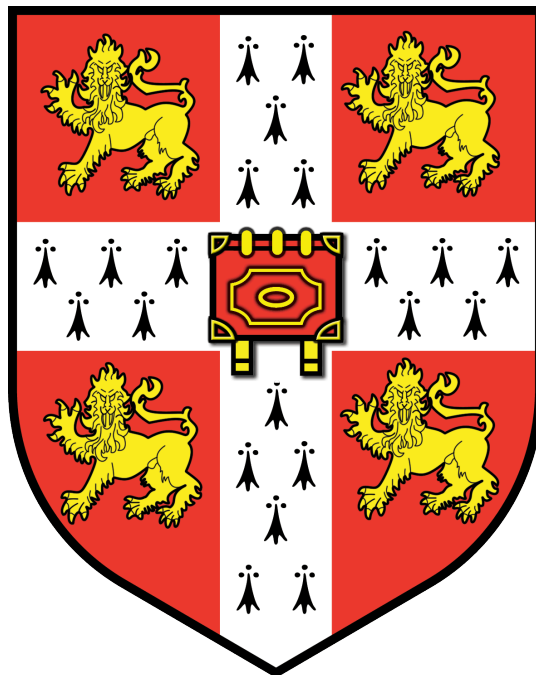# The Sea is the Limit: Foraging Ecology of Breeding Antarctic Procellariiformes

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DECLARATION

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the preface and specified in the text. It is not substantially the same as any work that has already been submitted before for any degree or other qualification except as declared in the preface and specified in the text. It does not exceed the prescribed word limit for the Biology Degree Committee.

Lily Kate Bentley
Cambridge
October 2022

For Mum, who should have been here to see this finished,
and for Walter, who was here instead.

Summary

In the dynamic marine environment, highly mobile predators are expected to select profitable foraging areas, especially when provisioning young in addition to meeting their own energy needs. Knowing how and where animals choose to forage is not only important to advance ecological theory, but also to assess and mitigate the impact of anthropogenic threats. In this thesis I examine the breeding-season foraging behaviour of several of the Procellariiformes, a wide-ranging, long-lived group of seabirds, many of which have experienced steep population declines since the mid-20th century. Advances in biologging technologies over the last four decades have made it possible not only to accurately track individual movements, but also to identify important behaviours at sea. In my first data chapter (Chapter 2), I combine data from multiple tag types to describe diving behaviour in three albatross species, and discuss the implications for both foraging ecology and bycatch susceptibility. Moving from foraging capability of the individual to foraging preferences at the level of genus, in Chapter 3 I analyse the divergent niches of a summer- and a winter- breeding species of *Procellaria* petrel. Here I compare the habitat preferences of Grey Petrels and White-chinned Petrels breeding at Gough Island and South Georgia, respectively. Using high-resolution remote sensing environmental data, I identify divergent foraging preferences in dynamic habitats. Finally, in Chapter 4, I compare habitat preferences and accessibility between the two species of *Phoebetria* albatrosses across six colonies. While most studies of habitat preference consider only a single species or site, here I investigate whether closely-related species inhabit the same ecological niche at sympatric and allopatric colonies throughout their range. I show that Light-mantled Albatrosses have a consistent foraging niche, whereas Sooty Albatrosses select different habitats in sympatry and allopatry. I then discuss the impact of interspecific competition on plasticity in habitat preferences in general. Overall, my thesis examines diverse aspects of seabird foraging ecology from the individual to community level, discusses habitat preferences (and their potential flexibility) in relation to species' evolutionary history and as drivers of community structure, and considers the implications for conservation planning.

Acknowledgements

It is not hyperbole to say that without the support of the people around me, this thesis would simply not exist. Losing a parent and becoming a parent on either side of a global viral pandemic has made the last five years a more difficult journey than I ever could have imagined. Nevertheless, here we are – and so it remains for me to attempt to express the gratitude I have for those who helped me along the way.

Moving across the world to undertake a PhD with supervisors you've only met via Skype – how very dated – is a risk indeed. It has been an immense privilege to work with both of mine. Thanks to Richard Phillips for introducing me to an extensive network of collaborators, patiently answering my (many) questions about seabirds, and for (as far as I am aware) being personally acquainted with every albatross in the Southern Ocean. Thank you also to Andrea Manica, for methodological, ecological, and pedagogical insight; for your unparalleled ability to distill complex (and, let's be honest, often scattered) ideas to complete clarity; and for your support for everyone in the lab both as scientists and as people. Our families are your beneficiaries as much as we are.

Many thanks also to my departmental advisors Nick Davies and Mike Brooke, for their insight and discussions on progress reports over the last few years. My gratitude also to Bill Sutherland and Lucy Hawkes for a thoughtful, challenging and affirming viva experience. The Department of Zoology has been a wonderful place to work, and thinking about distant birds has been made much easier by the good company found within it. For this I thank my fellow ornithologists, Caitlin Frankish and Billy Mills, and more recently Lizzie Pearmain and Paul Whitelaw. My thanks also to Henry North for almost a decade of friendship, from late-night undergraduate assignments to our PhDs here. The tracking data used in this thesis was collected across many sites and years – I am grateful to all the fieldworkers, from the British Antarctic Survey and other organisations, who deployed and collected tags, as well as the collaborators who generously shared data with me.

By far the most incredible influences on my Cambridge life have been the multiple communities I have had the privilege to be part of. Thank you to Corpus Christi College, for creating a remarkable graduate community at Leckhampton – I will never forget my time living there and the people I met: Jonathan Cushenan, Kerry Mackereth, Jakob Lundwall, Barney Row, John Clark, and Jasmine Aslan, to name just a few. Thank you also to Tessa Milne: whatever they pay you, it's not enough! I will also be forever

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CHAPTER 1:   **Introduction**

1.1 Movement and foraging ecology

Decisions about where, when and how to move shape all aspects of the lives of mobile animals, from individual survival to population and community structure (Nathan et al. 2008). One key driver of movement is the search for food: understanding how animals make foraging decisions is therefore a fundamental question in ecology (Sutherland et al. 2013, Hays et al. 2016). In theory, foraging is expected to be optimised when animals are searching in a patchy environment (Pyke 1984, Fauchald 1999). Optimal foraging theories are, however, based on simplifying assumptions which often belie the complexities of ecological systems (Nathan et al. 2022). Additionally, research has tended towards measuring and describing movements of organisms without consideration of the role of internal state or the influence of the surrounding environment (Holyoak et al. 2008). It is therefore critical to combine real-world measurements of movement with considerations of the intrinsic and extrinsic (both environmental and organismal) drivers of behaviour when attempting to understand animal distributions (Holyoak et al. 2008, Nathan et al. 2008, Kot et al. 2022).

Various constraints, be they physiological, ontogenetic, or ecological, influence realised foraging distributions in natural systems (Gilchrist et al. 1998, Spaethe et al. 2001, Shaffer et al. 2003, Green et al. 2005). A key constraint for many species is the requirement to return to a central place between foraging trips – this constraint affects many animals during the breeding season, when their energy needs are highest and their distributions are the most restricted within the annual cycle (Welcker et al. 2015). Adults are limited in how long they can be absent from the den or nest site due to the need to frequently feed young or to relieve a partner from guard, incubation or brooding duties (Orians and Pearson 1979, Kacelnik 1984, Burke and Montevecchi 2009, Jessopp et al. 2020), and theory predicts they should travel only the minimum distance that meets energy requirements when foraging (Schoener 1971). Individuals are only expected to forage at more distant sites if prey are more accessible (either more abundant, of higher quality, or there is reduced competition) (Houston and McNamara 1985). Understanding why some animals choose to travel thousands of kilometres despite a central-place

constraint is, therefore, of ecological interest, given the high cost of choosing unprofitable patches. Beyond choice of location, theory predicts that foraging constraints also influence phenology, i.e. that peak energy requirements should align with peak resource availability (Lack 1954, Perrins 1970, Van Balen 1973). There is evidence that temporal mismatches between peak prey availability and high energy demand during reproduction lead to reduced breeding success (Perrins 1970, Regular et al. 2014), and as such there is strong selection for most animals to breed during the spring and summer when resources are plentiful (Jönsson 1997, Durant et al. 2007). Why, then, we observe some species breeding in winter is largely unclear, though some have suggested these species are taking advantage of multiple peaks of resource availability, or avoiding competition (Dilley et al. 2019, Taylor et al. 2019).

1.2 Habitat preference and selection

By combining animal positions with environmental data it is possible to categorise utilised or preferred habitats beyond simple geographic space (Guisan and Zimmermann 2000, Patrick et al. 2014). While traditional home-range estimates remain useful, particularly for management, they do not provide insight into the processes by which observed distributions arise (Kie et al. 2010). Increasingly high-quality remote sensing data have become available in recent years, such that we can identify the particular environmental conditions in which individual foraging trips occurred (Dierssen 2010, Lellouche et al. 2018). We can then quantify how animals forage in heterogenous environments by comparing the proportion of habitat selected to what is available in the surrounding area (Rosenberg and McKelvey 1999, Boyce et al. 2002), with any habitat use that is disproportionate to availability defined as a preference (Johnson 1980). Models which account for availability by considering the movement capability of the species in question are thought to provide the most robust representation of habitat preferences (Aarts et al. 2008). While resource selection functions are often validated by how well they can predict the location of animals in new landscapes (Boyce et al. 2002), they are also useful in determining which environmental signals are most relevant for particular populations, which in turn is critical for predicting how animals may respond to climate change (Beyer et al. 2010).

Investigations of how animals use heterogenous habitat allow us to draw conclusions not only about foraging behaviour and energetic trade offs, but ultimately about fitness (Morris 2003, Beyer et al. 2010, Gaillard et al. 2010). However, there are gaps in our understanding of how habitat preferences link to evolutionary processes. The extent to which habitat preferences vary (or not) across breeding ranges remains a key question for ecologists: in particular, the way in which processes such as interspecific competition modulate realised niche is not fully understood (Svärdson 1949, Connell 1980, Miller et al. 2009). While there has been extensive theoretical discussion on these questions (Davic 1985, Schmidt et al. 2000), studies in natural systems are less common.

1.3 Study system and methods overview

1.3.1 The Procellariiformes

Procellariiform seabirds are a useful group of organisms for investigating habitat preferences in the marine realm. This order comprises four families: Diomedeidae (Albatrosses), Procellariidae (Petrels and Shearwaters), Hydrobatidae and Oceanitidae (Northern and Southern Storm Petrels, respectively) (Handbook of the Birds of the World and BirdLife International 2022). In this thesis I examine the foraging ecology of multiple species within the Diomedeidae and Procellariidae (Fig. 1.1). These are long lived, highly k-selected, colonially breeding species that exhibit strong monogamy and philopatry, and raise only one chick every year (or every two years in the case of great albatrosses *Diomedea* spp., the *Phoebetria* spp. and some *Thalassarche* spp.) (Brooke 2004). They nest in densely populated colonies on oceanic islands, either on the ground or, in the case of most small petrels, in burrows or crevices, and take regular trips to sea to forage for themselves and provision their chicks (Brooke 2004). These high population densities lead to high intra- and interspecific competition for prey close to breeding colonies (Ashmole 1963, Furness and Birkhead 1984, Birt et al. 1987). It is well established that this competition can be ameliorated via niche segregation across multiple axes, including choice of foraging areas (Araya et al. 2011, Kiszka et al. 2011, Jiménez et al. 2017, Gulka et al. 2019, Pastore et al. 2021).

Figure 1.1: *Select study species discussed in this thesis. Top row: Light-mantled Albatross, © Jamie Coleman (Chapter 2, Chapter 4). Middle left: Grey Petrel, © Bryce Robinson (Chapter 3). Middle right: Sooty Albatross, © Stefan Schoombie (Chapter 4). Bottom row: White-chinned Petrel, © Jamie Coleman (Chapter 3). All images used with permission.*

Traditional ship-based survey techniques can provide data on distributions and abundances around colonies, but are subject to a range of sampling biases, including vessel-following behaviour, and do not usually allow the colony of origin, sex or age of individuals to be determined (Hyrenbach 2001). For a nuanced understanding of how seabirds select and partition foraging habitat, individual tracking is crucial; indeed, tracking has already demonstrated niche partitioning in multiple sympatric seabird species (Hyrenbach et al. 2002, Phillips et al. 2004, Weimerskirch et al. 2009, Navarro et al. 2013). Choice of foraging area is important in a dynamic ocean environment, where prey are spatiotemporally patchy (Russell et al. 1992, Jessopp et al. 2020). Tracking has shown that seabirds frequently associate with specific types of productive habitat, including shelf edges, upwellings, fronts and eddies (Skov et al. 2008, Wakefield et al. 2009, Bost et al. 2009). In addition, seabirds make direct commuting flights to areas where they subsequently forage, indicating that they know where to find food, likely based on past experience (Weimerskirch 2007).

In addition to being ecologically appropriate to investigate foraging habitat selection, many Procellariiformes are of conservation concern. Monitored populations of the Diomedeidae and Procellariidae decreased in size by 69.0% and 79.6%, respectively, from 1950-2010 (Paleczny et al. 2015). Further, 15 of the 22 albatross species are threatened with extinction (ranked as Vulnerable or higher on the IUCN Red List) (IUCN 2022). This is due to the impact of multiple anthropogenic threats, including introduced species (Wanless et al. 2007), plastic pollution (Wilcox et al. 2015), competition for resources and bycatch in commercial fisheries (Grémillet et al. 2018, Clay et al. 2019). While there are marine protected areas (MPAs) surrounding some seabird colonies, effective conservation also requires policy interventions at much wider spatial scales given their extensive distributions at sea (Yorio 2009, Péron et al. 2013, Hindell et al. 2020). In particular, knowing the depths at which procellariiform species forage is critical, as dive capability is inextricably linked to the likelihood of incidental mortality (Anderson et al. 2011). Mitigation measures such as heavier line-weighting, night setting and use of bird-scaring lines are effective in some fisheries, but assessing the effectiveness of line weighting, for example, requires data on hook sink speed relative to descent rates and dive depths of vulnerable seabirds, and for some species the only dive

data available are maximum depths published over 25 years ago (e.g. Prince et al. 1994). There is a paucity of high-resolution dive data obtained using time-depth recorders (TDRs, see biologging section below) in the Diomedeidae compared to other seabird orders (e.g. Shaffer et al. 2009, Matsumoto et al. 2012). Further, matching dive events to landings on the water and location allows us to develop a holistic understanding of at-sea foraging, which is lacking for many albatross species.

1.3.2   Biologging devices

There is a long history of biologging in seabird research: because many Procellariiformes are large-bodied and return reliably to their nest (so are easily recaptured), they have been extensively studied since the first animal-borne tracking devices were deployed (Phillips et al. 2007, Geen et al. 2019, Bernard et al. 2021). Indeed, the first successful avian tracking using satellite telemetry was undertaken on Wandering Albatrosses *Diomedea exulans* (Jouventin and Weimerskirch 1990). Studies of predator distributions were previously difficult to undertake in the southern oceans due to extreme seasonality, remoteness, and rough seas (Bost et al. 2009), but technological advances in recent decades mean that we can now remotely obtain detailed information about animal space-use and behaviour with relative ease (Block et al. 2011). Over the last four decades, various types of biologgers have provided insights into topics as diverse as individual consistency (analyses of repeated measures, see Phillips et al. 2017 for a summary), feeding (Wilson et al. 1992), stress responses (Müller et al. 2017), thermal physiology (Handrich et al. 1997), flight development (Yoda et al. 2004), and habitat preferences (see Wakefield et al. 2009 for a summary; Chapter 3, Chapter 4).

In this thesis I combine data from multiple types of animal-borne tags. Time-depth recorders (TDR) measure pressure, and can be used to characterise diving behaviour (Navarro et al. 2014, Chapter 2). Archival light-level geolocators-activity loggers (GLS) measure both ambient light – allowing for approximate locations to be calculated – and water immersion – identifying periods when the animal is dry and wet, and therefore in flight or resting on water (Kürten et al. 2019, Schoombie et al. 2022, Chapter 2, Chapter 3). Satellite tags identify the locations of animals on scales of metres (Global Positioning System, GPS) to kilometres (Advanced Research and Global

Observation Satellite, Argos) (Hazen et al. 2012, Wakefield et al. 2009, Chapter 2, Chapter 3, Chapter 4).

1.4 Thesis outline

The major aims of this thesis are to:

I. Quantify foraging behaviour in pelagic seabird species;

II. Identify characteristics of key foraging habitat during the breeding season, and understand extrinsic drivers of variation in habitat selection between species;

III. Compare preferred foraging habitats across species, genera, communities and breeding sites, to understand the relative plasticity of these preferences.

By understanding how, where, and in what kinds of environments pelagic predators forage we will better be able to mitigate their exposures to anthropogenic threats – the most important in this context being commercial fisheries. There are complex and interconnected relationships between threats, ecology, environment, and behaviour, that ultimately influence fitness – which is difficult to directly measure – see Figure 1.2 for an overview.

In **Chapter 2**, I characterise the diving behaviour of three albatross species breeding at Bird Island, South Georgia. I show that Black-browed Albatrosses *Thalassarche melanophris*, Grey-headed Albatrosses *T. chrysostoma* and Light-mantled Albatrosses *Phoebetria palpebrata* are infrequent, shallow, diurnal divers. I combine dive behaviour with GPS and immersion data to characterise activity levels and discuss my findings in the context of bycatch susceptibility and foraging ecology.

In **Chapter 3**, I compare the habitat preferences of two congeners: the winter-breeding Grey Petrel *Procellaria cinerea* and summer-breeding White-chinned Petrel *P. aequinoctialis*. I identify periods of active foraging and use remote sensing data to determine the environmental characteristics of key habitat areas for both species. Here I highlight the potential for extreme divergence in habitat preference within a genus, and

discuss the implications of this divergence for these species across their range, as well as for our understanding of breeding allochrony in general.

In **Chapter 4**, I investigate the influence of interspecific competition on habitat preference, using data from 87 Sooty and Light-mantled Albatrosses breeding in six sympatric and allopatric colonies. I establish a natural experiment by examining the foraging behaviour of each species breeding in the presence and absence of their congener, and show that while Light-mantled Albatrosses have consistent habitat preferences throughout their range, Sooty Albatrosses vary their habitat preferences in sympatry and allopatry.

In **Chapter 5**, I discuss my findings in the wider context of foraging ecology, consider their implications for conservation of pelagic seabirds, and explore further areas of research arising from this thesis.
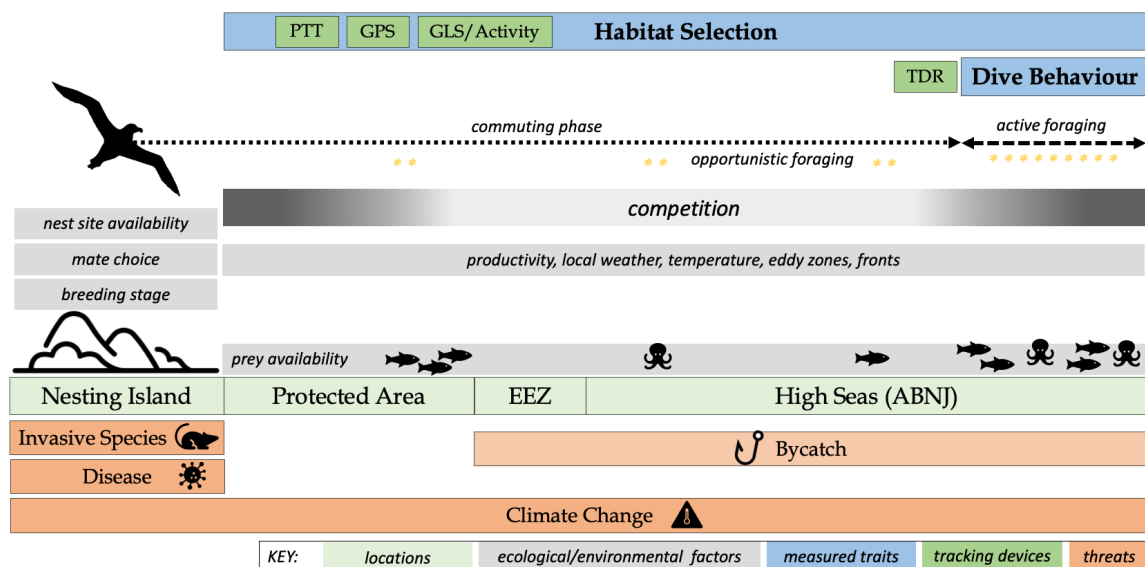
Figure 1.2: *Schematic showing various factors that can influence organism fitness at different stages and locations of a foraging trip in a breeding procellariiform seabird. EEZ: Exclusive Economic Zone. ABNJ: Areas Beyond National Jurisdiction. Abbreviations for tracking devices listed in section 1.3.2. NB: Though bycatch in illegal, unregulated, or unreported fisheries may occur inside protected areas, most seabird bycatch occurs in legal fisheries. Icons used with permission: flaticon.com.*

CHAPTER 2:   **Diving behaviour of albatrosses: implications for foraging ecology and bycatch susceptibility**

This chapter is published as Bentley, L. K., Kato, A., Ropert-Coudert, Y., Manica, A., & Phillips, R. A. (2021). Diving behaviour of albatrosses: implications for foraging ecology and bycatch susceptibility. *Marine Biology*, 168(3), 1-10. https://doi.org/10.1007/s00227-021-03841-y

Author contributions:

I conceived the ideas, designed the methodology, analysed data, made figures, and wrote up the chapter with supervision from R. A. Phillips and A. Manica.

R. A. Phillips oversaw animal tagging and provided the tracking data. A. Kato and Y. Ropert-Coudert processed the raw TDR data in IGOR pro to extract dive depths and durations and provided feedback on various versions of the manuscript. The pronoun 'we' is used in this chapter to recognise the collaborative nature of the published work.

Abstract

Diving is an ecologically important behaviour that provides air-breathing predators with opportunities to capture prey, but that also increases their exposure to incidental mortality (bycatch) in commercial fisheries. In this study, we characterised the diving behaviour of 26 individuals of three species, the Black-browed Albatross *Thalassarche melanophris*, Grey-headed Albatross *T. chrysostoma* and Light-mantled Albatross *Phoebetria palpebrata*, breeding at Bird Island, South Georgia. Individuals were tracked using Global Location Sensor (GLS)-immersion loggers and time-depth recorders (TDRs) and, for two species, Global Positioning System (GPS) loggers. Although the TDRs recorded 589 dives (defined in this paper as submersion >1 m), average dive depths and durations were just 1.30-1.49 m and 2.5-3.3 s, respectively, for the three species. In addition, many individuals (22% of Black-browed, 20% of Grey-headed, and 57% of Light-mantled Albatrosses; total n = 9, 10 and 7 individuals, respectively) did not dive at all. Most dives occurred at the distal end of foraging trips and were rare during the commuting phase. No dives took place in darkness, despite long periods spent on water at night. The limited and shallow dive activity contrasts with impressions from a previous study using capillary-tube depth gauges (which are less accurate than TDRs), and has implications for susceptibility of albatrosses to bycatch on longlines. This study provides further support for regulations requiring night setting and increased sink rates of baited hooks to help mitigate albatross bycatch.

2.1   Introduction

Many seabirds, including penguins, cormorants, alcids, diving petrels and some shearwaters are considered specialist divers, often foraging at depths >10 m, whereas most other seabird species undertake only brief, shallow dives or feed largely at the surface (Croxall and Prince 1980, Harper 1987, Navarro et al. 2014). As various types of fishing gear (e.g. gillnets, trawls, pelagic and demersal longlines) are set and operate at different depths, diving capability is a key determinant of the likelihood of incidental mortality (bycatch) (Anderson et al. 2011, Žydelis et al. 2013, Crawford et al. 2017). Many seabird species are of high conservation concern because of negative interactions with fisheries (Phillips et al. 2016). As such, quantifying their diving behaviour is fundamental to understanding not just their ability to access prey, but also their susceptibility to this anthropogenic threat.

