, some breeding seabirds adopt a 'dual foraging' strategy in which parents alternate frequent short foraging trips to ensure that chicks are fed regularly (Cuthill and Kacelnik, 1990) with less frequent longer trips to higher quality foraging grounds to replenish their own condition (Matsumoto, 2008). This strategy is usually employed when resources near the colony are not sufficient to provision both the adults and the chicks (Chaurand and Weimerskirch, 1994; Granadeiro et al., 1998; Weimerskirch, 1998; Weimerskirch and Cherel, 1998) or when there is more than one foraging patch accessible from the colony (Ropert-Coudert et al., 2004). Dual foraging has been studied most extensively in Procellariforms (e.g., Baduini and Hyrenbach, 2003). While dual foraging has not been studied as extensively in penguins, bimodal foraging trip durations have been identified in Adélie *Pygoscelis*

adeliae (Clarke et al., 1998), chinstrap *Pygoscelis antarcticus* (Jansen et al., 1998), Gentoo *Pygoscelis papua* (Carpenter-Kling et al., 2017), Humboldt *Spheniscus humboldti* (Taylor et al., 2002), little *Eudyptula minor* (Saraux et al., 2011), and macaroni penguins *Eudyptes chrysolophus* (Barlow and Croxall, 2002a). However, whether the quality of prey patches accessed during short and long foraging trips differ in penguins – as has been reported in Procellariforms (Shoji et al., 2015) – remains unknown.

This study addresses this question in macaroni penguins, the most abundant penguin species (Williams, 1995) and the greatest consumer of marine resources amongst all seabirds (with an annual consumption estimated at 9.2 million tonnes (Brooke, 2004)). Their primary foodstuff is krill (Barlow et al., 2002), though amphipods and fish can make up a significant portion of their diets, especially in years of low Antarctic krill *Euphausia superba* availability (Croxall et al., 1999; Waluda et al., 2010). South Georgia in the Scotia Sea has one of the largest breeding populations of macaroni penguins in the world (Williams, 1995) with just over a million breeding pairs (Trathan et al., 2012). There are about 46,500 breeding pairs at Bird Island on the north-western tip of South Georgia (Trathan et al., 2006; Trathan et al., 2012). Following egg-laying, both the male and female spend the first incubation shift at the nest (around 9 to 12 days) then the female incubates alone during the second shift (about 12 to 14 days); this is followed by a long fast by the male who remains at the nest for the third incubation shift (about 10 to 12 days) and throughout brood (an additional 23 to 25 days) (Williams and Croxall, 1991). When the chicks enter crèche they are fed every 1 to 2 days, at first by the female (7 to 10 days), then by both parents until they fledge 60 to 70 days after hatching (Williams, 1995).

In this study, we track 45 macaroni penguins rearing chicks on Bird Island, South Georgia with Global Positioning System (GPS) devices and time-depth recorders (TDR) to characterize the environmental conditions and the quality of the prey patches at their preferred foraging sites. More specifically, we aim to determine the following:

1. Whether the quality of prey patches penguins feed at differs during different breeding stages (brood vs. crèche), between putative chick-provisioning and putative self-

feeding bouts, and between patches close to and distant from the colony. We hypothesize that: a) penguins will feed at higher quality patches during crèche than brood because foraging macaroni penguins at Bird Island travel further during crèche than during brood (Barlow and Croxall, 2002b); b) parents will forage at higher quality patches when foraging for themselves compared to when foraging for chicks, as reported in many other seabirds (e.g., Weimerskirch, 1998; Shoji et al., 2015); and c) patch quality will be higher further from the colony than close to the colony, due to prey depletion by penguins close to the colony (Ashmole, 1963).

2. Whether prey patch quality of foraging locations used by penguins follows a daily temporal pattern. We hypothesize that patch quality of foraging locations is highest in the evening, due to the diel migration of krill to the surface at night (Zhou and Dorland, 2004) and to the fact that penguins require some light to see and catch prey.

3. Identify the environmental characteristics of preferred foraging sites of macaroni penguins. We hypothesize that these characteristics also predict the presence of krill.

3. Methods

3.1 Field Methods

All fieldwork was conducted at Bird Island, South Georgia, in the southern Atlantic Ocean between December 29th 2018 and February 11th 2019 at two sub-colonies, Fairy Point (54.011°S, 38.074°W) and Goldcrest Point (54.009°S, 38.071°W) (see Trathan (2004) for colony locations). We captured 45 breeding macaroni penguins (3 males, 42 females) at their nests during the brood and crèche periods. The sex bias was caused by the fact that males remain at the nest during brood, so we could only tag females during this period. Each bird was fitted with a GPS device and a TDR. The TDR were programmed to record depth and temperature every second, and the GPS to record location

every 4 minutes (The GPS location intervals were sometimes longer than 4 minutes when the GPS could not connect to satellites because the birds were diving (Tomkiewicz et al., 2010)). The GPS units used were Sirtrack™ Fastloc™ 33 F3G133A GPS (31.0 g in air, 63 x 24 x 22 mm with 40 mm whip antenna). The TDR units used were Lotek LAT 1810 TDR (6 g in air, 38 x 11 mm). The TDR and GPS devices were prepared as a single deployment package and attached with Tesa© tape and 2-part quick-setting glue on the back of the penguins (Warwick-Evans et al., 2018). We also measured the weight, bill depth, and bill width of each penguin. Penguin sex was determined by their bill depth (Williams and Croxall, 1991; Hart et al., 2009). Devices were retrieved after a mean (se) of 5.33 (0.52) days. Devices were recovered from 40 individuals (3 males, 37 females). The mean (se) handling time for deployment was 11.7 (0.6) minutes; handling time for retrieval did not exceed 5 minutes.

All fieldwork was approved by the University of Oxford's Local Ethical Review Process and by the British Antarctic Survey's Animal Welfare and Ethical Review process. It was performed under a Regulated Activity Permit issued by South Georgia and the South Sandwich Islands (permit number: 2018/025). All methods conformed to the Scientific Committee of Antarctic Research (SCAR) Code of Conduct for Use of Animals for Scientific Purposes in Antarctica (2011).

3.2 Analytical Methods

All analyses were performed in R 3.5.3 (R core team, 2019).

The time periods penguins were at sea were identified based on plots of their distance from the colony (GPS) and temperature (TDR) over the tracking period. We preliminarily used an upper temperature threshold of 5 degrees Celsius to identify times the bird was at sea and then validated this by visually inspecting the distance to the colony over that period. We defined foraging trips as periods at sea which lasted longer than 1h and contained at least 10 GPS points.

We identified 58,299 dives from the TDR depth data during foraging trips using the 'DiveMove' package (Luque, 2007). After visually inspecting the GPS points to remove obvious

erroneous locations, we estimated the GPS coordinates for each dive by interpolating the GPS records to the start time of each dive. To ensure the accuracy of these interpolations, we excluded dives that occurred during periods when there was more than 2 hours without GPS recordings, which resulted in excluding 17,884 of the 58,299 (30.6%) dives.

We identified the number of dive types using Calinski-Harabasz clustering (Caliński and Harabasz, 1974). The detailed classification criteria are described in the Identification of Dives section in Chapter 3 (page 101). Based on these criteria, we classified all dives into two types of diving behaviours: 14,389 'traveling dives', and 26,026 'foraging dives'. We also calculated the distance from each dive location to the penguin's colony of origin (i.e., Fairy Point or Goldcrest Point).

3.2.1 Index of Patch Quality (IPQ)

As described in Chapter 3 (page 102), we calculated IPQ using the method described by Mori and colleagues (2002). However, we estimated IPQ based on the dive parameters for each individual penguin rather than averaging them across all penguins (Shoji et al., 2014) to control for individual differences in diving capabilities. In brief, the IPQ is based on the premise that prey abundance can be inferred from the depth profiles of dives using time-allocation foraging models; it is calculated using an algorithm based on total dive duration, time taken to ascend and descend, time spent foraging at the bottom of the dive, and the duration of the recovery time on the surface prior to the subsequent dive (Mori et al., 2002). We calculated IPQ for all foraging dives, and then excluded dives with a surface pause of greater than 225 seconds (the inflection point of post-dive surface pause duration (Gentry and Kooyman, 1986; Zimmer et al., 2010)) because longer periods on the surface are unlikely to indicate the time taken to physiologically recover from the dive. We also defined "diving bouts" as a series of consecutive foraging dives that occur with less than 225 seconds of surface time between sequential dives.

3.2.2 Mixed models

We used linear mixed models (LMMs) to validate IPQ as a proxy measure of abundance by testing 1) whether dive IPQ increased with the distance travelled in the bottom phase of the dive (Mori and Boyd, 2004a); 2) whether bout IPQ (i.e., mean IPQ for all dives in the bout) increased with the number of dives in the bout (Mori et al., 2002); and 3) whether dive IPQ differed between single dives and dives which were part of a diving bout. Then, we also used linear mixed-models to test 4) whether bout IPQ differed with the distance from the colony where the bout occurred; 5) whether bout IPQ differed between brood and crèche; 6) whether bout IPQ differed between males and females (tagged during the same period); 7) whether bout IPQ differed with the hour of day; 8) whether bout IPQ differed between day and night; and 9) whether bout IPQ differed between putative self-feeding and putative chick-feeding.

For each of the mixed models we set penguin identity as a random effect to account for repeated measures because our dataset contained multiple dives per penguin, and we set the putative explanatory variables as a fixed effect. We then compared the model of interest with the null model (the same model without the explanatory variable of interest) with a likelihood ratio test (chi-square statistic) to identify statistically significant variables. We square-root transformed IPQ in all models to normalize its distribution. All estimates presented in the results section are mean ± standard error (se) unless indicated otherwise. As we only had data from three males, and all were tagged during crèche (males do not travel to sea until crèche), we compared them with the 6 females tagged during the same period (January 22nd to the 29th, 2019) when testing for sex differences in the quality of patches selected for foraging (model 6).

To test whether the quality of prey patches used for putative self-provisioning differed from those used to putatively provision chicks, we classified foraging dives that occurred more than 48 hours before returning to the colony as self-provisioning dives and those that occurred 48 hours or less before returning to the colony as potential chick-provisioning dives. The rationale for this cut-off is that 48 hours equals the product of multiplying the digestion rate of female macaroni penguins of

50g krill h^{-1} (Croxall et al., 1993) by the estimated maximum stomach capacity of female macaroni penguins of 2400g (Cresswell et al., 2007). Prey captured more than 48 hours before returning to the colony will be digested before the penguin returns and cannot be fed to the chick, whereas prey caught less than 48 hours before returning could be used to provision chicks. We compared the IPQ of self-provisioning diving bouts and potential chick-provisioning diving bouts to determine whether macaroni penguins feed at higher quality prey patches when foraging for themselves compared with when foraging for their chicks, as has been reported in other seabirds (Shoji et al., 2015). Previous studies have found that penguins provision chicks mostly with undigested prey caught later in the trip (Wilson et al., 1989; Peters, 1997; Peters, 2004; Thouzeau et al., 2004). Green and colleagues (2007) postulated that macaroni penguins digest food caught earlier in the trips while leaving prey caught towards the end of the trip undigested to feed their chicks, which supports our assumption that prey caught more than 48 hours before the return to colony is digested by adults. However, Green and colleagues (2007) also found that macaroni penguin parents only feed about 15% of the food they catch during chick rearing to chicks, so it is probable that only some of the prey caught within 48 hours of returning to the colony is fed to chicks.

3.2.3 Predictive models of distributions

3.2.3.1 Environmental variables.

We decided to investigate the impacts of seafloor depth, roughness, aspect and slope, as well as the distance to the shelf break, temperature, salinity, mixed layer depth, chlorophyll, and current speed (Table 1), as Barlow and colleagues (2002) previously found that breeding macaroni penguins from Bird Island mainly utilized shelf waters, and postulated that the core areas of activity were associated with bathymetry and oceanography which impact prey distributions. We also included the distance to colony, as this distance is limiting for central place foragers and has previously been found to predict distributions of breeding seabirds (Chivers et al., 2013; Karris et al., 2018).

Environmental data with a geographic resolution of 0.25 degrees were downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS) for the area where the penguins we

tracked travelled, 41 to 47°W and 50 to 55°S, from December 29th, 2018 to February 11th, 2019 (our tracking period). These variables were chlorophyll-a, sea surface temperature, mixed layer depth, salinity, and current speed (Table 1). Current speed data were available hourly and included northward and eastward current velocity; in this analysis we calculated current speed as the square root of the sum of the square of the north and east velocities.

Data on seafloor depth for the same area were downloaded with a resolution of 15 arc seconds; seafloor roughness, slope, and aspect were estimated from the seafloor depth data using the R package "raster" (version 2.8-4, (Hijmans, 2018)). Defining the shelf break – typically associated with high productivity – as the place where depth passes 1000m (Atkinson et al., 2008), we calculated the distance of each dive from the shelf break, assigning locations inshore of the shelf break as negative values (e.g., dives 5km inshore of the shelf break were assigned a value of -5).

Krill abundance data from the Western Core Box (Trathan et al., 2003; Fielding et al., 2014) near to Bird Island, were determined using bio-acoustic surveys undertaken with RRS Discovery on January 7th to 10th, 2019. Surveys were carried out during the macaroni penguin brood period. Detailed methods about how the krill survey was conducted are provided in Fielding et al. (2014).

Table 1. Environmental variables obtained for the area where GPS tracked macaroni penguins travelled on foraging trips.

Group	Variables	Resolution	Source
Static oceanographic features	depth	15 arc seconds (0.004 degrees)	(GEBCO, 2020)
	seafloor roughness		derived from depth
	seafloor slope		
	seafloor aspect		
Dynamic oceanographic features	current speed	Calculated from eastward and northward current velocity 0.25 degrees, hourly	(CMEMS, 2020a)
	temperature	0.25 degrees daily mean	(CMEMS, 2020b)
	salinity		
	mixed layer depth		
	chlorophyll-a		
Location	distance to colony	-	calculated with customized R code using the "raster" package (version 2.8-4, (Hijmans, 2018))
	distance to shelf break	-	

3.2.3.2 Predictive models of penguin foraging areas

To identify the environmental characteristics of penguins' preferred foraging locations within the study area, for each day during the survey we identified the time and GPS coordinates where penguins performed foraging dives and paired this with the environmental variables for the place and time where each dive occurred. To create a null distribution (Milne et al., 1989), we interpolated the penguin tracks in space, marking one point every 40 meters. We interpolated the tracks in space rather than in time in order to avoid having the penguin speed bias the random sample. To reduce 'noise' that decreases the accuracy of identified locations, we excluded points that occurred in periods of more than 2 hours without GPS data. We then randomly selected a set of points equal in size to the number of foraging dives on that trip. The environmental variables corresponding to each of these randomly identified points along penguin tracks were extracted and compared to the environmental characteristics at the locations of the observed foraging dives.

We used Generalized Additive Models (GAM) to assess the relationship between the outcome of interest (i.e., a foraging dive occurring) and the potential predictive environmental variables of interest. The GAMs were created using the 'mgcv' package in R (version 1.8-27, (Wood, 2017)). GAMs are widely used to help explain the at-sea distributions of seabirds from biologging data (e.g. Bertrand et al., 2012; Scales et al., 2014; Dehnhard et al., 2020); one reason for their popularity is that they can be used to assess non-linear and non-parametric relationships between environmental variables and the presence of different species (Hastie and Tibshirani, 1990; Wood, 2017). We identified the most important variables by setting penguin identity as a random effect and selecting the combination of variables that yielded the model with the lowest Akaike information criterion (AIC, Table 2). Distance to colony and depth are correlated, so only one of these variables could appear in any one model; similarly, seafloor roughness, aspect, and slope are all related measures of the seabed, so only one of these variables could appear in any one model. We retained seafloor depth and roughness because the model with these two variables had the lowest AIC. We used this model to predict penguin foraging locations within the minimum convex polygon of penguin tracks for each of the 45 days of tracking.

Table 2 Top five GAMs with lowest AIC for explaining macaroni penguin foraging locations, and top five GAMs for explaining krill density (grey shading indicates variables included in each model)

Variable group	Variables	Penguin models					Krill models				
		pen.1	**pen.2**	**pen.3**	**pen.4**	**pen.5**	**krill.1**	**krill.2**	**krill.3**	**krill.4**	**krill.5**
Static oceanographic features	depth[∏]	■	■	■	■	■				■	
	seafloor roughness[ൣ]	■	■	■	■	■					
	seafloor slope[ൣ]										
	seafloor aspect[ൣ∓]						■	■	■	■	
Dynamic oceanographic features	current speed	■	■			■	■		■	■	■
	temperature	■	■	■	■	■	■	■	■	■	■
	salinity	■	■	■	■		■	■	■	■	■
	mixed layer depth	■		■		■	■	■	■	■	■
	chlorophyll-a	■	■	■	■	■	■	■		■	■
Location	distance to colony[∏]						■	■	■		■
	distance to shelf break	■	■	■	■	■	■	■	■	■	■
Δ AIC[ℓ]		0.0	6.7	7.4	15.2	24.4	0.0	2.0	2.0	6.8	7.5

[∏] Distance to colony and depth are correlated and, thus, cannot be used in the same model

[ൣ] Seafloor roughness, seafloor slope, and seafloor aspect are correlated and, thus, cannot be used in the same model

[∓]Orientation of the slope of the seafloor

[ℓ]difference in AIC compared to penguin and krill models with lowest AIC respectively

3.2.3.3 Modelling krill distribution

We repeated this modelling process to predict krill abundance. Using krill abundance as the outcome variable, we identified the combination of environmental variables that produced the GAM with the lowest AIC. We then used this model to map krill abundance for the krill survey period (January 7th to 10th, 2019) across the minimum convex polygon of the krill survey area. Krill abundance was log-transformed to normalize its distribution. However, due to the low temporal and spatial overlap between penguin tracks and the area of the krill survey shown in Figure 1, we could not directly use krill abundance to predict penguin foraging across the area penguins used.

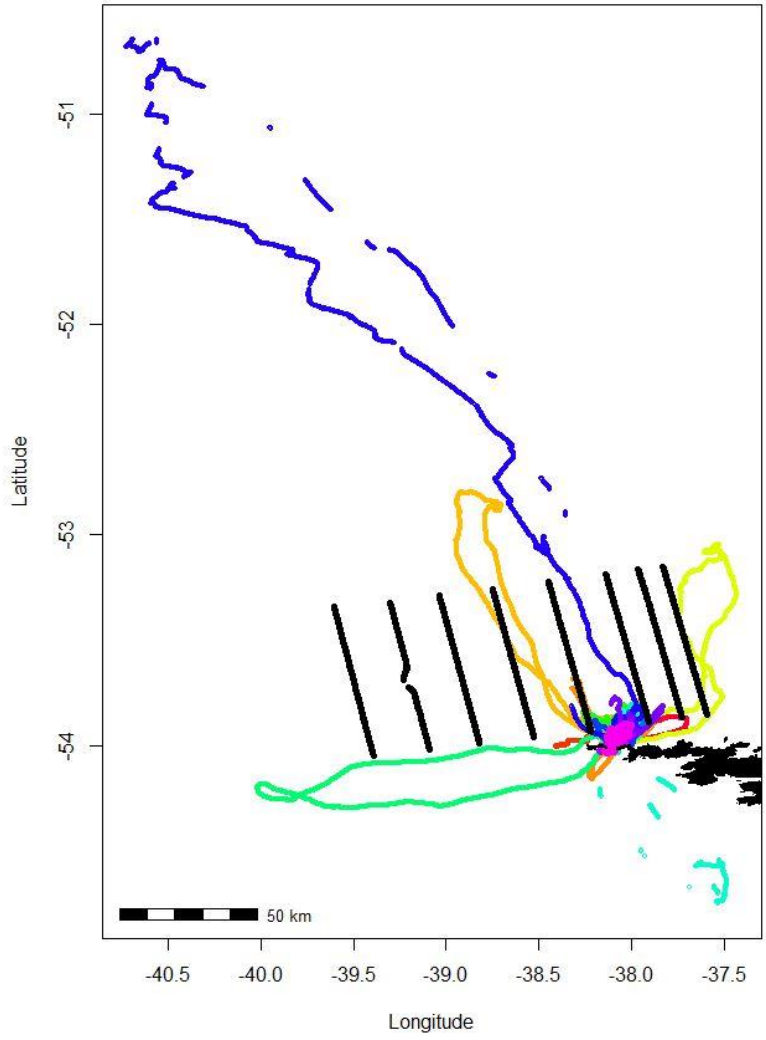


Figure 1. Foraging tracks of chick-rearing macaroni penguins breeding on Bird Island, colour-coded by penguin identity. The tracks are superimposed with transects of the krill survey (black), and a map of South Georgia (black). The projection used is WGS84.

