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**FORAGING ECOLOGY OF THE CAMPBELL
ALBATROSS: INDIVIDUAL SPECIALISATION AND
FISHERY INTERACTIONS**

by

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FORAGING ECOLOGY OF THE CAMPBELL ALBATROSS: INDIVIDUAL SPECIALISATION AND FISHERY INTERACTIONS

Lisa Ann Sztukowski

ABSTRACT

Most albatrosses are critically endangered, endangered or vulnerable due to the deleterious impact of fisheries, pollution, introduced species, habitat alteration, and climate change. Foraging behaviour influences many aspects of seabird biology, and a detailed understanding of foraging ecology is required to better predict the impacts of significant changes to the marine environment. Campbell Albatross (*Thalassarche impavida*) is a threatened endemic, confined to a small number of locations on Campbell Island, New Zealand and was recently split from the closely related Black-browed Albatross (*T. melanophrys*). We currently lack much basic information on the foraging behaviour of this species, hindering our ability to understand how change may have occurred in the past and make predictions about its long-term future. First, I used GPS loggers and stable isotope analysis of blood to investigate how distribution and foraging effort (distance travelled and duration) varied with sex and breeding stage. I found that Campbell Albatrosses are sexually dimorphic and showed sex-specific foraging behaviour and habitat use – although this varied by stage of reproduction.

Because males and females may be vulnerable to different threats, such as interactions with fisheries, I compared the spatial overlap and high resolution spatio-temporal overlaps between fisheries vessels and albatrosses within New Zealand's Exclusive

Economic Zone (EEZ). Albatrosses utilised 32% of the EEZ, however they overlapped with fisheries vessels in only 0.20% of the area. Previous research has demonstrated that the influence of fisheries vessels goes beyond the immediate location of the boat itself. Campbell Albatross have low levels of spatio-temporal overlap with fisheries – with males overlapping more than females. More generally, my results indicate that adding data on fine scale interactions will improve fisheries risk assessments, and provide information needed for the conservation and management of the Campbell Albatross.

A key development in recent ecological research has been a greater appreciation that inter-individual variation in foraging behaviour can have profound population-level consequences. Accordingly I tested for individual differences in foraging behaviour in Campbell Albatrosses. The majority of individuals demonstrated both annual and inter-annual individual consistency in foraging locations, and the degree of specialisation was influenced by both sex and year. Consistent terminal latitude and longitude of foraging trips indicated high foraging area fidelity with a degree of flexibility in the fine-scale location. During brooding, females used the Campbell Plateau and showed more consistent behaviours than males, which tended to forage in the Southern Ocean. This adds to a growing body of evidence of individual foraging specialisation among seabirds in general and albatrosses in particular and reveals marked inter-individual differences in vulnerability to threats.

In light of the evidence of individual foraging specialisations in the Campbell albatross, I also preformed a literature review of individual foraging specialisations across all seabirds. I found studies examining foraging specialisation for 35 species, with 28 (80%) providing evidence of consistent inter-individual differences (i.e. specialisation). Current studies suggest that specialisation is influenced by environmental variability

and resource predictability, however, with limited data in tropical regions, more studies are needed to test these links.

In summary, my thesis has provided new information on Campbell Albatross foraging ecology. Sex specific variations in behaviour and habitat use may influence conservation and management strategies. I have been able to contextualise the consistent individual differences in foraging distribution described for this species in light of global patterns of individual foraging specialisation in seabirds and highlight future areas of research.

Spécialisation individuelle du comportement de recherche alimentaire et interactions avec les pêcheries chez l'albatros de Campbell.

La plupart des albatros sont considérés 'en danger critique d'extinction', 'en danger' ou 'vulnérables' en raison de l'impact néfaste de la pêche, la pollution, les espèces introduites, l'altération de l'habitat et le changement climatique. Tous les aspects de la biologie des oiseaux marins étant influencés par le comportement de recherche alimentaire, son étude se trouve donc au cœur de la recherche appliquée sur ces derniers afin de prédire l'impact de changements significatifs de l'environnement marin. L'Albatros de Campbell (*Thalassarche impavida*), menacé et confiné à quelques petites zones de l'île de Campbell en Nouvelle Zélande d'où il est endémique, a récemment été taxonomiquement distingué de son proche parent L'Albatros à sourcils noirs (*T. melanophrys*). Nos connaissances sur le comportement de recherche alimentaire de cette espèce sont encore lacunaires ce qui gêne notre capacité à comprendre des changements passés et prédire son futur à long terme. J'ai d'abord utilisé des traceurs GPS et analysé la composition en isotopes simples du sang afin d'étudier comment leur répartition et leur comportement de recherche alimentaire (distance parcourue et durée)

varie en fonction du sexe et du stade de maturation. J'ai conclu que les Albatros de Campbell, présentent un dimorphisme sexuel et que le comportement de recherche alimentaire et l'utilisation de l'habitat sont spécifiques à chaque sexe bien qu'à des degrés variables selon le stade de reproduction.