Bycatch in commercial fisheries is a main cause of population declines in many albatrosses and large petrels (Phillips et al. 2016). These species mature slowly, have high adult survival, and low reproductive output, which means any additional adult mortality – e.g., as bycatch – can have major implications for demography (Thomson et al. 2015, Pardo et al. 2017). Research on bycatch mitigation in commercial fisheries has been extensive in recent years (Sullivan et al. 2018, Robertson et al. 2018, Jiménez et al. 2018). In longline fisheries, use of bird-scaring lines (BSLs; also called streamer or tori lines) aims to discourage birds from targeting hooks during setting, and heavier line-weighting regimes aim to sink baits more rapidly beyond their reach (Jiménez et al. 2018). Baits may also be released below the surface by a machine (Robertson et al. 2018), or devices (such as Hookpods) used to cover the sharp section of the hook until it reaches a particular depth (Sullivan et al. 2018, Goad et al. 2019). As pelagic and demersal longliners in the Southern Hemisphere set 100s of millions of hooks per year (Clay et al. 2019), it is critical to know at what depths these pose a threat to different seabirds in order to refine bycatch mitigation strategies, including minimum line-weighting regimes and aerial extents of BSLs. Information on diurnal activity patterns, including diving, of seabirds can also inform policies on restricting setting times.

In general, albatrosses appear morphologically to be poorly adapted to diving. Indeed while the typical relationship for most orders of seabirds is that maximum dive

depth scales positively with body mass, this does not apply in the Diomedeidae (Navarro et al. 2014). Early studies of albatrosses deployed capillary-tube depth gauges to measure the absolute maximum dive depth during the deployment period (Prince et al. 1994), whereas more recently, time-depth recorders (TDRs) have been used to record depth, duration and shape of all dives (Hedd et al. 1997, Huin and Prince 1997). Dive depths recorded by capillary depth gauges were unexpectedly high, ranging from mean ± SD and absolute maxima of 2.5 m ± 1.3 m and 4.5 m in Black-browed Albatrosses *Thalassarche melanophris*, to 4.7 m ± 3.4 m and 12.4 m, respectively, in Light-mantled Albatrosses *Phoebetria palpebrata*, which led the authors to speculate that the latter species was as proficient at diving as gannets (Sulidae) (Prince et al. 1994). Subsequent studies using TDRs have recorded shallower diving in other albatrosses, with mean and maximum dive depths of 0.6 m ± 0.2 m, and 2.5 m, respectively, in Black-footed Albatrosses *Phoebastria nigripes*, and of 1.9 m ± 1.7 m and 7.4 m in Shy Albatrosses *T. cauta* (Hedd et al. 1997, Kazama et al. 2019). A study of three Black-browed Albatrosses using a back-mounted camera with a pressure sensor also found that dives were infrequent and shallow (mean depth 1.46 m) (Sakamoto et al. 2009). Several studies have shown that capillary gauges overestimate depth, possibly because of high pressures experienced when birds hit the water at speed (Burger and Wilson 1988, Hedd et al. 1997, Navarro et al. 2014). Nor do they record dive frequency or duration, better indications of foraging style and breath-hold capability. As capillary gauges only record the single deepest dive during each deployment, this inflates the importance of these outliers when drawing ecological inferences. Therefore, TDRs allow more meaningful ecological conclusions to be drawn.

A detailed understanding of albatross behaviour at sea requires a combination of bio-logging devices. Global Positioning System (GPS) loggers, geolocators (Global Location Sensor or GLS loggers) and satellite transmitters allow habitat use to be determined, and saltwater immersion loggers allow flights and landings to be distinguished. Opportunistic foraging can be inferred by landings in the middle of directional transits, and area restricted search by higher turning rates and increased landings as the predator exploits a profitable patch of resources (Catry et al. 2004, Weimerskirch et al. 2007). Feeding attempts cannot be distinguished from resting using

immersion data, which is an important limitation given albatrosses spend long periods on the water overnight (Weimerskirch and Guionnet 2002, Catry et al. 2004, Phillips et al. 2005, Phalan et al. 2007). Albatrosses were initially thought to be primarily nocturnal foragers, as Grey-headed *T. chrysostoma* and Light-mantled Albatrosses in particular feed their chicks with substantial amounts of vertically-migrating squid, and all species were observed feeding at sea at night (Harper 1987, Prince and Morgan 1987). More recent studies propose that while some sit-and-wait feeding occurs at night, this strategy is only used because visual detection of prey is difficult in low light conditions (Phalan et al. 2007, Weimerskirch et al. 2007). Further evidence supporting largely diurnal foraging is that the eyes of albatrosses are adapted for visual pursuit of prey in daylight (Martin 1998). Timing of activity has important implications for conservation, as albatross bycatch is reduced when longlines are set at night (Bull 2007, Jiménez et al. 2020). Although immersion events can be interpreted in different ways, dive events are almost certainly indicative of feeding attempts, and their presence or absence can clarify foraging style.

The main objectives of this study were to quantify and contextualise dive events using both immersion and location data, and to construct a more comprehensive picture of albatross foraging behaviour in the breeding season. We aimed to accurately characterise diving depth, duration and frequency in three albatross species, including Black-browed Albatrosses and Grey-headed Albatrosses (both frequently caught in longline fisheries) and Light-mantled Albatrosses (previously suggested to be the most proficient divers; Prince et al. 1994). We hypothesised that typical dive depths for these species would be much shallower than the maximum depths previously reported using capillary gauges. As the eyes of albatrosses are adapted for diurnal foraging (Martin 1998), and they are generally more active in daylight than darkness (Phillips et al. 2007), we predicted that most dive activity would occur during the day. Results are discussed in the context of susceptibility to bycatch in longline fisheries, and the implications for refining approaches to bycatch mitigation.

2.2   Materials and methods

2.2.1   Device deployments

All devices were deployed at Bird Island, South Georgia (54° 00' S, 38° 03' W) on breeding birds during the austral summer 2009/10. Black-browed albatrosses (n = 9) and Grey-headed Albatrosses (n = 10) were tracked during brood-guard, and Light-mantled Albatrosses (n = 7) during incubation, in all cases for a single foraging trip. Three types of GPS logger were used: i-gotU GT-120 (MobileAction Technology, Taiwan; 25 g), MiniGPSlog (earth & OceanTechnology, Germany; 25 g) or MicroGPSlog (earth & OceanTechnology, Germany; 10 g). These were usually set to obtain a fix every 10 or 15 minutes and attached to mantle feathers using fabric (Tesa ®) tape. In addition, a combined GLS-immersion logger (Mk19, British Antarctic Survey, Cambridge, UK; 2.5g) attached by a cable-tie to a plastic ring was deployed on one tarsus, and a TDR (Cefas G5, Cefas Technology Ltd, Lowestoft, UK; 2.7g or 6.5g), also on a plastic ring, on the other tarsus. (Details of devices used for each individual available in Appendix 1, Table S1.) Attachment of devices took < 10 min. Maximum instrument loads were < 1.5% of mean body mass, and hence well below the threshold of 3% above which deleterious effects are more common in albatrosses (Phillips et al. 2003). TDRs had a 0.03 m depth resolution, and on Black-browed and Grey-headed Albatrosses recorded depth every 1 s for the duration of the foraging trip. Those on Light-mantled Albatrosses recorded depth every 1 s on every third day. GLS-immersion loggers tested for saltwater immersion every 3 s, and recorded every change of state from wet to dry and *vice versa* that lasted 6 s or more, providing the timing of landings and take-offs from the water. The calculated immersion times included all time that the bird had its legs in the water (i.e. resting, surface feeding, and diving). The term "diving" hereafter refers only to events during which the tarsus of the bird submerges to > 1m depth.

2.2.2   Dive analysis

Depth data were manually corrected for a drifting surface level. The dive threshold was set at 1 m depth (Navarro et al. 2014, Bennison et al. 2018), as this best reflects the accuracy of the pressure sensor (1% at 10 bar device range). This threshold

also reduces noise associated with surface pressure changes and wave action, and ensures recorded 'dives' reflect prey capture attempts rather than other surface behaviours. We acknowledge that because the TDR was mounted on the tarsus, a dive record of 1 m may represent a bird whose head can access prey beyond this depth, given a body length of ~ 0.8 m. Dives were analysed using IGOR pro (Wavemetrics, version 6.3, Portland, OR, USA). Dive parameters (maximum depth, duration) were extracted for each dive. Uncertainty, particularly at shallow depths, is hard to quantify without accurate data on *in-situ* barometric pressure, but by using a 1 m threshold we were able to more confidently remove false dive events from analysis if they did not meet minimum criteria as follows: (i) start depth ≥ 0 m, (ii) depth change rate at the start of the dive < 1 m/s, (iii) depth change rate at the end of the dive < 2 m/s, and (iv) depth change rate just before the start of the dive ≤ 0 m/s, confirmed by visual inspection of all dives. We calculated mean depth, duration and frequency of dives for each individual. A Fisher's exact test was used to compare the proportions of non-divers between species. Dives were also assigned to daylight (between sunset and sunrise), twilight (from civil twilight to the nearest sunset or sunrise), and darkness (between civil twilights) based on GPS location and time, using standard astronomical calculations in the R package *SGAT* (Sumner et al. 2009).

2.2.3   *GPS and immersion analysis*

GPS tracks were interpolated to 1-second intervals for behavioural matching and 5-minute intervals for visualisation using the R package *adehabitatLT* (Calenge 2006), and the start and end of each foraging trip was estimated to ± 5 mins from GPS locations, confirmed by immersion data (first wet event, as albatrosses almost always bathe before departing on a trip; Granadeiro et al. 2018). Immersion and dive events were then matched by time to GPS locations interpolated at 1-second intervals for Black-browed and Grey-headed Albatrosses. GPS data were unavailable for Light-mantled Albatrosses because of battery depletion or water ingress into the devices. Total immersion time was calculated for each trip. Immersion events were categorised as occurring in daylight, twilight or darkness in the same manner as dive events (described above). Sample sizes varied between analyses in cases where, for the same

bird, one type of data was unavailable (e.g. GPS). All processing of GPS tracks, summarising and cleaning of data, descriptive statistics and mapping were undertaken in R version 3.6.2 (R Core Team 2020). Values are given as the mean ± SD unless indicated otherwise.

2.3 Results

2.3.1 Dive characteristics

Average dive depths, durations, and frequencies (per day and per trip) for Black-browed and Grey-headed Albatrosses tracked during brood-guard, and Light-mantled Albatrosses tracked during incubation from Bird Island (South Georgia) are shown in Table 1.

Species	Breeding stage	Dive depth (m); max observed depth	Dive duration (s); max duration	Dives/trip	Dives/day	n dives	n birds tracked	n (%) non-divers
Black-browed Albatross	Brood-guard	1.49 ± 0.17; 6.0	3.30 ± 0.6; 15	36.55 ± 53.79	17.83 ± 27.15	329	9	2 (22%)
Grey-headed Albatross	Brood-guard	1.47 ± 0.34; 3.4	2.85 ± 0.9; 8	22.50 ± 44.74	9.13 ± 16.62	225	10	2 (20%)
Light-mantled Albatross	Incubation	1.30 ± 0.32; 2.0	2.50 ± 0.9; 5	NA	0.44 ± 0.23	10	7	4 (57%)

Table 1. Summary of dive events for three albatross species tracked from Bird Island (South Georgia), in austral summer 2009/10. 'Non-divers' indicates birds for which no dive events were recorded by the TDRs. All values are means ± SD unless otherwise stated.

No dives were recorded for two of the nine Black-browed, two of the 10 Grey-headed, and four of the seven Light-mantled Albatrosses that were tracked. There was no statistically significant difference between these ratios (two-tailed Fisher's exact test, $P = 0.28$). The mean maximum depths of diving individuals from all three species were < 1.5 m, and the deepest dive for any bird was 6.0, 3.4 and 2.0 m for Black-browed, Grey-headed and Light-mantled Albatrosses, respectively. Mean dive durations ranged from

2.5-3.3 s. Number of dives per trip, and maximum dive depths were highly variable between individuals (Figure 2.1). Grey-headed Albatrosses generally dived at the most distal portions of foraging tracks, and travelled north of Bird Island to the Antarctic Polar Front, whereas with one exception, foraging and dives in Black-browed Albatrosses took place closer to South Georgia (Figure 2.2).
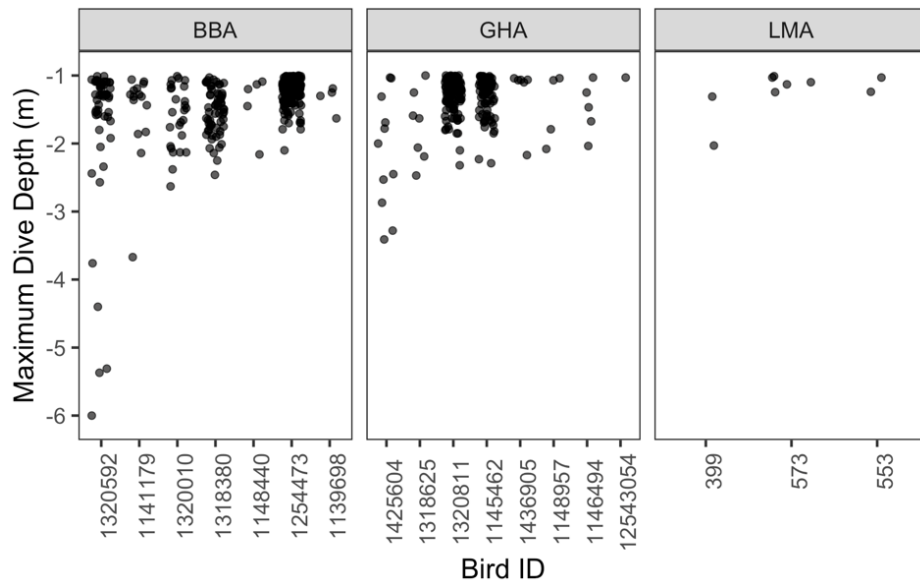
Figure 2.1: *Dive depths recorded from Black-browed Albatross (BBA) Grey-headed Albatross (GHA) and Light-mantled Albatross (LMA) tracked from Bird Island (South Georgia) during the 2009/10 breeding season. BBA and GHA tracked during brood-guard, and LMA tracked during incubation. Jitter is used to emphasise variation in number of points (dives) between individuals. Note that for all species only the IDs of birds that dived appear on the plot.*

2.3.2   Immersion behaviour and diving

Average proportion of time spent immersed was 25.5 ± 14.5% of brood-guard trips lasting 1.9 ± 0.7 days in Black-browed Albatrosses (n = 9) and 20.4 ± 2.6% of trips lasting 2.8 ± 0.4 days in Grey-headed Albatrosses (n = 8); in all cases, total time spent diving was < 0.5% of the trip (Figure 2.3a). Light-mantled Albatrosses (n = 7) spent an average of 27.2 ± 7.8% of incubation trips of 14.2 ± 5.0 days immersed; total time spent diving was always < 10 s (Figure 2.3b).
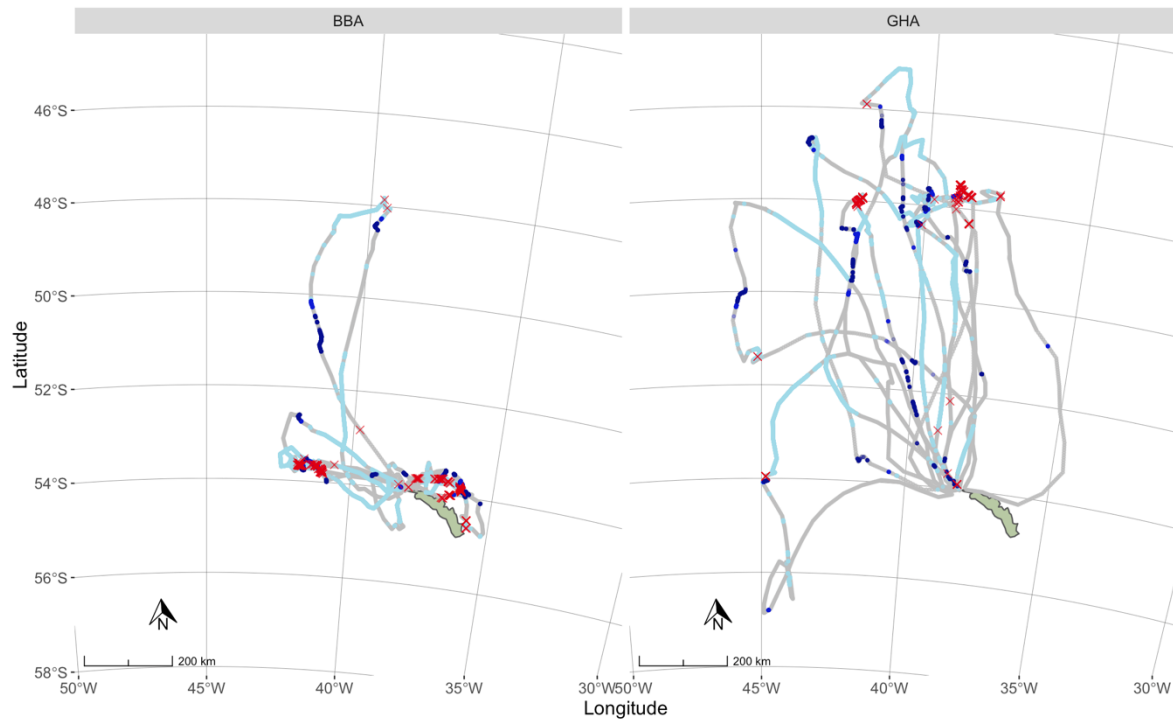
Figure 2.2*: GPS tracks (grey), immersion events during the day (light blue points), twilight (medium blue points) and night (dark blue points) and dive events (red X) for Black-browed Albatrosses (left, n = 8), and Grey-headed Albatrosses (right, n = 8) tracked from Bird Island, South Georgia (light green), during brood-guard in austral summer 2009/10. NB: Continuous daylight immersion events covering large distances do not represent fast on-water drifting, but rather repeated switching between flight and landings, i.e. likely foraging.*

a)

b)
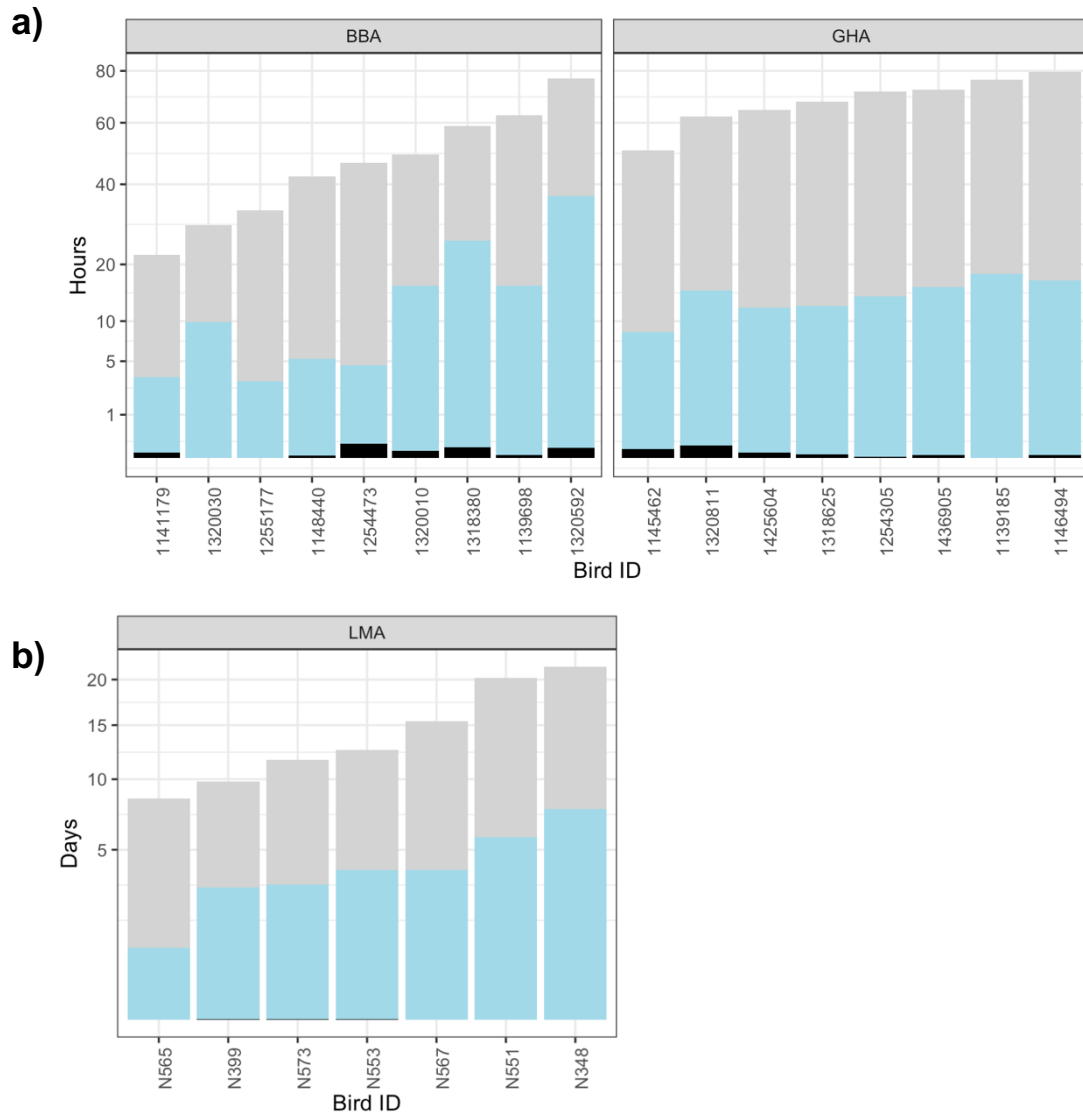
Figure 2.3: *Time spent diving (black), immersed (light blue) and flying (grey) for: a) individual Black-browed (left panel) and Grey-headed (right panel) Albatrosses tracked during brood-guard; and b) for individual Light-mantled Albatrosses tracked during incubation from Bird Island (South Georgia), in austral summer 2009/10. Note the square root scale on the Y axis and variation in Y axis scale between panels a and b.*

2.3.3   Diurnal activity patterns

Of the total time that Black-browed Albatrosses (n = 8) spent on water, 42.7 ± 16.9% occurred during the day, 4.1 ± 3.4% during twilight, and 53.2 ± 18.3% at night. In Grey-headed Albatrosses (n = 8), 25.2 ± 8.3% of immersion occurred during the day, 2.8 ± 3.2% during twilight, and 72.0 ± 10.5% at night. (Figure 2.4).
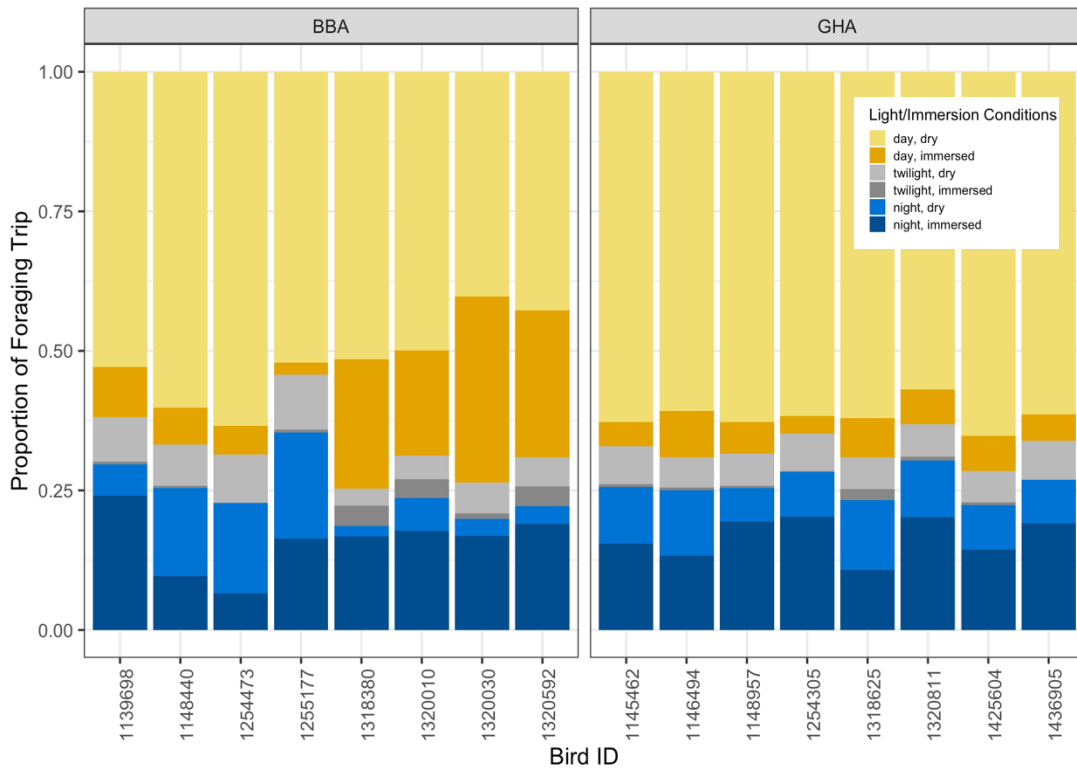
Figure 2.4: *Total proportions of foraging trip spent immersed (dark shades) and dry (light shades) during daylight (yellow), twilight (grey) and darkness (blue), for individual Black-browed (BBA) and Grey-headed (GHA) Albatrosses tracked during brood-guard from Bird Island (South Georgia), in austral summer 2009/10.*

More than 95% of dives that could be matched to GPS locations (n = 308, Black-browed Albatrosses; n = 219, Grey-headed Albatrosses) occurred during daylight, with all others (3.6% and 4.1% of dives for Black-browed Albatrosses and Grey-headed Albatrosses, respectively) occurring during twilight. No dives were recorded in darkness.