4. Results

We recorded data on 145 foraging trips from 32 macaroni penguins, ranging from 1 hour to 15.4 days (median 9.4 hours). These trips contained a total of 40,415 dives, including 26,026 foraging dives and 14,389 traveling dives.

4.1 Validation of IPQ as a measure of patch quality

IPQ significantly increased with the vertical distance travelled in the bottom phase of the dive (slope=0.045±0.00021, LMM: $\chi^2_1 = 25898$, $p<0.0001$); bout IPQ significantly increased with the number of dives in a bout (slope=0.005±0.0003, LMM: $\chi^2_1 = 252.71$, $p<0.0001$); and foraging dives occurring in bouts had a significantly higher IPQ that those not in bouts (0.298 ± 0.003 vs. 0.131 ±0.007, LMM: $\chi^2_1 = 190.23$, $p<0.0001$). Taken together, these results validate our use of IPQ as a proxy for patch quality.

4.2 Factors associated with variation in patch quality

Bout IPQ increased significantly with the distance to colony (slope=0.001±0.0001, LMM: $\chi^2_1 = 105.09$, $p<0.0001$). In other words, IPQ increased by ~0.1 for every extra 100km from the colony. Foraging bouts during brood had a significantly higher IPQ than those during crèche (0.22±0.004 vs. 0.11±0.007, LMM: $\chi^2_1 = 8.67$, $p=0.003$), a difference which remained when controlling for distance to colony (LMM: $\chi^2_1 = 8.28$, $p=0.004$). The IPQ of the foraging bouts of the 3 males tagged during crèche was less than that the 6 females tagged during the same period (0.10 ± 0.006 vs. 0.22 ± 0.008, LMM: $\chi^2_1 = 8.55$, $p=0.003$), a difference that remained significant after controlling for the distance to colony (LMM: $\chi^2_1 = 4.60$, $p=0.032$). The hour of day was also a significant predictor of bout IPQ (LMM: $\chi^2_1 = 24.7$, $p<0.0001$), a difference that remained significant after controlling for distance to colony (LMM: $\chi^2_1 = 17.1$, $p<0.0001$). As shown in Figure 2, bout IPQ was highest during 5pm to 8pm. Foraging bouts during daylight had a significantly higher IPQ than foraging bouts performed at night (0.206 ± 0.004 vs. 0.186 ±0.012, LMM: $\chi^2_1 = 9.01$, $p=0.0027$).

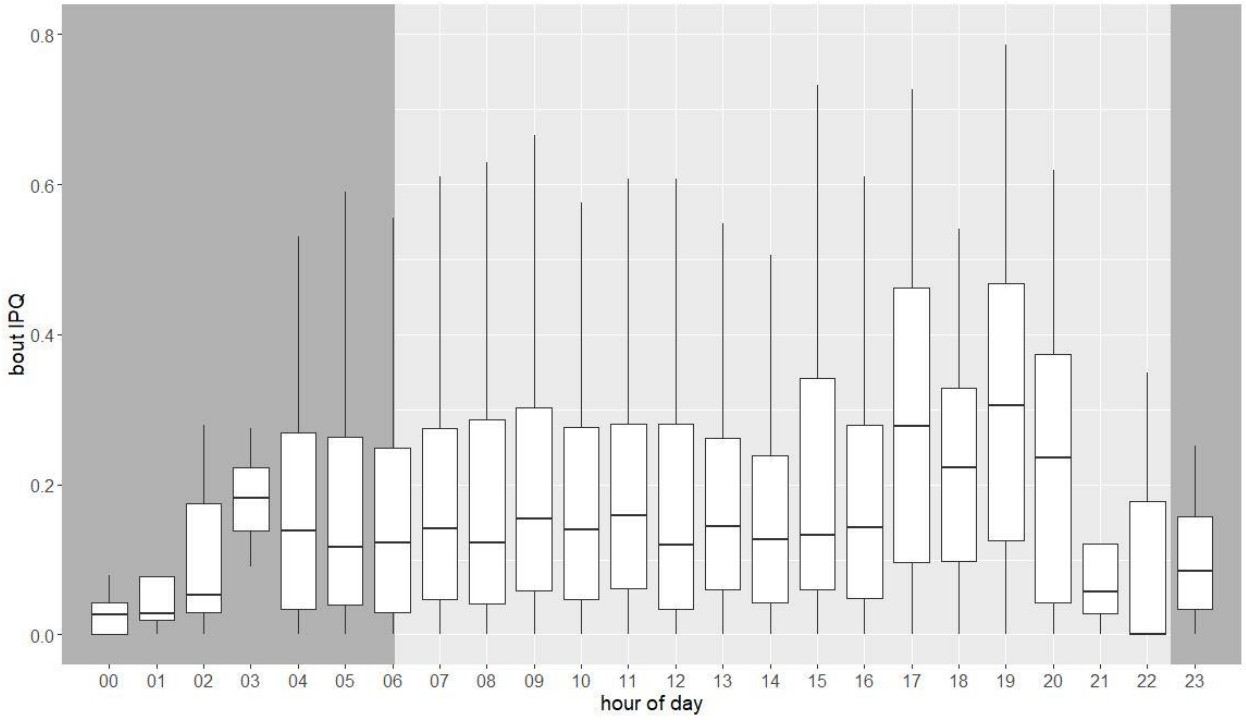


Figure 2. IPQ of foraging bouts by hour of day (local time). The area shaded dark grey indicates the period between the average sunset time (22:30) and average sunrise time (6:04) during our tracking period

While we found no evidence of a bimodal pattern in trip lengths, we did find that penguins foraged in higher quality patches when foraging for themselves (i.e., on foraging bouts more than 48 hours before return to the colony) compared to foraging that could be fed to chicks (foraging bouts within 48 hours before return to the colony) (0.296 ± 0.018 vs. 0.195 ±0.004, LMM: $\chi^2_1 = 9.43$, p=0.002). However, this difference did not remain statistically significant after controlling for distance to colony (LMM: $\chi^2_1 = 0.67$), suggesting that parents were able to forage at higher quality patches when provisioning their own condition because when self-provisioning they were further from the colony where prey patches had higher quality.

4.3 Factors associated with foraging preferences

The GAM that best predicted the location of foraging dives with the lowest AIC retained depth, seafloor roughness, current speed, temperature, salinity, the depth of the mixed layer,

chlorophyll-a, and the distance to the shelf break (Figure 3). We used this model to predict the suitability of habitats for foraging during brood and crèche within the minimum convex polygon covered by our GPS tracks (Figure 4). The predicted foraging locations for brood and crèche were very similar, with favourable foraging conditions to the northwest beyond the shelf break.

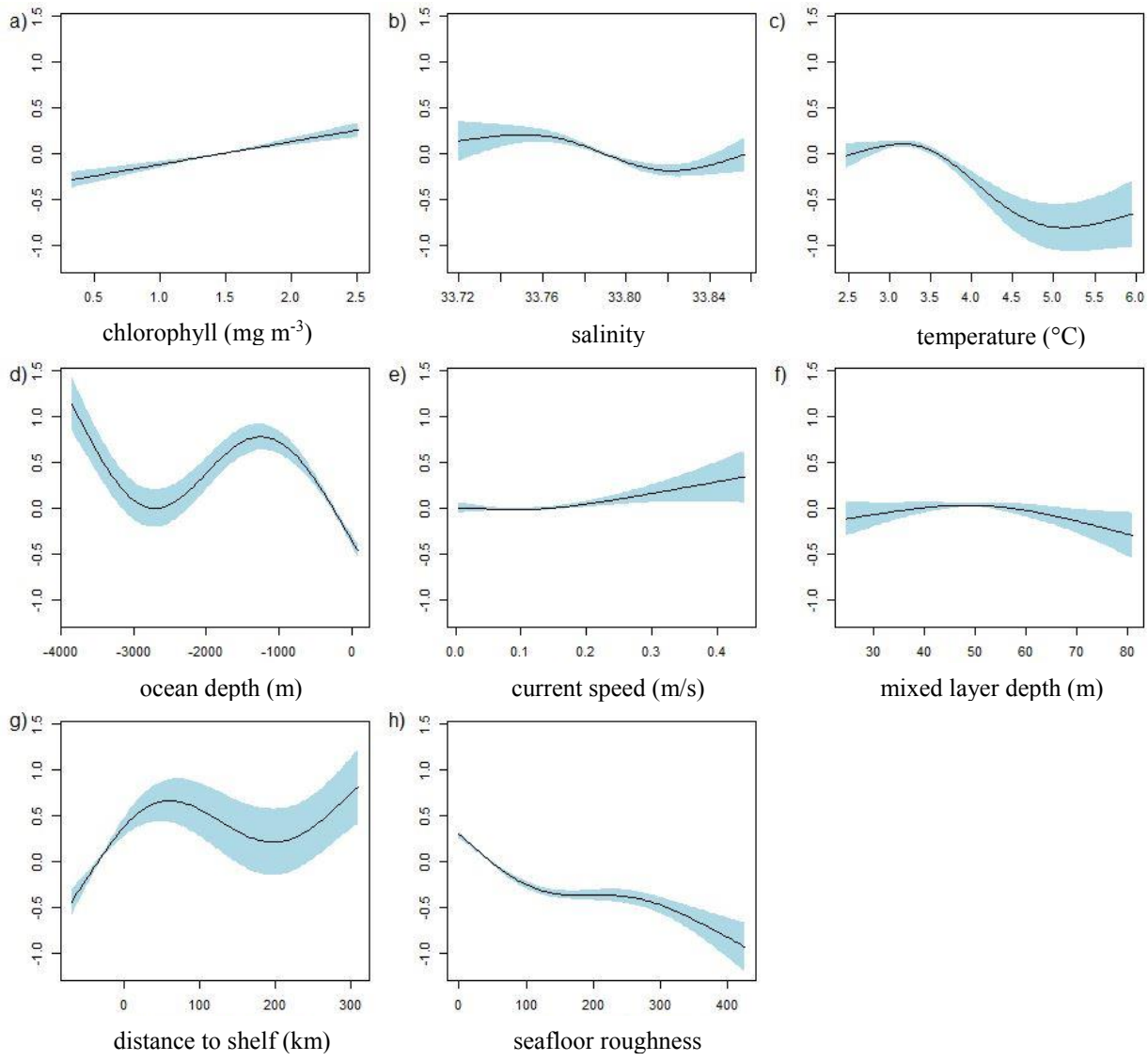
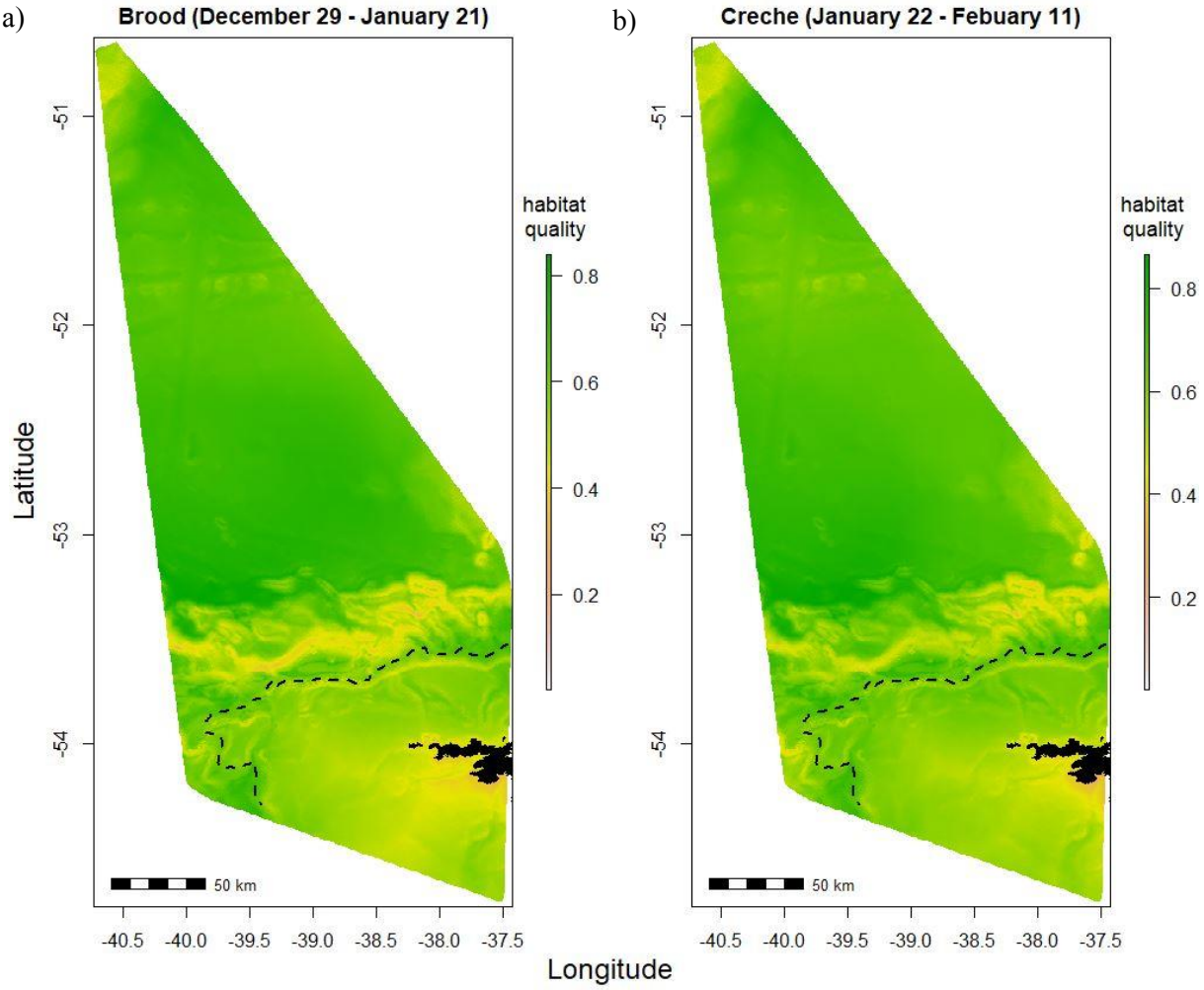


Figure 3. Partial effect plots of variables retained in the GAM which best predicts penguin foraging (with 95% confidence intervals). For a) chlorophyll-a; b) salinity; c) temperature; d) ocean depth; e) current speed; f) depth of the mixed layer; g) distance to shelf (negative values on the x-axis indicate distance from the shelf from the inside); and h) seafloor roughness.

Figure 4. GAM predictions of preferable foraging locations for breeding macaroni penguins during a) brood (December 29th 2018 to January 21st 2019), and b) crèche (January 22nd to February 11th 2019). Where the dotted black lines indicate the shelf break (1,000m contour line).



The best GAM for krill abundance retained salinity, temperature, distance to colony, current speed, seafloor aspect, mixed layer depth, chlorophyll, and distance to shelf as predictors (Figure 5). We used this model to map krill abundance across the minimum convex polygon of the krill survey transects (Figure 6). The map shows a band of high krill abundance just outside of the shelf break.

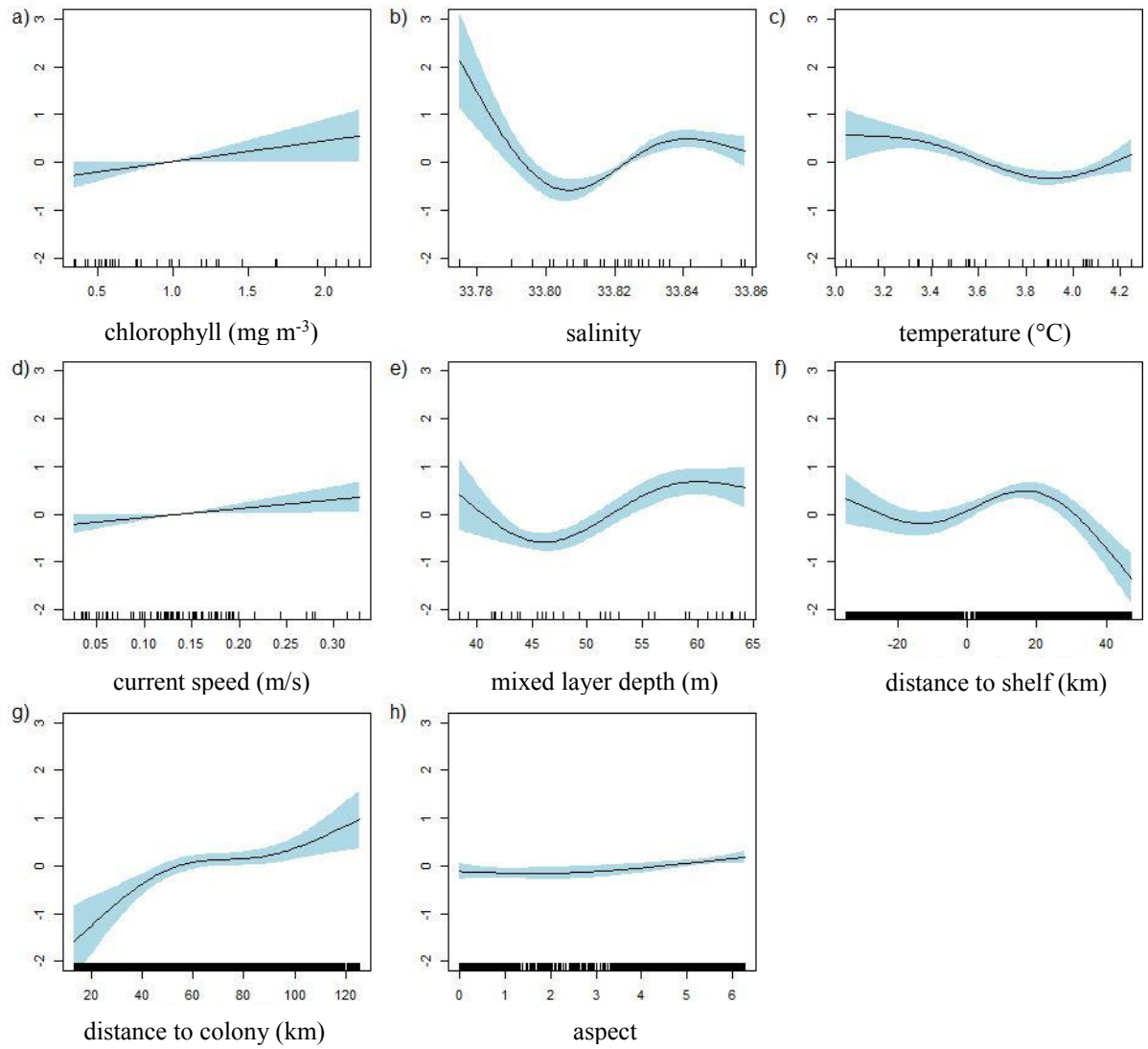


Figure 5. Partial effect plots of variables retained in the GAM which predicts krill abundance (with 95% confidence intervals). For a) chlorophyll-a; b) salinity; c) temperature; d) current speed; e) mixed layer depth; f) distance to shelf (negative values on the x-axis indicate distance from the shelf from the inside); g) distance to colony; and h) seafloor aspect.

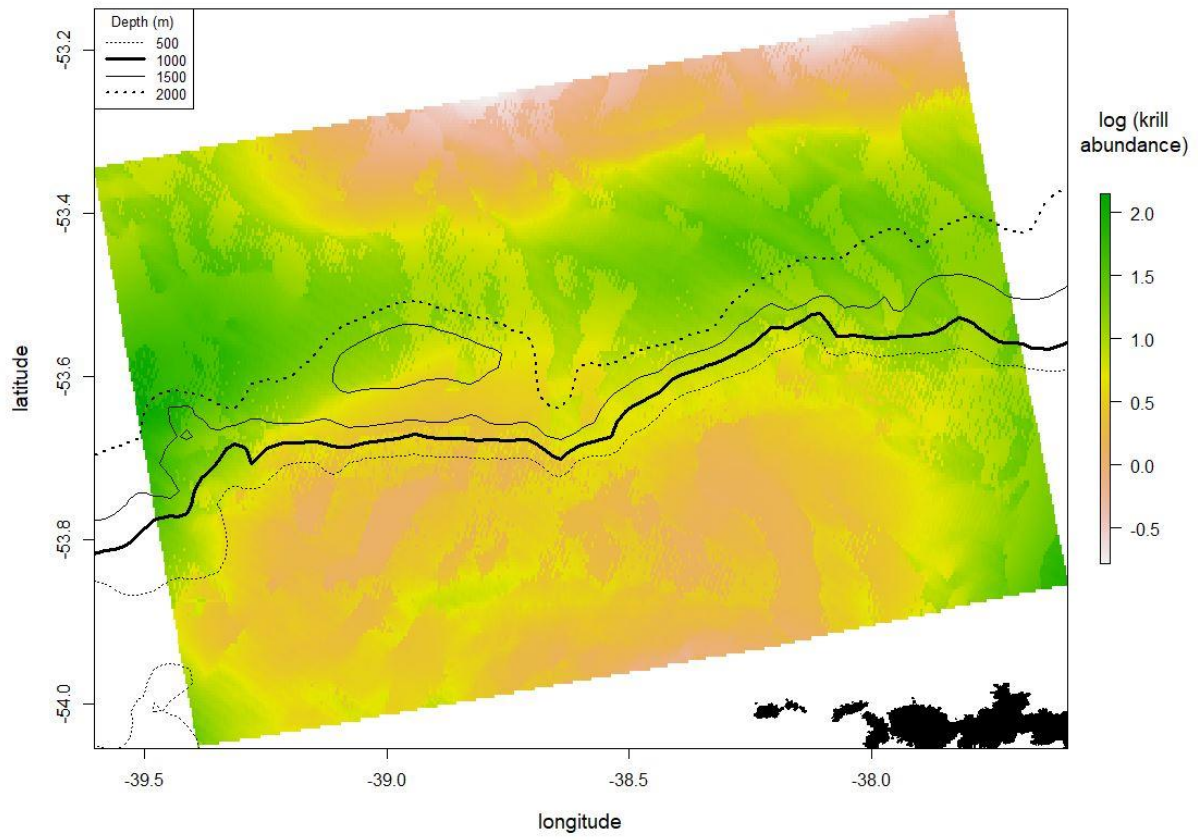


Figure 6. Predicted distribution of krill in the minimum convex polygon of survey transects for the period of January 7th to 10th, 2019.