Ainsi, les mâles et les femelles peuvent être vulnérables à différentes menaces, telles que les interactions avec les pêcheries. J'ai donc comparé le chevauchement spatial et les interactions spatio-temporelles à haute résolution entre les navires de pêche et les albatros au sein de la Zone Economique Exclusive (ZEE) de la Nouvelle-Zélande. Les albatros utilisaient 32 % de la ZEE mais le chevauchement avec la présence de navires de pêche était observé dans seulement 0,20 % de la superficie. De précédentes recherches ont montré que l'influence des navires de pêche va au-delà de leur localisation immédiate. Il y a peu de chevauchements dans le temps et l'espace entre l'activité des albatros et les pêcheries, cependant, ceci est plus fréquent chez les mâles que chez les femelles. De façon plus générale, mes résultats indiquent que l'apport de données sur les interactions à petite échelle permettra d'améliorer l'évaluation des risques liés aux pêcheries, et de fournir des informations nécessaires à la conservation et la gestion de l'albatros de Campbell.

Récemment, une avancée majeure de la recherche en écologie a consisté en la découverte des conséquences importantes de la variabilité interindividuelle (*i.e.* spécialisation) sur le comportement de recherche alimentaire au niveau de la population. Par conséquent, j'ai tenté de déterminer l'étendue et l'incidence de la spécialisation du comportement de recherche alimentaire à l'échelle de l'individu chez les albatros. La majorité des individus montraient une tendance à la fois annuelle et inter-annuelle dans l'orientation de leurs trajets, avec un degré de spécialisation influencé par le sexe et l'année. La redondance des latitudes et longitudes à l'extrémité des trajets indiquait une

importante fidélité à des zones de recherche alimentaire, avec cependant un certain degré de flexibilité à petite échelle dans la localisation de ces zones. Pendant l'élevage du poussin, les femelles utilisaient le plateau de Campbell et montraient des comportements plus redondants que les mâles, qui avaient tendance à se nourrir dans l'océan Austral. Ceci s'ajoute à un faisceau de preuves de l'existence de spécialisation individuelle dans la recherche alimentaire chez les oiseaux marins et, en particulier, des albatros et révèle également des différences interindividuelles marquées en termes de vulnérabilité aux menaces.

Ayant observé un certain degré de spécialisation individuelle des albatros de Campbell dans leur recherche alimentaire, j'ai recherché dans la littérature scientifique des informations sur ce trait chez d'autres espèces d'oiseaux marins. Les documents que j'ai étudiés concernaient au total 35 espèces, dont 28 (80%) apportaient la preuve d'importantes différences interindividuelles. Bien que les études actuelles suggèrent que cette spécialisation est influencée par la variabilité environnementale et la prévisibilité des ressources, les données restent limitées dans les régions tropicales et d'autres études sont nécessaires pour tester ces liens.

En résumé, ce manuscrit apporte de nouvelles informations sur l'écologie des albatros de Campbell. Des variations de comportement et d'utilisation de l'habitat selon le sexe peuvent influencer les stratégies de gestion et de conservation. J'ai aussi pu replacer les différences individuelles persistantes de localisation des zones de recherche alimentaire déjà observés chez cette espèce dans le contexte générale de la spécialisation individuelle du comportement de recherche alimentaire chez les oiseaux marins et mis en évidence de nouveaux champs de recherche.

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AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee. Work submitted for this research degree at the Plymouth University has not formed part of any other degree either at Plymouth University or at another establishment.

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CHAPTER 1: GENERAL INTRODUCTION

1.1. Introduction

My thesis was set out as a series of independent research chapters with limited cross reference between chapters. When integrated together, the overall goal of the doctorate was to investigate the foraging ecology of the vulnerable, and endemic, Campbell albatross (*Thalassarche impavida*) and their interaction with fisheries. As well as studying the general foraging ecology of this poorly studied species, I also tested for individual foraging specialisation. Such intra-population variation has been linked to fitness correlates (i.e. Golet et al. 2000; Litzow et al. 2002; Votier et al. 2004a; Votier et al. 2004b; Wanless et al. 2005) and has conservation implications as threats may not be uniformly distributed within a population. For example, some species have been found to specialise on fisheries discards (Votier et al. 2010, Patrick et al. 2015), with implications for population-level response to fisheries activity. Indeed, this may have led to the selective removal of some individuals via bycatch, leading to divergent population trends (Barbraud et al. 2013; Tuck et al. 2015). These findings also prompted a review of the incidence and implications of foraging specialisation among seabirds. In this general introduction, I briefly outline the rationale behind this project, provide background information on the species and highlight the main aims of each chapter.