2.4   Discussion

Here we integrate measures of albatross activity at sea, combining geographic location, flights, landings, and diving behaviour during the brood guard (Black-browed, Grey-headed) and incubation (Light-mantled) stages of the breeding season. We provide detailed data on diving depths, durations, frequencies, and timing for albatrosses using TDRs, and show that dives are infrequent, diurnal and shallow in all species. Indeed, albatrosses show greatly reduced diving activity than might be inferred from the

maximum dive depths estimated using capillary depth gauges for these species at the same study site close to 30 years ago (Prince et al. 1994).

2.4.1   Defining dive events

Defining what constitutes a dive is critically important when comparing dive metrics among species. Reaching prey located at 0.5 - 0.7 m depths may only require a surface dive for a large bird, whereas in smaller species where this distance is at least one – maybe two – times their body length, it will represent a wing-propelled pursuit dive (Harper 1987). Previous work on grey-headed albatrosses using TDRs considered a dive to be any record deeper than 0.1 m (Huin and Prince 1997), whereas we only considered dives to occur when the tarsus exceeded a threshold of 1 m (a common threshold used in more in recent work using the same logger type (albeit for deeper diving species), e.g. Navarro et al. (2014), Bennison et al. (2018)). This not only better accounts for levels of sensor accuracy and data noise, but we consider it to be more ecologically appropriate as the average body length of these birds is 0.8 m (Warham 1996). For a bird of this size to record a tarsus depth > 1 m, we can be more confident that we have measured a meaningfully different behaviour than surface foraging. Moreover, all immersions (whether or not they involve diving), can be recorded more efficiently and consistently using immersion sensors rather than relying on shallow depth values recorded by a TDR.

The distinction between all landings and just dives is important when drawing conclusions about physiology and ecology. For example, Huin and Prince (1997) suggested that in grey-headed albatrosses, the percentage of energy gained by diving might be as high as 45%, whereas this seems unrealistic using a dive threshold of 1 m as in our study, because three (30%) of the ten birds of this species tracked dived < 5 times, and two (20%) did not dive at all. The most common strategy for prey acquisition was therefore likely to be feeding within 1 or 2 m of the surface, with occasional dives (or "plunges", as in Harper 1987) both while in transit and while undertaking area-restricted search, and rare bouts of numerous successive surface dives, seen only in a few individuals (e.g. see GHA 1320811, GHA 1145462 in Figure 2.1). Further work combining tracking with both TDRs and stomach temperature probes is required to make any claims about energy gain with certainty. Had these bouts of successive dives

occurred in areas with known fishing activity, it may have indicated vessel interactions; however, this was not the case given there is a seasonal closure of fisheries in the waters around South Georgia and no evidence for illegal fishing in recent years (Tancell et al. 2016). For further analyses of foraging habitat selection in these Grey-headed Albatrosses, see Scales et al. (2016).

2.4.2   *Activity patterns and diving behaviour*

Our study affirms the large amounts of time spent feeding at depths < 2 m for these species, because diving was very infrequent and shallow, and a high proportion of foraging trips was spent on the water's surface. The absence of diving overnight reinforces previous work noting the importance of daylight foraging, despite the long periods of time on the water at night (Catry et al. 2004, Phalan et al. 2007). The proportion of time spent on the water was broadly similar within and between species, although as in previous studies of at-sea activity patterns (Phalan et al. 2007, Mackley et al. 2011), there were very large differences in behaviour between individuals (Figure 2.2). The high variability in landing and diving rates suggest possible individual specialisation, and perhaps that diving is undertaken only by birds with particular skills or preferences. Alternatively, the few individuals that dived numerous (> 100) times on a single trip may have simply encountered a highly productive patch of prey for which this technique allowed efficient exploitation, or that was driven upwards by subsurface predators. Further tracking of multiple foraging trips by individuals over an extended period might indicate if this large variation in dive behaviour is due predominantly to extrinsic (e.g. prey availability) or intrinsic (e.g. energy needs) factors.

Energy requirements during brood-guard are higher than during incubation: parents must meet both their own and their chick's energy requirements while foraging, are constrained to shorter and closer foraging trips, and Wandering Albatrosses *Diomedea exulans* are known to lose mass during this period (Weimerskirch and Lys 2000). Nonetheless, there was no statistically significant difference in dive rates between species, even though the Light-mantled Albatross in incubation appeared to dive less frequently than Black-browed or Grey-headed Albatross in brood-guard. Based on immersion data, foraging bout lengths and frequencies are broadly similar between

incubation and brood-guard (Weimerskirch and Guionnet 2002, Phalan et al. 2007), and hence dive frequency and characteristics may also be comparable across breeding stages. Any potential effects of breeding stage on diving behaviour would need to be confirmed by further tracking.

Our results confirm that all three genera of small albatrosses (*Phoebetria* and *Thalassarche*, this study*; Phoebastria*, (Kazama et al. 2019)) are infrequent, short and shallow divers compared with most other seabirds, reaching < 1.5 m on average. In contrast, many shearwaters are far more proficient, attaining mean maximum depths of 17.8 m *Puffinus yelkouan*, 9.6 m *P. puffinus*, and 15.9 m *Ardenna grisea* (Shaffer et al. 2009, Péron et al. 2013, Shoji et al. 2016), whereas the *Calonectris* shearwaters only dive to mean depths of 1-2 m (Paiva et al. 2010, Matsumoto et al. 2012, Grémillet et al. 2014). The *Procellaria* petrels are also proficient divers; Grey Petrels *Procellaria cinerea* and White-chinned Petrels *Procellaria aequinoctialis* reach mean and absolute maximum diving depths, respectively, of 3.2 ± 2.2 m and 22 m, and 2.9 ± 2.4 m, and 17 m (Rollinson et al. 2014, 2016).

2.4.3 *Diving behaviour and bycatch mitigation*

Although they are mostly shallow divers, albatrosses are clearly at high risk of bycatch behind longline vessels (Jiménez et al. 2014, Phillips et al. 2016). In accordance with our results indicating fewer landings and no diving in darkness, night setting of longlines is known to significantly reduce bycatch rates (Jiménez et al. 2020). In terms of compliance-monitoring, night setting has the advantage over BSLs and specific line-weighting regimes as a mandatory mitigation measure, as it can be assessed remotely and in near real-time by inferring fishing activity from satellite detected automatic identification system (AIS) data on vessel movements (de Souza et al. 2016). While one reason night-setting may be successful is because albatrosses rarely forage nocturnally, our results only apply to dive behaviour during the breeding season when targeting natural prey. As such, they do not necessarily indicate a physiological maximum, and it is possible that birds feeding behind vessels might dive deeper. Further work could usefully involve tracking of diurnal activity patterns of albatrosses in contact with fisheries, as it

cannot be assumed that the patterns seen here are representative of all populations or times of year.

In some regions, the smaller, deeper-diving *Procellaria* petrels and *Ardenna* shearwaters bring baited hooks to the surface, where they become accessible to albatrosses, putting the latter at risk. Jiménez et al (2012) observed that 41% of albatrosses killed on longlines were hooked on gear with which a medium-sized diving seabird had first made contact. Similar dynamics were reported in Melvin et al. (2014), where over half of primary attacks (bait brought to the surface by a diving *Procellaria* petrel) led to a secondary attack on the bait, usually by an albatross. Despite their poor diving abilities, *Thalassarche* albatrosses are often the most frequently-killed surface-foraging birds at feeding assemblages, indicating the critical importance of mitigation designed to keep hooks beyond reach of deeper-diving birds (Petersen et al. 2009, Melvin et al. 2013, 2014). In feeding assemblages where White-chinned Petrels are the dominant species, a combination of two bird-scaring lines, weighted branch lines and night setting has the potential to reduce seabird bycatch to zero (Melvin et al. 2014). Further research into areas of spatial overlap between deeper divers, threatened albatross species, and commercial longline fisheries would better identify potential bycatch hotspots where monitoring and mitigation efforts could be focused. In addition, the use of additional tracking devices such as high-resolution TDRs mounted on the head, accelerometers to reveal very shallow dives (Cianchetti-Benedetti et al. 2017), or stomach temperature probes, which provide information on the timing of ingestion and size of prey (Catry et al. 2004), would provide insights into the prey capture rate and profitability of diving compared with feeding close to the surface.

CHAPTER 3:   Divergent foraging habitat preferences between summer-breeding and winter-breeding *Procellaria* petrels

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Author contributions:

I conceived the ideas, designed the study, analysed data, made figures, and wrote up the chapter with supervision from R. A. Phillips and A. Manica.

R. A. Phillips, B. J. Dilley, and P. G. Ryan provided tracking data and all coauthors gave feedback on various versions of the manuscript. The pronoun 'we' is used in this chapter to recognise the collaborative nature of the published work.

Abstract

Foraging niche specialisation is thought to occur when different members of speciose communities divide resources in either time or space. Here we compared habitat preferences of the congeneric Grey Petrel *Procellaria cinerea* and White-chinned Petrel *P. aequinoctialis*, tracked in the same calendar year using GPS loggers from Gough Island and Bird Island (South Georgia), respectively. We identified periods of active foraging, and determined habitat characteristics using remote-sensing data. Although these highly pelagic species could potentially overlap at sea across large areas, they showed markedly different foraging preferences during their incubation periods, which are temporally offset because Grey Petrels breed during the austral winter. Grey Petrels foraged mostly in pelagic cold-water areas to the north-west of South Georgia, whereas White-chinned Petrels foraged almost exclusively in the warm, shallow waters of the Patagonian Shelf. Within each species, foraging habitat characteristics were highly consistent. Our results demonstrate the diversity of habitat preferences within genera, and provide further evidence that colony-specific information on habitat preference is crucial to identify important feeding areas for pelagic predators.

3.1   Introduction

Foraging in dynamic environments challenges predators to locate and capture prey that are temporally and spatially unpredictable. While optimal foraging strategies are complex and often variable, their key objective is to maximise prey consumption while minimising the effort required to travel and feed (Orians and Pearson 1979, Stephens et al. 2008, Waggitt et al. 2018). A wide variety of environmental and physiological factors may constrain foraging behaviour (Tucker et al. 1995, Gilchrist et al. 1998, Spaethe et al. 2001). Although we expect foraging animals to target habitats that yield the highest prey capture rates, this involves trade-offs between resource abundance and levels of inter- and intra-specific competition, which in speciose communities often leads to high levels of spatial and temporal segregation in habitat use (Masello et al. 2010, Navarro et al. 2013). Understanding habitat specialisation in closely-related species can provide insights into how these communities are maintained (Vilchis et al. 2006, Granroth-Wilding and Phillips 2019).

Coexistence is often promoted in highly diverse communities via specialisation, which allows a greater number of species and individuals to partition resources (Schoener 1974, Phillips et al. 2017). This has been shown across diverse taxa, including reptiles and amphibians (Toft 1985), mammals (Aldridge and Rautenbach 1987), and birds (Feinsinger and Colwell 1978). Given their high diversity and abundance, coupled with the central-place foraging constraints imposed by breeding on land, seabirds provide ideal models for investigating specialisation. During breeding, they must balance traveling to access the best resources with the needs of incubation and chick-rearing (Phillips et al. 2017). The depletion of resources around their nesting islands has been long discussed (Ashmole 1963, Birt et al. 1987), and specialisations on particular prey, habitats or in other aspects of foraging behaviour have been shown to occur among species, populations, sexes and age classes (Bearhop et al. 2006, Thiebot et al. 2012, Wakefield et al. 2013, Mendez et al. 2017, Votier et al. 2017). When interspecific competitors are morphologically similar, specialisation is often via behavioural variation, such as in timing or location of foraging (Nicholls and Racey 2006). Partitioning of resources is a potential driver of speciation if behavioural or phenotypic changes ultimately lead to reproductive isolation (Bolnick et al. 2007). If selection leads to

differences in timing of breeding of related taxa (allochrony), speciation is possible even in sympatry (Friesen et al. 2007a, 2007b, Taylor and Friesen 2017).

Extreme allochrony in Antarctic seabirds can lead to the phenomenon of winter breeding (Poupart et al. 2019a). The underlying ecological drivers remain unclear, particularly because chick provisioning is energetically expensive (Welcker et al. 2015) and so we expect reproduction to coincide with the most favourable foraging conditions; for the great majority of temperate and polar seabirds, this is during the austral summer, when longer days and warmer conditions enhance phytoplankton blooms, in turn supporting abundant primary and secondary consumers (Poupart et al. 2019a). By comparison, productivity in the Southern Ocean is reduced in autumn and at its minimum in winter (Alvain et al. 2008). As such, the shift during speciation to winter breeding is counter-intuitive, particularly as many summer breeders avoid the seasonal decline in food availability by migrating to lower latitudes.

The *Procellaria* petrels are long-lived, highly *k*-selected species which often forage at sites long distances from their colonies (Bugoni et al. 2009, Rollinson et al. 2018, Frankish et al. 2020). Two of the five species (Grey Petrels *P. cinerea*, and Westland Petrels *P. westlandica*) are winter breeders. Westland Petrels, Spectacled Petrels *P. conspicillata* and Black Petrels *P. parkinsoni* are each endemic to only one or two breeding islands, whereas Grey Petrels and White-chinned Petrels *P. aequinoctialis* are much more abundant, breeding in highly speciose seabird communities at several island groups around the Southern Ocean (Phillips et al. 2016).

Tracking studies in the last 1–2 decades suggest that the contrasting distribution, abundance and phenology among *Procellaria* petrels may partly be explained by differences in foraging habitat availability and preferences. Habitat use also determines fisheries overlap, which has major implications for conservation; Grey and White-chinned Petrels are listed as Near-threatened and Vulnerable, respectively, by the IUCN because of high bycatch rates in longline fisheries (Phillips et al. 2016). Here we compare habitat preferences of Grey Petrels and White-chinned Petrels from the largest populations in the South Atlantic: Gough Island and South Georgia, respectively. Spectacled Petrels also breed in the region (at Inaccessible Island), but feed in much warmer waters than Grey Petrels and White-chinned Petrels (Bugoni et al. 2009, Reid et

al. 2014). Previous tracking of White-chinned Petrels from South Georgia indicated that they target warm, shallow waters at the Patagonian Shelf during the non-breeding season and incubation, then switch to colder waters around and south of the Antarctic Polar Front during chick-rearing (Berrow et al. 2000, Phillips et al. 2006). Grey Petrels are known to target particular broad-scale oceanographic features during the non-breeding season (oceanic ridges with moderate current velocities and average surface temperatures of 7–13°C), but preferences vary among study colonies (Kerguelen, Antipodes and Prince Edward Islands) to such an extent that habitat models are not transferable across ocean basins (Torres et al. 2015). In our study, we classified behavioural states during trips to sea by these two species tracked in the same region, breeding stage and calendar year, and identified oceanographic features of key habitats. We predicted that habitat choice would be consistent within species, based on previous indications of high site fidelity in these species (Rollinson et al. 2018, Delord et al. 2019). We also predicted that foraging would be more likely at locations furthest from the colony. By comparing results from closely-related species we can better understand the extent to which habitat preferences are fixed or flexible, which has important implications for the capacity of organisms to adapt to environmental change. Further, understanding the types of foraging habitat targeted by winter-breeding Grey Petrels can help to explain the evolution of this uncommon strategy.

3.2   Methods

3.2.1   *Device deployments and initial processing*

Grey Petrels are winter breeders, attending colonies from February to September, whereas White-chinned Petrels breed in the summer, attending colonies from September to May (Phillips et al. 2006, Torres et al. 2015). GPS tags (IgotU; Mobile Action Technology Inc., Taiwan), weighing c. 25 g including heat-shrink packaging, were attached by Tesa® tape to the mantle feathers of 16 White-chinned Petrels and 20 Grey Petrels. All White-chinned Petrels and eight Grey Petrels were also fitted with either a geolocator-immersion logger (Intigeo C250, Migrate Technology, Cambridge, UK; 2.6 g) attached to a plastic band on the tarsus, or a Time Depth Recorder (TDR, G5, Cefas Technology; mass 2.7 g) housed in heat-shrink with the GPS logger, respectively. Grey

Petrels were tagged during the incubation period in April–May 2014 (austral winter), and White-chinned Petrels in December 2014 to January 2015 (austral summer). Mean mass of the tracked Grey Petrels was 1152 g. To minimise handling time, the White-chinned Petrels were not weighed, but the mean mass of other birds weighed during the deployment period was 1307 g ($n = 32$ birds). GPS devices were retrieved after an average of 22.4 and 30.8 days, respectively, from 18 (90%) of Grey Petrels (all 20 birds were recaptured but two had lost the GPS logger) and from 13 (81%) of the White-chinned Petrels, possibly because some of the other three birds were non-breeders, or the chick hatched so the adult was missed during burrow checks. Thirteen of the GLS devices on White-chinned Petrels were retrieved along with the GPS loggers, and the three others in the following austral summer. The maximum combined mass of the two devices and tape or ring attachments was < 3% of mean body mass for both species, which is below the threshold at which deleterious effects are more common in pelagic seabirds (Phillips et al. 2003), but does not guarantee there will be no impact (Geen et al. 2019). Devices were set to record at 30-minute intervals and removed after a single foraging trip (most birds), or after two foraging trips (two birds only). Fourteen (Grey Petrel) and twelve (White-chinned petrel) devices downloaded successfully. There were insufficient good-quality locations for four Grey Petrels and one White-chinned Petrel. The retained tracks were interpolated to 30 minute intervals to ensure consistency between the data sets using the *redisltraj* function from the R package *adehabitatLT* (Calenge 2006).

3.2.2   *Behavioural classification*

Behavioural states were determined using expectation-maximisation binary clustering (EMbC), an algorithm which uses speed and turning angles to categorise behaviour into four states (Garriga et al. 2016). High turning angles were presumed to be associated with foraging behaviour regardless of speed (thus merging two of the states together), low turning angles at high speed with transit behaviour, and low tortuosity at low speed with resting (Garriga et al. 2016). This algorithm is suitable for modelling behavioural responses to dynamic environmental variables, and is robust for use on data of our temporal scale (Bennison et al. 2018). For White-chinned Petrels, the immersion

data were used to check whether the locations classified as foraging using EMbC corresponded to landings on the water (Appendix 2, Fig. S1). Locations classified as transit or resting were pooled as "not foraging" and compared with foraging points in binomial analyses (clustering for all categories is shown in Appendix 2, Fig. S2).

3.2.3 Habitat modelling

To assess habitat selection, pseudoabsences were generated by retaining track shape and observed step length but randomising the angle at which birds left the colony, removing any generated tracks that went over land. This ensured total flight distance, sinuosity, turning angles etc. were realistic. Fifty pseudoabsence tracks were generated per real track (see Appendix 2, Fig. S3), and environmental variables were extracted for each point of both the generated and real tracks. Environmental predictors were selected as follows: (1) sea-surface temperature (SST, indicating cold fronts and water mass: CMEMS/Copernicus Marine) measured daily, 0.083° grid; (2) chlorophyll *a* concentration (chl *a*, a proxy for marine productivity: CMEMS/Copernicus Marine) measured daily, 0.25° grid and log transformed; (3) sea-level anomaly (height above geoid (m), index of mesoscale oceanic activity: CMEMS/Copernicus marine) measured daily, 0.083° grid; and (4) eddy kinetic energy (EKE, index of mesoscale oceanic activity calculated from eastward and northward sea water velocities) measured daily, 0.083° grid and log transformed, CMEMS/Copernicus marine. Two static variables were also calculated for each track location/pseudoabsence: (5) bathymetry (identifying shelf and pelagic zones, 0.00833° grid, GEBCO) and (6) Euclidean distance from colony (as a proxy for the effect of accessibility). All layers were resampled to the coarsest scale (0.25°) using the package *raster* in R (Hijmans and van Etten 2012). Sea-level anomaly was removed from final models as it was 94% correlated with sea-surface temperature. A binomial (presence/pseudoabsence) generalised additive model (GAM) was used to assess the influence of these environmental variables on habitat selection in each species. Model terms were initially selected via the *dredge* function (Bartón 2020) using AICc values, and unique and total deviance explained for each model term was calculated to help contextualise biological significance. The influence of environmental variables (as above) on behaviour (foraging or not foraging, classified using EMbC) was assessed

using binomial GAMs with cubic spline smoothing. Model fitting and selection was undertaken using AICc values.

3.3 Results

3.3.1 Trip characteristics and habitat selection

Primary foraging areas were highly consistent within species. During the winter, the Grey Petrels (n = 10) tracked during incubation travelled over 3000 km from Gough Island to forage predominantly west-northwest of South Georgia, in a region that was overflown with minimal foraging or resting by White-chinned Petrels in the following austral summer. Instead of utilising this area, the incubating White-chinned Petrels (n = 11) travelled over 2000 km from South Georgia to forage primarily on the Patagonian Shelf (Fig. 3.1). Grey Petrels were tracked for a mean of 9.56 ± 3.69 days, but batteries in the loggers depleted before the bird returned and the tracking data were incomplete. It is likely that these loggers depleted quickly due to the impact of cold temperatures on the batteries, and potentially because the GPS devices had been used in previous studies. While the GPS loggers collected data on average for 67% of the duration of foraging trips, the vast majority of dives (682 of 775; 88%) recorded by TDRs (which ran for the entire trip) were within the period for which there was GPS data, suggesting that the area to the west-northwest of South Georgia is indeed the key foraging area for this species (full dive details reported in Rollinson et al. 2016; see Appendix 2, Fig. S4 showing the last available GPS location from each bird). White-chinned Petrels were tracked for 13.83 ± 3.57 days, which represented their entire foraging trip.