5. Discussion

We found that the quality of prey patches visited by penguins varied with distance from the colony, time of day, sex , breeding stage, and whether the birds were provisioning themselves or potentially collecting food for their chick. The quality of prey patches visited by penguins followed specific daily patterns and was highest between 5 and 8pm followed by a steep drop at 9 to10 pm. This may be associated with penguins returning to the colony before dark. Many seabirds have foraging activity peaks at dawn and dusk (Gaston and Jones, 1998; Fayet et al., 2015). Common murres *Uria aalge* increase their dive frequency during twilight when their capelin prey migrate up the water column (Regular et al., 2010), and to that for chinstrap penguins at Seal Island with peak dive frequency between 10am to 3pm and 10pm to 2am (Bengtson et al., 1993). However, a study on

razorbills by Shoji and colleagues (2014) found a daily peak in IPQ at midday; a finding that the authors attribute to birds identifying the good patches in the morning, maximizing foraging at midday, and then commuting back to the colony later in the day.

Contrary to our hypothesis, we found that females foraged at higher quality patches than males. Green and colleagues (2007) found that during chick-rearing, for every minute submerged during foraging male macaroni penguins obtained about 2.8g of prey, whereas females only obtained about 2.3g. However, this greater intake of prey by males could be due to their tendency to dive deeper and longer than females (Green et al., 2005) and to their greater body mass, rather than because males accessed better quality patches than females. In our study the sampling of males was limited to individuals at the start of crèche after 44 to 48 days of fasting (Williams and Croxall, 1991), whereas the females they were compared with had been foraging for weeks, so it is possible that the difference in patch quality accessed by males and females was due to the females' more up-to-date knowledge about prey patch locations or better body condition due to the males having fasted for a longer time. Constraints on information of prey locations are known to limit predators' ability to target prey (Fauchald, 2009). However, given the dynamic nature of prey fields, predators should value new information on prey distributions over previous experience (McNamara and Houston, 1985; McNamara and Houston, 1987), so we would expect that patch quality exploited by males would improve with time as they accumulate new foraging experience after ending their long fast. Importantly, the comparison of foraging patch quality by sex was limited to data from 3 males and 6 females, so these results should be interpreted with caution. Future studies with larger samples are needed to validate our finding of lower patch quality utilized by males in comparison with females at the start of crèche; and to determine whether patch quality utilized by males improves over time after the start of crèche as they accumulate current at-sea experience. This sex bias may also affect our predictions for penguin foraging areas during crèche, as females provision chicks at higher rates (Barlow and Croxall, 2002a), and travel on longer and more direct tirps (Barlow and Croxall, 2002b).

We found patch quality improved with increasing distance from the colony. This is likely a result of prey depletion by macaroni penguins as well as other central-place foraging krill-predators on Bird Island. In particular, Antarctic fur seals *Arctocephalus gazelle* and macaroni penguins breed sympatrically in South Georgia, where they are the top mammalian and avian predators of Antarctic krill *Euphausia superba* (Barlow et al., 2002). They also breed synchronously, with penguins breeding November to February and seals breeding November to April (Waluda et al., 2010). During this time, both species act as central place foragers and are constrained to feed near the colony. At Bird Island, there is substantial overlap in the foraging areas used by the two species (Barlow et al., 2002). Though there is significant separation in the core feeding areas, they likely feed on the same krill populations (Barlow et al., 2002). The two species also dive to similar depths (Croxall et al., 1988; Boyd and Croxall, 1992; Croxall et al., 1993) and feed on similar-sized krill (Barlow et al., 2002). While the population of macaroni penguins in South Georgia has declined drastically since the 1970s from ~5.4 million to ~1 million breeding pairs (Trathan et al., 2012), the population of Antarctic fur seals has steadily recovered from near extinction in the 1950s to ~4 million breeding individuals (Waluda et al., 2010; Trathan et al., 2012; BAS unpublished data). Some authors (Barlow et al., 2002; Trathan et al., 2012) speculate this decline in the penguin population may be associated with competition with fur seals for Antarctic krill. Waluda and colleagues (2010) found that in years of low Antarctic krill availability, breeding macaroni penguins at Bird Island adapted by foraging further at sea, diving deeper, and switching prey, while fur seals did not change their foraging behaviour. Together, these studies indicate fur seals likely contribute to the depletion of macaroni penguin prey near Bird Island. Besides fur seals, macaroni penguins also breed sympatrically with numerous other kill-predators on Bird Island, including Gentoo penguins, light-mantled sooty albatross *Phoebetria palpebrata,* black-browed albatross *Thalassarche melanophris,* grey-headed albatrosses *T. chrysostoma* and white-chinned petrels *Procellaria aequinoctialis* (Mori and Boyd, 2004b; Phillips et al., 2005), which may also contribute to the near-colony prey depletion to varying degrees.

We also found that self-provisioning diving bouts occurred at higher quality patches than those likely aimed at collecting food for the chick, though this difference disappeared when we controlled for distance to the colony, suggesting distance was the driver of this difference. This indicates that parents travel to higher-quality patches further from the colony to maintain their own condition, presumably because resources near the colony are not sufficient to provide for both the chick and themselves. Similar results have been reported for other seabirds (Chaurand and Weimerskirch, 1994; Granadeiro et al., 1998; Weimerskirch, 1998; Weimerskirch and Cherel, 1998). Lower quality of local prey patches could be due to intraspecific competition, or less favourable environmental conditions for the plankton which attract the krill. Parents may be limited to foraging for chicks relatively close to the colony if food obtained further away would be digested by the time they retun.

The previously reported 'dual foraging strategy' involves alternate short trips to ensure chicks are fed regularly (Cuthill and Kacelnik, 1990) with long trips for self-provisioning (Matsumoto, 2008). However, birds in our study did *not* display a bimodal pattern of trip lengths, indicating that they may not perform separate short and long foraging trips to feed their chick or themselves. But even in birds that use the dual foraging strategy, the division of satisfying chick needs versus satisfying their own needs is not always binarily divided between short and long trips. Shoji and colleagues (2015) found that Manx shearwaters returning from long self-provisioning trips fed the chicks on their return. As penguins travel more slowly than flying seabirds (Alerstam et al., 2007; Watanabe et al., 2011), it is possible that foraging at lower quality patches on the way to or from the better quality patches at greater distances from the colony optimizes energy acquisition per unit time for long trips while allowing trips to meet the dual goals of self-provisioning and feeding chicks (Trathan et al., 2006). Our findings are different from those of Barlow and colleagues (2002a) who found bimodal distributions of trip duration (supporting the dual foraging strategy hypothesis) for both male and female macaroni penguins at Bird Island during chick-rearing in 1997 to 2000. Thus, the distance from the colony and the quality of prey patches is probably dynamic over time, both within and between years (Trathan et al., 2006). These contradictory results may reflect a higher

availability of prey around Bird Island in the 2018 to 2019 chick-rearing season compared with that of 1997 to 2000. Australasian gannets *Morus serrator* have also been found to utilize bimodal trip durations in certain years and unimodal trip durations in other years from the same colony, which suggests that the different trip patterns could be associated with changes in prey availability near the colony (Besel et al., 2018). Future research that includes weighing the food fed to chicks, and adult mass change after both short and long trips would help establish the function(s) of trips of different lengths.

Due to limited spatial and temporal overlap in the krill survey and penguin foraging distributions, we could not directly test whether krill abundance was a good predictor of penguin foraging. However, we were able to show that amongst locations penguins visited, the probability of foraging were highest at ocean depths of 1000m and 4000m, indicating a preference for foraging at the shelf break as well as deep waters beyond the shelf break (Figure 3d). The likelihood of foraging was lowest inside the shelf, and highest about 80km and 300km outside of the shelf break (Figure 3g). The density of krill was also highest within 20km of the shelf break (Figure 5i). Together, these findings indicate that krill congregated near the shelf break, a location that provided good foraging opportunities for penguins. This also echoes previous findings that macaroni penguins at Kerguelen island in the southern Indian Ocean targeted foraging grounds beyond the shelf break (Thiebot et al., 2011). The probability of foraging also declined with increasing seafloor roughness (Figure 3h), and increasing temperatures (Figure 3c). Krill abundance was highest at low salinity levels (Figure 3b).

Whereas Hunt and colleagues (1992) previously found that the density of Antarctica krill around Bird Island declined from 18km to 120km from the colony, our model shows an increase in abundance across these distances (Figure 5e). These contradictory findings could reflect dynamic changes in the distribution of Antarctic krill between years (Trathan et al., 2003; Fielding et al., 2014).

We found penguins foraged at higher quality patches during brood than crèche, even when controlling for distance to colony. This implies that patches at the same distance to the colony were of poorer quality during crèche than brood, which could be due to depletion of prey by the penguins

themselves (Ashmole, 1963) or temporal changes in prey availability (Deagle et al., 2008). As the predicted foraging locations were similar between brood and crèche, prey were likely congregating in similar areas in brood and crèche, but the availability or quality of prey in these areas were lower in crèche compared with brood.

One limitation of our study is that by comparing locations where penguins performed foraging dives with a random distribution of locations penguins visited, our habitat model described the probability that penguins will forage in locations they had actually travelled through during their at-sea trips. Thus when using this model to predict the probability of penguins foraging in locations they did not visit on trips, it will only account for the suitability of the habitat for foraging, but not whether the penguin can access it. We attempted to mitigate this limitation by restricting the geographic range of our predictive map. However, further analyses are needed to address how foraging patch accessibility and quality interact to affect penguin foraging decisions.

5.1 Conclusion

We found a positive correlation between the quality of prey patches and distance from the colony, quality improved as the distance increased. Penguins foraged at poorer quality patches in crèche compared to brood, either due to prey depletion by the penguins themselves or temporal changes in prey availability. At the start of crèche, males foraged on poorer quality patches than females. Penguins travelled to higher quality prey patches further from the colony to replenish their own condition and foraged at poorer quality patches closer to the colony to obtain food for chicks.

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7. Author contributions

Jessica A. Phillips: Penguin biologging fieldwork (lead), Formal analysis (lead), Writing-original draft (lead), Writing review & editing (equal); **Annette L. Fayet**: Methodology (lead), Formal analysis (supporting), Writing-original draft (supporting), Writing-review & editing (equal); **Tim Guilford**: Methodology (supporting), Formal analysis (supporting), Writing-original draft (supporting), Writing-review & editing (equal); **Sophie Feilding**: Krill abundance data (lead)**; Phil Trathan**: Project design (lead), Ecological context (lead), Formal analysis (supporting), Writing-review & editing (equal).

8. Data availability statement

The code used in this analysis will be available on github upon publication (https://github.com/JAP2018/macaroni-penguin-analysis).

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Chapter 5

Systematic review of dual foraging across seabirds: probability of dual foraging varies with habitat quality and taxa

Jessica Ann Phillips, Annette L. Fayet, Tim Guilford

1. Abstract 166
2. Introduction 166
3. Methods 170
4. Results 184
5. Discussion 194
6. Acknowledgements 203
7. Author contributions 203
8. Data availability statement 203
9. References 203

1. Abstract

To investigate whether habitat quality around seabirds' breeding colonies drives the use of the dual foraging strategy when feeding offspring, we conducted a systematic review of the seabird dual-foraging literature, compiling the results of 103 studies on 50 seabird species across 9 families from all 6 orders. We estimated the mean distance from colony of short and long foraging trips of each species and obtained remote-sensed data on chlorophyll concentrations present during each month of data collection at each colony within the radius of both short and long trips. We used generalized linear models to assess the relationship between the use of dual foraging strategies across seabird families and the magnitude of the difference in the quality of foraging locations available during short-distance and long-distance foraging trips. We found the probability of dual foraging increased with increasing differences in the quality of foraging locations available during short-distance and long-distance foraging trips. We also found that when controlling for differences in habitat quality, albatrosses and penguins were significantly less likely to dual forage than Procellariidae, while Sulids were significantly more likely to dual forage than Procellariidae. This study enhances our understanding of core questions regarding how environmental conditions and taxa interact in driving seabird foraging decisions.

2. Introduction

Long-lived species must balance investment in current offspring with investment in future offspring to maximize their lifetime reproductive potential (Ricklefs, 1977). As life-history theory predicts that investment in current offspring will come at a cost to parental survival and future reproductive success (Williams, 1966; Charnov and Krebs, 1974; Charlesworth, 1980), this creates a conflict of interest between parents and offspring. For central place foraging animals, this conflict is expected to be especially pronounced in animals that feed at distant and inaccessible prey patches (Abrams, 1991; McNamara and Houston, 1997), as the range and duration of foraging trips tend to decrease with the onset of chick rearing, potentially putting the most productive foraging locations

beyond reach (Weimerskirch et al., 1993). Understanding the drivers of foraging decisions in adults provisioning offspring, including the role of habitat quality, can provide valuable insights into how long-lived parents balance their own needs with the needs of their current offspring.

One tactic some long-lived animals (Skinner et al., 2012; Hernandez-Pliego et al., 2015; Hoskins et al., 2017) use to solve this problem is called dual foraging. First defined in 1993 by Weimerskirch and colleagues (1993), the dual foraging strategy involves parents alternating short foraging trips to provision their offspring with long foraging trips to primarily provision themselves. Short trips allow offspring to be fed regularly but are energetically costly for parents (Cuthill and Kacelnik, 1990; Weimerskirch, 1998; Weimerskirch and Cherel, 1998), whereas long trips allow adults to mainly forage for themselves to maintain their own body condition and only secondarily forage for their offspring (Weimerskirch et al., 1994; Granadeiro et al., 1998). One reason why long trips are not suitable for offspring provisioning is that the food will be digested by the time the parent returns. Alternatively, for birds that carry prey in their beaks they would have to transport the prey a long way which may be impractical or costly and may also prevent the adult from feeding for long periods. Dual foraging is especially prevalent in seabirds, which are the focus of this analysis. But it has been noted in other taxa including seals (Skinner et al., 2012) and kestrels (Hernandez-Pliego et al., 2015; Hoskins et al., 2017).

Both time and distance are important to the dual foraging concept; the energetic cost of travel is largely determined by the distance to foraging sites, while chick survival is partly determined by the time between feeding events. In the dual foraging literature, short and long trips have been defined either in terms of distance from the colony (e.g., Weimerskirch et al., 1993) or duration away from the nest (e.g., Weimerskirch et al., 1994).

Theory predicts that chick-rearing seabirds will employ a mixture of short- and long-distance foraging trips when the resources near the colony are insufficient to provision both themselves and their offspring (Chaurand and Weimerskirch, 1994; Granadeiro et al., 1998; Weimerskirch, 1998; Weimerskirch and Cherel, 1998). In support of this theory, a few studies reporting that the use of dual

foraging differs between years in the same population of seabirds (Irvine et al., 2000; Besel et al., 2018) posit that the use of different foraging strategies may be due to changes in prey availability over time. Additionally, Baduini and Hyrenbach (2003) published a review of the dual foraging literature in Procellariiformes which found that the long-distance foraging patches targeted by species that used dual foraging had higher concentrations of chlorophyll than short-distance foraging patches, suggesting that the long-distance patches had greater prey availability.

Major advances in biologging technology since these foundational studies on dual foraging have enabled the emergence of a new generation of studies that track the foraging movements of chick-rearing seabirds with GPS loggers. While previous studies mainly estimated trip duration by measuring how long birds were away from their nest, these tracking studies provide data on the exact locations and distances foraging seabirds travel from their colonies. By combining GPS locations with remote-sensed environmental variables, we can estimate the primary productivity of habitat birds can access at different distances from the colony. An updated review about the use of dual foraging strategies that integrates the results of these newer studies is warranted.

Another critical issue that has not previously been systematically assessed that could be addressed in an updated review is the potential role differences in habitat quality available during short and long foraging trips have in promoting (or discouraging) use of a dual foraging strategy by different seabird taxa. The importance of differences in habitat quality near to and far from the colony in affecting seabirds' use of the dual foraging strategy when feeding chicks may be moderated by several species-specific differences, including differences in flight costs, in whether fresh or pre-digested prey are brought back to the chick, and in the risk of chick starvation or predation. Cross-taxa approaches are needed to clarify similarities and differences in the drivers of the use of the dual foraging strategy between different seabird families.

Some studies (e.g. Ydenberg and Davies, 2010) consider dual foraging or related issues from a theoretical perspective. Ropert-Coudert and colleagues (2004) developed a model based on chick-rearing Adélie penguin *Pygoscelis adeliae* tracking data that hypothesizes that adults adjust the time

they spend foraging and the distance from the colony they forage based both on their own stomach capacity and digestion rates and on that of their chicks. Based on this model, there are occasions when alternatively using short and long foraging trips can maximize the net gain for adults and chicks. Olsson and colleagues (2014) developed a general habitat selection model based on Central Place Foraging Theory; in this model a central place forager's decision to forage in a prey patch depends on whether foraging there would positively contribute to the animal's fitness – which is a function of its patch quality and distance from the colony. Their model predicts that the maximum distance an animal is willing to travel to forage is a function of prey availability, so when prey availability near the colony is poor, animals should be willing to travel further from the colony to forage than when prey availability near the colony is good. Their model also predicts that the trade-offs different species make between patch-quality and distance from colony depend on their travel costs – species with low travel costs can profitably access patches at greater distances from the colony than species with high travel costs. However, the roles of travel cost and near-colony habitat quality in driving dual foraging are not well understood.

This analysis identifies all studies published on dual foraging in seabirds to date, extracts data on the distance from colony each seabird travels on short and long trips, and integrates these data with large-scale data on the density of chlorophyll at different distances from the colonies at the time the seabird data were collected. Using the chlorophyll data as a proxy for habitat quality, we assess the association of habitat quality with the use of the dual foraging strategy during chick-rearing in different species of seabirds. Based on predictions from Central Place Foraging Theory that animals will only travel further to forage if the farther patches offer better foraging opportunities than closer patches (Houston and McNamara, 1985; Cuthill and Kacelnik, 1990; Waite and Ydenberg, 1996), we expect that the probability of dual foraging will increase as the difference in the quality of foraging patches seabirds can access during short and long trips increases.

This systematic review combines the results of 103 studies on 50 seabird species across 9 families to investigate whether habitat quality around breeding colonies drives the use of the dual

foraging strategy. More specifically, we test whether the difference in habitat quality between locations close to the colony and locations further from the colony (but still within feasible foraging distances) predicts use of the dual foraging strategy and explore how this relationship differs between seabird families. We use data from numerous tracking studies across different colonies of Cory's shearwaters *Calonectris borealis* and little auks *Alle alle* to conduct two detailed case studies that analyse the distribution of chlorophyll near specific colonies in the months when dual foraging did and did not occur.

3. Methods

3.1 Literature Search

To identify all studies that consider dual foraging in seabirds, we used the Google Scholar search engine – which searches the full text of all available articles – using the search terms 'dual foraging' (exact phrase) and 'seabird' on July 20th, 2020. After excluding patents and citations, this search yielded 348 unique results.

Many studies report unimodal or bimodal foraging trips of seabirds based on the duration or distance of the foraging trips but do not specifically mention 'dual foraging'; in order to identify such studies, on August 14th, 2020 we conducted a second search using the advanced search function in Google Scholar for articles that included the terms 'seabird', ' foraging trip' (exact phrase) and 'bimodal' or 'unimodal' while excluding papers that included the term 'dual foraging' (exact phrase) (which were identified in the first search). This second searches yielded an additional 388 unique results.