1.1.1. Rationale

Many seabirds are top predators in marine ecosystems that spend much of their lives at sea, only returning to land to reproduce. They are declining faster than any other

comparable group of birds, primarily due to the deleterious impact of fisheries, pollution, introduced species, habitat alteration, and climate change (Croxall et al. 2012). Albatrosses are particularly susceptible to these threats, and most species are critically endangered, endangered or vulnerable (BirdLife International 2012). Recently, albatross research has focused on understanding their at-sea distribution and foraging behaviour, as this influences demography and alters risk from threats such as fisheries and climate change. One key aspect of foraging ecology is inter-individual trait variation, which has important implications for ecological and evolutionary processes. Consistent individual variation in foraging behaviour, also referred to as foraging specialisation, can impact predator-prey interactions, parasitism risk, and population and community dynamics; all of which can lead to disruptive selection and evolutionary divergence (Darimont et al. 2007; Johnson et al. 2009; Duffy et al. 2010).

The Campbell albatross is listed as vulnerable due to its restricted breeding range, habitat degradation, and threats associated with fisheries (BirdLife International 2012). They only breed on Campbell Island, New Zealand, a remote, uninhabited Sub-Antarctic island in the Southern Ocean (52°32'24"S 169°8'42"E), and thus may have an increased risk of extinction. The population has declined by around 30%, from 31,300 pairs in the 1940s to 21,648 pairs in 2012 (Waugh et al. 1999b; Sagar 2014). However information on the drivers of this population decline are limited, in part because it has only recently been recognised as a separate species. The Campbell albatross was previously considered to be a subspecies of the black-browed albatross (*Thalassarche melanophrys*), but evidence from morphology, biometrics, behaviour, mitochondrial DNA, and microsatellites indicate that they are best treated as two distinct species (Robertson and Nunn 1998; Sangster et al. 2013). The large gaps in the information

available for Campbell albatrosses are of concern given their recent upgrade to species level, as well as their long-term population decline. Therefore, improving our knowledge of the status and future prospects of this species requires a detailed understanding of the way in which Campbell albatrosses use the marine environment and how this may expose them to natural and anthropogenic threats.

1.1.2. Species Background

Campbell albatrosses, while endemic to Campbell Island, travel to southern Australian waters, the Tasman Sea, and the southern Pacific Ocean during the non-breeding season (Waugh et al. 1999b). Breeding begins in early August with pairs producing a single egg (Cherel et al. 1999; Waugh et al. 2000). Chicks hatch in late-November and December, fledging after 120-140 days. The average age of first breeding is 10 years (range 6-13 years) and the majority of the population breed annually (Waugh et al. 1999b). Campbell albatross forage primarily on fish (93%), particularly southern blue whiting (*Micromesistius australis*), but also consume cephalopods, crustaceans and carrion (Cherel et al. 1999; Waugh et al. 1999a; Cherel et al. 2000). We currently lack basic information on at-sea behaviour and distribution of Campbell albatrosses during incubation and chick brooding. However studies have shown that during the post-guard chick rearing phase, two foraging strategies are present: short neritic trips (2.0-3.7 days) over the Campbell Plateau and longer (>5 days) oceanic trips to the Polar Front and in the southern Antarctic Zone (Waugh et al. 2000).

1.2. Methods

To investigate the foraging ecology of Campbell albatross and their interaction with fisheries, I used a combination of high-resolution bird-borne GPS loggers, Vessel

Monitoring System (VMS) data, and analysis of stable isotopes of carbon and nitrogen in blood. Each data chapter used some or all of these data sets (see Table 1.1).

Table 1.1. Data sets used for each chapter.