Comparison of presences and pseudoabsences from real and rotated tracks indicated that both species selected habitat in a narrower band of sea surface temperature than that available, with Grey Petrels mostly foraging in water ~5 °C and White-chinned Petrels ~10-15°C (Fig. 3.2a). Additionally, White-chinned Petrels targeted a specific bathymetric profile, the shallow shelf area < 500 m (Fig. 3.2b), and both species preferred the upper range of available chlorophyll-*a* values (Fig. 3.2c).
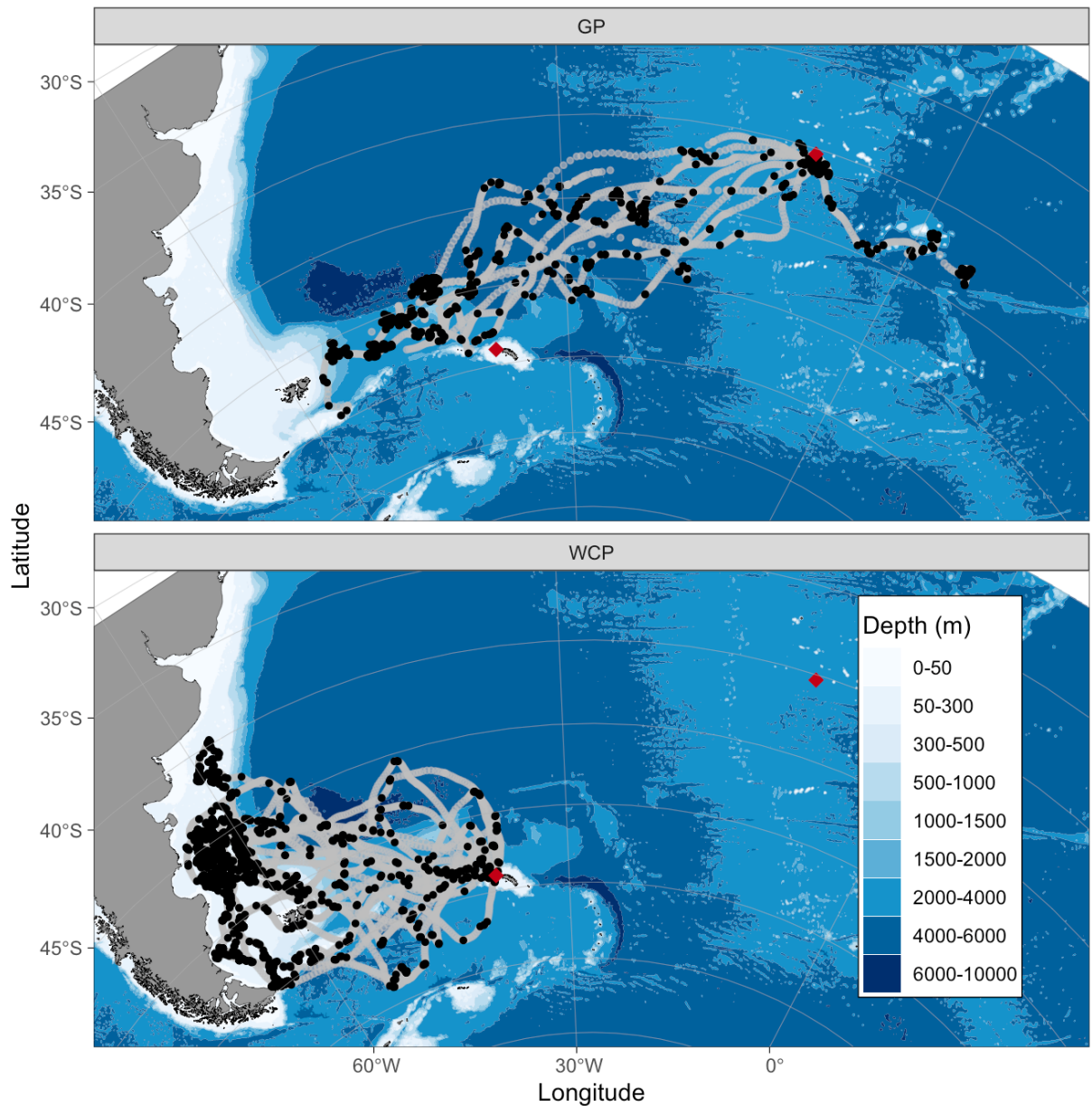
Figure 3.1: *Foraging (black points) and resting/transit (grey points) behaviour of (upper) Grey Petrels (GP) from Gough Island (April to May 2014; austral winter), and (lower) White-chinned Petrels (WCP) from South Georgia (December 2014 to January 2015; austral summer) tracked during the incubation period. Behaviours were classified using the EMbC R package* (Garriga et al. 2016)*. Study colonies are marked with red diamonds. Map generated using tools from the* ggOceanMaps *R package (Vihtakari 2020). Bathymetry layer from NOAA (Amante and Eakins 2009).*
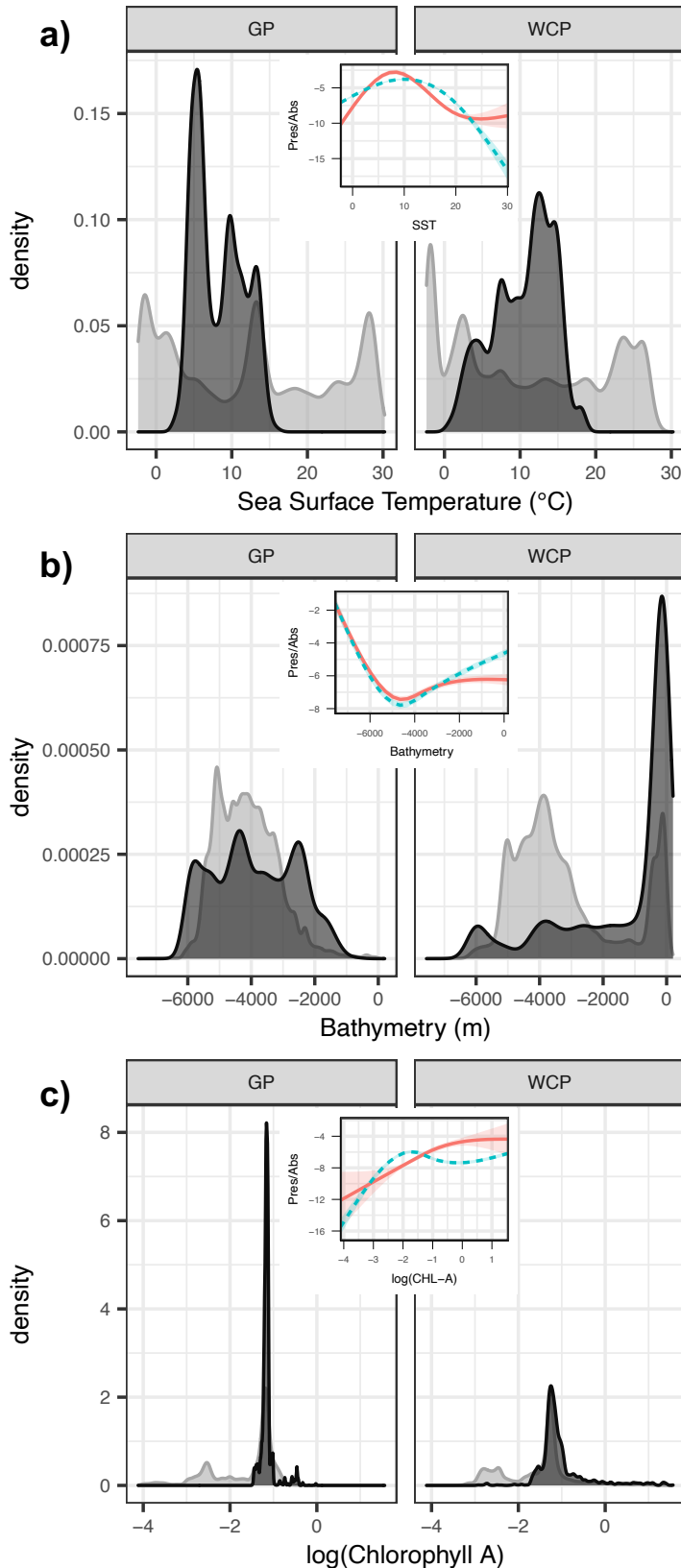
Figure 3.2: *Density plots showing the proportion of presences (dark grey) and pseudoabsences (pale grey) that occurred across environmental gradients (A: sea surface temperature, °C; B: bathymetry (m); C: $\log_{10}$ (chlorophyll a concentration, mg/L) in Grey Petrels (GP) from Gough Island (tracked in April–May 2014; austral winter), and White-chinned Petrels (WCP) from South Georgia (tracked in December 2014–January 2015; austral summer). Insets show significant GAM smooths for Grey Petrels: red/solid, and White-chinned Petrels: blue/dashed (see Appendix 2, Table S1 and Fig. S5 for all smooths).*

3.3.2   Foraging habitats

Foraging behaviour, in comparison to transit or resting behaviour, was observed at sea surface temperatures of 0–18 °C, with a marked peak around 5 °C for Grey Petrels, and a broader peak between 10 and 15 °C for White-chinned Petrels (Fig. 3.3a), reflecting their greater range in latitudes on the Patagonian Shelf. Grey Petrels foraged across a wide depth gradient in colder, deeper waters, whereas White-chinned Petrels foraged almost exclusively in shallow shelf waters < 500 m (Fig. 3.3b). In both species, foraging behaviour was more likely to occur at maximal distances from the colony (~3000 km for Grey Petrels and ~2000 km for White-chinned Petrels) (Fig. 3.3c).

3.4   Discussion

Habitat preferences, and flexibility in habitat use, are fundamental to our understanding of ecological processes, community structure and population dynamics, and critical for effective conservation and management in a world where human impacts are pervasive. In this study, we compared the oceanographic characteristics of incubation foraging trips by the winter-breeding Grey Petrel and their summer-breeding congener, the White-chinned Petrel. We identified the habitats where feeding behaviour occurred, as opposed to transit or resting. We observed a clear divergence in habitat preference between congeners, despite the potentially large area of overlap of birds from the two populations. Grey Petrels tracked from Gough Island targeted a specific cold-water area to the northwest of South Georgia, likely related to the relatively high primary productivity at that time of year. In contrast, White-chinned Petrels transited that region, preferring to feed in the shallow (< 500 m) waters of the Patagonian Shelf, without a specific preference for temperature regime. Both species targeted areas of relatively high productivity.
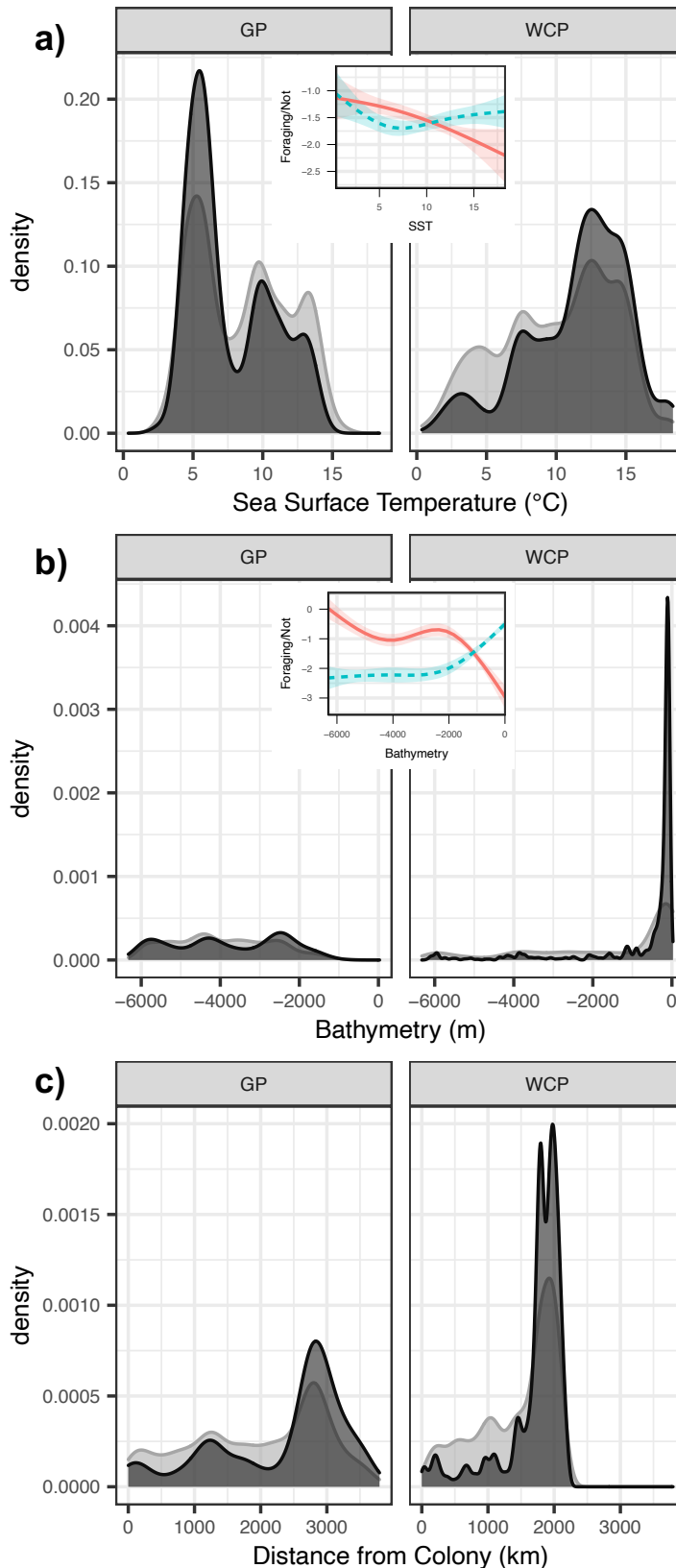
Figure 3.3: Density plots showing foraging points (black) and non-foraging points (grey) that occurred across selected environmental gradients (A: sea surface temperature, °C; B: bathymetry (m); C: distance from the breeding colony (km), in Grey Petrels (GP) from Gough Island (tracked in April–May 2014; austral winter), and White-chinned Petrels (WCP) from South Georgia (tracked in December 2014–January 2015; austral summer). Insets show selected GAM smooths for Grey Petrels: red/solid, and White-chinned Petrels: blue/dashed (see Appendix 2, Table S2 and Fig. S6 for all smooths). No inset indicates that the term was not modelled.

The preference for foraging in cold, pelagic habitat by Grey Petrels from Gough Island was consistent among individuals, whereas evidence from fisheries bycatch in New Zealand shows that at least for part of the breeding season, some Grey Petrels from Antipodes Island travel to the north coast of New Zealand, where temperatures are likely much higher than the ~ 5°C peak observed in our study (Mischler and Bell 2017). The Antipodes population also appears to show sexual segregation in foraging areas during breeding (Mischler and Bell 2017), which was not evident at Gough Island (Rollinson et al. 2016). To our knowledge, the Grey Petrels from Gough Island represent the only population tracked with GPS devices during breeding. Fine-scale habitat preferences of Grey Petrels at Kerguelen, Antipodes, and Marion Islands differed markedly during the non-breeding season (Torres et al. 2015), and hence tracking at other colonies is needed to determine whether the same applies during the breeding season.

Contrasting habitat preferences among colonies are also apparent in the White-chinned Petrel. In our study, birds did not target a specific temperature profile, although all travelled to shallow, productive waters on the Patagonian Shelf. This contrasts with White-chinned Petrels from Iles Kerguelen, which foraged during the entire breeding season in Antarctic and sub-Antarctic waters of 1–5 °C (Péron et al. 2010); those from Marion Island, which tended to forage either in waters close to the colony or off the southern coast of South Africa (Rollinson et al. 2018); and those from Iles Crozet, which foraged both north and south of the colony during incubation, but targeted cold waters to the south while rearing chicks (Weimerskirch et al. 1999, Catard et al. 2000). White-chinned Petrels from South Georgia also forage in cold, southerly waters, as far as the ice edge, but not until the chick-rearing period (Phillips et al. 2006). It could be argued that the consistent targeting of the Patagonian Shelf by White-chinned Petrels during the incubation period might be a new behaviour since the advent of industrial fishing, but it seems unlikely given the huge numbers of other predators – many of which do not scavenge behind vessels – that also use this highly productive region (Song et al. 2016). Our study also reaffirms that this area is critical habitat for White-chinned Petrels during breeding every year, as our new data indicate the use of similar foraging areas to White-chinned Petrels tracked in incubation over a decade earlier (Phillips et al. 2006).

Differences among congeners in habitat use can vary from subtle to distinct, and can involve temporal segregation when niches are very similar. Both MacGillivray's *Pachyptila macgillivrayi* and Broad-billed Prions *Pachyptila vittata* target similar foraging areas at the same points in their breeding cycle, but do not compete due to a temporal offset of breeding by around three months (Jones et al. 2020). The same mechanism also reduces competition between Northern *Macronectes halli* and Southern Giant Petrels *M. giganteus*, which lay on average around 6 weeks apart, and also show sexual segregation (Brown et al. 2015, Granroth-Wilding and Phillips 2019). In contrast, the oceanographic characteristics of foraging areas chosen by Grey and White-chinned Petrels are much more distinct, and the temporal offset in timing of breeding much longer (approximately 3–4 months). The high consistency in foraging habitat preferences within Grey and White-chinned Petrels, and its strong divergence between species, as well as the markedly different phenology, may have originally developed during sympatric speciation. Further study focusing on islands where these two species breed in sympatry (Marion, Crozet, Kerguelen and New Zealand) would help determine the mechanisms by which this is maintained. The observed flexibility in habitat choice of *Procellaria* species across populations and between breeding stages suggests that temporal segregation of peak resource-demand (i.e. breeding allochrony) is as effective for partitioning resources as habitat specialisation, and also more likely to lead to reproductive isolation and therefore speciation.

The most extreme example of breeding allochrony in seabirds is winter breeding, which in the *Procellaria* occurs in both Grey and Westland Petrels. Although most seabirds appear to time reproduction such that the most energetically-intensive phase (chick-rearing) coincides with peak resource availability, there may be a benefit to instead aligning the non-breeding period with the productivity peak. Grey Petrels and Westland Petrels have unusually long chick-rearing periods, and laying is more protracted than in other petrels and shearwaters, which has been attributed to the scarcity and variability of food in the austral winter (Zotier 1990). This long breeding period means that the slowest parents have < 80 days for post-breeding moult and to restore their body condition prior to the onset of the subsequent season (Zotier 1990, Chastel 1995). While such a short period between fledging and expected return would usually

result in biennial breeding, as in the Wandering Albatross *Diomedea exulans*, this is not the case for Grey Petrels. It has been argued that such a quick recovery is possible for winter breeders due to the abundant resources available in the summer, which they can exploit without the central-place restrictions experienced by breeding birds (Chastel 1995).

Alternatively, allochrony may develop simply because winter resource levels *are* high enough to support alternative breeding strategies. Seven reciprocally monophyletic clades of band-rumped storm-petrels (*Hydrobates* spp.) have now been revealed, which likely comprise cryptic species or sub-species that show strong allochrony caused (or at least maintained) by multiple temporal peaks in resource availability (Monteiro and Furness 1998, Taylor et al. 2019). It may be that despite lower overall productivity in winter, there is a secondary peak of food *accessibility* for Grey Petrels, due to a reduction in interspecific competition in waters around South Georgia. Grey Petrels from Gough Island show temporal segregation in peak demand for resources both from White-chinned Petrels at South Georgia, and Spectacled Petrels, which breed on nearby Inaccessible Island (Reid et al. 2014). Demand for resources other than food may also contribute to breeding allochrony; indeed, it has been suggested that winter breeding in seabirds emerged in response to competition for burrows (Harrison et al. 1983). Winter breeding at South Georgia is not possible for burrow-nesting species due to frozen ground and persistent snow cover; however, at lower-latitude sites such as Marion Island, there is strong evidence for competition (in the form of chick evictions) between Grey and White-chinned Petrels at the start or end of their respective breeding seasons (Dilley et al. 2019). Winter breeding may have evolved in sympatry as a mechanism to reduce such competition and then carried over to islands where these species breed in allopatry. In addition, because zooplankton remain abundant in the area north of South Georgia well into winter (Atkinson et al. 2001), the absence of local breeders may more than compensate for the commuting costs borne by Grey Petrels coming from Gough. It has been suggested that winter breeding in Westland Petrel is sustained by sufficient prey abundance in the absence of summer-breeding competitors (Poupart et al. 2020). It may be that winter breeding also provides Grey Petrels with a dual advantage, allowing access

to sufficient prey resources in the south, while avoiding peak competition for burrows on their temperate breeding islands.

Our study highlights the importance of tracking for identifying key foraging areas and habitats for pelagic predators, which can be located thousands of kilometres from the nest. Here we report results for two congeners with distinct foraging preferences, but we infer that their strategies are also influenced by the highly speciose communities in which they breed: specialisation is therefore likely to occur at even smaller scales, and be further influenced by individual preferences (Navarro et al. 2013, Phillips et al. 2017). Such comparisons help develop a deeper understanding of the relationships between foraging behaviour, niche partitioning and life history.

CHAPTER 4: **Habitat preferences of the *Phoebetria* albatrosses in sympatry and allopatry**

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Author contributions:

I conceived the ideas, designed the study, analysed data, made figures, and wrote up the chapter with supervision from R. A. Phillips and A. Manica.

R. Alderman, T. Carpenter-Kling, R. Crawford, R. Cuthbert, K. Delord, B. J. Dilley, R. Gales, A. B. Makhado, S. Oppel, P. Pistorius, P. G. Ryan, S. Schoombie, H. Weimerskich, and R. A. Phillips provided tracking data. T. Carpenter-Kling separated Marion Island tracking data into individual trips. The pronoun 'I' is used in this chapter as it has not yet been reviewed by all coauthors.

Abstract

Competition is proposed to drive niche segregation along multiple axes in speciose communities. Understanding spatial partitioning of foraging areas is particularly important in species that are constrained to a central place. Here, I present a natural experiment examining habitat preferences in sympatry and allopatry of congeneric Southern Ocean predators. The two *Phoebetria* albatrosses breed on islands located from ~ 30-55 °S – Sooty Albatrosses (*P. fusca*) in the north and Light-mantled Albatrosses (*P. palpebrata*) in the south) – with sympatric overlap at locations ~ 45 °S. Using foraging tracks from 87 individuals during their incubation periods (from 2002-2017) I show that while foraging habitat preferences are consistent in Light-mantled Albatrosses, there is divergence of preferences in Sooty Albatrosses depending on whether they are in sympatry with their congener or in allopatry. Light-mantled Albatrosses demonstrated a cold-water preference across their range, whereas allopatric Sooty Albatrosses in the north preferred cold-water habitats, but those at more southern sympatric colonies foraged in warm-water areas. This study represents the most comprehensive work undertaken on this genus to date. My findings highlight how habitat preferences and behavioural plasticity influence species distributions under different competitive conditions, and also have wider implications for our understanding of niche partitioning within complex communities.

4.1 Introduction

Interspecific competition occurs when closely-related species overlap in space and share the same habitats and resources (Svärdson 1949, MacArthur and Levins 1964, Tilman 2007). Responses to interspecific competition vary, but include agonistic or territorial behaviour if species remain specialised on the same resources, or niche differentiation if either selection or plasticity results in one or both species shifting to alternative resources (Kokkoris et al. 1999, Grant and Grant 2006, Stuart and Losos 2013, Tarjuelo et al. 2017). The latter has been observed, for example, in hydrological niches in plants (Araya et al. 2011), feeding niches in predatory fish (Young et al. 2010), microhabitat use in reptiles (Pianka and Huey 1978), and sensory abilities in bats (Siemers and Schnitzler 2004). Segregation along multiple axes relating to habitat use, phenology or trophic level has also been reported in speciose communities across diverse taxa (Croxall and Prince 1980, Kiszka et al. 2011, Ito et al. 2021). Habitat segregation of mobile predators is well-studied in terrestrial and marine systems, as an adaptive response to interspecific competition which allows for competitors to coexist (Ziv et al. 1993, Martin and Martin 2001, Morris 2003, Jankowski et al. 2010).

For highly mobile species, foraging habitat selection is of critical importance, particularly when the environment is dynamic and prey are unpredictable at small spatial scales (Weimerskirch 2007). Whether we consider the drivers of habitat selection at the proximate level (the environmental cues used to locate prey patches) or ultimate level (the evolutionary costs and benefits of using a particular habitat), it is assumed that individuals should forage such that their expected fitness is maximised (subject to constraints) (Pyke 1984, Hutto 1985). It has been suggested as a general rule that competitors with similar ecological niches are more confined to their specific, divergent niches when in sympatry, but expand into the niche of their absent competitor when in allopatry (Hildén 1965). While often argued that niche divergence between competitors is evidence of competition driving coevolution (e.g. Jones and Barmuta 2000, Salewski et al. 2003, Cloyed 2014), demonstrating the supposed coevolutionary shaping of niches is difficult, particularly as there are other potential drivers (Connell 1980). When studying an ecological community, it is often impossible to tell whether observed traits are truly coevolved – i.e. that they represent reciprocal evolutionary change in traits between two co-occurring species (Janzen 1980) – or instead are adaptations over shorter timescales (Connell 1980, 1985). If habitat preferences are coevolved at a species level due to

historical competition, they are likely to be less variable than those that emerge within populations due to behavioural plasticity or density-dependent mechanisms. Regardless of the mechanism of segregation it is important to understand the extent to which species can change their foraging strategy in response to competition and a dynamic environment, particularly in the context of anthropogenic environmental change.