3.2 Inclusion and exclusion criteria

Identified papers satisfying any of the following five criteria were included in the analysis.

1. The author(s) conclude that 'dual foraging' does or does not occur during chick-rearing.

2. The author(s) conclude that the duration of foraging trips during chick-rearing was either 'bimodal' or 'unimodal'.
3. The author(s) conclude that the maximum distance from the colony of foraging trips during chick-rearing was 'bimodal' or 'unimodal'.
4. Short and long foraging trips during chick-rearing are analysed separately based on previous studies which found that the same species conducts short and long trips.
5. The author(s) present histograms of the duration or maximum trip distance of foraging trips during chick-rearing that visually demonstrate a clear unimodal or bimodal pattern (even if the authors do not discuss this).

Based on these criteria we identified 103 papers that reported data collected between August 1987 and August 2018 that could be used to determine whether or not 50 species of seabirds from 9 families used the dual foraging strategy during chick-rearing. We only included studies where maximum distance to colony or duration of foraging trips was clearly unimodal or bimodal.

If the authors' assessment about the presence or absence of dual foraging and the raw data provided in the paper's tables or histograms about the bimodality of foraging trip distance or duration contradicted each other, we excluded the paper. For the purpose of this analysis, we only included data from studies that provided clear evidence about the presence or absence of dual foraging or about the bimodal duration or distance of foraging trips. In cases where the data on the duality of the maximum distance of foraging trips from the colony and the duality of the maximum duration of foraging trips came to a different conclusion about the use of dual foraging, the final decision about the presence or absence of dual foraging was based on the results about the maximum distance of foraging trips. Papers were excluded if the presented data on duration and distance from the colony of foraging trips were not clearly stratified by breeding stage.

3.3 Data extracted

We extracted the following information from each paper (and for each separately reported colony in each paper) that met the above inclusion and exclusion criteria: species studied, colony

location (latitude and longitude), months and years of data collection (limited to the chick-rearing phase if data were collected in multiple breeding stages), data collection method(s) (e.g., GPS, isotope analysis, nest entrance monitoring, etc.) sample size (number of individuals studied), and whether or not dual foraging occurred (see Table 1).

When a study included data from multiple colonies that were analysed separately, we only included data from colonies that met the inclusion and exclusion criteria. For studies that included data from multiple seasons in which dual foraging occurred in some seasons but not in other seasons, we recorded data for the seasons in which dual foraging occurred separately from data for the seasons in which it did not occur. If multiple papers used the same datasets, we only included one of the papers; when deciding which paper to include, we initially prioritized peer-reviewed papers over theses and then prioritized papers that included more detailed data over papers that included less detailed data.

Table 1. Data extracted from studies included in the systematic review

Species	Colony location	Data collection years*	Study method	Dual foraging?	Citation
Adélie penguin	Bechervaise Island, East Antarctica	1991-1992, 1995-1996	weigh bridge	Y	(Clarke et al., 1998)
		1991-2003	PTT	Y	(Clarke et al., 2006)
		1993-1994	nest attendance	N	(Irvine et al., 2000)
		1998-1999	nest attendance	Y	(Irvine et al., 2000)
	Edmonson Point, Ross Sea	1994-1996	weigh bridge	N	(Clarke et al., 1998)
	Ross Island, Antarctica	1997-2007	weigh bridge	N	(Ballard et al., 2010)
African penguin	Robben Island, South Africa	2011-2013	GPS	N	(Campbell, 2016)
Antarctic prion	Île Verte, Kerguelen islands, Southern Indian Ocean	1995-1996	nest attendance, chick weighing	Y	(Weimerskirch et al., 1999)
Australasian gannet	Hawke's Bay, New Zealand	2007-2009	GPS, blood	Y	(Besel et al., 2018)
Barau's petrel	Reunion Island, Indian Ocean	2008-2009	GLS	Y	(Pinet et al., 2012)
Black petrel	Mount Hobson, New Zealand	2006	GPS	Y	(Freeman et al., 2010)
Black-browed albatross	Bird Island, South Georgia	1990,1992-1994, 2002	radio transmitter, PTT	N	(Phillips et al., 2009)
	Kerguelen island, Southern Indian Ocean	1992	nest attendance, adult weighing	N	(Weimerskirch et al., 1994)
Black-legged kittiwake	Sor-Gjaeslingan, central Norwegian sea	2011-2014	GPS	Y	(Christensen-Dalsgaard et al., 2018)
	Anda, northern Norwegian Sea	2011-2014	GPS	Y	(Christensen-Dalsgaard et al., 2018)
	St. George, south-eastern Bering sea	2009	GPS, activity loggers, blood, diet	Y	(Paredes et al., 2012)
	The Pribilof Islands, Bering sea	2009	GPS, activity loggers, blood, diet	Y	(Paredes et al., 2012)
Blue petrel	Mayes Island, Kerguelen Islands, Southern Indian Ocean	1990	nest attendance	Y	(Chaurand and Weimerskirch, 1994)
		1990-2000	Chick and adult weighing	Y	(Weimerskirch et al., 2003)
		1998	nest attendance	Y	(Cherel et al., 2002)
	Kerguelen islands, Southern Indian Ocean	1989	nest attendance, adult weighing	Y	(Weimerskirch et al., 1994)

Table 1. Data extracted from studies included in the systematic review (continued)

Species	Colony location	Data collection years*	Study method	Dual foraging?	Citation
Blue-footed boobie	Isla Lobos de Tierra, northern Peru	2002-2003	Depth logger, flight sensor, diet	Y	(Zavalaga et al., 2007)
Brown Pelican	Gaillard Island, Alabama, USA	2012	GPS	N	(Walter et al., 2014)
	Raccoon island, Louisiana, USA	2012	GPS	N	(Walter et al., 2014)
	Shallow Bayou island, Louisiana, USA	2012	GPS	N	(Walter et al., 2014)
	Queen Bess Island, Louisiana, USA	2012	GPS	N	(Walter et al., 2014)
Cape gannet	Bird Island, Algoa Bay, South Africa	1994-1995	activity meter, stomach contents	Y	(Adams and Klages, 1999)
Cape verde shearwater	Raso Islet, Cape Verde	2013 - 2014	GPS	Y	(Paiva et al., 2015)
Chinstrap penguin	Nyroysa, west coast of Bouvetoya	2007-2008	PTT, TDR	Y	(Blanchet et al., 2013)
Common guillemot	Isle of May, south-east Scotland	1999, 2001-2003, 2005	activity logger or TDR	N	(Thaxter et al., 2010)
Cory's Shearwater	Corvo Island, Azores archipelago, North Atlantic	2004-2006	radio transmitter, PPT, blood	Y	(Magalhaes et al., 2008)
		2007	GPS	Y	(Paiva et al., 2010a)
		2007	compass-temperature, TDR	Y	(Paiva et al., 2010b)
		2010	GPS	N	(Ceia et al., 2015)
		2010	GPS, isotope	N	(Ceia, 2013)
	Cima Islet, Porto Santo Island, North Atlantic	2011 - 2012	GPS, isotope	Y	(Soares, 2013)
		2011, 2012, 2014	GPS	Y	(Lliguin, 2015)
		2011-2012, 2014-2015	GPS	Y	(Avalos et al., 2017)
	Selvagem Grande, Selvagens, North Atlantic	1997	nest attendance, chick weighing	Y	(Granadeiro et al., 1998)
		2007-2008	compass-temperature, TDR	Y	(Paiva et al., 2010b)
		2008	GPS	Y	(Paiva et al., 2010a)
		2010	GPS, diet	N	(Alonso et al., 2012)

Table 1. Data extracted from studies included in the systematic review (continued)

Species	Colony location	Data collection years*	Study method	Dual foraging?	Citation
Cory's Shearwater	Berlengas islands, Portugal	1987	nest attendance, chick weighing	N	(Granadeiro et al., 1998)
		2005-2007	compass-temperature, TDR	Y	(Paiva et al., 2010b)
		2007	GPS	N	(Paiva et al., 2010a)
		2011-2012, 2014-2015	GPS	N	(Avalos et al., 2017)
	Faial, Azores archipelago, North Atlantic	2006	compass-temperature, TDR	Y	(Paiva et al., 2010b)
	Vila Islet, Azores archipelago, North Atlantic	2004-2006	radio transmitter, PPT, blood	Y	(Magalhaes et al., 2008)
	Praia Islet, Azores archipelago, North Atlantic	2004-2006	radio transmitter, PPT, blood	Y	(Magalhaes et al., 2008)
	Gran Canaria Island, Canary Island	2005	PTT, isotope	N	(Navarro and Gonzalez-Solis, 2009)
	Desertas, Madeira archipelago	2006	compass-temperature, TDR	Y	(Paiva et al., 2010b)
Desertas petrel	Bugio island, Madeira archipelago	2007-2009	GLS	Y	(Ramirez et al., 2013)
Common diving petrel	Kerguelen island, Southern Indian Ocean	1992	Nest attendance, adult weighing	N	(Weimerskirch et al., 1994)
Flesh-footed shearwater	Lord Howe Island, Australia	2004-2005	nest attendance, light and temperature loggers, chick weighing	Y	(Thalmann et al., 2010)
Fulmar	Hirta, St. Kilda, Scotland	1994	chick weighing	N	(Hamer and Thompson, 1997)
Gentoo penguin	Trypot Beach, Marion Island, subantarctic Indian Ocean	2014	GPS, TDR	Y	(Carpenter-Kling et al., 2017)
Great frigatebird	Europa Island, Mozambipue Channel	2003	PTT, altimeters, diet	N	(Weimerskirch et al., 2004)
Great shearwater	Gough Island, Atlantic Ocean	2014	GPS, TDR	Y	(Schoombie et al., 2018)
Grey-headed albatross	Marion Island, subantarctic Indian Ocean	1998	PTT, GLS	Y	(Nel et al., 2000)[ʎ]
	Bird Island, South Georgia	1993-1996, 2001	radio transmitter/ PTT	N	(Phillips et al., 2009)
Humboldt penguin	Punta San Juan, Peru	1999	TDR	Y	(Taylor et al., 2002)
	Isla Pan de Azucar, northern Chile	1994 - 1995	TDR	Y	(Luna-Jorquera, 1999)

Table 1. Data extracted from studies included in the systematic review (continued)

Species	Colony location	Data collection years*	Study method	Dual foraging?	Citation
Hutton's shearwater	Kaikoura Peninsula, New Zealand	2017-2018	GPS, TDR	N	(Bennet et al., 2019)
Laysan albatross	Kilauea Point, Hawaii	2007	radio transmitters	Y	(Sprague, 2009)
Light-mantled albatross	Bird Island, South Georgia	2003	radio transmitter/ PTT	N	(Phillips et al., 2009)
Little auk	Hornsund, southwest Spitsbergen, Norway	2004, 2006	nest attendance	Y	(Wojczulanis-Jakubas et al., 2010)
		2004, 2016, 2017	nest attendance	Y	(Wojczulanis-Jakubas et al., 2020)
		2007	TDR, nest attendance	Y	(Welcker et al., 2009a)[T]
		2009 - 2010	GPS, temperature loggers	Y	(Kidawa et al., 2012)
		2011, 2016, 2018	GPS	Y	(Jakubas et al., 2020)
	Magdalenefjorden, northwest Spitsbergen, Norway	2008-2010	nest attendance, chick diet	Y	(Hovinen et al., 2014)
		2009	temperature loggers	Y	(Jakubas et al., 2014)
		2009 - 2010	GPS, temperature loggers	Y	(Kidawa et al., 2012)[ǂ]
		2009, 2010	nest attendance	Y	(Wojczulanis-Jakubas et al., 2020)
		2009-2010	nest attendance	Y	(Wojczulanis-Jakubas et al., 2018)
	Kongsfjorden, Norway	2007	TDR, nest attendance	Y	(Welcker et al., 2009a)[T]
		2006- 2007	nest attendance	Y	(Welcker et al., 2009b)
	Bjørndalen, Isfjorden, Norway	2005	nest attendance, plankton survey	Y	(Steen et al., 2007)
		2006- 2007	nest attendance	Y	(Welcker et al., 2009b)
		2007	TDR, nest attendance	Y	(Welcker et al., 2009a)
		2008	nest attendance, weighing	Y	(Welcker et al., 2012)
		2008- 2010	nest attendance, chick diet	Y	(Hovinen et al., 2014)
	Kap Høegh, Greenland	2007	TDR, nest attendance	Y	(Welcker et al., 2009a)
	Bear Island (Bjørnøya), Norway	2007	TDR, nest attendance	Y	(Welcker et al., 2009a)
		2013	GPS	Y	(Jakubas et al., 2016)
Macaroni penguin	Nyroysa, west coast of Bouvetoya	2007-2008	PTT, TDR	Y	(Blanchet et al., 2013)
	Bird Island, South Georgia	1997-2000	radio transmitters, diet	Y	(Barlow and Croxall, 2002)

Table 1. Data extracted from studies included in the systematic review (continued)

Species	Colony location	Data collection years*	Study method	Dual foraging?	Citation
Magnificent frigatebird	Little Cayman, Cayman islands	2017	GPS, GPS-GSM, bird-borne camera, diet	Y	(Austin et al., 2019)
Manx shearwater	Skomer Island, southwest Wales	1999	nest attendance	N	(Gray and Hamer, 2001)
		2002	meal size, feeding frequency	N	(Hamer et al., 2006)
		2003	GPS, TDR	Y	(Shoji et al., 2015)
		2009-2011	GPS	Y	(Dean et al., 2015)
	Copeland, Northern Ireland	2009-2011	GPS	Y	(Dean et al., 2015)
	Lundy, England	2009-2011	GPS	Y	(Dean et al., 2015)
	Rum, Scotland	2009-2011	GPS	Y	(Dean et al., 2015)
	Great Balsket, Ireland	2014-2015	GPS, nest attendance	Y	(Wischnewski et al., 2019)
	High Island, Ireland	2014	GPS, nest attendance	Y	(Wischnewski et al., 2019)
Nazac boobie	Punta Cevallos, Isla Espanola	2007	GPS, TDR	N	(Zavalaga et al., 2012)
Northern gannet	Les Etacs, Alderney	2011,2013-2015	GPS	Y	(Warwick-Evans et al., 2016)
Pink-footed Shearwater	Isla mocha, Chile	2015-2017	GPS	Y	(Carle et al., 2019)
Razorbill	Isle of May, southeast Scotland	1999, 2002, 2003, 2005, 2006	activity logger, TDR	Y	(Thaxter et al., 2010)
Red-tailed tropicbird	Christmas island, Indian Ocean	2006	nest attendance, immersion loggers, TDR	Y	(Sommerfeld and Hennicke, 2010)
Scopoli's shearwater	island of Linosa, Mediterranean	2008, 2009, 2012	GPS	Y	(Cecere et al., 2014)
	Tuscan Archipelago, Mediterranean	2010, 2011	GPS	N	(Cecere et al., 2014)
	La Maddalena Archipelago, Mediterranean	2013	GPS	N	(Cecere et al., 2014)
	Strofades Island complex, Ionian sea	2014	GPS	N	(Karris et al., 2018)
	Menorca Island, Cala Morell, Menorca	2012-2015	GPS	Y	(Pereira de Felipe, 2020)

Table 1. Data extracted from studies included in the systematic review (continued)

Species	Colony location	Data collection years*	Study method	Dual foraging?	Citation
Short-tailed shearwater	Althorpe Island, South Australia	2005 – 2007	nest attendance, chick feeding rate	Y	(Einoder et al., 2013)
		2005-2007	satellite transmitters, chick weighing	Y	(Einoder et al., 2011)
	Montague Island, New South Wales, Australia	1997	nest attendance, adult and chick weighing	Y	(Schultz and Klomp, 2000)
	Bruny Island, Tasmania	1997	nest attendance	Y	(Weimerskirch and Cherel, 1998)
	Wedge Island, Southern Tasmania	2008	GLS, TDR	Y	(Vertigan, 2010)
Shy albatross	Albatross Island, western Bass Strait	1995-1998	nest attendance, chick weighing	N	(Hedd et al., 2002)
Sooty shearwater	Kidney Island, Falkland islands	2008-2010	GLS	N	(Hedd et al., 2014)
	Snares Islands, New Zealand	2003	GLS	Y	(Shaffer et al., 2009)
	Codfish Island, New Zealand	2005	GLS	Y	(Shaffer et al., 2009)
	Mana Island, New Zealand	2005	GLS	Y	(Shaffer et al., 2009)
	North-east Island, Snares Island, New Zealand	1995	nest attendance, chick weighing	Y	(Weimerskirch, 1998)
Streaked shearwater	Nago area, Mikura Island, Japan	2003, 2006	TDR, stomach contents	Y	(Matsumoto et al., 2012)
		2005	nest attendance, automatic weighing	N	(Ochi et al., 2010)
	Mikura island, Japan	2003-2006	nest attendance, weight	Y	(Ochi et al., 2016)
	Awashima Island, Japan	2011-2013	GPS	Y[ß]	(Matsumoto et al., 2017)
	Sangan Island, Japan	2005	nest attendance, weight	Y	(Ochi et al., 2016)
Thick-billed murre	Coats Island, Nunavut, Canada	2000 – 2007	TDR, prey inspection	N	(Elliott et al., 2009a)
Thin-billed prion	Mayes Island, Kerguelen Islands, Southern Indian Ocean	1993	chick weighing	Y	(Weimerskirch et al., 1995)
		1997	chick weighing	Y	(Duriez et al., 2000)
	Kerguelen Island, Southern Indian Ocean	1992	nest attendance, adult weighing	Y	(Weimerskirch et al., 1994)

Table 1. Data extracted from studies included in the systematic review (continued)

Species	Colony location	Data collection years*	Study method	Dual foraging?	Citation
Wandering albatross	Bird Island, South Georgia	1996-1997, 2002, 2004	radio transmitter, GPS	N	(Phillips et al., 2009)
		1997	nest attendance, chick weighing	Y	(Berrow and Croxall, 2001)
		2009	GPS, salt water immersion, stomach temperature probe	Y	(Pereira et al., 2018)
	Crozet island, southern Indian Ocean	1990 -1992	nest attendance, adult weighing	Y	(Weimerskirch et al., 1994)
	Kerguelen Island, Southern Indian Ocean	1990 -1992	nest attendance, adult weighing	Y	(Weimerskirch et al., 1994)
	Possession Island, Crozet Islands, southern Indian Ocean	1990	ARGOS transmitters	Y	(Weimerskirch et al., 1993)
		1992	nest attendance	Y	(Weimerskirch et al., 1997)
	Marion Island, subantarctic Indian Ocean	1996-1997	PTT, GLS, nest attendance, diet	Y[ß]	(Nel et al., 2002)
Waved albatross	Isla Espanola, Galapagos	1996	PTT	Y	(Fernandez et al., 2001)
Wedge-tailed shearwater	Heron Island, Australia	2001	nest attendance, weighing of chick and adults	Y	(Congdon et al., 2005)
		2003	nest attendance, chick weighing	Y	(Peck and Congdon, 2005)
		2006, 2011, 2012	PTT, nest attendance	Y	(McDuie et al., 2015)
		2015	nest attendance, chick weighing, isotope, GPS	Y	(Miller, 2018)
	Lord Howe Island, southwest Pacific Ocean	2004	nest attendance, chick weighing	N	(Peck and Congdon, 2005)
		2015	nest attendance, chick weighing, isotope, GPS	Y	(Miller, 2018)
		2016	nest attendance, chick weighing, isotope, GPS	N	(Miller, 2018)
	Grand Anse, Reunion Island, Indian Ocean	2016-2017	GPS	Y	(Keys, 2018)
	Tern Island, Hawaii	1996-1997	nest attendance, weighing adults and chicks	N	(Baduini, 2002)

Table 1. Data extracted from studies included in the systematic review (continued)

Species	Colony location	Data collection years*	Study method	Dual foraging?	Citation
Westland petrel	Punakaiki, Westland, New Zealand	2012, 2015, 2016	I-got-u loggers	N	(Waugh et al., 2018)
		1995-1996	PTT, diet	Y	(Freeman et al., 2001)
White-chinned petrels	Possession Island, Crozet Islands, southern Indian Ocean	1997	nest attendance, satellite tracking	Y	(Catard et al., 2000)
Yellow-nosed albatross	Amsterdam islands, southwestern Indian Ocean	1991-1992	weighing adult, monitor return	Y	(Weimerskirch et al., 1994)
	Pointe d'Entrecasteaux, Amsterdam Island, southern Indian Ocean	1995-1996	nest attendance	N	(Weimerskirch et al., 2000)
		1996	PTT, nest attendance, diet	N	(Pinaud et al., 2005)
		2001	PTT, nest attendance, diet	Y	(Pinaud et al., 2005)

*Any year where data were collected during chick-rearing

[ʎ] This data is also reported by Nel in a PhD thesis (2002).

[ד] A subset of this data, the TDR data, is also reported in Brown and colleagues' paper (2012).

[ǂ] A subset of this data collected in Magdalenefjorden in 2009 was first reported by Jakubas and colleagues (2012).

[ß] Only males performed the dual foraging strategy.

3.4 Estimating distance from colony of short and long foraging trips

For the 50 species of seabirds represented in the included papers, we identified the mean distance of short and long foraging trips during chick-rearing reported in the paper or – if separate data were not available for short and long trips – the average distance of all foraging trips during chick-rearing. However, for 28 species, the relevant papers neither reported the distance of short and long trips nor the overall mean of all foraging trips, so we searched for studies in Google Scholar (using the species name (exact phrase) and 'distance to colony' as search terms) to identify studies that could provide this information. When trip distance during chick-rearing was not available, we considered studies that reported trip distance during breeding generally or during incubation. When no information at all was available for a species about foraging trip distance during breeding, we considered studies that reported trip distance during breeding in a closely-related species (this was done for 5 species, see Table 2) based on the assumption that the maximum distance from colony on foraging trips would be similar. When there were multiple studies that provided information on trip distances for a particular species, we averaged the distances reported across colonies or studies (without weighting by sample size).

When we were only able to find studies that reported the overall mean maximum distance of foraging trips without providing the mean distances of short and long trips, we estimate these values as follows. If the study reported minimum and maximum trip distances, we used these as the distances for short and long trips (done for 19 species, shown in Table 2). When the study only provided mean trip distance and the corresponding standard deviation or standard error, we estimate long trip distances as the mean value plus one standard deviation and short trip distances as the mean value minus one standard deviation (done for 13 species). When the standard deviation was larger than the mean, we estimated short trip distance as ¼ of the mean trip distances (done for 4 species). We used this fraction of the mean to estimate short-trip distance because in the 19 studies of 12 species for which we had data on the mean distance of all trips and on the distance travelled in both short and long foraging trips during chick-rearing, the mean maximum distance from the colony of short trips was approximately ¼ (0.241) of that of all foraging trips. When a paper presented the minimum and

maximum or the mean and standard deviation of trip distances stratified by sex, colony, or season without an overall mean, we estimated the mean distances of short and long trips for each subsample and averaged them (without weighting for the size of the subsamples).

3.5 Assessment of habitat quality

To assess the potential role of habitat quality on foraging patterns, we used chlorophyll as our metric of habitat quality. Nutrient-rich water promotes the primary production of phytoplankton (Abreu et al., 1995), phytoplankton attracts zooplankton (Noges, 1997), and zooplankton attract the fish prey that seabirds forage for (Ware and Thomson, 2005). Thus chlorophyll concentration – a measure of primary production – can provide an estimate of foraging habitat quality for seabirds. Specifically, we compare the maximum chlorophyll concentration accessible within the range of short and long foraging trips based on the assumption that seabirds are capable of locating the best available prey-patches. Numerous studies report that seabirds depart colonies in specific directions (Trathan et al., 2006; Weimerskirch, 2007), which suggests that they know where the best prey patches are likely to be located on a mesoscale; so using the *maximum* chlorophyll concentration accessible within their foraging range is probably a more accurate proxy for the quality of the prey patches they use than using the average chlorophyll concentration within their foraging range. Data on chlorophyll concentrations around colonies at the time the studies were conducted were extracted from the Global Ocean Biogeochemistry Hindcast dataset, which was downloaded from the Copernicus Marine Environment Monitoring Service (CMEMS, 2020).

The CMEMS dataset contained monthly means of global chlorophyll-a concentrations in mg m^{-3} from January 1st 1993 to December 23rd 2019, on a grid of 0.25 by 0.25 degrees. Dual foraging data during chick-rearing collected before 1993 were excluded from this analysis; this resulted in excluding data on 1 of the 50 species considered (the common diving petrel *Pelecanoides urinatrix*) and excluding 80 of the 822 months of dual foraging data we had collected.

Using the raster of global chlorophyll concentrations for the months the studies were conducted and the GPS location of each colony, we defined chlorophyll accessible on short trips as

the maximum chlorophyll concentration within the radius of the species' short-trip distance from the colony, and chlorophyll accessible on long trips as the maximum chlorophyll concentration outside of the areas accessible during short trips but within the radius of long trips from the colony. The chlorophyll data were available as monthly averages, so we calculated the maximum chlorophyll concentrations available during short and long foraging trips from the colony for each month during which foraging data on chick-rearing seabirds were collected.

3.6 Statistical analysis

To assess whether the difference in habitat quality is a driver of dual foraging, we used linear mixed effects models (LMMs) to test (1) whether locations with different chlorophyll concentrations were available during long and short trips in the months seabirds employed dual foraging, and (2) whether the magnitude of the difference in chlorophyll concentrations in areas accessible during long versus short trips differed between the months in which dual foraging was and was not used. In model (1) the response variable was the maximum chlorophyll concentration accessible, and the fixed effect was short or long trip. In model (2) the response variable was the difference in chlorophyll concentrations between areas accessible during short and long trips, and the fixed effect was whether or not dual foraging was employed. For both models we set species and study as a random effect and square-root transformed chlorophyll concentration to normalize its distribution.

We built a generalized linear mixed model (GLMM) to assess whether the probability of dual foraging changed with changing differences in the quality of habitat accessible between short and long trips. This model had a binomial family distribution: we set seabird taxa as a random effect, the difference in maximum chlorophyll concentrations accessible between short and long trips in each month as a fixed effect, and whether dual foraging occurred as the response variable. We then compared each of these three models with a null model (without the fixed effect) using a likelihood ratio test to identify statistical significance.

We then built a generalized linear model to assess differences in the use of dual foraging by different seabird taxa based on the difference in habitat quality available on short and long trips. This

model had a binomial family distribution in which the difference in maximum chlorophyll concentrations between the areas accessible during short and long trips in each month is a fixed effect, the family group of the species is a fixed effect, and whether or not dual foraging occurred in that month is the binary response variable.

4. Results

We identified 103 studies that presented data that could be used to determine whether or not dual foraging occurred. These studies reported data on 50 species (Table 1) across nine families: auks (Alcidae), albatrosses (Diomedeidae), frigatebirds (Fregatidae), gulls (Laridae), pelicans (Pelecanidae), tropicbirds (Phaethontidae), shearwaters (and prions and some petrels) (Procellariidae), penguins (Spheniscidae), and sulids (Sulidae), spanning all 6 orders containing seabirds (Charadriiformes, Procellariiformes, Suliformes, Pelecaniformes, Phaethontiformes, and Sphenisciformes). The locations of the colonies reported in the 103 studies encompass all oceans and continents (Figure 1). The mean maximum distances travelled from the colony on short-distance and long-distance foraging trips during chick-rearing for each of these 50 species are shown in Table 2.

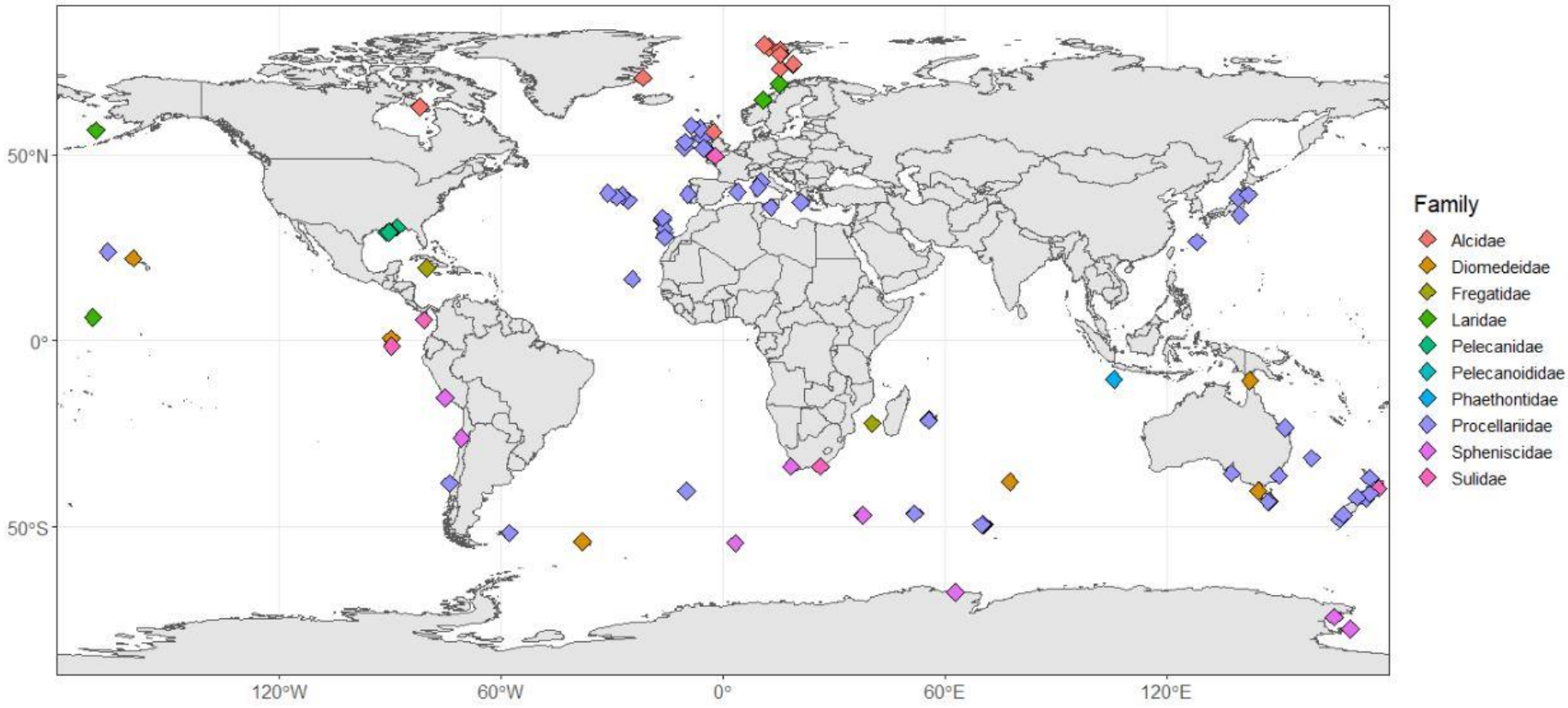


Figure 1. Location of study colonies reported in the 103 studies included in the analysis of dual foraging in seabirds

Table 2. Mean maximum distance to colony of short- and long-distance trips for the 50 seabirds species considered

Species	Short trip distance (km)	Long trip distance (km)	Estimation method	Breeding stage ǂ	Data from closely-related species ʎ	Source
Adélie penguin	35	98	min max ʈ	C	N	(Wienecke et al., 2000)
African penguin	8	33	min max	C	N	(Pichegru et al., 2010)
Antarctic prion	800	1546	SD ɜ	I	Thin-billed prion	(Quillfeldt et al., 2019)
Australasian gannet	20	50	given ɥ	C	N	(Besel et al., 2018)
Barau's petrel	150	1355	given	C	N	(Pinet et al., 2012)
Black petrel	98	1128	min max	C	N	(Freeman et al., 2010)
Black-browed albatross	10	129	min max	C	N	(Arata et al., 2014)
Black-legged kittiwake	28	304	given	C	N	(Christensen-Dalsgaard et al., 2018)
	29	71	given	C	N	(Paredes et al., 2012)
	34	135	given	C	N	(Paredes et al., 2012)
	37	64	given	C	N	(Christensen-Dalsgaard et al., 2018)
	9	48	given	C	N	(Kotzerka et al., 2010)
Blue petrel	800	1546	SD	I	Thin-billed prion	(Quillfeldt et al., 2019)
Blue-footed booby	8	46	SD	C+I	N	(Weimerskirch et al., 2009)
Brown pelicans	21	83	min max	I	Peruvian pelicans	(Zavalaga et al., 2011)
Cape gannet	29	322	min max	C	N	(Botha and Pistorius, 2018)
Cape Verde shearwater	140	242	SD	C	N	(Paiva et al., 2015)
Chinstrap penguin	9	27	SD	C	N	(Kokubun et al., 2015)
Common diving petrel	21	33	SD	I	N	(Dunphy et al., 2020)
Common guillemots	34	134	SD	C	N	(Thaxter et al., 2012)
Cory's shearwater	52	596	given	C	N	(Paiva et al., 2010a)
	64	548	given	C	N	(Paiva et al., 2010a)
	62	1060	given	C	N	(Soares, 2013)
Desertas petrel	1268	4690	min max	C+I	Murphy's petrel	(Clay et al., 2019)
Flesh-footed shearwater	92	923	1/4, SD ß	C+I	N	(Waugh et al., 2016)
Gentoo penguin	3.1	11	given	C	N	(Carpenter-Kling et al., 2017)
Great frigatebird	376	1022	min max	I	N	(Weimerskirch et al., 2010)
Great shearwater	299	2814	given	C	N	(Schoombie et al., 2018)
Grey-headed albatross	399	2162	min max	C	N	(Xavier et al., 2003)
Humboldt penguin	7	30	min max	C	N	(Boersma et al., 2007)
Hutton's shearwater	124	306	min max	C	N	(Bennet et al., 2019)
Laysan albatross	103	865	1/4, SD	C+I	N	(Montoya et al., 2019)

Table 2. Mean maximum distance to colony of short- and long-distance trips for the 50 seabirds species considered (continued)

Species	Short trip distance (km)	Long trip distance (km)	Estimation method	Breeding stage ǂ	Data from closely-related species ^	Source
Light-mantled albatross	50	1650	min max	C	N	(Phillips et al., 2009)
Little auk	12	66	given	C	N	(Jakubas et al., 2016)
	16	58	given	C	N	(Jakubas et al., 2020)
Macaroni penguin	16	60	SD	C	N	(Trathan et al., 2006)
Magnificent frigatebird	26	928	1/4, max Θ	C	N	(Austin et al., 2019)
Manx shearwater	19	1109	min max	C	N	(Wischnewski et al., 2019)
Nazca booby	98	329	given	C	N	(Zavalaga et al., 2012)
Northern fulmar	154	646	SD	C	N	(Thaxter et al., 2012)
Northern gannet	79	268	SD	C	N	(Warwick-Evans et al., 2016)
Pink-footed shearwater	23	216	given	C	N	(Carle et al., 2019)
Razorbill	3	73	1/4, max	C	N	(Isaksson et al., 2019)
Red-tailed tropicbird	27	317	SD	C	Red-billed tropicbirds	(Diop et al., 2018)
Scopoli's shearwater	46	210	given	C	N	(Pereira de Felipe, 2020)
Short-tailed shearwater	130	312	min max	C	N	(Einoder and Goldsworthy, 2005)
Shy albatross	24	267	min max	C	N	(Brothers et al., 1998)
Sooty shearwater	515	1970	given	C	N	(Shaffer et al., 2009)
Streaked shearwater	15	775	min max	C	N	(Matsumoto et al., 2017)
Thick-billed murre	4	161	min max	C	N	(Jones et al., 2002)
Thin-billed prion	800	1546	SD	I	N	(Quillfeldt et al., 2019)
Wandering albatross	441	2192	given	C	N	(Pereira et al., 2018)
Waved albatross	13	1397	min max	C+I	N	(Awkerman et al., 2014)
Wedge-tailed shearwater	69	262	given	C	N	(Keys, 2018)
Westland petrel	88	232	SD	C	N	(Waugh et al., 2018)
White-chinned petrel	62	1868	given	C	N	(Catard et al., 2000)
Yellow-nosed albatross	11	594	min max	C	N	(Weimerskirch and Guionnet, 2002)

ǂ When species-specific distance to colony during the chick-rearing stage (C) was unavailable, either the distance from colony during breeding (incubation and chick-rearing, I+C) or the distance from colony during incubation (I) was used, depending on what data were available
^ When unable to obtain species-specific distances to colony, distances to colony of closely related species was used
ד Short and long trip distances estimated from minimum and maximum trip distances
ᶟ Short-trip distance estimated as mean plus one standard deviation, long-trip distance estimated as mean minus one standard deviation
µ Short and long trip distances are given in the study
ß Long trip distance estimated as mean plus one standard deviation, short trip distance estimated at ¼ of mean trip distance (see methods section for details)
Θ Long trip distance estimated as maximum trip distance, short trip distance estimated at ¼ of mean trip distance (see methods section for details)

Dual foraging occurred in 81 (78.6%) of the 103 studies and did not occur in the remaining 22 (20.4%) studies. Eleven of the 81 studies reporting dual foraging also reported instances in which no dual foraging occurred (for specific species, colonies, or years). In 2 of the 81 studies dual foraging was only recorded in males. Dual foraging was always used in 100% of studied Phaethontidae and Laridae species, 80% of Sulidae species, 67% of Spheniscidae species, 55% of Procellariidae species, 50% of Alcidae and Fregatidae species, 25% of Diomedeidae species, and 0% of Pelecanidae species (Table 3). There was little difference in the use of dual foraging strategies between seabirds located in breeding colonies in different geographic regions: 69% of colonies in the tropics or subtropics (0-35°N or S, n=42) used dual foraging, compared with 74% of colonies in temperate regions (35-50°N or S, n=58), and 75% of colonies in subpolar or polar regions (>50°N or S, n=52).

Table 3. Probability of dual foraging across seabird families

Family	Species that only used dual foraging (%)*	Species that sometimes used dual foraging (%)*	Species that never use dual foraging (%)*	Number of species	Number of studies
Laridae	100% (1)	0% (0)	0% (0)	1	2
Phaethontidae	100% (1)	0% (0)	0% (0)	1	1
Sulidae	80% (4)	0% (0)	20% (1)	5	5
Spheniscidae	67% (4)	16.6% (1)	16.6% (1)	6	10
Procellariidae	55% (12)	31% (7)	14% (3)	22	54
Alcidae	50% (2)	0% (0)	50% (2)	4	14
Fregatidae	50% (1)	0% (0)	50% (1)	2	2
Diomedeidae	25% (2)	37.5% (3)	37.5% (3)	8	10
Pelecanidae	0% (0)	0% (0)	100%	1	1

*number in brackets indicate the number of species

4.1 Influence of habitat quality on the probability of dual foraging

Three results supported our hypothesis that habitat quality is a driver of dual foraging in seabirds. First, in months when seabird species used dual foraging chlorophyll concentrations accessible during long trips were higher than those accessible during short trips (2.030 ± 0.08 vs. 0.946 ± 0.06, LMM: $\chi^2_1 = 304.14$, $p<0.0001$). Second, the difference in chlorophyll concentrations accessible in short and long trips was greater when dual foraging occurred than when it did not occur

(1.083 ± 0.08 vs. 0.820 ± 0.08, LMM: $\chi^2_1 = 18.416$, $p<0.0001$). Third, the probability of dual foraging increased significantly with increases in the magnitude of the difference in habitat quality accessible between short and long trips (slope=0.160±0.060, GLMM: $\chi^2_1 = 7.643$, $p=0.0057$). In other words, birds were more likely to use a dual foraging strategy if better quality habitat was available further from the colony.

Results of the generalized linear model identified differences between seabird families (Table 4). Using Procellariidae as the reference group (because its known that they commonly use the dual foraging strategy (Baduini and Hyrenbach, 2003)), we found that within the observed range in differences in habitat quality available during short and long foraging trips, auks (excluding little auks), albatrosses, and penguins were significantly less likely to use the dual foraging strategy than Procellariidae, while Sulids were significantly more likely to use the dual foraging strategy than Procellariidae. There were no statistically significant differences in the probability of using the dual foraging strategy between the remaining families (*Alle alle*, Fregatidae, Laridae, Pelecanidae, Phaethontidae) and Procellariidae (Table 4). Little auks were analysed separately from other auks because their unique ability among auks to carry prey in a gular pouch (Stempniewicz, 2001) – unlike other auks which carry fish in their beaks (e.g., Burke and Montevecchi, 2009) – could result in the use of different foraging strategies.

Table 4. Results of generalized linear model with a binomial family distribution*

Seabird Family	Estimate	Standard Error	z value	P-value
Intercept	0.887465	0.142296	6.236741	**4.47E-10**
Procellariidae (reference family)	0.159841	0.059598	2.682	**0.007318**
Alcidae	-1.41719	0.316089	-4.48352	**7.34E-06**
Alle alle	17.62117	815.0689	0.021619	0.982752
Diomedeidae	-1.94466	0.235057	-8.27314	**1.30E-16**
Fregatidae	-0.24643	0.876559	-0.28113	0.778608
Laridae	17.57919	1190.4	0.014767	0.988218
Pelecanidae	-19.6081	2300.816	-0.00852	0.9932
Phaethontidae	17.34224	3255.677	0.005327	0.99575
Spheniscidae	-0.92484	0.242544	-3.81309	**0.000137**
Sulidae	1.665297	0.743279	2.240474	**0.02506**

* The model uses the difference in maximum chlorophyll concentrations between the area accessible during short and long trips in each month as a fixed effect, the family group of the seabird species as a fixed effect, and whether or not dual foraging occurred in that month as the binary response variable

The relationship of the probability of dual foraging occurring with the magnitude of the difference in chlorophyll concentrations between near and far prey patches for the 5 families with data available from more than two studies is shown in Figure 2.