Seabirds provide a suitable system to study effects of competition on habitat preference, because they breed in densely populated, speciose communities with highly constrained central-place foraging (Phillips et al. 2017, Antolos et al. 2017). This forced overlap during an energetically expensive life stage has led to segregation across multiple axes, both within and between species (Cooper and Klages 1995, Navarro et al. 2013, Campioni et al. 2016, Bolton et al. 2019, Granroth-Wilding and Phillips 2019, Reisinger et al. 2020). However, almost all studies to date have focused on competition within a single breeding community, thus making it difficult to ascertain the drivers of observed niche differentiation at a broader level. A suitable study system to investigate the impact of competition on habitat preference exists in the *Phoebetria* albatrosses (Sooty Albatross *P. fusca* and Light-mantled Albatross *P. palpebrata*). This genus has a circumpolar distribution, and the two species breed both in sympatry and allopatry. Sooty albatrosses are distributed largely from 30-50 °S, and breed north of the Antarctic Polar Front, whereas Light-mantled Albatrosses breed in the subantarctic region (below 40 °S); the species co-occur at their respective southern/northern limit, at the Prince Edward Islands and Iles Crozet (~ 47 °S) (Berruti 1979, Phillips et al. 2016, Schoombie et al. 2017). There is extensive overlap of the ~ 7 month breeding seasons in both species, though on average Sooty Albatrosses lay ~ 2 weeks earlier than Light-mantled Albatrosses (Tickell 2000). This allochrony means that there is little overlap of the ~ 3-week brood-guard stage, but significant overlap of the longer incubation and chick-rearing periods.

In this study I compare the habitat preferences of the *Phoebetria* albatrosses at multiple colonies across their breeding ranges, including in sympatry and allopatry (Figure 4.1). My aim was to ascertain consistency in habitat preferences within species, and whether preferences changed in the presence of the congener. I hypothesised that if habitat preference coevolved in sympatry or was otherwise innate, I would observe consistent preferences within species across breeding sites. The alternative is that habitat preferences are shaped on shorter timescales by interspecific competition, in which case I hypothesised that colony-specific preferences would be apparent in one or both species.

4.2 Methods

4.2.1   Data collection

Light-mantled and Sooty Albatrosses were tracked during incubation at multiple islands from the years 2002 to 2017 (for full details, see Table 4.1).
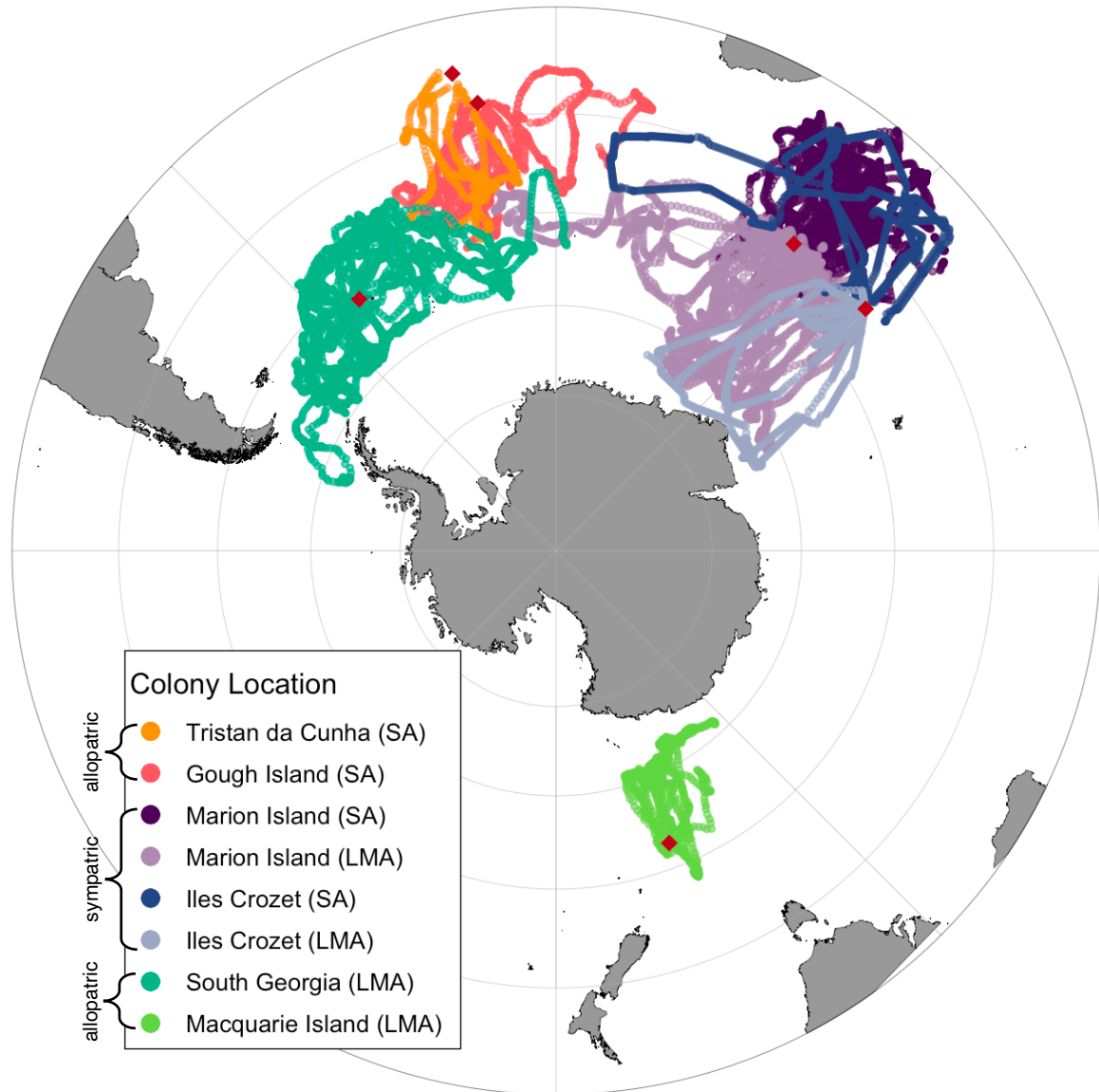
Figure 4.1: *Tracks from Light-mantled Albatrosses (LMA) and Sooty Albatrosses (SA) during incubation from multiple colonies across their breeding range. Study colonies indicated by red diamonds. For deployment details, see Table 4.1.*

Site Name	Species	Est. population (breeding pairs)	% of global population	Sympatric/allopatric	Year(s)	Device	Further information
Tristan da Cunha	SA	2000-3000	~18.7%	allopatric	2015	GPS: CatTraQ (Mobile Action Technology, Inc. 2013) loggers, 42 × 25 × 10 mm, 25 g (incl. tape)	(Schoombie et al. 2017)
Gough Island	SA	< 5000	< 37.5%	allopatric	2013	GPS: CatTraQ (Mobile Action Technology, Inc. 2013) loggers, 42 × 25 × 10 mm, 25 g (incl. tape)	(Schoombie et al. 2017)
South Georgia	LMA	5000	~24.5%	allopatric	2009, 2014	GPS: i-gotU GT-120 (MobileAction Technology, Taiwan; 25 g)	NA. (BAS unpublished data.)
Marion Island	LMA	507	~2.4%	sympatric	2015-17	GPS: CatLog-S loggers, Perthold Engineering LLC USA, 50 × 22 × 8 mm, 34 g	(Carpenter-Kling et al. 2020)
Marion Island	SA	1283	~9.6%	sympatric	2015-17	GPS: CatLog-S loggers, Perthold Engineering LLC USA, 50 × 22 × 8 mm, 34 g	(Carpenter-Kling et al. 2020)
Iles Crozet	LMA	2273-2323	~11.2%	sympatric	2008	PTT: Microwave Telemetry, Solar, duty cycle 10/24, 62 × 18 × 14 mm, 18g	(CNRS unpublished data, see Delord et al. 2014)
Iles Crozet	SA	2084-2264	~15.8%	sympatric	2008	PTT: Microwave Telemetry, Solar, duty cycle 10/24, 62 × 18 × 14 mm, 18g	(CNRS unpublished data, see Delord et al. 2014)
Macquarie Island	LMA	1281	~6.3%	allopatric	2002	PTT: Microwave Telemetry. 50 × 15 × 15 mm, 30 g	(Cleeland et al. 2019)

Table 4.1: *Summary of tracking data from light-mantled albatrosses (LMA) and sooty albatrosses (SA) during the incubation period used in analyses. 'Year' refers to the timing of egg laying, although incubation at some colonies extends into January the following year. Population sizes from ACAP (2010a, 2010b).*

4.2.2 Track processing

Tracks were visually inspected and removed from analysis if trips were incomplete due to of device malfunction. Trips were counted as incomplete if they did not show a clear departure from and return to the colony, or if large portions of the middle of the trip did not register locations. Where multiple trips for the same individual were successfully recorded, only the first trip was selected from each bird to avoid pseudo-replication. Not all nests were monitored until hatching, in which case I used trip duration and the average hatching dates at each colony (Agreement on the Conservation of Albatrosses and Petrels 2010a, 2010b) to select a trip likely made during incubation. All tracks were filtered (*trip* R package (Sumner et al. 2009)) to remove points indicating flight speeds > 90 km/hr (Phillips et al. 2007), and interpolated to 60-minute intervals for consistency, as this was the coarsest temporal resolution of data collected. Characteristics (duration, distance travelled, and maximum displacement) were calculated from the interpolated tracks. For each track, 20 pseudoabsence tracks were generated by randomising the departure direction from the colony, while retaining step length and turning angle to ensure flight patterns were biologically appropriate. Various remote sensing and other environmental variables were extracted for each presence and pseudoabsence location (Table 4.2).

Variable (units)	Data Source	Temporal scale	Spatial Scale
Sea surface temperature (SST, °C)	Global ocean ensemble physics reanalysis, CMEMS (Global Monitoring and Forecasting Centre 2021).	Monthly composite	0.25 x 0.25 degrees
log(Chlorophyll *a* gradient)	Calculated from Global ocean biogeochemistry hindcast, CMEMS (Global Monitoring and Forecasting Centre 2021) using R package 'grec' (Lau-Medrano 2020)	Monthly composite	0.25 x 0.25 degrees
Bathymetry (m)	Global Bathymetric Chart of the Oceans (GEBCO Compilation Group 2020).	Static	0.00833 x 0.00833 degrees, resampled to 0.25 x 0.25 degrees using the 'terra' package (Hijmans et al. 2022).
log(eddy kinetic energy)	Calculated from north and east current velocities, Global ocean ensemble physics reanalysis, CMEMS (Global Monitoring and Forecasting Centre 2021).	Monthly composite	0.25 x 0.25 degrees

Table 4.2: *Environmental layers used in habitat models for Light-mantled and Sooty Albatrosses tracked during incubation.*

4.2.3   Modelling

Binomial generalised additive models using the environmental variables extracted at the presence and pseudoabsence locations were constructed for each species. Additive models are appropriate when relationships with predictors are likely to be non-linear, and were constructed using the R package *mgcv* (Wood 2011). Full models were constructed for each species, using all environmental variables (see Table 2) by colony type (sympatric or allopatric), and model selection was undertaken using AICc values. Models for each colony were subsequently constructed using the environmental variables selected for the full model. Spatial autocorrelation was accounted for in all cases using a Gaussian correlation structure on the latitude and longitude terms. All model formulae and outputs are available in in supplementary tables 1 through 6. All data manipulation and analyses were undertaken in R version 4.0.3 (R Core Team 2020). Means are provided ± SD unless indicated otherwise.

4.3 Results

4.3.1   Trip characteristics

Trips of Light-mantled Albatrosses were on average 12.66 ± 4.62 days and covered on average 5723 ± 2151 km, whereas those of Sooty Albatrosses were on average 11.25 ± 4.58 days and covered an average 5154 ± 2132 km. The average maximum displacement from the colony was 1562 ± 675 km for Light-mantled Albatrosses and 1318 ± 495 km for Sooty Albatrosses (see Table 4.3). When pooling trips from all years, Light-mantled Albatrosses from South Georgia took the shortest trips (10.17 ± 4.57 days), and those from Marion Island the longest (12.72 ± 4.57 days). There much higher variation in average trip lengths among Sooty Albatross colonies, with birds from Gough Island foraging for 8.45 ± 4.54 days, and birds from Tristan da Cunha and Iles Crozet foraging for almost twice as long: 16.17 ± 2.16 and 16.5 ± 10.4 days, respectively. However, the longest-lasting foraging trips were not always those where birds reached the greatest distances from their breeding colonies. In both light-mantled and Sooty Albatrosses, birds from Crozet attended the most distant foraging areas, 2456 ± 161 and 2210 ± 1091 km from their respective colonies. Light-mantled albatrosses from Macquarie Island and Sooty Albatrosses from Marion Island accessed the most proximate foraging areas, at a maximum 1203 ± 267 and 1145 ± 323 km away,

respectively. Finally, the average distance travelled in a foraging trip was greatest for
Marion Island Light-mantled Albatrosses and Crozet Island Sooty Albatrosses, at 6255 ±
2205 and 6913 ± 5019 km. The shortest average distance travelled was 4810 ± 399 km
for Light-mantled Albatrosses from Macquarie Island, and 4826 ± 2328 km for Sooty
Albatrosses from Gough Island.

Season	Breeding site	Species	n	Mean trip length (days)	Mean distance travelled (km)	Mean max displacement from colony (km)
2015	Tristan da Cunha	SA	3	16.17 ± 2.16	6339 ± 986	1682 ± 227
2013	Gough Island	SA	11	8.45 ± 4.54	4826 ± 2328	1307 ± 327
2009	South Georgia	LMA	6	7.61 ± 3.83	4828 ± 2128	1546 ± 633
2014	South Georgia	LMA	12	11.45 ± 4.50	5715 ± 2600	1259 ± 474
2015	Marion Island	LMA	4	14.48 ± 5.58	5782 ± 2308	1312 ± 704
2015	Marion Island	SA	3	11.72 ± 2.09	4402 ± 1101	1225 ± 360
2016	Marion Island	LMA	6	17.00 ± 3.99	7696 ± 2057	2135 ± 690
2016	Marion Island	SA	10	12.05 ± 2.11	5601 ± 1568	1273 ± 237
2017	Marion Island	LMA	11	13.56 ± 4.45	5640 ± 2064	1548 ± 762
2017	Marion Island	SA	8	10.10 ± 2.29	4226 ± 1296	953 ± 347
2008	Iles Crozet	LMA	4	13.84 ± 2.54	5666 ± 1938	2455 ± 161
2008	Iles Crozet	SA	3	16.50 ± 10.40	6913 ± 5018	2210 ± 1090
2002	Macquarie Island	LMA	6	12.17 ± 2.29	4809 ± 399	1202 ± 267

Table 4.3: *Trip characteristics of incubating Light-mantled Albatrosses (LMA) and Sooty
Albatrosses (SA) for each year tracked.*

4.3.2   Habitat preferences

Light-mantled Albatrosses, whether in sympatry or allopatry with Sooty
Albatrosses, preferentially foraged during the incubation period in cold-water areas of 0 –
5 °C, and avoided water temperatures > 15 °C (Fig. 4.2(a)). At Crozet, Marion and
Macquarie Islands, Light-mantled Albatrosses mainly travelled south to forage in areas
close to the ice edge, whereas at South Georgia they foraged at the ice edge and to as far
north as the Antarctic Polar Front. There was a slight tendency to use areas with high
chlorophyll *a* gradients (indicating frontal zones), particularly at Iles Crozet. Preferred
water depths were 2000-4000 m (Fig. 4.2 (c)). The best model included all environmental

variables, though the most influential was sea surface temperature (Appendix 3, Tables S1 and S2).

In contrast to Light-mantled Albatrosses, the Sooty Albatrosses did not show consistent preferences across sites. When in allopatry, Sooty Albatrosses foraged preferentially in cold (0 – 5 °C) and cool waters (10 – 15 °C), even though most available habitat was 15-25 °C (Fig. 2 (e)). In contrast, Sooty Albatrosses breeding in sympatry with Light-mantled Albatrosses foraged preferentially in waters of 15 – 20 °C and targeted areas with high chlorophyll *a* gradients. Sooty albatrosses avoided the cold-water areas (< 5 °C) frequented by their congener, even though sites where the two species breed in sympatry are further south than those where only Sooty Albatrosses are present. Zones of high eddy kinetic energy were targeted by Sooty Albatrosses across their range (Fig. 4.2(f)). The best model included all environmental variables, with markedly different relationships displayed at sympatric and allopatric colonies (Appendix 3, Tables S4 and S5).

Sea-surface temperature was the most important predictor in models for both species, with similar shapes for all smooths at all colonies of Light-mantled Albatrosses, and clear differences in smooths between colonies of Sooty Albatrosses, depending on whether they were breeding in sympatry or allopatry (Fig. 4.3, Appendix 3, Tables S3 and S6).

Light–mantled Albatross, all colonies

Dark Grey = Presences, Light Grey = Absences
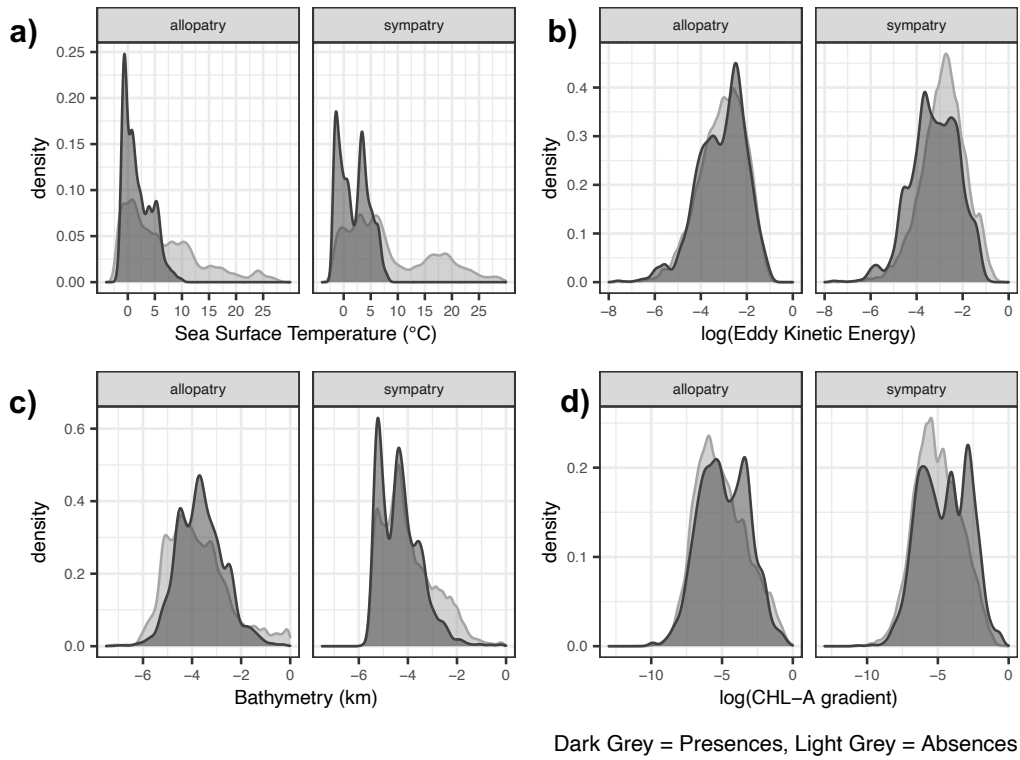
Sooty Albatross, all colonies

Dark Grey = Presences, Light Grey = Absences
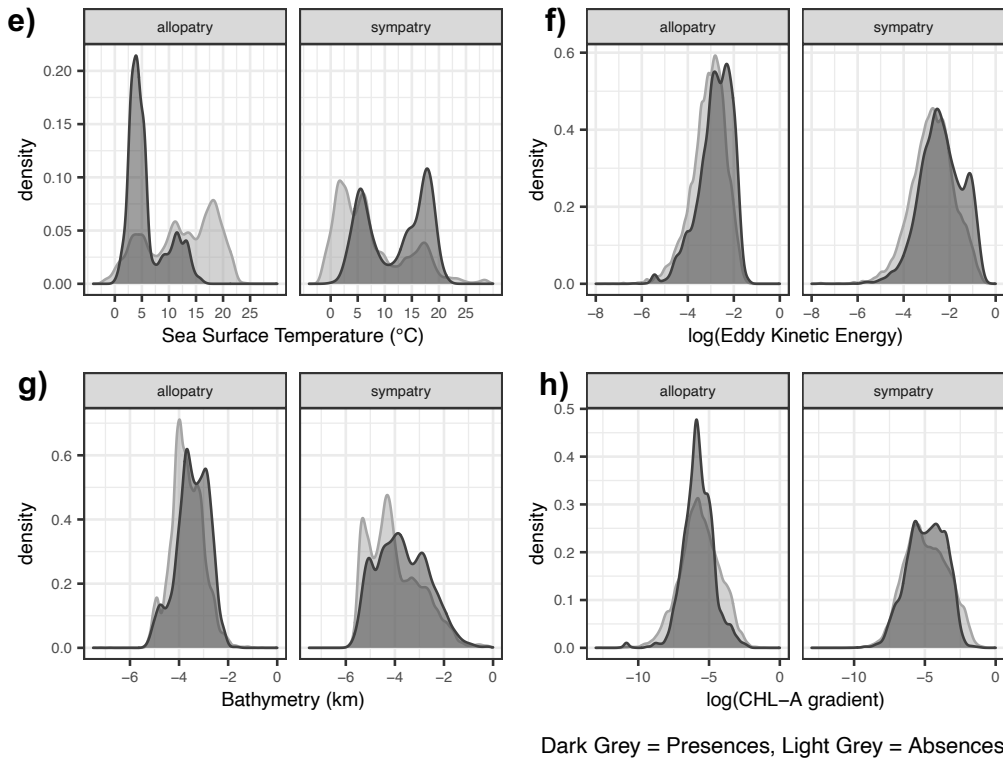
Figure 4.2: *Density plots showing the proportion of presences and pseudoabsences across key environmental variables for incubating Light-mantled and Sooty Albatrosses.*