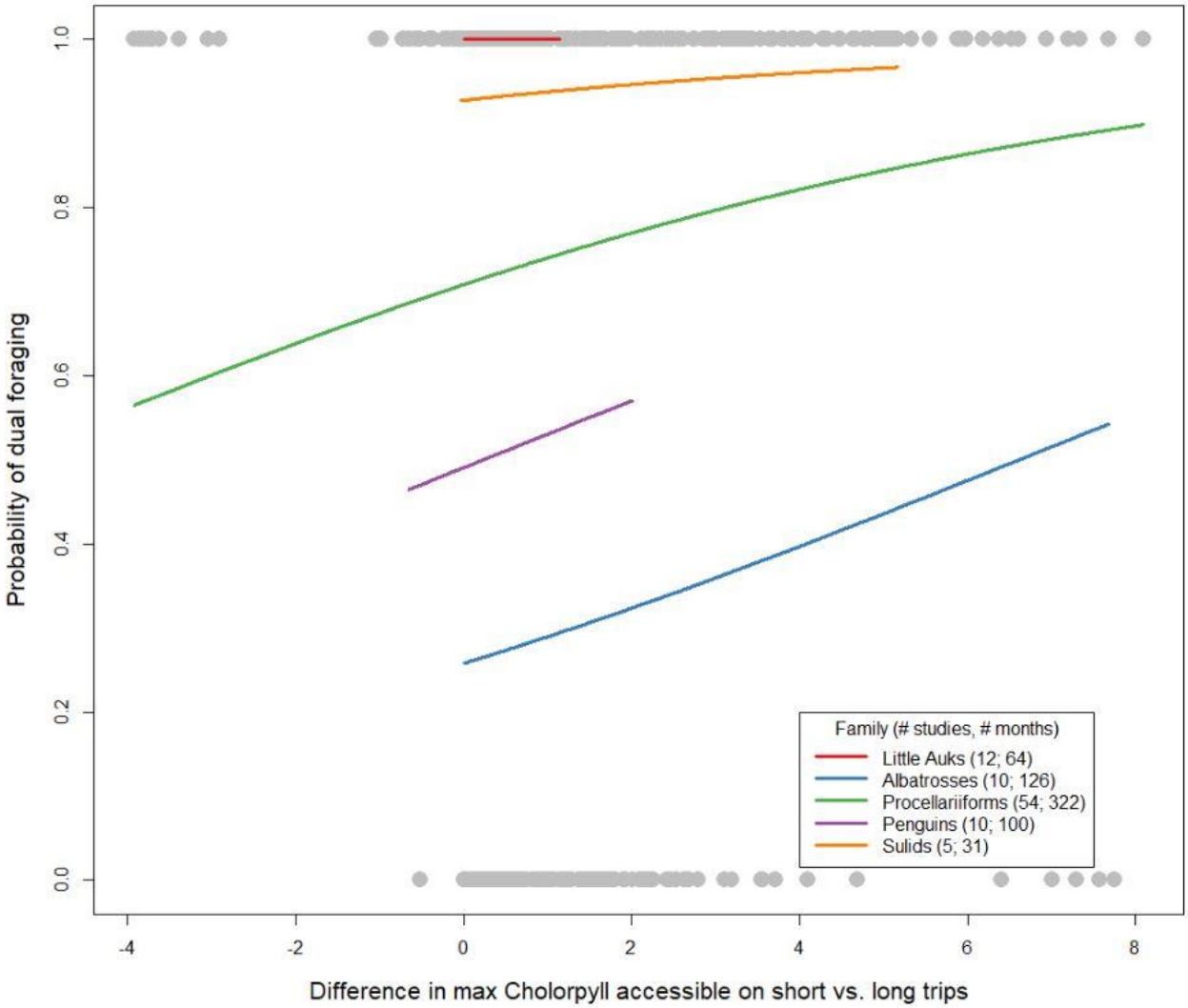


Figure 2. Probability of dual foraging during chick-rearing as a function of the difference in patch quality accessible during short and long foraging trips for 5 of the 9 families of seabirds considered.

Negative values on the X-axis indicate cases where the maximum chlorophyll concentrations within the area accessible for long trips (i.e., outside the area accessible during short trips) was poorer than the maximum chlorophyll concentrations in areas accessible during short trips. To avoid extrapolating beyond our dataset, the lines predicted from the generalized linear model are constrained (on the X-axis) to the chlorophyll differences recorded in that family. Grey dots are observed data points that indicate months when seabirds did (Y-axis=1) and did not (Y-axis=0) use the dual foraging strategy when the difference in patch quality available during short and long trips in the month was at the level specified by the X-axis coordinate of the dot.

4.2 Case studies: Cory's shearwaters and little auks

Eleven studies conducted at 9 colonies provided information on whether Cory's shearwaters used the dual foraging strategy. We focus our case study on data from 3 colonies reported in 10 of the 11 studies (Selvagem Grande, Cima Islet, and Corvo Island) in which it was possible to estimate the mean distances of short- and long-distance foraging trips. Studies at Selvagem Grande in the North Atlantic found that chick-rearing Cory's shearwaters used the dual foraging strategy in some – but not all – months. Contrary to our *a priori* hypothesis, dual foraging occurred in a month with the highest maximum chlorophyll concentrations *near* the colony but did not occur in other months when chlorophyll concentrations near the colony were lower (Figure 3a). All the studies at Cima Islet in the North Atlantic found that Cory's shearwaters used the dual foraging strategy; at this colony, chlorophyll concentrations were generally low within 500km of the colony; in most months the maximum chlorophyll concentrations 600 to 800km from the colony were much higher (Figure 3b). Studies at Corvo Island in the North Atlantic (Figure 3c) found that dual foraging was used in some months while in other months it was not; during one month when the chlorophyll concentrations at all distances from the colony were higher than during any other month (Figure 3c), Cory's shearwaters did not use the dual foraging strategy.

All 12 studies of little auks at 6 colonies found that dual foraging occurred. We focus our case study on 5 of these colonies, including data from 11 of the 12 studies for which we were able to estimate chlorophyll concentrations (our proxy for habitat quality) in 20km intervals from the colony. In most months at most colonies maximum chlorophyll concentrations improved with increasing distance from the colony (Figure 4). However, during two months at the Magdalenefjorden site, chlorophyll concentrations at the mean long-trip distance from the colony were slightly lower than those at the mean short-trip distance.

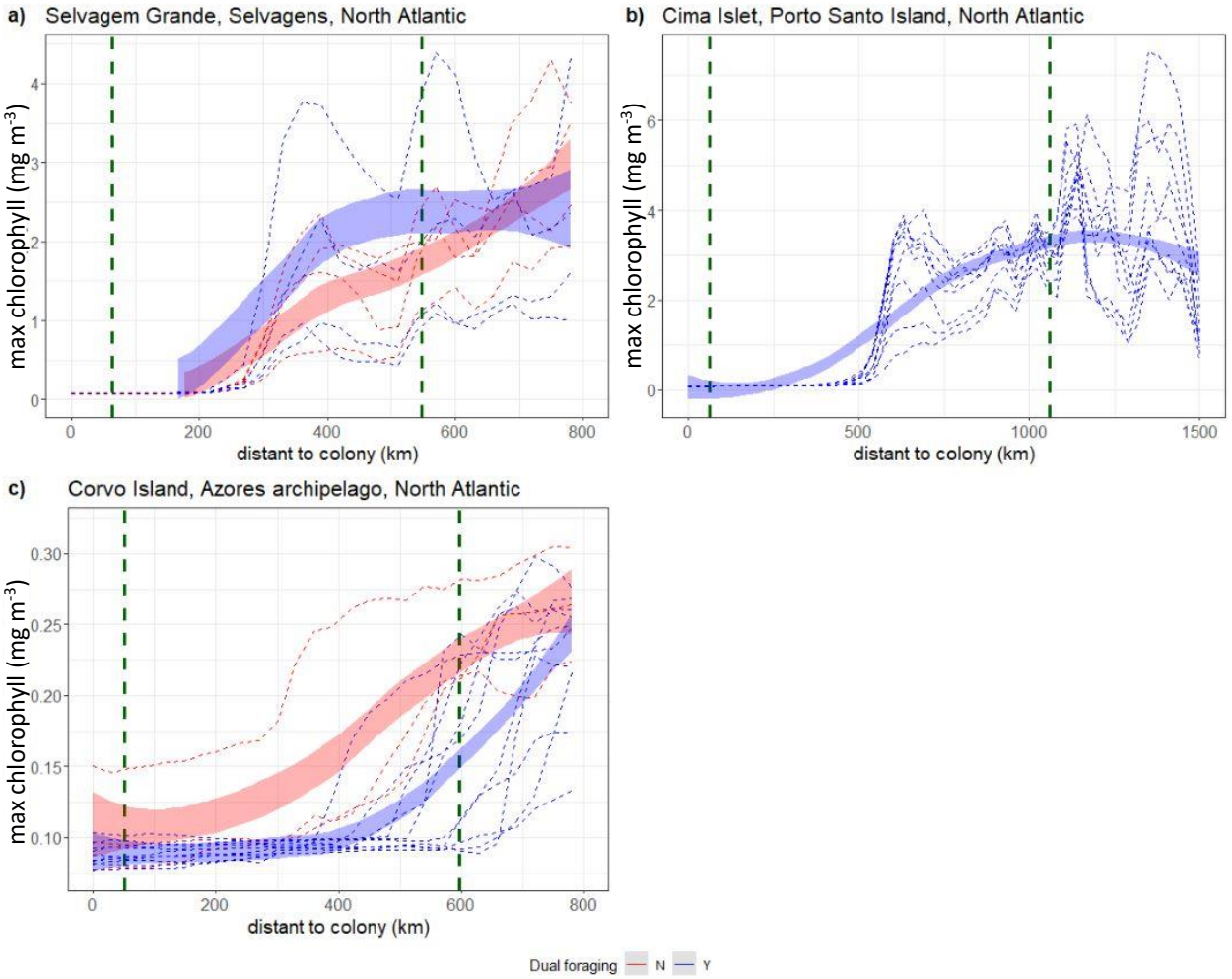


Figure 3. Case study of Cory's shearwaters.

Each panel represents one colony; each line in each panel represents a month during chick-rearing when foraging data were collected. The (x,y) coordinate of points on each line represents the distance from the colony and the maximum chlorophyll concentration within 30km of that distance from the colony during the specified month. If the line is blue, dual foraging occurred; if the line is red, dual foraging did not occur. The dashed vertical lines indicate the mean maximum distance from the colony of short and long trips at each of the colonies. The blue and red shaded areas represent the mean (standard error) of the maximum chlorophyll concentration of the months in which dual foraging did (blue) and did not (red) occur.

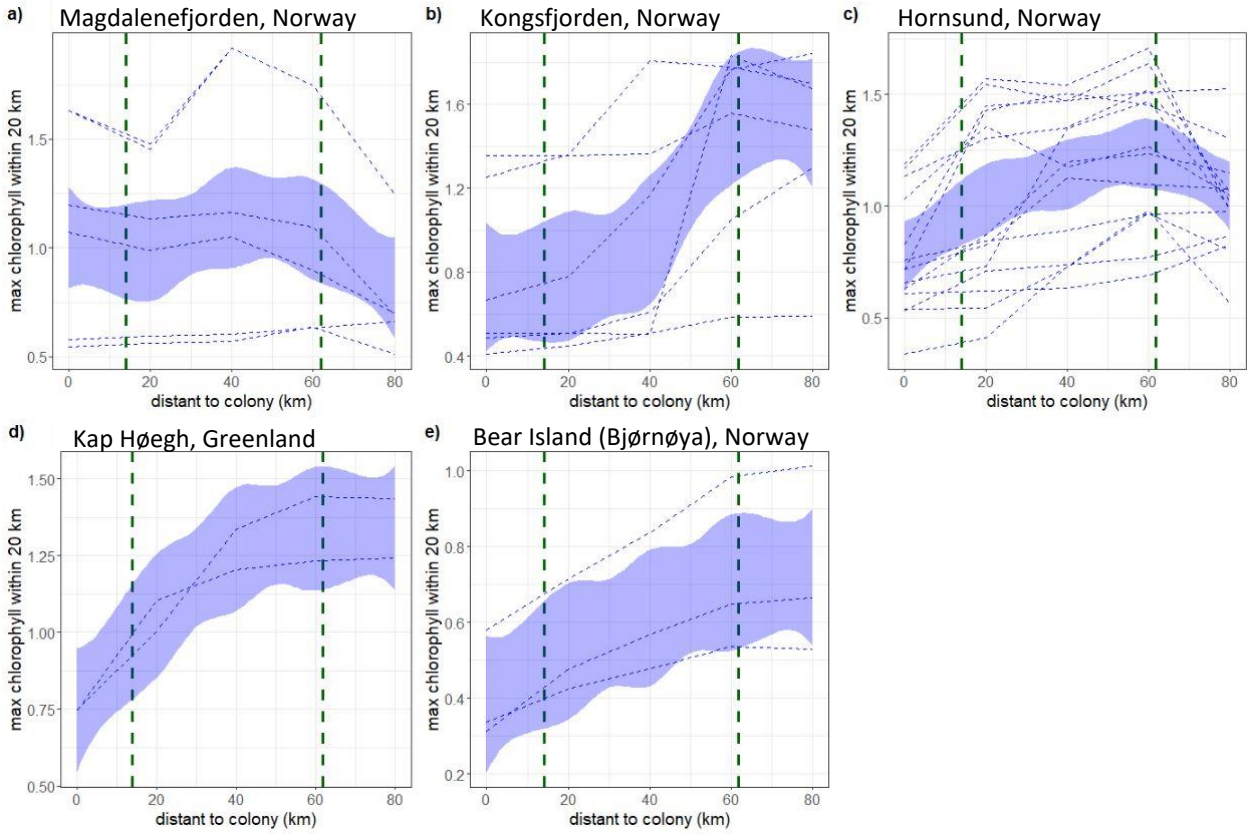


Figure 4. Case study of little auks

Each panel represents one colony; each line in each panel represents a month during chick-rearing when foraging data was collected. The (x,y) coordinate of points on each line represents the distance from the colony and the maximum chlorophyll concentration within 20km of that distance from the colony during the specified month. The dashed vertical lines indicate the mean maximum distance from the colony of short and long trips. The blue shaded area represents the mean (standard error) of the maximum chlorophyll concentration. Dual foraging occurred during all months at all colonies.

5. Discussion

Our study reviewed 103 studies from the literature and used additional data on habitat quality to show that (i) dual foraging is common among seabirds, and (ii) the probability of dual foraging across seabird families increases with increasing differences in patch quality between close and far prey patches.

5.1 Differences in dual foraging across seabird families

Reviewing 103 studies across 9 families, we found that dual foraging was a commonly employed foraging strategy in seabirds, occurring in 50% to 100% of seabird species in each family (Table 3). The exception was the Pelecanidae family, but we only located a single study for this family and so their propensity to use dual foraging should be re-assessed in subsequent studies. The propensity for using dual foraging varied between families. Auks (excluding little auks), albatrosses, and penguins were all significantly less likely to use the dual foraging strategy during chick-rearing than Procellariidae, while Sulids were significantly more likely to use the dual foraging strategy than Procellariidae.

In some seabirds, chicks accumulate such large amounts of fat that their mass exceeds that of their parents. This is particularly extreme in Procellariiforms (albatrosses, shearwaters, and petrels) among which some chicks attain a mass 60% greater than that of their parents (Warham, 1990), though they subsequently lose this fat prior to fledging (Lack, 1968; Ricklefs et al., 1980; Warham, 1990). Building on an earlier theory by Lack (1968), Ricklefs and Schew (1994) hypothesized that these fat deposits were a result of parental over-feeding, a strategy that provides chicks with enough resources to weather the natural stochastic variation in food deliveries. This hypothesis is supported by empirical evidence in little shearwaters *Puffinus assimilis*, showing that the accumulation of fat in chicks relates to stochastic variation in parental food delivery rates (Hamer, 1994). These fat deposits likely buffer shearwater, albatross, and petrel chicks against starvation during longer periods without feeding, reducing the risks of their parents employing the dual foraging strategy. Also, feather growth is likely to be energetically demanding, so fat may ensure that high-quality feathers are grown over a relatively short period.

While this may help to explain why dual foraging is common in Procellariidae (shearwaters, prions, and some petrels), it does not explain why albatrosses were the least likely to use the dual foraging strategy (amongst the five seabird families in which we had enough power to detect a significant difference: Alcidae, Diomedeidae, Procellariidae, Spheniscidae, and Sulidae). One

possible explanation for this unexpected result is that albatrosses forage over such large distances that there is a certain amount of self-maintenance built into all trips, and they are less likely to embark on short trips near the colony. Auks were also not very likely to employ dual foraging. They have very high flight costs because of their high wing loading (Pennycuick, 1987). Thus the energy expenditure of auks increases drastically with increasing travel distances (Gaston, 1985), so they are likely to adopt foraging strategies that minimize flight time, only foraging in prey patches further from the colony when those immediately around the colony become severely depleted – as often occurs around large colonies (Elliott et al., 2009b). Also, most auks carry prey to chicks in their beaks (e.g., Burke and Montevecchi, 2009), restricting the amount of food they can bring back from each trip in comparison to Procellariidae which regurgitate food for their chicks (Prince and Morgan, 2009). Auks' more restricted food load may require parents to stay close to the colony to ensure frequent food deliveries. Auk chicks also have lower nestling obesity than Procellariidae chicks (Visser, 2001), making them more susceptible to starvation during long periods without feeding. Together, these factors may explain our finding that auks are significantly less likely to use the dual foraging strategy than Procellariidae (but see below for little auks).

The distances from the colony penguins travelled on short and long foraging trips tended to be on the lower end of the foraging distances of all seabirds included in this analysis (Table 2). This could be due to the smaller distances reachable through swimming compared to flying and/or to the availability of sufficient food resources at shorter distances from penguin colonies (reducing the need to travel further). In support of the latter theory, temperate and polar waters are more productive and more predictable than tropical waters (Longhurst and Pauly, 1987; Weimerskirch, 2007); so the polar waters in which penguin colonies are located are therefore more likely to have sufficient resources to provision both parents and offspring near the colony than the waters surrounding colonies of seabirds breeding in the tropics. This may explain why penguins are less likely to use the dual foraging strategy than Procellariidae. A similar rationale may explain why we found that Sulidae, including gannets and boobies, are more likely to use dual foraging than Procellariidae. Boobies are tropical seabirds that breed at colonies in resource-poor tropical waters (Longhurst and Pauly, 1987;

Weimerskirch, 2007) where it is less likely that parents can meet the needs of both themselves and their offspring in near-colony waters alone.

5.2 Case study of little auks

Unlike the findings in other auk species, all 12 studies on little auks from 6 colonies identified in this review reported the use of dual foraging. Little auks chicks have more fat deposits than any other auks, which would buffer them against starvation during longer periods without food (Taylor and Konarzewski, 1989). Little auks also carry prey back to their chicks in a gular pouch (a small sac under their beaks) (Stempniewicz, 2001), which may allow them to carry prey over longer distances than other auks which carry prey in their beaks.

Little auks also have a very high growth rate, with chicks gaining more mass per day than any other auk as a proportion of adult body mass (Stempniewicz, 2001). Indeed, parents must make multiple trips a day to meet their needs (Welcker et al., 2009a). Furthermore, many little auk breeding colonies are located in shallow fjords (including four of the six colonies studied here), where parents would need to make long trips to the continental shelf break to access high quality prey (Steen et al., 2007). High energy demands from chicks combined with poor near-colony habitat quality, likely favour the use of the dual foraging strategy in little auks.

Little auks also often breed in very large colonies: the Spitsbergen region in Norway (where four of the six colonies included in this analysis are located) contains over 728,000 pairs of little auks (Keslinka et al., 2019). Like other members of the auk family, little auks have high flight costs (Gabrielsen et al., 1991) due in part to having small wings optimized for underwater propulsion during prey capture (Taylor, 1994). Given the combination of high densities of individuals and high flight costs, little auks are likely to deplete resources immediately around their colonies, creating an Ashmole's halo, and necessitating longer trips for parents to replenish their own condition (Welcker et al., 2009a).

This is supported by our finding that in most months at most colonies maximum chlorophyll concentrations improved at greater distances from the colony (Figure 4). However, for two of the months assessed at Magdalenefjorden the chlorophyll concentrations at the mean long-trip distance were slightly *lower* than those at the mean short-trip distance (Figure 4a). This mismatch may have occurred because the chlorophyll measure is not a precise proxy for the quality of prey patches, as high primary productivity may not translate to high prey availability for apex predators if competition for food depletes these resources.