GAM smooths, Light–mantled albatross
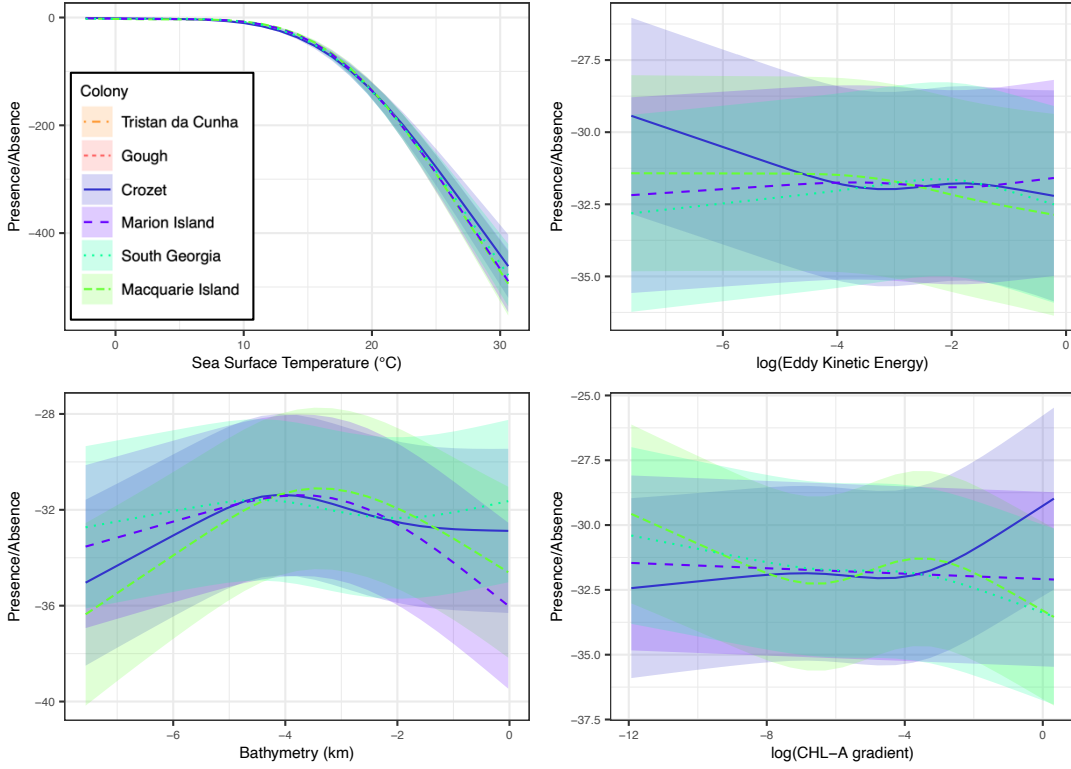
GAM smooths, Sooty albatross
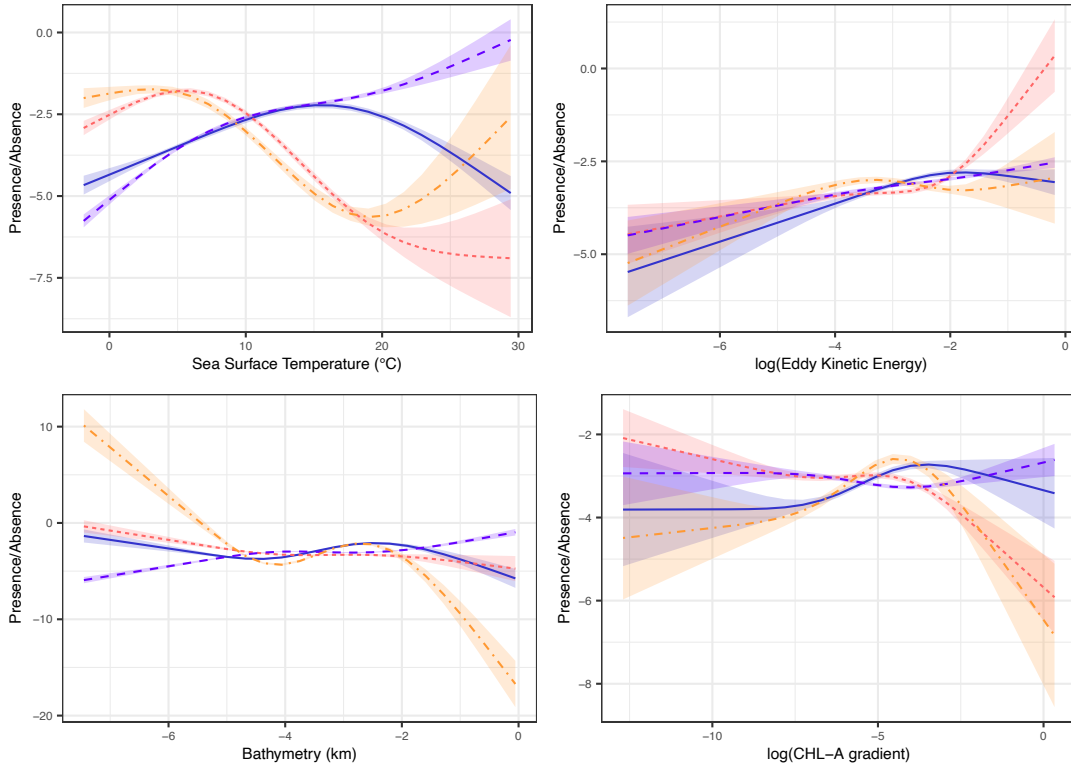
Figure 4.3: *GAM smooths for colony-specific habitat preference models for Light-mantled and Sooty Albatrosses tracked during the incubation period. Green and teal lines: allopatric LMA colonies; red and orange lines: allopatric SA colonies; blue and purple lines: sympatric colonies. Individual colonies indicated by line type in the legend. Y-axes on log-odds scale.*

4.4 Discussion

Despite their morphological and behavioural similarities, the foraging habitat preferences of the two species of *Phoebetria* albatross differ significantly from one another when breeding in sympatry. The preference of Light-mantled Albatrosses for cold-water areas (either cold upwelling zones or the ice edge) remain consistent throughout their range. In contrast, habitat preferences of Sooty Albatrosses differ whether they breed in sympatry with their congener or in allopatry. Even though the islands where they breed in sympatry are further south, the Sooty Albatrosses at those sites foraged preferentially in warm water areas, which was not a preferred habitat when breeding in allopatry in the northern portion of their range. This suggests that there is a competitive mechanism at work driving habitat segregation.

Given the absence of consistent preferences in both species across their global distributions, the observed niche segregation between sympatric *Phoebetria* albatrosses is unlikely to be driven by coevolution under competition. Competition is often considered to drive coevolved niche specialisation in speciose communities, but demonstrating coevolutionary shaping of competitors' niches is challenging, especially as there are alternative, more plausible drivers (Connell 1980). In general, ecological niche theory predicts that differentiation of some kind (e.g. prey specialisation, spatio-temporal segregation) should occur when multiple species with similar niches compete for resources (Tilman 2007). Specialist foraging strategies coevolved at a species level due to historical competition (i.e. following reciprocal divergent selection for different phenotypes) are likely to be less flexible than strategies that emerge within populations due to behavioural plasticity or density-dependent mechanisms. In an ecological community, it is often impossible to tell whether the observed specialisations are coevolved or are adaptations that were selected for over shorter timescales. In general, sympatric speciation – particularly on isolated islands where the population is under divergent ecological selection – is accepted as a plausible route to the formation of novel species (Jiggins 2006). Indeed, there is recent empirical evidence for this in some seabird species (Friesen et al. 2007b). Had *Phoebetria* speciation occurred in sympatry – with competition driving selection for resource segregation and leading to subsequent reproductive isolation – I would expect fixed habitat preferences within each species that carried over to any allopatric populations that were subsequently established. However, this 'ghost of competition past' (Connell 1980) was not observed in our study: although

the foraging habitat preferences of Light-mantled Albatrosses were consistent across sites, those of Sooty Albatrosses were not. If sympatric speciation *did* occur in these species it is therefore unlikely to have been driven by competitive segregation of foraging niches. Based on simulation models, the alternative mechanism – speciation in allopatry with subsequent reestablishment of sympatric populations – is considered to be the more common mode of avian speciation (Phillimore et al. 2008). If this is the case, the observed niche segregation in sympatry cannot be the product of coevolution, as co-occurrence is a critical requirement for reciprocal selection to occur (Connell 1980, 1985, Janzen 1980).

Even if the habitat preferences of the *Phoebetria* albatrosses are not the result of coevolved niche differentiation, this does not preclude the possibility that competition influences their realised niches in sympatry. As such, there are three alternative mechanisms I see for the patterns observed. Firstly, ecological character displacement – the concept that sympatric species competing for limited resources should experience selection for divergent resource use (Brown and Wilson 1956) – may be occurring at a population level. There are few cases with truly unequivocal support for ecological character displacement, with one review finding only nine of 144 case studies convincingly ruled out alternative explanations (Stuart and Losos 2013). In our study, character displacement is difficult to confirm as the trait in question is behavioural rather than morphological, and multiple measures from the same individuals through time are required to confirm whether this trait is fixed or plastic.

Secondly, habitat segregation of the sympatric populations may be demonstrating a socially-mediated variation of the Ideal Free Distribution (IFD), the theory assuming that equally competitive organisms will act to maximise their foraging efficiency by moving to areas with decreased densities of competitors (Fretwell 1969). It is theoretically possible that the observed segregation developed because individuals avoided areas of highest competition and is now maintained through social learning or preferred associations. However, multiple studies have shown that the space-use of seabirds and their prey rarely appears as expected under the IFD (Logerwell and Hargreaves 1996, Swartzman and Hunt 2000). This is most likely because seabirds rarely conform with the associated IFD assumptions of individuals having perfect environmental information and cost-free movement (Fauchald 2009). In many colonial seabirds, density dependent habitat segregation has been observed among colonies (e.g. Wakefield et al. 2013), but I did not find this. The speciose nature of seabird breeding

aggregations means both intra- and interspecific competition are high. There is evidence in geese that the density of multispecies assemblages can influence fitness more than the density of conspecifics alone (Schmutz and Laing 2002), and it is plausible that similar effects occur at seabird breeding islands, however this has not been formally tested. In our study, I observed segregation between presumably unequal competitors (i.e. between the two species), and use of the same foraging areas by equal competitors (i.e. consistent habitat preferences within species, often among colonies). There was within-species overlap of foraging areas in both Light-mantled and Sooty Albatrosses from Marion and Crozet (Fig. 1), though they were tracked in different years. Future tracking of birds from neighbouring colonies in the same year is needed to rule out among-colony habitat partitioning in the *Phoebetria* albatrosses.

Thirdly, the observed differences in habitat preference among populations of Sooty Albatrosses may reflect behavioural plasticity. This I consider to be the most likely explanation. Strict resource preferences have been shown to relax in conditions of scarcity (Bergström et al. 2004, Snell-Rood and Papaj 2009), which is adaptive in novel or dynamic environments where preferred resources are unavailable. Indeed, there should be selection for reversible phenotypic plasticity in environments that vary within the lifetime of an individual, due to the high costs of mismatch between preference and availability of resources (Snell-Rood 2013). This is particularly relevant for long-lived species such as albatrosses, which can live for > 40 years (Froy et al. 2017), as they presumably encounter greater environmental variability than shorter-lived species. There is evidence that habitat preferences in other Procellariiformes are not consistent between breeding populations (Torres et al. 2015, Clay et al. 2016, Péron et al. 2018). This suggests that flexibility of habitat preferences is adaptive at a species level. Further evidence for plasticity in habitat preference comes from Marion Island, where Sooty Albatrosses tracked during incubation showed high inter-annual variability in foraging behaviour, and Light-mantled Albatrosses targeted specific eddy fields only in years when eddy kinetic energy was particularly high (Carpenter-Kling et al. 2020). I observed divergent habitat preference among colonies of Sooty Albatross, which supports the conjecture that this trait is behaviourally plastic. The consistency of preferences among Light-mantled Albatross colonies does not, however, confirm that this species is inflexible. To truly understand the flexibility of albatross habitat preferences we require repeated measures on individuals (to determine if there is individual-level specialisation), across years (to determine the response within populations to changes in local conditions)

and a combination of both (to understand within-population variation of individual responses to changing conditions). If any colony-level habitat preferences are shown to be fixed, further research is then required to ascertain whether this inflexibility is genetic (due to past selection) or cultural (due to learning).

Flexibility in habitat preferences can buffer the effects of anthropogenic environmental change, which is occurring at an unprecedented rate (Gruber et al. 2019), allowing for immediate individual adaptation to changing conditions rather than species adaptation on the scale of evolutionary time. Nevertheless, selection also acts on these individuals (whether they display this flexibility or not). High philopatry in seabirds minimises gene flow across breeding ranges, and there has been some suggestion that differentiation is occurring in Sooty Albatrosses, although citing unpublished data (Robertson 1998). If this is the case, we are more likely to see differential responses among colonies of this species to environmental change. Unfortunately, albatrosses are unsuitable for cross-fostering studies which could explore the varying influences of genotype and the local environment on habitat preferences. Studies of ontogenetic changes in habitat preferences can at least help us to understand the potential flexibility of preferences within individuals (Frankish et al. 2020). Importantly, even if birds are flexible in their habitat preferences, this may not be sufficient to compensate for poor environmental conditions: evidence from South Georgia shows that in years when grey-headed albatrosses foraged mostly on krill in Antarctic waters – rather than cephalopods in the Antarctic Polar Frontal Zone, which is more common in years with favourable environmental conditions – they experienced poorer breeding success (Xavier et al. 2013). Flexible preferences do not always manifest as a shift to a generalist niche, as there is also evidence that when foraging conditions deteriorate, the diets of sympatric species show greater divergence (Barger and Kitaysky 2012). Increased niche segregation in response to stress, such as greater anthropogenic pressures, can exacerbate impacts affecting particular aspects of the niche space.

Foraging habitat location influences exposure to threats, and, ultimately, the population trend. Sooty albatross are listed as Endangered, and Light-mantled Albatross as Near-threatened by the IUCN (2022), and both species are listed by the Agreement on the Conservation of Albatrosses and Petrels (Phillips et al. 2016). Decreasing population trends have been observed at almost all Sooty Albatross colonies, with the exception of Marion Island (Delord et al. 2008, Agreement on the Conservation of Albatrosses and Petrels 2010a, Schoombie et al. 2016, Weimerskirch et al. 2018). This is proposed, in

part, to be the result of increased overlap with subtropical tuna fisheries (Delord et al. 2008). It is also possible the extreme southerly latitudes of cold-water habitats near Marion and Crozet (~60°S) are generally inhospitable to a species such as the Sooty Albatross, which presumably evolved in the subtropics. Conversely, the Light-mantled Albatross population has likely increased at Iles Crozet in recent years (Delord et al. 2008). However, the cold-water specialism of Light-mantled Albatrosses may increase their vulnerability to warming seas due to climate change (Inchausti et al. 2003, Schoombie et al. 2016). The distribution of Antarctic krill, an important prey item for this species (Green et al. 1998, Jaeger et al. 2010), is rapidly contracting southwards (Atkinson et al. 2019), and the increased costs associated with foraging even further to the south may reduce fitness in Light-mantled Albatrosses and contribute to future population declines.

Evidence from stable isotopes indicates that the cold-water preferences observed in incubating Light-mantled Albatrosses persist through chick-rearing and the non-breeding season. By measuring the isotopic ratios in chick and adult feathers, one can approximate the latitude of foraging during chick-rearing and moult, respectively (Jaeger et al. 2013). Studies from both Crozet and Marion Islands show that Light-mantled Albatrosses forage further to the south than Sooty Albatrosses during chick rearing (Jaeger et al. 2010, Connan et al. 2014, 2018), as well as in incubation (this study). Interestingly, there is some indication that Sooty Albatrosses from Crozet forage in subantarctic waters during chick-rearing (Jaeger et al. 2010), rather than the subtropical waters observed during incubation. It is likely they utilise a diet of squid and penguin carrion taken from near Crozet Island during this period, whereas Light-mantled Albatrosses showed greater reliance on Antarctic krill *Euphausia superba*, which is not available outside of the Antarctic zone (Jaeger et al. 2010). However, dietary studies on Crozet Sooty Albatrosses also showed squid beaks from subtropical species during this time, so their dietary niche remains equivocal (Connan et al. 2014). The reasonably consistent isotope ratios found in adult Light-mantled Albatross feathers indicate an annual fidelity to the Southern Ocean (Connan et al. 2014). Sooty albatrosses, however, appear to overwinter in the subtropics, with the exception of those from Gough Island, which join their congener at higher latitudes (Connan et al. 2018). Given that breeding Sooty Albatrosses from Gough Island also target cold-water areas, this may indicate some consistency between breeding and non-breeding habitat preferences across the genus, which merits further study. Indeed, further work on foraging habitat choice in the

non-breeding season is important to understand the factors influencing distribution when these species are not constrained to a central place.

Finally, I acknowledge that comparisons of species pairs in sympatry and allopatry do not account for the reality that resource competition occurs within a wider community (Bodey et al. 2014). The speciose nature of seabird breeding assemblages results in multiple layers of morphological segregation between e.g. small petrels, penguins and albatrosses (Abrams and Griffiths 1981), but more detailed comparative studies are required to identify how niche space is partitioned among sympatric (and morphologically more similar) *Thalassarche* and *Phoebetria* albatross species.

CHAPTER 5: **General discussion**

5.1 Synopsis

Understanding factors affecting species distributions is a fundamental goal in ecology, and one critical driver of movement is the search for food. By equipping pelagic predators with miniaturised tracking devices, we can reveal where and how they forage in the open ocean – particularly during the energetically expensive breeding period. Using tracking data from Antarctic seabirds, I investigated aspects of foraging ecology from the behaviour of individuals to the habitat preferences of populations and species. Not only does this work provide insights into the at-sea behaviour of pelagic seabirds, a group of high conservation concern, but it also considers how habitat accessibility, habitat preference, and interspecific competition may impact realised distributions.

In this thesis I focus on foraging during the breeding season, when individuals are constrained to a central place. In Chapter 2, I show that – in contrast to maximum depths shown in previous studies using capillary depth gauges – diving behaviour in two genera of small albatrosses is mostly infrequent, shallow, and diurnal. This work supports wider adoption of bycatch mitigation measures including night-setting and line weighting to increase sink rates of baited hooks. In Chapters 3 and 4, I show that multiple populations of albatrosses and petrels use consistent, distant foraging areas while incubating, and that competition is a likely driver of distribution patterns. Building on existing evidence for niche segregation (on multiple axes) in response to interspecific competition, I show multiple examples of population-specific habitat preferences during the incubation period (Chapters 3, 4). Additionally, I show that while habitat preferences in some species are consistent across populations, in other species preferences differ depending on whether breeding is in sympatry with a congener (Chapter 4). This variation among populations indicates that species-level variability in habitat preference may be adaptive, and that extrinsic factors (competition) as well as intrinsic physiology and preferences are likely strong drivers of foraging habitat selection. In this final chapter, I discuss the implications of my work for foraging ecology at multiple functional levels. I then consider the necessary advances (some underway, some still to come) that will improve our knowledge of pelagic seabird species from both fundamental ecological research and conservation perspectives.

5.2 Foraging ecology: from the individual to the community

5.2.1 Individual behavioural measures

Knowing how seabirds capture prey can inform both our understanding of their foraging ecology and their likelihood of incidental mortality fisheries. The extent of commercial fishing in the world's oceans means that, at least for some stage of their life cycle, geographic overlap between pelagic seabirds and commercial fisheries is highly likely (Clay et al. 2019). Beyond simple co-occurrence, species vary in their likelihood of being bycaught according to gear type and any bycatch mitigation measures deployed (extrinsic factors), their behaviour and physiology (intrinsic factors), and interactions between the two (Dias et al. 2019). For example, bird-scaring (tori) lines repel foragers until hooks have sunk beyond their dive capabilities (Løkkeborg 2011) – it is therefore critical to accurately determine what these capabilities are. For the small albatrosses (*Thalassarche* spp., *Phoebetria* spp., *Phoebastria* spp.) it has been shown that most dives are short and shallow (Chapter 2, Kazama et al. 2019). However, other intrinsic behaviours, such as tendency to follow fishing vessels, have been shown to vary not only between species, but also between colonies of the same species (Granadeiro et al. 2011, Torres et al. 2011). It is likely that diving behaviour also varies among colonies: Guilford et al. (2022) showed that for Black-browed Albatrosses from the Falkland Islands, many dives > 6 m were recorded, including some that appeared to be wing-propelled. Black-browed Albatrosses have consistently been found to dive only during the day, and at distal portions of their foraging trips (Chapter 2, Guilford et al. 2022). This diurnal diving is likely to be a physiological limitation linked to visual systems, and is a likely explanation for the observed effectiveness of night setting in reducing albatross bycatch (Melvin et al. 2013). However, variations in dive depth observed between studies may be linked to variation in prey type and availability. It may be that Black-browed Albatrosses from South Georgia were not observed to dive to depths > 6 m simply because there is ample prey at shallower depths. The different dive depths observed between studies highlight the fact that when measuring foraging behaviour, we are unlikely to be measuring maximum capabilities, rather, we can only ever take a snapshot of individual behaviour. There are a great number of reasons why animals would not frequently demonstrate physiological maxima in regular monitoring (Shepard et al. 2009). It is therefore critical that ship-based observers continue to identify the way birds are caught, such that future mitigation strategies account for the complexities of behaviour *in situ*

that lead to mortality. In particular, understanding the impact of multi-species assemblages is important, because even shallow diving species are often killed due to secondary hooking when deeper divers such as White-chinned Petrels return baited hooks to the surface (Jiménez et al. 2012, Frankish et al. 2021). This reinforces the need to mitigate not necessarily only for the species of conservation concern, but also for the deepest-diving species commonly encountered.

5.2.2   *Colony-level habitat preferences*

In this work I found highly consistent habitat preferences within colonies of White-chinned Petrels, Grey Petrels, Light-mantled Albatrosses and Sooty Albatrosses during their incubation periods (Chapter 3, Chapter 4). Birds may use particular foraging areas consistently because they are linked to stable oceanographic features: for example, White-chinned Petrels from South Georgia use the Patagonian Shelf at multiple times of year, which is likely a preference learned through ontogeny via exploration and refinement (Chapter 3, Phillips et al. 2006, Frankish et al. 2020). Other explanations for this within-population consistency relate to information sharing between conspecifics – either at the foraging patch, or at the colony. The theory of local enhancement proposes that there is a social attraction between conspecifics that draws them to the same foraging patches (Kiester 1979). This is more likely to occur when birds are foraging close to their nesting colony (e.g. Black-browed Albatrosses in brood-guard, Chapter 2), rather than for many incubating Procellariiformes which forage thousands of kilometres from their colony (Chapter 3, Chapter 4), and therefore are within visual range of fewer conspecifics. Alternatively, the information centre hypothesis posits that colonial breeders can 'inform' others about the direction of foraging habitat via behaviours such as the bearing on which they return to the colony (Ward and Zahavi 1973). This theory has, however, been criticised for ignoring more parsimonious explanations for observed shared habitat use (Mock et al. 1988, Richner and Heeb 1995), but it has been demonstrated in some species which raft close to the colony (Weimerskirch et al. 2010). Importantly, not all the observed habitat preferences were linked to consistent geographic features, but rather to habitat types – Light-mantled Albatrosses from South Georgia, for example, preferentially use pelagic, productive, cold-water areas all around the island (Chapter 4). This implies that individuals may be using olfactory or other local environmental cues rather than social or learned information to identify appropriate

foraging habitat (Nevitt 2000, Abolaffio et al. 2018). The Procellariiformes in particular have highly developed olfactory systems (Cobb 1968, Nevitt 2004, Nevitt et al. 2008).

Previous studies have found inter-colony segregation of foraging areas by intrinsic factors (e.g. sex) in many seabirds including Wandering Albatrosses (Nel et al. 2002), Black-browed and Grey-headed Albatrosses (Phillips et al. 2004), and Giant Petrels *Macronectes halli, M. giganteus* (González-Solís et al. 2000)). It is, however, by no means ubiquitous: sexual segregation is not apparent in Shy Albatrosses *T. cauta* (Hedd et al. 2001) and Westland Petrels *P. westlandica* (Poupart et al. 2020). In sexually dimorphic species differences in factors such as competitive advantage or wing loading are often used to explain sexual habitat segregation (González-Solís et al. 2000, Shaffer et al. 2001b). Conversely, consistency in foraging area choice has been shown in male and female White-chinned Petrels from Marion Island (non-breeding) and South Georgia (breeding) (Berrow et al. 2000, Rollinson et al. 2018), or not explicitly tested for, as in the *Phoebetria* albatrosses across their breeding range (Schoombie et al. 2017). I also did not observe segregation of foraging areas by sex in this thesis. This was not quantified due to either limited sample sizes, birds of unknown sex, and (most importantly) due to high consistency of foraging location within populations.

It is of particular interest that all except one of the Grey Petrels from Gough Island travelled to a foraging area to the north-west of South Georgia, over 3000 km from their nesting colony (Chapter 3). As they are winter breeders, it is unlikely that they experience the same levels of interspecific competition at their colony as most procellariiform seabirds do when breeding during the austral summer, yet they travelled very far from their colony to forage. Atlantic Petrels *Pterodroma incerta* also travel from Gough Island to a similar foraging area near South Georgia during their pre-laying exodus, which occurs at the time that Grey Petrels are incubating (Cuthbert 2004, Pastor-Prieto et al. 2019). While these two winter-breeding species at Gough Island forage at great distances from the colony (Chapter 3, Pastor-Prieto et al. 2019), multiple winter breeders from New Zealand forage relatively close to their colonies (Waugh et al. 2018, Poupart et al. 2019a, 2019b, 2020). This indicates that prey are more available near colonies in the New Zealand region than at Gough, where the slow growth rates of chicks have been attributed to poor feeding conditions (Cuthbert 2004). Simultaneous tracking of winter-breeding species at Gough is required to better understand interspecific niche segregation in foraging depth, time, area and diet during this period when food availability is assumed to be poor. At Marion Island, habitat preferences vary among

years by different extents in *Thalassarche* and *Phoebetria* species (Carpenter-Kling et al. 2020). More multi-year tracking studies are needed to understand consistency in habitat preferences under different environmental conditions, given the relevance for identifying and protecting important habitats for species of conservation concern.

5.2.3   *Species-level insights*

To draw unequivocal conclusions about foraging behaviour at a species level, we require data from multiple breeding colonies across species ranges. Many multi-colony studies are from the North Atlantic, and focus on the partitioning of coastal habitats accessible from colonies at distances of tens or, at most, hundreds of kilometres (e.g. Wakefield et al. 2013, Dean et al. 2015, Corman et al. 2016, Bogdanova et al. 2017, Buckingham et al. 2022). In comparison, capturing all (or a large part) of the at-sea range of seabirds breeding in the Antarctic and subantarctic requires tracking at breeding sites that are thousands of kilometres apart, across multiple jurisdictions. Results in Chapter 4 show that individuals from different breeding colonies can vary enormously in their foraging behaviour – Sooty Albatrosses in particular show markedly different habitat preferences at the northern and southern limits of their range.

When foraging behaviour varies between colonies it indicates a trait or preference has been adjusted according to local conditions – either because it is under local selection, or due to behavioural plasticity (or both). On the other hand, physiological traits such as metabolic rates are likely to be reasonably fixed within species (Nagy et al. 1999, Shaffer et al. 2001a). Similarly, morphological traits such as wing loading are inflexible, except on evolutionary timescales (Warham 1977). Identifying which factors are variable and which are fixed is important when considering the capacity of species to adapt to anthropogenic climate change. Changes in wind speed, for example, generate behavioural adjustments (i.e. a greater reliance on flapping flight, and therefore higher flight costs, if wind speeds drop) that impact all members of a species in the same way (Suryan et al. 2008). Changes in sea-surface temperature, however, are unlikely to generate consistent responses in all colonies, given the evidence that current habitat preferences encompass a broad temperature range (Chapter 3, Chapter 4). Ultimately, animal movements are shaped by both evolutionary and ecological processes: we will be able to better identify the evolutionary processes by investigating habitat preferences at the species level.

5.2.4   Considering communities

The logical extension of the work in this thesis is to consider how habitat preferences are shaped by both competition and accessibility at a community level. While ambitious, simultaneous tracking of multiple species at the same breeding island would allow us to better understand how habitat is partitioned in real time between birds experiencing the same environmental conditions. Identifying how foraging habitat preferences differ among species during the breeding season would provide insights into the relationship between niche partitioning and community structure. For example, at South Georgia there are seven species with broadly overlapping habitat preferences, including Wandering, Black-browed, Grey-headed and Light-mantled Albatrosses, Northern and Southern Giant Petrels, and White-chinned Petrels. Few studies to date have analysed individual movement data to understand broader-scale community ecology, but recent conceptual work shows there is great potential for animal tracking to inform our understanding of communities and the processes that shape them (Costa-Pereira et al. 2022).

5.3 Advances in biologging and movement ecology

Here I discuss three key areas – technological, analytical, and political – in which advances must continue, in order to ensure high quality research output and conservation outcomes for pelagic seabirds into the future.

5.3.1   Technological

The last decade has been called a "golden age of animal tracking", in which technological advances have allowed scientists to build an increasingly detailed understanding of animal movement in the wild (Kays et al. 2015). Early Argos tags were large and expensive (>£2K), and required funding for satellite time (Bridge et al. 2011). Archival geolocators were the first truly miniature tags to be developed, and although the mean error was ~180-200km, they were (and remain) appropriate for tracking movement on a migratory scale and could be deployed on species as small as terns (Bridge et al. 2013). Lightweight GPS tags weighing < 1 g are now available, enabling tracking of seabirds as small as European Storm-petrels *Hydrobates pelagicus* (25 g, Bolton 2021). In addition to tag miniaturisation increasing the number of species that can be tracked, the development of new sensors has diversified the types of movement data that can be

collected. Tri-axial accelerometers have now been used to identify behaviour such as dive type (i.e. plunge, foot propelled or wing-propelled), and can detect diving behaviour on a shallower scale than that of TDRs (Cianchetti-Benedetti et al. 2017, Guilford et al. 2022). The development of lightweight, bird-borne cameras has given new insight into associations between seabirds and whales (Sakamoto et al. 2009), fisheries (Votier et al. 2013), and other birds (Tremblay et al. 2014), as well as allowing researchers to identify prey types consumed (e.g. natural vs. fishery discards, Michel et al. 2021). New GPS tags equipped with a radar detector and Argos antenna have been used to relay information on the location of illegal fishing vessels in real time (Weimerskirch et al. 2020). As new devices become more innovative and affordable, our understanding of seabird foraging behaviour can expand to include events such as competitive interactions at foraging areas and individual interactions with anthropogenic threats – this type of data can ultimately help elucidate the links between individual movement and fitness (and, indeed, work of this sort is now being published, see Carneiro et al. 2022, Ouled-Cheikh et al. 2022).

5.3.2   *Analytical*

The new types, and increasing volumes, of data collected by animal-borne tags have provided detailed insight into fields from animal navigation and cognition, to flight performance, to responses to anthropogenic change (Weimerskirch et al. 2016, Tucker et al. 2018, Toledo et al. 2020), but these data require increasing capability in data storage and computational analysis in order to be interpreted (Kays et al. 2015, Nathan et al. 2022). Researchers can now access diverse high-resolution remote-sensing products (see Chapter 3, Chapter 4), handle big datasets on smaller and more powerful portable computers (often remotely using high performance computers; HPCs), and take advantage of the proliferation of free, open-source software packages – at least 60 in the R programming ecosystem alone (Joo et al. 2020). As has also been discussed for other frequently-tracked marine megafauna (e.g. sea turtles, Godley et al. 2008, Hays and Hawkes 2018), for tracking data to reach maximum utility they must be available and accessible to researchers and policymakers. This applies equally to procellariiform seabirds. Seabirds are unique in that there is a dedicated online database (hosted by BirdLife International) for tracking data from seabirds (initially Procellariiformes and later all seabird species). Globally at least 13 movement data repositories have been developed, with most hosting tracks from a wide variety of species (but see seaturtle.org)

(Campbell et al. 2016). As we look to the future, ensuring compatibility (and avoiding redundancy) of new packages and repositories is an important goal to effectively use animal tracking data. Early challenges related to standardising data types and formats, such as dates, times, coordinates and species names, have been well-discussed (Campbell et al. 2016). New proposals clearly outline how this standardisation is possible, and in fact necessary, as new tracking data are being generated at unprecedented rates (Sequeira et al. 2021, Kays et al. 2022).

A more challenging issue is how to balance the interests of data owners, who have often collected tracking data at great cost, with the interests of the broader scientific and conservation community, to whom these data could be useful. Offering multiple levels of data sharing is a solution to this challenge. At minimum, registering species, region, numbers, and types of tags deployed with a data repository would avoid duplication of studies, and facilitate requests to collaborate. Publishing aggregate data sets (e.g. kernel density estimates (KDEs), reduced-resolution tracks, or species-wide summaries) provides an intermediate level of transparency, but prevents the data being used for other studies. Ideally, high resolution tracking data would be stored publicly once grant obligations have been fulfilled and data owners have addressed their primary research questions. This will ensure the maximum value is extracted from the datasets, which often can be used in innovative ways in synergy. When considering optimal outcomes from data sharing, it is also important to factor in the types of re-use that are most valuable. Researchers are more likely to use and re-process raw data, to ensure compatibility of multiple datasets. On the other hand, policymakers, conservationists, and managers are likely get more use from derived data products – for example, species-level maps of area use and overlap with threats (Carneiro et al. 2020). Indeed, there are now databases that exist for the purpose of re-using tracking data to ask ecosystem-scale questions, such as understanding migratory connectivity in the oceans to inform conservation and management policy (e.g. MiCO, see Dunn et al. 2019, Beal et al. 2021). The studies in this thesis were only possible due to the generous data-sharing of collaborators, and indeed it is likely that the mechanism through which data will be most effectively shared into the future is increased collaborative research (Hays and Hawkes 2018, Bernard et al. 2021).

5.3.3 Political

It has been well established that movement data can provide insights that inform biodiversity conservation (Burger and Shaffer 2008, Dias et al. 2017, Hays et al. 2019, Requena et al. 2020). Analysing seabird tracking data has been specifically highlighted as one way in which researchers can identify key candidate areas for Marine Protected Areas (MPAs), which are key conservation tools (Lovejoy 2006, Lascelles et al. 2012). Many studies have already used tracking and bio-logging techniques to identify species foraging hotspots and migratory routes, and propose Important Bird and Biodiversity Areas (IBAs), Ecological and Biologically Significant Areas (EBSAs), and no-take zones for commercial fisheries (e.g. Arcos et al. 2012, Montevecchi et al. 2012, Pichegru et al. 2012, Perrow et al. 2015, Soanes et al. 2016, Bolton 2021). There are, however, problems that arise including a bias towards protected areas located directly surrounding seabird colonies or along national coastlines, and a lack of techniques for integrating at-sea survey data and individual tracking data (Lascelles et al. 2012). Moving from proposed protected area to formal, legal protection often takes many years – even when the area in question is within the exclusive economic zone (EEZ) of a single country. There is, then, significantly increased complexity when designing an MPA network for highly pelagic species such as the Procellariiformes, which spend an estimated ~40% of their life on the high seas (Beal et al. 2021). Although human activities including commercial fishing, shipping and seabed mining have rapidly increased the impacts on biodiversity in these areas beyond national jurisdiction (ABNJ), there has been a lag in developing appropriate international governance to regulate them (Wright et al. 2021). The Southern Ocean is, so far, the only location where regulations on resource use are caveated with an explicit aim to conserve biodiversity – the Convention on the Conservation of Marine Living Resources (CCAMLR) shows that international cooperation on the high seas is possible, though challenging (Ban et al. 2014).

To ensure effective protection for procellariiform seabirds throughout their range, scientific evidence – including findings from tracking data –must be synthesised and well-publicised such that policymakers can interpret and act upon it (Dunn et al. 2019), and intergovernmental cooperation on a global high seas treaty must be forthcoming. While suggestions to streamline the complex processes involving hard and soft laws (e.g. the UN Convention on the Law of the Sea (UNCLOS), the Sustainable Development Goals (SDGs), respectively), and various management organisations for fisheries and shipping are outside the scope of this thesis, finalising a treaty (as was supposed to occur

at the Fifth Intergovernmental Conference on Marine Biodiversity of Areas Beyond
National Jurisdiction in August 2022 (United Nations 2022)) is of critical importance to
enable establishment of MPAs in ABNJs – this is crucial if we are to meet the goal of
protecting 30% of the world's oceans by 2030 (O'Leary et al. 2016, Roberts et al. 2020,
Sala et al. 2021). A global treaty to this effect will allow tracking data to be used
worldwide to inform development of high seas protected areas, as has successfully
occurred in the North Atlantic, where nearly 600,000 km^2 have recently been protected
under the OSPAR Convention (Davies et al. 2021b). The designation of this MPA is a
key example showing how seabird tracking data, when shared, collated and re-analysed,
can inform ground-breaking conservation policy (Davies et al. 2021a, 2021b). Area-
based conservation measures such as this form a key element in successful conservation
of Procellariiformes, but are insufficient on their own. As discussed in section 5.2.1,
incidental mortality in fisheries is a significant threat to albatrosses and petrels (Dias et
al. 2019), and fisheries are currently excluded from negotiations on a high seas treaty.
Future negotiations between countries and regional fisheries management organisations
(RFMOs) must reach a consensus to formalise and increase bycatch mitigation measures,
increase transparency around reporting, and countries must improve national fishing
practices to regulate vessels under their jurisdiction on the high seas (Beal et al. 2021).
Global diplomatic collaboration is necessary to both establish protected areas and enforce
threat-based conservation measures (e.g. bycatch mitigation) – this is key if we are to
ensure the effective conservation of Procellariiformes into the future.

5.4 Future priorities

Though at various points in this thesis I have highlighted knowledge gaps that
could be closed with further tracking studies, a broad-brush approach of *more tags in
more places at more times* is not nuanced enough to be effective or, I would argue,
ethical. There are certain scenarios where new tags should be deployed, such as when the
foraging areas of a particular species are unknown, especially if the population is
experiencing declines of unknown drivers. As I have demonstrated, habitat preferences
are often distinct for individual colonies (Chapter 3, Chapter 4), and models are often
poorly transferrable (Torres et al. 2015, Péron et al. 2018) – therefore there is a good
argument for tracking populations for which data are entirely absent. Furthermore,
identifying global research gaps and collaborating to fill them is important (Bernard et al.

2021). However, researchers should be clear on the fundamental ecological, conservation, or management case for collecting new tracking data prior to doing so, as there is increasing evidence that the cost of bearing a tag for individual animals is non-trivial (Bodey et al. 2018, Geen et al. 2019). This is particularly important when tracking species of high conservation concern, as there is a trade-off between the benefits of knowledge gained via tracking and the potentially high costs of impacting individuals in the breeding population.

Ensuring maximum utility is extracted from all tracking data that has been collected (often via sharing, re-use, and synthesis with other datasets, as discussed in section 5.3.2) is, in my view, an ethical imperative. One of the challenges, however, with synthesising tracking data from multiple sources is that they have been collected across many years – this unavoidably means that individuals experienced different environmental conditions. Priority, therefore, should be given to ambitious projects that will allow us to understand habitat use (and partitioning) among species at the same place and time. For example, simultaneous tracking of the two winter-breeders on Gough Island (Grey Petrels and Westland Petrels), or across the community of sympatric Procellariiformes on Bird Island, South Georgia, would help to answer ecological questions about allochrony and community dynamics, respectively.

Finally, priority should be given to tracking data that can be integrated at multiple levels (and with other data types) to ensure effective conservation outcomes. For example, when considering the threat of incidental mortality in fisheries: firstly, protected area planning is required to reduce spatial overlap with fishing vessels (Tancell et al. 2016); secondly, regulations such as seasonal closures and night setting can reduce temporal overlap with seabird foraging behaviour (Melvin et al. 2013, Zou and Wang 2021); and thirdly, mitigation measures such as tori lines, hook encapsulation devices and line weights can reduce the chance a bird is hooked if the first two measures have not prevented co-occurrence (Goad et al. 2019, Jiménez et al. 2020). Different kinds of tracking data are critical in designing policies and technologies to achieve each of these aims, as no single intervention can eliminate bycatch mortality on its own (Fig. 5.1).
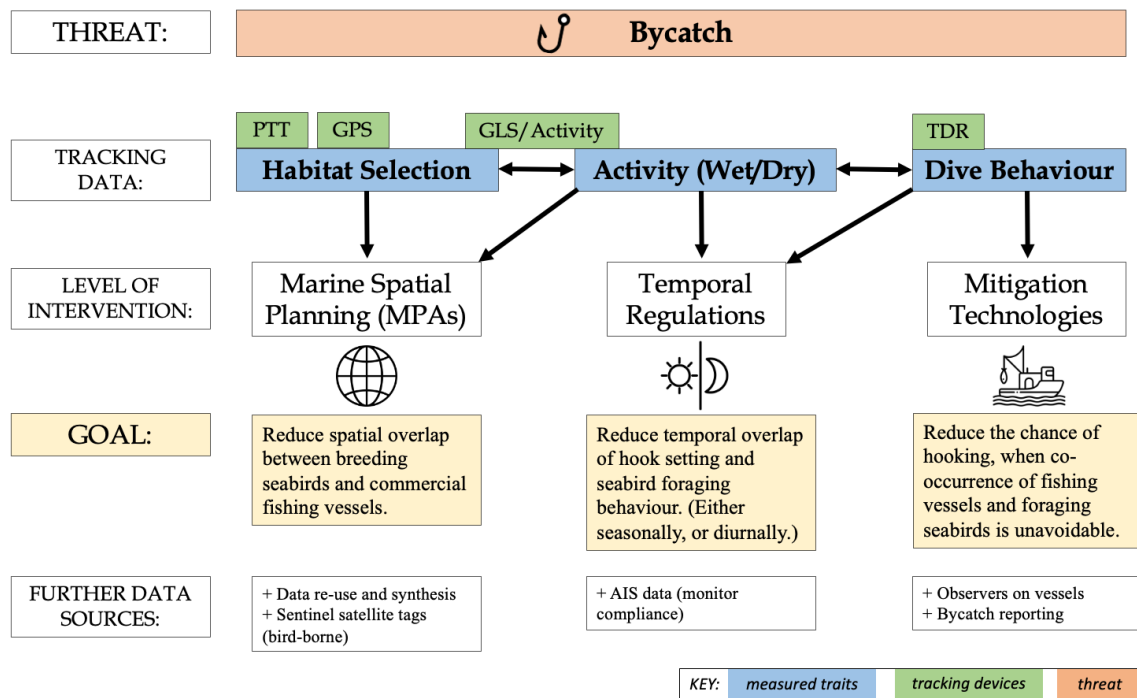
Figure 5.1: *Integration of tracking data at different levels for a particular anthropogenic threat (fisheries bycatch). Icons used with permission: flaticon.com.*

CHAPTER 6: **References**

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Appendices

Appendix 1: Supplementary information for Chapter 2

Appendix 2: Supplementary information for Chapter 3

Appendix 3: Supplementary information for Chapter 4

Appendix 1: Supplementary information for Chapter 2

Appendix 1, Table S1. Individuals included in dive analyses.

Ring Number	Species	Breed Stage	Sex	GPS Started	GPS Model	Sampling Interval	GLS	TDR Sampling Rate	n Dives	Time Spent Immersed	Trip Length (hours)
1320592	BBA	BR	unknown	08/01/2010	E&O	10	Y	1 sec, daily	50	37.6	77
1318380	BBA	BR	F	05/01/2010	IGotU	15	Y	1 sec, daily	62	25.6	58.9
1254473	BBA	BR	M	02/01/2010	E&O	10	Y	1 sec, daily	167	5.4	46.5
1320030	BBA	BR	M	09/01/2010	E&O	10	Y	1 sec, daily	0	14.8	29
1255177	BBA	BR	M	12/01/2010	E&O	10	Y	1 sec, daily	0	6.3	32.7
1139698	BBA	BR	F	07/01/2010	E&O	10	Y	1 sec, daily	4	21	62.6
1148440	BBA	BR	M	04/01/2010	IGotU	15	Y	1 sec, daily	5	7.1	42.4
1141179	BBA	BR	F	04/01/2010	IGotU (failed)	15	Y	1 sec, daily	15	3.5	22.1
1320010	BBA	BR	M	09/01/2010	E&O	10	Y	1 sec, daily	26	19.6	49.1
1145462	GHA	BR	unknown	07/01/2010	E&O	10	Y	1 sec, daily	68	10.2	50.6
1254305	GHA	BR	unknown	13/01/2010	E&O micro	10	Y	1 sec, daily	1	16.9	71.6
1425604	GHA	BR	unknown	07/01/2010	iGotU	10	Y	1 sec, daily	11	13.6	64.7
1146494	GHA	BR	unknown	02/01/2010	E&O	10	Y	1 sec, daily	5	17.5	79.4
1436905	GHA	BR	unknown	12/01/2010	E&O	10	Y	1 sec, daily	6	17.2	72.4
1318625	GHA	BR	unknown	08/01/2010	iGotU	10	Y	1 sec, daily	7	13.3	67.9
1320811	GHA	BR	unknown	12/01/2010	E&O	10	Y	1 sec, daily	123	16.8	62.3
1148957	GHA	BR	unknown	09/01/2010	E&O	10	Y	1 sec, daily	4	19.8	78.3
1147587	GHA	BR	unknown	07/01/2010	E&O	10	N	1 sec, daily	0	NA	26.4
1139185	GHA	BR	unknown	12/01/2010	E&O micro	15	N	1 sec, daily	0	NA	76.3
N553	LMSA	Inc	unknown	29/12/2009	IGotU (failed)	NA	Y	1 sec, every 3rd day	2	3.9 days	12.6 days
N573	LMSA	Inc	unknown	30/12/2009	IGotU (failed)	NA	Y	1 sec, every 3rd day	5	3.2 days	11.7 days
N565	LMSA	Inc	unknown	28/12/2009	IGotU (failed)	NA	Y	1 sec, every 3rd day	0	0.9 days	8.5 days
N348	LMSA	Inc	unknown	20/12/2009	IGotU (failed)	NA	Y	1 sec, every 3rd day	0	7.7 days	21.5 days
N399	LMSA	Inc	unknown	19/12/2009	IGotU (failed)	NA	Y	1 sec, every 3rd day	2	3.0 days	9.8 days
N551	LMSA	Inc	unknown	17/12/2009	IGotU (failed)	NA	Y	1 sec, every 3rd day	0	5.8 days	20.2 days
N567	LMSA	Inc	unknown	18/12/2009	IGotU (failed)	NA	Y	1 sec, every 3rd day	0	3.9 days	15.4 days

Appendix 2: Supplementary information for Chapter 3

Appendix 2, Table S1. Outputs for parametric coefficients and smooth terms of best fitting (by AICc values) generalised additive models for habitat selection (presence/pseudoabsence). Bolded *P* values indicate statistical significance below 0.001.

PARAMETRIC	estimate	se	Z value	Pr(>|z|)
Intercept	-6.92	0.09	-73.39	**< 0.001**

SMOOTHS		edf	χ2	*P*
s(bathymetry):GP		2.99	903.46	**< 0.001**
s(bathymetry):WCP		2.99	3872.40	**< 0.001**
s(sea_surface_temp):GP		2.98	3269.40	**< 0.001**
s(sea_surface_temp):WCP		2.98	1877.01	**< 0.001**
s(EKE_log):GP		2.76	5.82	0.088
s(EKE_log):WCP		2.98	116.01	**< 0.001**
s(CHL-A_log):GP		2.15	166.47	**< 0.001**
s(CHL-A_log):WCP		2.99	588.61	**< 0.001**

Appendix 2, Table S2. Outputs for parametric coefficients and smooth terms of best fitting (by AICc values) generalised additive models for foraging behaviour. Italicised *P* values indicate statistical significance below a threshold of 0.05, bolded *P* values indicate statistical significance below 0.0001.