5.3 Case study of Cory's shearwaters

At Corvo Island, Cory's shearwaters did not use the dual foraging strategy in the month with equally high chlorophyll concentrations at all distances from the colony, perhaps because the quality of prey patches near the colony were sufficient to provision both offspring and parents. At all distances from the colony, the averaged mean maximum chlorophyll concentrations during the months in which dual foraging did not occur (the red shaded area in Figure 3c) was greater than that of the months when dual foraging occurred (the blue shaded area in Figure 3c). This finding of consistently lower concentrations of chlorophyll surrounding colonies when dual foraging occurred supports the hypothesis that birds engage in the dual foraging strategy when resources near the colony are insufficient to provision both themselves and their offspring. The reason why chlorophyll concentrations were much lower than those at Cima Islet or Selvagem Grande may be because Corvo Island is much further from the continental shelf.

At Cima Islet, Cory's shearwaters always used the dual foraging strategy. For all months studied, there were much higher quality prey patches available beyond 500km from the colony than within 500km. Given the huge difference in the mean short-trip distance from the colony compared to the mean long-trip distance (62km versus 1060km) (Soares, 2013), the higher quality patches over 500km from the colony are out of reach during short trips. In this situation, the dual foraging strategy was the best available method for simultaneously meeting chicks' requirements for frequent feeding and parents' requirements for replenishment.

We had an unexpected finding at Selvagem Grande, where Cory's shearwaters used the dual foraging strategy in a month when the maximum chlorophyll concentration near the colony was greater than that farther from the colony and did not use the dual foraging strategy in months when the maximum chlorophyll concentration was lower near the colony than that further from the colony. A possible explanation is that chlorophyll concentrations may not reflect the amount of prey available near colonies of Cory's shearwaters because large colonies may deplete prey patches near the colony which cannot be measured by chlorophyll concentrations. In support of this hypothesis, Selvagem Grande has an estimated population of ~29,540 breeding pairs (Granadeiro et al., 2006). In contrast, Porto Santo has an estimated ~3500 breeding pairs (Ramos et al., 2013), and Corvo Island has an estimated 6,000 to 12,000 breeding pairs (Monteiro et al., 1996).

5.4 Influence of habitat quality on the probability of dual foraging

The habitat selection model developed by Olsson and colleagues (2014) assumes that animals should only forage in locations where foraging contributes positively to the animal's fitness. Building on the prediction based on the Central Place Foraging Theory that animals should only travel further to forage if more distant foraging locations offer better foraging conditions (Houston and McNamara, 1985; Cuthill and Kacelnik, 1990; Waite and Ydenberg, 1996), Olsson and colleagues' model predicts that animals should travel shorter distances to forage when environmental quality is good and travel longer distances to forage when environmental quality is poor. Applied to a dual foraging context, this model predicts that seabirds should only forage in locations far from the colony if foraging there positively contributes to their fitness. Our findings provide support for this hypothesis: the probability of using the dual foraging strategy across seabird families increases with increasing differences in patch quality between close and far prey patches. In other words, dual foraging was more likely to occur if the quality of distant foraging patches far exceeded that of closer patches.

Baduini and Hyrenbach's review (2003) of dual foraging in Procellariiformes found that chlorophyll concentrations were higher in areas Procellariiformes targeted during long trips than in

areas they targeted during short trips. Our results show that this is also the case in other families of seabirds; when seabirds used the dual foraging strategy, the chlorophyll concentrations accessible during long trips were significantly higher than those accessible during short trips. Moreover, we found that as the magnitude of the difference in the chlorophyll concentrations between areas accessible in long and short trips increase, the likelihood of using the dual foraging strategy also increased. Although there were differences between families, the fact that we found this trend across numerous seabird families, provides convincing evidence that habitat quality is an important driver of dual foraging

Some of the studies included in Baduini and Hyrenbach's review (2003) were not included in our analysis because they did not meet our inclusion criteria. While Baduni and Hyrenbach classified foraging reported in studies in which they could not identify 'distinct bimodality' as 'unimodal', we only included papers in which there was clear evidence of unimodal or bimodal foraging. Their more relaxed criteria of unimodal foraging may have resulted in the misclassification of some instances of unimodal foraging. This may partly explain why they found no differences in the use of dual foraging across tube-nosed families, while we found that albatrosses were significantly less likely to dual forage than Procellariidae.

Parent-offspring conflict can be exacerbated by various factors, including parasitism (Romano et al., 2011), heightened predation risk (Tilgar et al., 2011), and degrading climate conditions (Dupoué et al., 2015). However, scarce (Martin, 1987; Montgomerie and Weatherhead, 1988), patchy, or inaccessible prey are perhaps the most common causes of heightened parent-offspring conflict (Abrams, 1991; McNamara and Houston, 1997). While discrepancy in the locations of the most productive foraging grounds and the colony may be a pre-requisite for the use of the dual foraging strategy (this study; Chaurand and Weimerskirch, 1994; Weimerskirch et al., 1994; Granadeiro et al., 1998; Welcker et al., 2009a; Tyson et al., 2017) the timing and frequency of short and long trips is likely driven by parent and/or chick condition (Weimerskirch, 1998; Weimerskirch and Cherel, 1998; Ochi et al., 2010; Wischnewski et al., 2019), and the type of trip the partner is performing (Tyson et

al., 2017). However, whether the needs of the parents , offspring, or both determine foraging trip distance is far from clear (Wischnewski et al., 2019). Studies have found that whether adults feed close to or far from the colony is either determined solely by adult condition [short-tailed shearwaters *Puffinus tenuirostris*(Weimerskirch and Cherel, 1998); sooty shearwater *Ardenna grisea* (Weimerskirch, 1998)], determined solely by chick condition [Manx shearwaters *Puffinus puffinus* (Wischnewski et al., 2019)], or determined by both adult and chick condition [Streaked shearwater *Calonectris leucomelas* (Ochi et al., 2010)]. This is an important question that needs further research across seabird taxa. **5.5 Limitations**

Other factors not considered in this study may influence the likelihood that seabirds use dual foraging. For instance, we did not consider whether the target species feed offspring different food from the food they feed themselves, a factor that could increase the likelihood that the seabird uses a dual foraging strategy, foraging in one location to feed their offspring and in another to feed themselves.

Surprisingly, few studies reported the distance from the colony that seabirds travelled for both short and long foraging trips. These data were only available from 20 of the 103 studies, covering 13 of our 50 species. For the remaining species considered, we had to estimate short-trip and long-trip foraging distances, either based on the reported minimum and maximum trip distances or based on the reported mean maximum distance for all foraging trips. This may have decreased the precision of the distance estimates used in our analysis.

Another limitation is the use of maximum chlorophyll concentration as a proxy for prey availability. This may not always be appropriate (Gremillet et al., 2008); for example, in cases where seabirds in large colonies deplete prey near the colony. However, this potential overestimation of patch quality near colonies would *decrease* the estimated difference in the quality of near and far prey patches; that is, the 'real' differences in patch quality available during short- and long-distance foraging may be larger than what we have reported. Thus, the relationship between dual foraging and the difference in patch quality in near and far patches may be stronger than we estimated.

Another limitation of this study is that we did not investigate the impact of fronts, shelf edges or other oceanographic features. Both fronts and shelf edges create upwellings of nutrient-rich water, which stimulates phytoplankton growth and reproduction (Huete-Ortega et al., 2011; Eichler et al., 2019). Zooplankton prey on phytoplankton (Noges, 1997), and fish feed on zooplankton (Ware and Thomson, 2005), creating areas of high fish abundance. Thus at-sea seabirds often forage near oceanographic features that produce nutrient-rich water which are likely to have high prey abundances (van Franeker et al., 2002), and this would be a valuable metric to include in the analysis. While some of these oceanographic features would be visible as high chlorophyll areas in our analysis, we would not be able to determine which oceanographic features they were.

5.6 Conclusion and future directions

We found that the probability of dual foraging increased with increasing differences in maximum chlorophyll concentrations accessible during short versus long foraging trips, providing support for predictions of the Central Place Foraging Theory that animals should only travel further to forage if more distant foraging locations offer better foraging conditions. We also found that different seabird taxa have different rates of using the dual foraging strategy during chick-rearing, differences that may only be partially explained by differences in maximum chlorophyll concentrations accessible between short versus long foraging trips. This analysis is the first step in addressing core questions regarding how environmental conditions and taxa interact in driving breeding seabirds' foraging decisions. Large-scale data on fronts and other oceanographic features known to concentrate prey could be used in combination with chlorophyll data as additional metrics of prey abundance in future analyses. Additionally, colony size should be accounted for in future predictive models of prey abundance, as larger colonies are more likely to create Ashmole's halo and, thus, result in a greater mismatch between chlorophyll concentrations and prey abundance near the colony. Finally, the factors driving differences in the use of dual foraging across different seabird families should be investigated further; such work will help clarify the relative roles of external environmental stimuli and internal genetic and biological determinants in the selection and 'moulding 'of seabirds' foraging strategies.

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7. Author contributions

Jessica A. Phillips: Conceptualization (lead), identifying relevant papers and extracting information (lead), formal analysis (lead), Writing-original draft (lead), Writing review & editing (equal); **Annette L. Fayet**: Conceptualization (supporting), Methodology (lead), Formal analysis (supporting), Writing-original draft (supporting), Writing-review & editing (equal); **Tim Guilford**: Conceptualization (supporting), Methodology (supporting), Formal analysis (supporting), Writing-original draft (supporting), Writing-review & editing (equal).

8. Data availability statement

The code used in this analysis will be available on github upon publication (https://github.com/JAP2018/dual-foraging-analysis).

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Chapter 6

General Discussion

1. Introduction 216
2. Main results 216
3. Limitations 223
4. Recommendations for future research 227
5. Conservation implications for Balearic shearwaters in the UK 229
6. Conclusions 232
7. References 232

1. Introduction

This thesis provides new insights into the at-sea behaviour and distribution of several species of seabird. It identifies factors that influence seabird foraging decisions and describes how local habitat quality determines the foraging strategies breeding seabirds use to balance their own needs with the needs of their offspring. We obtained these results using three different techniques: 1) combining at-sea sightings of a critically endangered seabird with fish abundance and remote-sensed environmental data to predict their distribution in UK waters; 2) calculating foraging patch quality from GPS loggers and time-depth recorders (TDRs) deployed on penguins to investigate how it changed with distance to the colony and across the breeding season; and 3) a systematic review of the seabird literature to identify the effects of local habitat quality on the use of the dual-foraging strategy across taxa. This chapter summarizes our main results, discusses their relevance to the wider literature, examines the limitations of the methods used, suggests directions for further research, and, based on the results of Chapter 2, describes the conservation implications of the results for Balearic shearwaters in the UK.

2. Main results

2.1 Relative importance of oceanographic and prey availability variables in predicting the at-sea movements of seabirds

Understanding how oceanographic conditions and prey distributions affect seabird distributions at sea has been a longstanding question in seabird ecology, but associations between seabirds and their prey have been surprisingly hard to prove (but see Fauchald et al., 2000; reviewed by Cox et al., 2018). In this thesis, we investigated the environmental drivers of seabird distributions at sea in both non-breeding (Chapter 2) and breeding seabirds (Chapter 4) by evaluating the association of seabird distributions with static and dynamic oceanographic variables and prey abundance. We directly compared the distribution of non-breeding Balearic shearwaters counted from

vessels with bio-acoustics data of prey abundances collected simultaneously from the same vessel (Chapter 2). However, in our analysis of chick-rearing macaroni penguin foraging preferences, we were unable to directly investigate the relationship between krill abundance and foraging behaviour due to temporal and spatial mismatch of the foraging and prey abundance data (Chapter 4). Nevertheless, we were able to identify oceanic variables that predicted penguin foraging locations and krill abundance. However, even when foraging and prey data were collected simultaneously, as was the case for the Balearic shearwater survey (Chapter 2), oceanic variables were better predictors of Balearic shearwater distributions than abundances of individual fish species.

There are several potential explanations for this finding. Firstly, the mismatch between fish abundance and foraging location could have occurred because the acoustic measurement of fish abundance excluded the top 12 meters of the water column, thereby excluding the main foraging depth of Balearic shearwaters (Meier et al., 2015). Fish abundance within the main foraging depths of Balearic shearwaters may have been better predictors of their distributions at sea. Secondly, a variable that measured overall fish abundance, including all fish species, may have had better predictive power, as it would portray prey abundance overall. Unfortunately, we could not calculate this as Mackerel had a different acoustic signature than the other species. Thus the units for their abundances were not comparable with that of other species. Thirdly, prey may engage in anti-predator movements (Crook and Davoren, 2014), which, if present, could have reduced our ability to detect fine-scale associations between Balearic shearwaters and their prey. In support of this suggestion, some researchers hypothesize that the lack of fine-grain knowledge of prey distributions leads to mismatches between predator and prey associations (Gremillet et al., 2008). Our findings reaffirm the difficulty of identifying spatiotemporal relationships between mobile marine top-predators and their prey (Fauchald, 2009). Although direct measurements of prey distributions have, in theory, the highest potential of shedding new light on how seabirds' movements at sea are driven by prey availability, currently available measures of prey distribution are unable to provide the high-resolution data on dynamic changes in prey distributions at the depths accessible to different species of seabird that would be required to really understand how prey availability drives fine-scale seabird

movements. However, chlorophyll-a remains a useful proxy of habitat quality for analyses across large or global scales.

2.2 Drivers of dual foraging in chick-rearing seabirds

While dual foraging in breeding seabirds is assumed to occur only when the quality of foraging grounds near the colony are insufficient to provide for the needs of both adults and chicks (Chaurand and Weimerskirch, 1994; Granadeiro et al., 1998; Weimerskirch, 1998; Weimerskirch and Cherel, 1998), the drivers of dual foraging are not well understood. In the systematic review of dual foraging in seabirds (Chapter 5) we found that the likelihood that chick-rearing seabirds use a dual foraging strategy increased with expanding differences in maximum chlorophyll concentrations available for foraging at short versus long (but reachable) distances from the colony, in other words, the better the foraging habitat quality at further distances compared to habitat close to the colony, the more likely birds were to engage in dual foraging. This provides convincing evidence that habitat quality influences whether or not chick-rearing seabirds employ dual foraging. However, we also found significant differences in the use of dual foraging across taxa. For instance, penguins were significantly less likely to employ dual foraging than shearwaters and petrels (Procellariidae). Indeed we found no evidence of dual foraging in either chinstrap penguins at the South Orkney Islands (Chapter 3) or macaroni penguins in South Georgia (Chapter 4). Superior habitat quality at further foraging patches may be a pre-requisite for seabirds to travel on longer foraging trips – as predicted by the Central-Place Foraging theory (Houston and McNamara, 1985; Cuthill and Kacelnik, 1990; Waite and Ydenberg, 1996) – but other factors such as the resilience of chicks against starvation probably also play a role in determining how widespread this strategy is across seabird taxa (Ropert-Coudert et al., 2004). Abundant fat storage in albatross and shearwater chicks (Warham, 1990) may make them more resilient to starvation when not fed for longer periods, so in terms of chick survival the dual foraging strategy may be less costly for shearwaters than for penguins. Also penguins travel more slowly than other seabirds, which limits the distance they can travel before chick starvation.This may explain why dual foraging is more common in shearwaters than penguins.

For both chinstrap penguins in the South Orkney islands over four breeding seasons (Chapter 3) and macaroni penguins at Bird Island, South Georgia in one season (Chapter 4), we found no evidence of a bimodal distribution of the maximum distance from the colony of foraging trips, and, thus, no evidence for the use of dual foraging during chick-rearing. This lack of dual foraging occurred in an environment in which habitat quality (as measured by the Index of Patch Quality (IPQ)) improved with increasing distance from the both chinstrap (Chapter 3) and macaroni penguin colonies (Chapter 4), that is, when there was evidence for the existence of Ashmole's halo surrounding the colonies. Taken together, the findings from Chapters 3 and 4 suggest that factors other than prey depletion near the colony, such as how likely chicks are to starve if not fed for long periods, play a role in whether seabirds use the dual foraging strategy.

Despite the lack of evidence for use of the dual foraging strategy by macaroni penguins, we found that they foraged at higher-quality patches when foraging for themselves than when foraging for their offspring. This may be because they are limited to forage at lower quality feeding grounds when foraging for offspring, as prey captured at distant, high-quality feeding grounds would likely be digested before the return to the colony. Even among birds that use the dual foraging strategy, the division of chick provisioning and self-provisioning is not binarily split between short trips and long trips. For example, Shoji and colleagues (2015) found that Manx shearwaters returning from long self-provisioning trips still fed the chicks when they returned. Instead, foraging trip distance tends to be mediated by trade-offs between chick and adult condition (Weimerskirch, 1998; Weimerskirch and Cherel, 1998; Ochi et al., 2010; Wischnewski et al., 2019). Adult condition was the sole determinant of foraging trip duration in short-tailed shearwaters *Puffinus tenuirostris* (Weimerskirch and Cherel, 1998) and sooty shearwater *Ardenna grisea* (Weimerskirch, 1998), whereas chick condition was the sole determinant of trip distance in Manx shearwaters *Puffinus puffinus* (Wischnewski et al., 2019). In Streaked shearwater *Calonectris leucomelas*, both adult and chick condition were found to impact trip duration (Ochi et al., 2010).

2.3 Drivers of spatial and temporal variation in habitat quality around breeding colonies

Theory predicts that seabirds in large colonies will create a zone of prey depletion around the colony, known as "Ashmole's halo" (Ashmole, 1963; Birt et al., 1987). In support of this theory, we found that patch quality, derived from the depth profiles of foraging dives, improved with increasing distance from the colony in both chinstrap and macaroni penguins (Chapters 3 and 4). We were unable to test for the existence of Ashmole's halos around colonies studied in Chapter 5, as we used chlorophyll as a metric of habitat quality in this global review, and prey depletion in upper trophic levels will not be reflected in chlorophyll levels. Our results in Chapters 3 and 4 are similar to findings in razorbills as measured by the same Index of Patch Quality (Shoji et al., 2014) and to evidence that the density of benthic fish increased with distance from a double-crested cormorant colony (Birt et al., 1987). This indicates that there are better foraging opportunities for penguins further from the colony, potentially justifying the higher costs of travel associated with longer foraging trips. Future research could use penguin-borne cameras to estimate patch quality (Fayet and Houston, 2021) and test for evidence of Ashmole's halo.

Ashmole (1963) predicts that prey near the colony will be depleted over time in large colonies as seabirds continue to feed during the breeding season. However, this is *not* what we found in chinstrap penguins breeding in the South Orkney Islands, where the quality of near-colony prey patches improved over the breeding season (Chapter 3). One possible reason for this unexpected finding could be that chinstrap penguins time their reproduction so that the period of maximum energy requirement in late chick-rearing coincides with maximum resource availability in the environment, as reported for many other birds (Lack, 1968; Crick et al., 1997; Crick and Sparks, 1999). However, our findings for macaroni penguins supported Ashmole's hypothesis: the quality of prey patches used were poorer in crèche than in the earlier brood period (in Chapter 4). This is likely due to a combination of inter- and intra-specific competition. South Georgia is home to numerous central-place foraging krill-predators, with macaroni penguins and Antarctic fur seals *Arctocephalus gazelle* being the top avian and mammalian krill-predators of the region (Barlow et al., 2002). With

approximately ~1 million breeding pairs of macaroni penguins (Trathan et al., 2012) and ~4 million breeding individual Antarctic fur seals (Waluda et al., 2010; Trathan et al., 2012; BAS unpublished data), breeding sympatrically and synchronously (Waluda et al., 2010) on South Georgia, both species likely contributed to the near-colony prey depletion during breeding. Gentoo penguins *Pygoscelis papua*, light-mantled sooty albatross *Phoebetria palpebrata,* black-browed albatross *Thalassarche melanophris,* grey-headed albatrosses *T. chrysostoma* and white-chinned petrels *Procellaria aequinoctialis,* which also breed sympatrically with macaroni penguins on South Georgia (Mori and Boyd, 2004b; Phillips et al., 2005) may also contribute to the near-colony prey depletion to varying degrees. The deterioration in prey availability over time could also be explained by temporal changes in prey availability unrelated to foraging behaviour (Deagle et al., 2008). Ashmole's hypothesis of prey depletion (1963) was originally proposed for seabird colonies in tropical waters where productivity is lower and less predictable than in polar waters (Longhurst and Pauly, 1987; Weimerskirch, 2007), though prey depletion near colonies of seabirds has also been reported at higher latitudes (Furness and Birkhead, 1984; Elliott et al., 2009). Taken together, the results from Capter 3 and 4 provide evidence that krill-eating predators can create zones of prey depletion around their colonies during breeding, though natural variation in prey availability during the breeding period may influence the severity of the depletion of prey near the colony.