PARAMETRIC	estimate	se	Z value	Pr(>|z|)
Intercept	-1.56	0.04	-36.28	**< 0.001**

SMOOTHS	edf	χ2	*P*
s(bathymetry):GP	2.98	83.32	**< 0.001**
s(bathymetry):WCP	2.76	183.27	**< 0.001**
s(sea_surface_temp):GP	1.45	21.68	**< 0.001**
s(sea_surface_temp):WCP	2.73	10.88	*0.027*
s(EKE_log):GP	2.95	31.87	**< 0.001**
s(EKE_log):WCP	2.16	33.99	**< 0.001**
s(CHL-A_log):GP	2.94	43.59	**< 0.001**
s(CHL-A_log):WCP	2.78	6.28	0.108
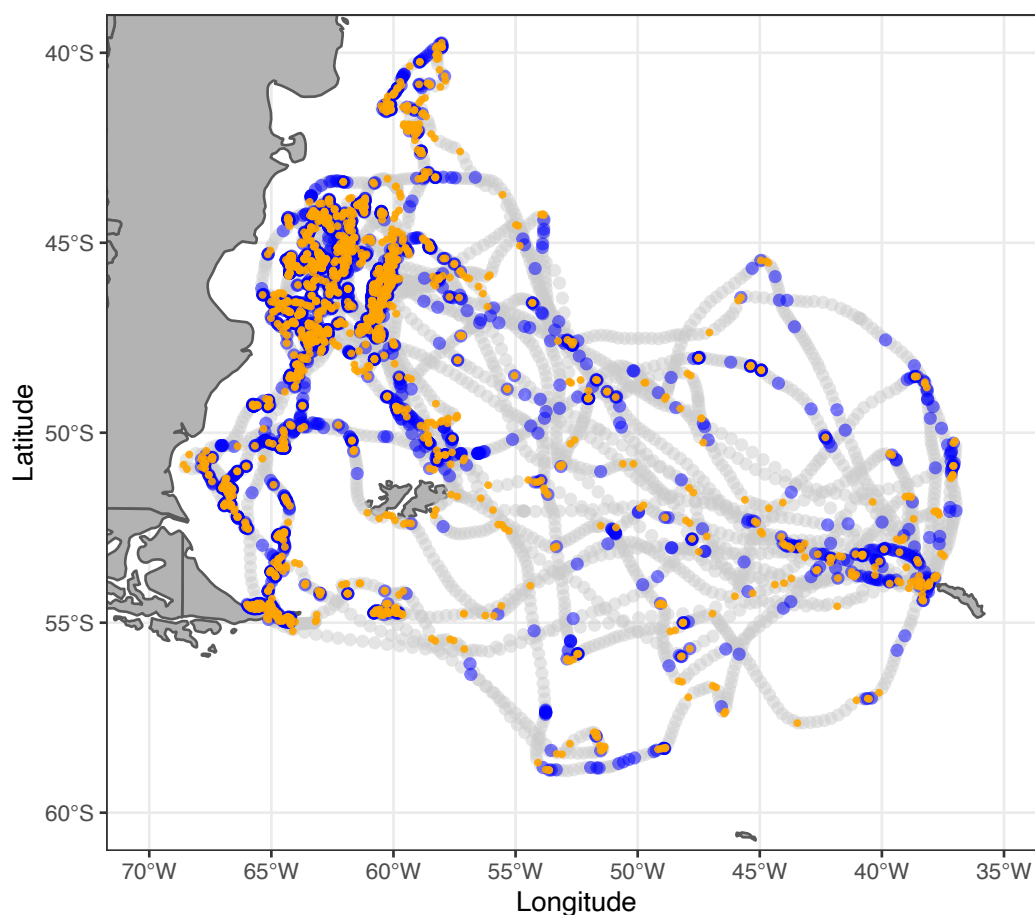
Appendix 2, Figure S1. Locations of landing (from immersion loggers; blue points) of White-chinned Petrels (*n* = 11) tracked during the incubation period, overlaid with foraging behaviour (according to EMbC; orange points). Locations where the bird was flying and the EMbC classification was 'not foraging' are indicated as grey points. 24% of the total trip was classified as foraging, and 33% of on-water points were classified as foraging. 39% of total trip points were on water, while 52% of foraging points were on-water.
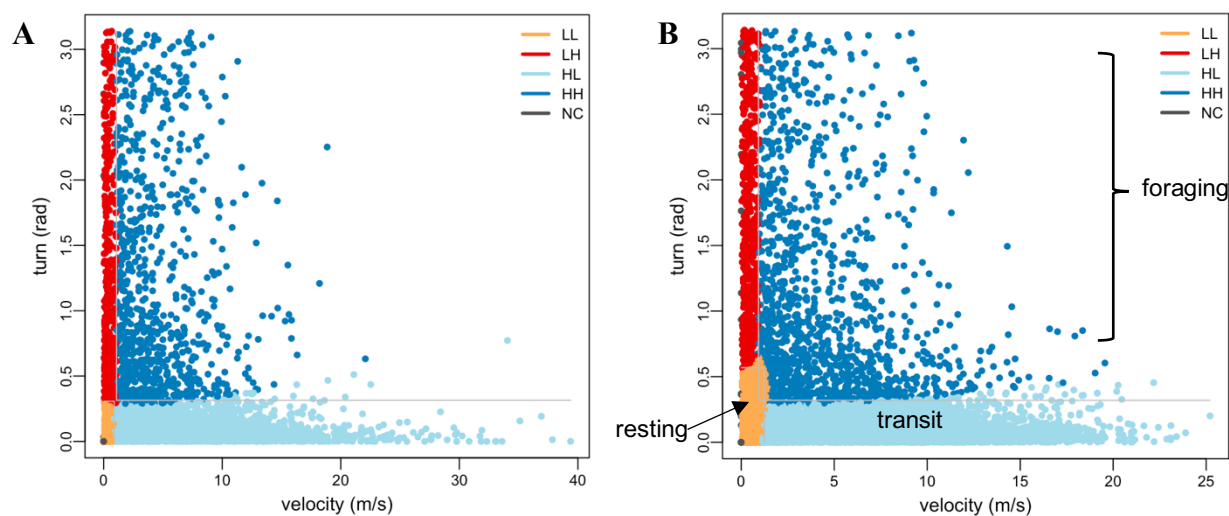
Appendix 2, Figure S2. Scatterplots showing clustering of points into behavioural categories for Grey Petrels (A) and White-chinned Petrels (B). Annotations indicate behavioural states.

LL, orange = low speed, low turning angles. Categorised as resting/not foraging.

LH, red = low speed, high turning angles. Categorised as foraging.

HL, light blue = high speed, low turning angles. Categorised as transit/not foraging.

HH, dark blue = high speed, high turning angles. Categorised as foraging.
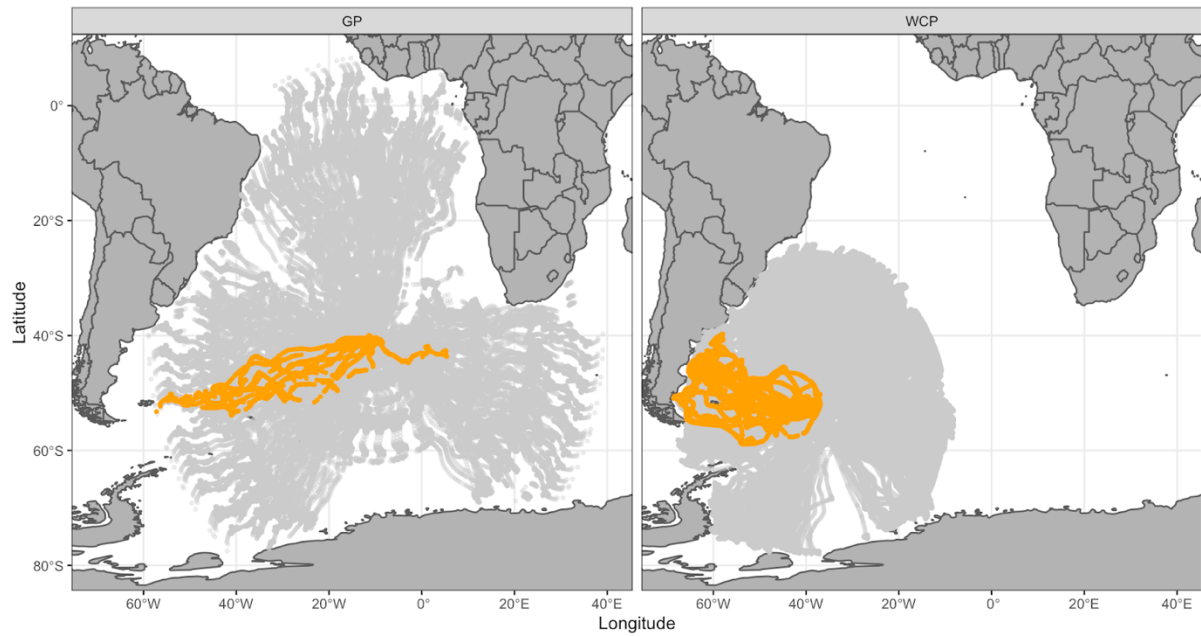
Appendix 2, Figure S3. Pseudoabsences (grey points) and real tracks (orange points) for Grey Petrels (left panel) and White-chinned Petrels (right panel) tracked during the incubation period.
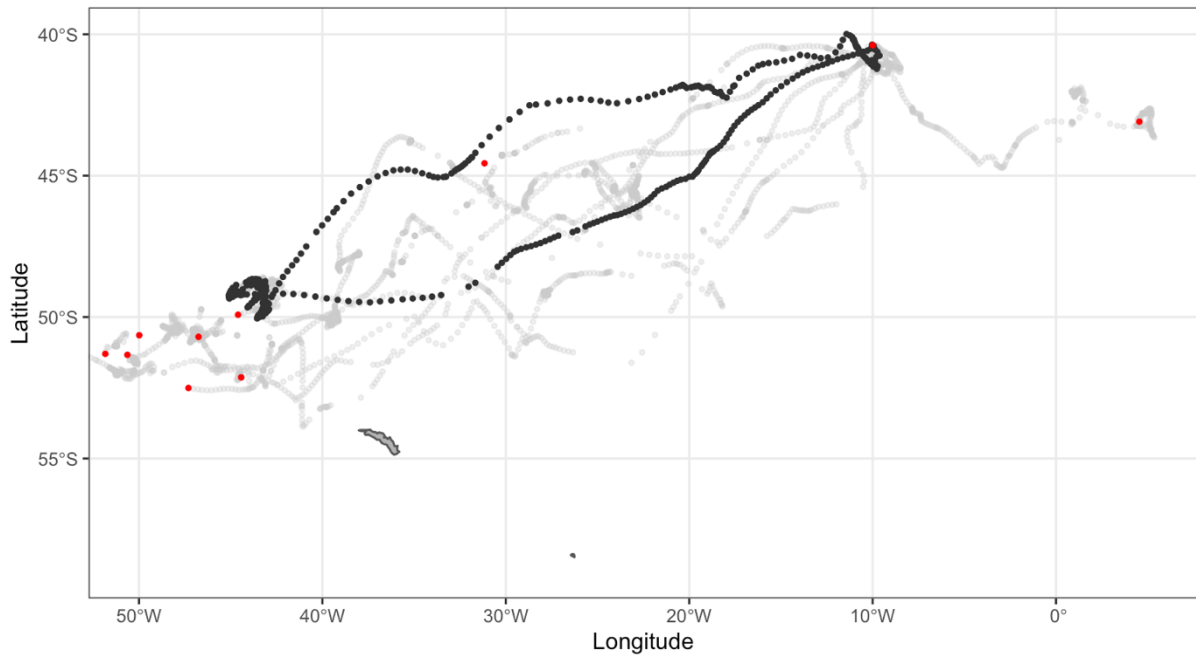
Appendix 2, Figure S4. Tracks from incubating Grey Petrels foraging from Gough Island. GPS data were available for the entire foraging trip of individual A (dark grey points), and for the majority of the trips of the other birds (light grey points, with the final GPS location marked in red).
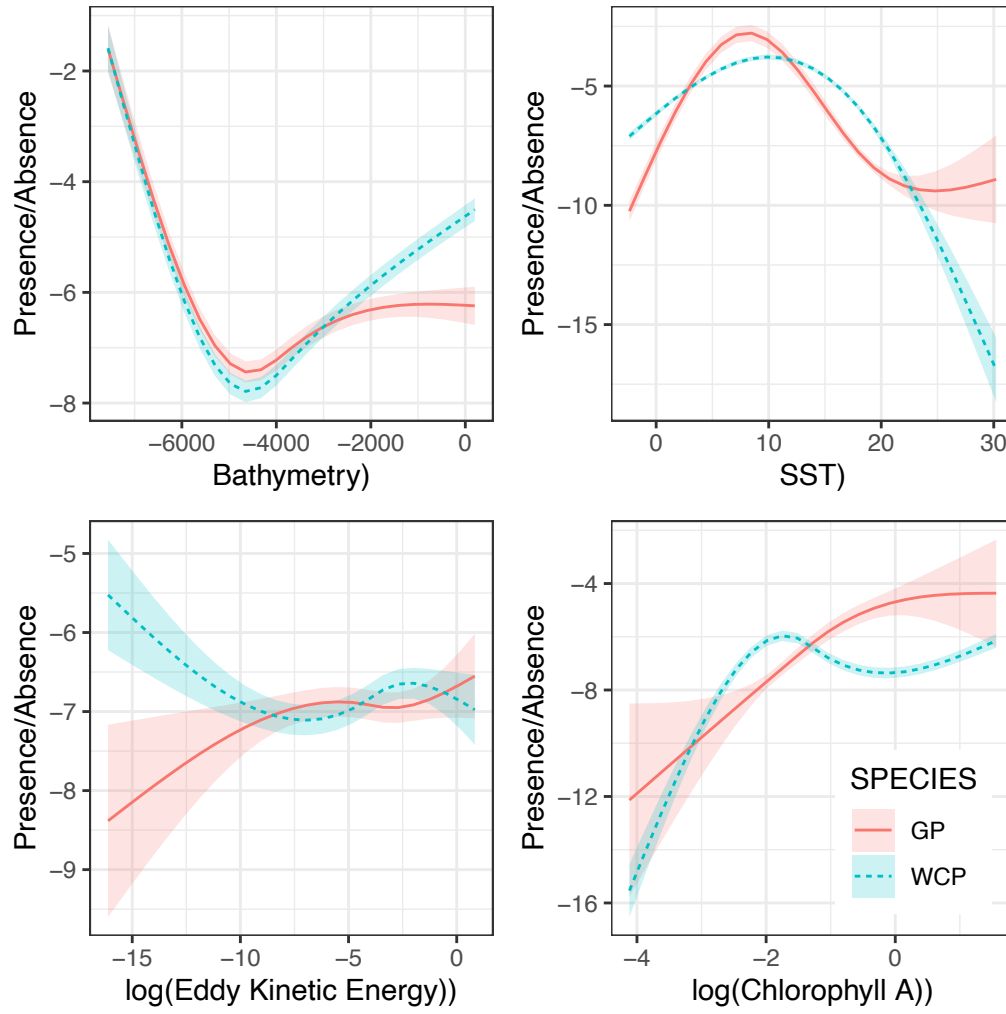
Appendix 2, Figure S5. All GAM smooths for full model in table S1.
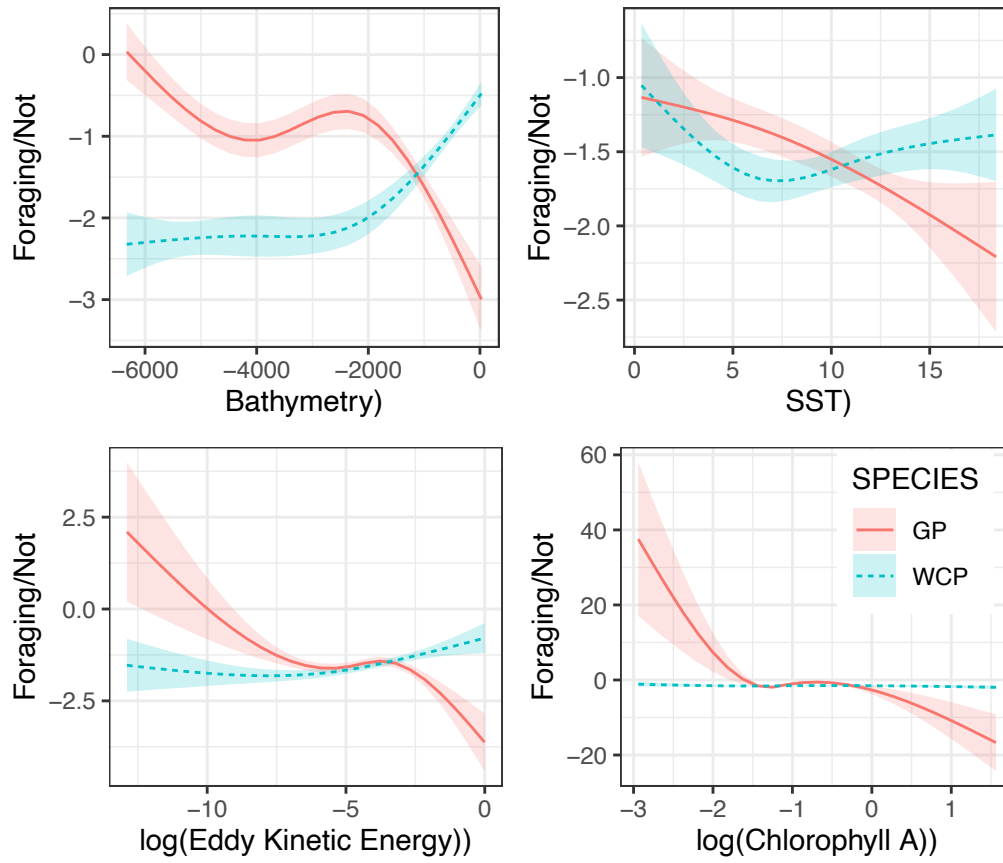
Appendix 2, Figure S6. All GAM smooths for full model in table S2.

Appendix 3: Supplementary Information for Chapter 4

Appendix 3, Table S1. Model selection for binomial generalised additive model (GAM) of presence/absence in light-mantled albatrosses, in symatric and allopatric colonies. Models ranked by AICc values. Full model structure:

pres_abs ~ s(SST, by = symallo, k = 4) + s(log(EKE), by = symallo, k = 4) + s(bathym, by = symallo, k = 4) + s(log(CHL-Agradient), by = symallo, k = 4), family = binomial(link = "logit"), correlation = corGaus(1, form = ~latitude + longitude))

Intercept	Bathymetry	log(Chlorophyll a gradient)	log(Eddy kinetic energy)	Sea surface temperature	df	logLik	AICc	delta	weight
-28.37	+	+	+	+	**22**	**-48209.61**	**96463.37**	**0.00**	**1**
-28.66	+	+	+	+	17	-48252.47	96538.97	75.60	3.83E-17
-26.94	+		+	+	18	-48329.82	96696.04	232.67	2.99E-51
-27.20	+	+		+	12	-48378.24	96782.41	319.04	5.27E-70
-27.61		+	+	+	16	-48520.82	97073.85	610.48	2.72E-133
-27.89		+		+	11	-48556.50	97135.04	671.67	1.41E-146
-25.13		+	+	+	10	-48707.03	97435.73	972.36	7.14E-212
-25.77			+	+	6	-48747.60	97509.19	1045.82	7.98E-228
-3.05	+	+	+		16	-53678.64	107390.98	10927.61	0
-3.06	+	+	+		12	-53939.21	107902.47	11439.10	0
-3.04	+	+			12	-54167.67	108361.31	11897.94	0
-3.03	+				6	-54586.81	109187.36	12723.99	0
-2.95		+	+		10	-54668.82	109359.54	12896.17	0
-2.94		+	+		5	-55042.47	110095.15	13631.78	0
-2.94		+			6	-55045.54	110105.07	13641.70	0
-2.92					0	-55610.75	111223.49	14760.12	0

Appendix 3, Table S2. Outputs for parametric coefficients and smooth terms of best fitting (by AICc values) generalised additive model for habitat selection (presence/pseudoabsence) in Light-mantled Albatrosses, in sympatry and allopatry. Bolded *P* values indicate statistical significance below 0.001.

PARAMETRIC	estimate	se	Z value	Pr(>|z|)
Intercept	-28.38	1.65	-17.26	**< 0.001**

SMOOTHS	edf	χ^2	*P*
s(SST):allopatry	2.99	644.56	**< 0.001**
s(SST):sympatry	2.99	1149.96	**< 0.001**
s(log(EKE)):allopatry	2.07	5.57	0.085
s(log(EKE)):sympatry	2.33	77.35	**< 0.001**
s(bathym): allopatry	2.76	131.86	**< 0.001**
s(bathym):sympatry	2.91	434.95	**< 0.001**
s(log(CHL-Agrad)): allopatry	2.98	196.77	**< 0.001**
s(log(CHL-Agrad)): sympatry	1.00	23.86	**< 0.001**

Appendix 3, Table S3. Outputs for parametric coefficients and smooth terms of best fitting (by AICc values) generalised additive model for habitat selection (presence/pseudoabsence) in Light-mantled Albatrosses, by breeding location. Bolded *P* values indicate statistical significance below 0.001.

PARAMETRIC	estimate	se	Z value	Pr(>|z|)
Intercept	-31.82	1.72	-18.52	**< 0.001**

SMOOTHS		edf	χ^2	*P*
s(SST):Crozet		2.99	517.44	**< 0.001**
s(SST):Macquarie		2.99	469.46	**< 0.001**
s(SST):Marion		2.99	953.04	**< 0.001**
s(SST):SouthGeorgia		2.99	479.51	**< 0.001**
s(log(EKE)):Crozet		2.60	135.40	**< 0.001**
s(log(EKE)):Macquarie		2.34	38.92	**< 0.001**
s(log(EKE)):Marion		2.84	23.56	**< 0.001**
s(log(EKE)):SouthGeorgia		2.89	95.63	**< 0.001**
s(bathym):Crozet		2.95	117.96	**< 0.001**
s(bathym):Macquarie		2.85	97.14	**< 0.001**
s(bathym):Marion		2.96	376.29	**< 0.001**
s(bathym):SouthGeorgia		2.98	199.83	**< 0.001**
s(log(CHL-Agrad)):Crozet		2.91	39.31	**< 0.001**
s(log(CHL-Agrad)):Macquarie		2.98	114.77	**< 0.001**
s(log(CHL-Agrad)):Marion		1.01	20.43	**< 0.001**
s(log(CHL-Agrad)):SouthGeorgia		2.94	172.60	**< 0.001**

Appendix 3, Table S4. Model selection for binomial generalised additive model (GAM) of presence/absence in sooty albatrosses, in sympatric and allopatric colonies. Models ranked by AICc values. Full model structure:

$pres\_abs \sim s(SST, by = symallo, k = 4) + s(log(EKE), by = symallo, k = 4) + s(bathym, by = symallo, k = 4) + s(log(CHL\text{-}Agradient), by = symallo, k = 4), family = binomial(link = "logit"), correlation = corGaus(1, form = \sim latitude + longitude))$

Intercept	Bathymetry	log(Chlorophyll a gradient)	log(Eddy kinetic energy)	Sea surface temperature	df	logLik	AICc	delta	weight
-3.20	+	+	+	+	20	-38016.34	76074.41	0.00	1
-3.17	+		+	+	18	-38083.78	76205.22	130.81	3.94E-29
-3.14		+	+	+	16	-38166.52	76367.03	292.62	2.87E-64
-3.13			+	+	12	-38242.68	76511.34	436.93	1.33E-95
-3.20	+	+		+	18	-38425.26	76887.05	812.64	3.44E-177
-3.18	+			+	12	-38507.66	77041.09	966.68	1.23E-210
-3.16		+		+	12	-38571.45	77167.88	1093.47	3.60E-238
-3.14				+	6	-38644.13	77302.26	1227.85	2.37E-267
-3.11	+	+	+		18	-41278.10	82594.13	6519.72	0
-3.06	+		+		12	-41517.44	83060.72	6986.30	0
-3.08		+	+		12	-41952.81	83931.41	7857.00	0
-3.02	+	+			12	-42267.20	84560.32	8485.90	0
-3.01			+		6	-42335.34	84684.68	8610.27	0
-2.96	+				6	-42609.20	85232.37	9157.96	0
-3.01		+			6	-42829.54	85673.05	9598.64	0
-2.94					0	-43299.15	86600.30	10525.88	0

Appendix 3, Table S5. Outputs for parametric coefficients and smooth terms of best fitting (by AICc values) generalised additive model for habitat selection (presence/pseudoabsence) in Sooty Albatrosses, in sympatry and allopatry. Bolded *P* values indicate statistical significance below 0.001.

PARAMETRIC	estimate	se	Z value	Pr(>|z|)
Intercept	-3.20	0.01	-206.1	**< 0.001**

SMOOTHS	edf	$\chi 2$	*P*
s(SST):allopatry	2.98	2295.28	**< 0.001**
s(SST):sympatry	2.99	2731.04	**< 0.001**
s(log(EKE)):allopatry	1.00	38.96	0.085
s(log(EKE)):sympatry	2.56	237.53	**< 0.001**
s(bathym): allopatry	2.97	222.00	**< 0.001**
s(bathym):sympatry	2.87	604.35	**< 0.001**
s(log(CHL-Agrad)):allopatry	2.98	139.65	**< 0.001**
s(log(CHL-Agrad)):sympatry	1.00	3.12	0.078

Appendix 3, Table S6. Outputs for parametric coefficients and smooth terms of best fitting (by AICc values) generalised additive model for habitat selection (presence/pseudoabsence) in Sooty Albatrosses, by breeding location. Bolded *P* values indicate statistical significance below 0.001.

PARAMETRIC	estimate	se	Z value	Pr(>|z|)
Intercept	-3.14	0.02	-193.2	**< 0.001**

SMOOTHS	edf	χ^2	*P*
s(SST):Crozet	2.96	418.15	**< 0.001**
s(SST):Gough	2.96	1448.95	**< 0.001**
s(SST):Marion	2.95	2465.96	**< 0.001**
s(SST):Tristan	2.95	542.98	**< 0.001**
s(log(EKE)):Crozet	2.70	85.16	**< 0.001**
s(log(EKE)): Gough	2.91	119.99	**< 0.001**
s(log(EKE)):Marion	2.30	155.78	**< 0.001**
s(log(EKE)): Tristan	2.60	19.82	0.003
s(bathym):Crozet	2.86	446.05	**< 0.001**
s(bathym): Gough	2.87	84.19	**< 0.001**
s(bathym):Marion	2.99	452.32	**< 0.001**
s(bathym): Tristan	2.99	521.09	**< 0.001**
s(log(CHL-Agrad)):Crozet	2.81	119.35	**< 0.001**
s(log(CHL-Agrad)): Gough	2.90	47.43	**< 0.001**
s(log(CHL-Agrad)):Marion	2.79	38.78	**< 0.001**
s(log(CHL-Agrad)): Tristan	2.93	129.87	**< 0.001**