To assess the relative importance of intraspecific competition and unrelated temporal changes in prey availability in the creation and dynamics of Ashmole's halo surrounding colonies of seabirds, future research could combine tracking seabird foraging movements throughout the season with ongoing surveys of prey abundance throughout the entire breeding season in areas within and just beyond the range of seabird foraging trips. In such a study, if prey abundance changes at similar rates in both locations, it could be assumed that intraspecific competition does not substantially affect prey availability, though parallel increases or decreases in prey availability at both locations would indicate natural temporal changes in prey availability unrelated to foraging. Alternatively, if prey abundance near the colony declined while abundance outside of the foraging range remained unchanged (Bonal and M. Aparicio, 2008), the change could reasonably be attributed to intra- and inter-specific

competition by central-place foraging krill predators. If prey abundance decreased in both locations but more quickly near the colony (or increased in both locations but more slowly near the colony), it would be likely that both intraspecific competition and unrelated temporal changes play independent roles. Interspecific competition from sympatric seabirds feeding on similar prey, if any, should also potentially be considered (Lynnes et al., 2002).

2.4 Validation of IPQ

Few studies have validated the use of the IPQ as a measure of the quality of prey patches. This thesis provides new evidence that the IPQ is an appropriate proxy for patch quality in penguins. For both chinstrap and macaroni penguins (Chapters 3 and 4) we found that the IPQ increased significantly with the vertical distance travelled on the bottom phase of foraging dives, a measure of the amount of 'wiggles' in the dive. Previous studies in different species attribute this behaviour to the active pursuit of prey (Adélie penguins (Rodary et al., 2000), emperor penguins (Kirkwood and Robertson, 1997; Zimmer et al., 2010), Magellanic penguins (Simeone and Wilson, 2003), and king penguins (Bost et al., 2007)). We also found that the IPQ of a diving bout increased significantly with the number of dives in the bout for both chinstrap and macaroni penguins. This finding both echoes the findings of Mori and colleagues (2002) on Brünnich's guillemots and provides a second empirical test of their hypothesis about optimal foraging strategies which posits that seabirds should perform more foraging dives in higher quality prey patches (Mori et al., 2002). Furthermore, in both species we found that foraging dives occurring in bouts had significantly higher IPQ than individual foraging dives that were not part of foraging bouts. This suggests that penguins were more likely to make further foraging attempts in the same location when they encountered higher patch quality during a dive. In combination, these three methods of validating IPQ across two penguin species from a total of five colonies support the validity of IPQ as a measure of patch quality. However, since we used dive data to calculate the IPQ, these three measures of the validity of IPQ are not fully independent of the measure itself. More independent validations of IPQ, such as using camera data to compare observed prey abundance with the IPQ measure, are needed to definitively confirm the validity of the

IPQ as a proxy for patch quality in diving animals. This has already been done successfully in Weddell seals by Mori and colleagues (2005), who found that IPQ correlated with prey abundance measured by on-board cameras; and in fur seals by Mori and colleagues (2004a), who found that IPQ correlated with krill abundance measured by hydro-acoustic surveys. In one of our studies (Chapter 4) we aimed to conduct such a validation by deploying video cameras on four macaroni penguins, but unfortunately, the cameras all failed, so we were unable to provide this validation.

In this thesis we excluded foraging dives occurring in periods over one (Chapter 3) or two (Chapter 4) without GPS data. While this improved the accuracy of the GPS locations of the dives remaining in our analyses, which is important when calculating differences in IPQ at different distances to the colony, this also reduces our sample sizes. As the lack of GPS fixes is likely associated with diving behaviour (Tomkiewicz et al., 2010), we may be excluding periods of continuous foraging dives in high-quality areas or excluding periods of fast travelling dives in which opportunistic foraging may occur. Other studies have used linear interpolation (Whitehead et al., 2016; Sabrina et al., 2020) or random walk models (Clewlow et al., 2019) to simulate dive locations during longer periods without GPS data. Location accuracy and sample size should be weighed against each other when determining dive location inclusion criteria.

3. Limitations

3.1 Lack of data on prey availability

A limitation of our work is that we did not have data that reflected the amount of prey available to seabirds at the locations and times when they were foraging. This limited our ability to directly access how seabird distributions are influenced by the prevalence of their prey. As presented in Chapter 2, our prey data reflected the abundance of fish in depths of the water column beyond the reach of most Balearic shearwater dives, thus we do not know whether prey abundances in the depths accessible to Balearic shearwaters would have been good predictors of their distributions. Similarly,

the krill acoustic survey data used in Chapter 4 were not collected at the exact place and time of the foraging trips of breeding macaroni penguins included in our study, preventing direct comparison of krill abundance with penguin foraging. In an ideal world, prey abundance data would be available both at the exact locations, depths, and times foraging occurs and at other locations, depths, and times where foraging does not occur. As discussed in an earlier section of this discussion, such data are rarely available.

3.2 Chlorophyll as a measure of habitat quality

In Chapters 2 and 4, we found that several oceanographic variables were good predictors of seabird distributions at sea. One of these variables was chlorophyll, which we also used in Chapter 5 as a proxy measure of prey availability. Chlorophyll-a concentration is a measure of primary production. Nutrient-rich water promotes the primary production of phytoplankton (Abreu et al., 1995), phytoplankton attracts zooplankton (Noges, 1997), and zooplankton attract the fish prey that seabirds forage for (Ware and Thomson, 2005). Remotely-sensed estimates of chlorophyll concentrations have been widely used as a proxy of foraging habitat quality and to investigate environmental drivers of at-sea movements of numerous marine top predators, including marine mammals, seabirds, turtles, and predatory fish (Fayet et al., 2015; Guzman et al., 2019; Kane et al., 2020; Speakman et al., 2020; Vayghan et al., 2020). There are, however, several potential limitations to using chlorophyll concentrations as proxies for prey abundance. First, remote-sensed chlorophyll concentrations measure the levels of phytoplankton in the upper layers of the ocean (Raitsos et al., 2013), but top marine predators do not consume phytoplankton. They consume prey one to four trophic levels above phytoplankton (Barnes and Hughes, 1988). Thus the association of chlorophyll concentrations with prey abundance will be weaker for seabirds that feed at higher trophic levels. Second, the depletion of prey around breeding colonies by the seabirds (Ashmole's halo) will not be reflected in corresponding reductions in chlorophyll concentrations. Third, there can be temporal delays in the reactions of zooplankton and tertiary consumers to changes in phytoplankton levels (Suryan et al., 2012), creating time lags between peaks in phytoplankton, zooplankton, and fish.

Fourth, there can also be spatial mismatches between remote-sensed chlorophyll and zooplankton associated with high chlorophyll concentrations at depths beyond the detection of remote-sensing (Gremillet et al., 2008). Finally, the spatial mismatches between zooplankton and fish and between fish and seabirds (Gremillet et al., 2008) also need to be considered. Taken together, these limitations add noise to the associations between seabird distributions and remote-sensed chlorophyll-a concentrations.

Some studies have found that the variability in chlorophyll concentrations is as important a predictor of seabird distributions as mean chlorophyll concentrations (Henson and Thomas, 2007; Suryan et al., 2012). Frequent cycles of phytoplankton production and subsequent depletion by zooplankton may increase variation in remote-sensed chlorophyll concentrations, indicating areas of high abundances of zooplankton, which are favourable to tertiary consumers (Suryan et al., 2012). In Chapter 5, we used a dataset of global chlorophyll concentrations, which presented data in monthly averages, which limited our ability to investigate daily or weekly variations in chlorophyll concentrations. Future research using chlorophyll data with higher temporal resolution should compare the relationship of maximum chlorophyll concentrations and variability of chlorophyll concentrations with the use of different foraging strategies to identify the best predictor of seabird distributions.

Despite these limitations, chlorophyll-a concentrations can nonetheless serve as proxies for seabird foraging habitat quality. Fayet and colleagues (2015) found immature Manx shearwaters *Puffinus puffinus* gained less food per unit time while visiting regions with lower chlorophyll-a levels. In another study, Fayet and colleagues (2017) found that chlorophyll in winter habitat predicted Atlantic puffin *Fratercula arctica* breeding success the following season. Suryan and colleagues (2012) found that the frequency of chlorophyll peaks explained 90% of the variation in seabird distributions in the Gulf of the Farallones off central California, as well as 73% of the variation in seabird densities in the Southern California Bight in spring and 27% in summer. Given the difficulties

of directly measuring prey availability (see section 2.1), chlorophyll-a concentrations can provide an estimate of habitat quality that is comparable across locations (Suryan et al., 2012).

3.3 Unknown foraging gains

Given the logistic challenges of weighing parents and chicks after each foraging trip, and to minimise disturbance to tagged birds and their chicks, in Chapters 3 and 4, we were not able to measure chick and adult mass before and after each trip. This would have helped us distinguish whether penguins take separate trips which prioritize self-feeding and chick-feeding as well as whether trip distances were driven by chick or adult condition, or both. Data on parents' weight changes and mass of food fed to chicks after trips would have also provided more information for us to distinguish the functions of long and short trips in Chapter 5. Some studies have found chick-rearing seabird foraging trip distance is driven solely by adult condition (Weimerskirch, 1998; Weimerskirch and Cherel, 1998), solely by chick condition (Wischnewski et al., 2019), or is mediated by both (Ochi et al., 2010). However, whether the needs of the parent, offspring or both determine foraging trip length is far from established (Wischnewski et al., 2019) and more research is needed to understand how chick and adult condition mediate trip distance and duration and whether the relationship differs across seabird taxa.

In the absence of such data, in Chapter 4 we assumed that foraging dives performed more than 48 hours before returning to the colony were self-provisioning dives and those that occurred 48 hours or less before returning to the colony were potential chick-provisioning dives. This assumption was made based on maximum stomach capacity and digestion rate of macaroni penguins (Croxall et al., 1993; Cresswell et al., 2007), which indicates that prey captured more than 48 hours before returning to the colony will be digested before the penguin returns to its chick while prey caught within 48 hours of return can be fed to chicks. This criterion has a number of inherent limitations, however. Firstly, parents may still forage for themselves within 48h of returning to the colony. However, we cannot establish what proportion of foraging dives performed within 48 hours of returning to the colony are for the parent and chick. Consequently, at best, we are comparing dives for

the parent with dives that could be either for the chick or parent. Secondly, penguins can halt their digestion (e.g., Thouzeau et al., 2004). However, a study by Green and colleagues (2007) which supports our assumption, found that macaroni penguins digest prey caught in the early and middle parts of their trips and halt digestion before the return journey to feed chicks largely undigested prey caught towards the end of the trip. Other studies have also found that penguins provision chicks mostly with undigested prey caught later in the trip (Wilson et al., 1989; Peters, 1997; Peters, 2004; Thouzeau et al., 2004). Together, these studies support our assumption that prey caught more than 48 hours before they return to the colony is digested by adults. Data on changes in parent and chick weights after foraging trips would provide essential information on the function of each trip, making it possible to develop a more definitive method of distinguishing self-feeding, chick-feeding, and combined self- and chick-feeding foraging trips and helping us gain a better understanding of drivers of foraging strategies in chick-rearing seabirds. This type of data would also allow a systematic review of dual foraging (such as Chapter 5 of this thesis) to draw more neuanced conclusions about how parents make decisions on when to prioritize chick feeding and when to prioirtize self provisioning, rather than treating the occurance of dual foraging as binary.

4. Recommendations for future research

I have several recommendations for future research on predator-prey associations based on the findings from the projects undertaken as part of this thesis and on the difficulties that arose when conducting these studies. First, when investigating the relationship between the distribution of prey and the foraging behaviour of a specific marine predator, it is important to take account of the diving depths of that predator when collecting data on the prey available to the predator. Second, given the dynamic nature of prey abundance and predator movements, assessment of the predator-prey association should ideally be based on measurements of prey abundance and predator distributions that occur in the same location, at the same depth, and over the same time period.

While this thesis provides new insight into drivers of dual foraging in seabirds, much remains to be understood about when and why this strategy arises. We identified several factors that potentially influence seabirds' foraging behaviour that should be considered in future research about seabirds' use of the dual foraging strategy. Specifically, investigations of drivers of the dual foraging strategy across seabird species should consider several potential moderators of the influence of differential prey availability for short- and long-distance foraging, including 1) colony size, which may affect the degree of prey depletion near the colony; 2) travel costs, which determine the net energy gain of long-distant foraging; 3) fat storage capacity of chicks, which directly affects the risk of starvation during long periods without feeding; 4) predation risk; and 5) biogeographic area, which is associated with overall prey availability and predictability. Multiple factors can simultaneously influence seabirds foraging strategies. For example, all little auks from six colonies reported in 12 studies assessed in our systematic review used the dual foraging strategy. We postulate that high densities at breeding colonies, very high travel costs, and the ability to store more prey in their gular pouch than other auks could carry in a single trip made little auks more likely to deplete prey near their colonies. This would thus necessitate longer trips to find adequate prey to provision themselves and their chicks. Thus travel costs and colony size can simultaneously influence seabirds' foraging decisions, a relationship that needs to be assessed in future investigations, both for tracking studies and reviews investigating prey depletions around different colonies. We postulate that the fat deposits in shearwater, albatross, and petrel chicks buffer them against starvation and, thus, reduce the risk to chicks when their parents go on long trips, but we do not provide an actual test of this hypothesis. Investigating whether parents of chicks with higher fat reserves are more likely to use the dual foraging strategy, both within and between species, is a potentially fruitful area for future research. We also postulate that albatrosses forage over such large distances that there is a certain amount of self-maintenance built into all trips, and they are less likely to embark on short trips near the colony. Cross-taxa examination of the relationship between foraging trip distance and the levels of self-provisioning on trips would be an interesting question for future research.

While we have not done a full phylogenetic analysis of dual foraging in seabirds, preliminary work on a subset of 30 of the 50 species considered in our systematic review indicates that dual foraging is not completely phylogenetically confounded. The three patterns of dual foraging in seabirds – always use dual foraging, selectively use dual foraging, and never use dual foraging – all occur multiple times across the phylogenetic tree. Further research is needed to understand how phylogeny influences dual foraging in seabirds.

5. Conservation implications for Balearic shearwaters in the UK

In Chapter 2 we employed a model based on oceanographic variables to estimate the spatial distribution of Balearic shearwaters in southwestern UK waters, estimates which make it possible to overcome a major stumbling block in advancing the conservation of one of the most endangered species to depend on UK waters. The results of this study have important implications for protecting Balearic shearwaters in the UK, either through a Special Protection Area (SPA) or through regulations on fisheries practices in the areas of high probability of presence. As part of my thesis, I engaged in policy-related activities to protect seabirds and worked on this project to protect Balearic shearwaters in collaboration with relevant conservation organizations, primarily Natural England and MarineLife.

Population viability models predict that Balearic shearwaters – the most endangered seabird in Europe – will become extinct in the next few decades without action (Oro et al., 2004; Genovart et al., 2016). Bycatch in fishing gear is a leading cause of decline (Oro et al., 2004; Louzao et al., 2006; Genovart et al., 2016; Cortes et al., 2017), so reducing bycatch is essential to helping the species recover (Cooper et al., 2003; Oro et al., 2004; Louzao et al., 2006; Louzao et al., 2011; Abelló and Esteban, 2012; Genovart et al., 2016). However, fishery discards often make up a substantial portion of Balearic shearwater diets, particularly during the late breeding season when the surface waters of the Mediterranean become depleted, but also during the rest of the breeding season and moulting and wintering to lesser extents (Arcos and Oro, 2002). When designing fisheries management strategies to

protect Balearic shearwaters, it is important to simultaneously consider the effects of both bycatch and discards on their short-term and long-term viability (Oliveira et al., 2015).

The number of Balearic shearwaters in southwest UK waters during the post-breeding period has been increasing since the 1990s (Wynn and Yésou, 2007; Darlaston and Wynn, 2012; Jones et al., 2014), possibly due to changing prey distributions (Wynn et al., 2007; Wynn et al., 2008; Luczak et al., 2011; Jones et al., 2014) associated with increasing sea surface temperatures (Wynn et al., 2007; Luczak et al., 2011). Nevertheless, the UK has not yet taken any steps to protect the species. Based on the timing of the surveys reported in Chapter 2, most of the birds identified in UK waters were immature Balearic shearwaters. Prior to this study little was known about the at-sea distribution of immature Balearic shearwaters, and no country had instituted conservation measures specifically targeted at immature Balearic shearwaters. However, demographically informed population viability models suggest reducing bycatch of immatures could increase their survival rates from 0.4 to 0.6, resulting in a corresponding increase in the total population growth rate from 0.856 to 0.972 (Genovart et al., 2016). Thus mitigating bycatch at the key foraging grounds for immature Balearic shearwaters in the area we identified at the Celtic Sea front could improve the population growth rate as a whole. Balearic shearwater survival rates would have to be on par with those of closely related Procellariforms for the population growth rate to exceed one (Genovart et al., 2016). There are, as yet, no reports of Balearic shearwater bycatch in UK waters of which we are aware, but there are reports of non-breeding Balearic shearwaters bycaught off the coast of Portugal in Purse seine and Setnets (Oliveira et al., 2015). There is mounting evidence of frequent mortality of Balearic shearwaters due to bycatch and of relatively frequent ‘mass’ mortality events killing over a hundred birds at once (Genovart et al., 2016). Bycatch of Balearic shearwaters is usually linked to the use of demersal longlines (ICES, 2013; Cortes et al., 2018), though other fishing gear including trawlers and purse-sein vessels have also been implicated (Oliveira et al., 2015). Developing conservation policies that focus on reducing bycatch from these types of fishing practices where Balearic shearwater bycatch is known to occur should be a priority.

In 1979, the Birds Directive (amended in 2009) (Directive 2009/147/EC) established a regime to protect birds occurring naturally in the European Union, including the classification of SPAs for particularly threatened species. In England, Wales, and Scotland, SPAs are classified under The Wildlife and Countryside Act (1981) and The Conservation of Habitats and Species Regulations (2010). One requirement for an area to be considered for selection as a SPA is that it must protect 1% of the national population of the species (JNCC, 2020). While this criteria generally applies to species breeding in the country, Article 4 of the EU Birds Directive (Directive 2009/147/EC) requires member states to classify suitable territories as SPAs for "regularly occurring migratory specices … as regards their breeding, moulting and wintering areas and staging posts along their migration routes". So there is not a requirement for the species to breed in the UK to benefit from a protected area. Indeed, there are several protected areas in the UK that protect the wintering areas of waders and waterfowl (Ramsar, 2021). Now that the UK has exited the EU, it is critical that the ethos of the EU Birds and Habitat Directives are not undermined going forward. This will ensure species living in the UK receive a level of protection that is at least on par with other countries in Europe.

There is currently no estimate of the total population of Balearic shearwaters in UK waters, posing a barrier to establishing protected areas in the UK for Balearic shearwaters (and for other rare species for which there are no estimates of the total national population). Despite the lack of UK-specific estimates, there are global population estimates for Balearic shearwaters, which range from 10,000 to 30,600 individuals (Ruíz and Martín, 2004; Arcos, 2011; Arroyo et al., 2016). Based on the highest global population estimate of 30,600 individuals (Arcos, 2011) – which is an estimate of the entire population size inferred from observed densities on the Iberian Mediterranean shelf in November and December - our study indicates that the study area in the UK annually supports between 2% and 23% of the global population of Balearic shearwaters. Our lowest estimated proportion, 2% of the global population, is, by definition, above 1% of the number of Balearic shearwaters in the UK, so it *should* meet the requirement for the creation of a SPA, even in the absence of a specific estimate of the national population in the UK. To allow for the creation of protected areas in cases such as the Balearic shearwater for which there are no nation-specific

population data, there should be a policy change that allows the use of the estimated proportion of the global population (for example, at least 0.5% of the global population) to meet the 1% national population criteria. Such a policy change to accommodate the lack of national population estimates for rare species would reduce barriers to protecting the most threatened species. Future research estimating the latest global Balearic shearwater numbers would provide critical information to inform conservation policies.

6. Conclusions

This thesis provides empirical evidence for Ashmole's halo, showing that krill-eating predators in the South Orkney Islands and South Georgia can deplete near-colony prey during the breeding season. It also shows that near-colony prey depletion does not necessarily worsen over the breeding season, as seabirds time their reproduction to make the most of seasonal abundances in food availability. This thesis also provides the most complete understanding of Balearic shearwater distribution in UK waters available to date, identify an important foraging ground at the Celtic Sea front. It also shows that the probability of dual foraging amongst seabirds increases with expanding differences in the quality of short-distance and long-distance foraging patches. Overall, the findings of this thesis advance our understanding of the environmental drivers of seabirds' foraging distributions and provide valuable information for their conservation. Future research on the downstream effects of prey depletion around breeding colonies could shed light on its role in regulating population sizes and how it impacts inter- and intra-specific competition.

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