Chapter	Type of data used
2: Foraging ecology	GPS loggers, VMS, stable isotopes
3: Interactions between Campbell albatross and fisheries	GPS loggers, VMS
4: Individual foraging specialisation	GPS loggers
5: Review	Literature, results from Chapter 4

Biologging

Biologging is defined as the deployment of miniaturized tags on free-living animals to collect data on movements, behaviour, physiology and/or the environment (Robert-Coudert and Wilson 2005; Rutz and Hays 2009). Over the past two decades, seabird research has seen a marked expansion in the application of tracking technology as well as advancements in analytical techniques, to investigate habitat use, environmental impacts, threat assessments, migration, and foraging ecology (Burger and Shaffer 2008; Tremblay et al. 2009; Wakefield et al. 2011). Among these technological advances is the use of Global Positioning System (GPS) loggers, which have improved in accuracy, data resolution, battery life and size (becoming smaller and lighter). Early deployments were limited to large species due to tag-to-body size ratios (180g:10-12kg); the first successful tracking of a foraging bird using satellite telemetry focused on the wandering albatross (*Diomedea exulans*; Jouventin and Weimerskirch 1990). But more recently, miniaturized GPS technology has allowed the logging of fine scale movements (< 20 m) of a wide variety of species as well as the ability to track smaller species, such as the 400 g Manx shearwater, *Puffinus puffinus* (Guilford et al. 2008), and 345-500g black-

legged kittiwake, *Rissa tridactyla* (Kotzerka et al. 2010). Along with these technological innovations, new analytical methods, advancing from grid-based to particle-based analyses, have arisen to deal with large spatial data sets, enabling researchers to study individual behaviour, age and sex differences, spatial overlap and to link distributions and movement data to environmental covariates.

Vessel Monitoring System (VMS) Data

Vessel monitoring systems (VMS) are deployed by both national and international programs to understand the spatial and temporal patterns of fishing activities (e.g. Witt and Godley 2007); requirements for VMS on fishing vessels vary by program. New Zealand Ministry of Fisheries have been collecting VMS data since 1994 and granted access to fisheries information during my study period (10 November 2011 to 29 December 2011 and 19 October 2012 to 27 December 2012). This data was necessary to examine spatio-temporal overlaps between albatrosses and boats, highlighting potential interactions and areas with increased risk of mortality to Campbell albatross. VMS information provides fine-scale data on the distribution and movement of fishing vessels via ship-borne GPS transponders that record vessel identification, speed, and location every 1 to 2 hours. These data covered all fishing vessels >28 m in length operating within the exclusive economic zone (EEZ). Additionally, smaller vessels fishing for orange roughy (*Hoplostethus atlanticus*) or New Zealand scampi (*Metanephrops challengeri*) were tracked.

Stable Isotope Analysis

Ecological applications of stable isotopes analysis use the naturally occurring ratio of heavier (enriched) to lighter atoms within tissues to infer information on trophic level and habitat. The ratios of heavier to lighter atoms, which are incorporated into the body primarily through ingestion, are reported in relation to an international standard. Using the evidence-based assumption that stable-isotope concentrations of consumers are associated with the concentration found in prey tissues, researchers can exploit subtle variations in stable isotope abundance within different tissue types to provide information on short- and long-term space use and diet (Hobson and Clark 1992; Kelly 2000). Each tissue type has a different turnover time based on the tissue's metabolic rate; turnover times range from a few days to years (plasma < red blood cells < muscles < bones) while inert tissues, such as feathers, represent the timeframe when they were formed (Hobson & Clark 1992, 1993). Carbon signatures ($\delta^{13}\text{C}$) largely reflect isotopic variation due to broad-scale gradients relating to water depth, temperature, distance to land, and latitude, and thus reveal variation in habitat use (Cherel and Hobson 2007). Nitrogen signatures ($\delta^{15}\text{N}$) show consistent stepwise enrichment relating to differences in trophic status and variation in food-chain length, and thus serve as a proxy for variation in prey type and food chain length (Hobson et al. 1994; Cherel and Hobson 2007).

1.3. Aims of the Thesis

Because we currently lack movement and distribution information for Campbell albatross during incubation and chick brooding, in **Chapter 2** I focus on their foraging ecology during these breeding stages. To accomplish this, I combined data gained through GPS tracking and stable isotope analysis across two years to provide a detailed study of individual foraging behaviour. I assessed the effects of seasonal, annual and

sex-specific interactions on foraging behaviour and stable isotope signatures. There were two main findings: 1) Campbell albatross are sexually dimorphic. 2) Despite feeding at the same trophic level ($\delta^{15}\text{N}$), habitat use, and terminal latitude showed significant sex differences. Females tended to forage on the Campbell Plateau and slope areas, whereas males travelled farther south into deeper waters of the Southern Ocean. These potential differences in foraging behaviour could impact the level of risk associated with various threats, such as interactions with fisheries (ex. Ryan 1999; Bugoni et al. 2011) and thus this information can be used in conservation and management plans.

Campbell albatrosses are attracted to offal and bycatch, making them vulnerable to fisheries-related entanglement. They, and the closely related black-browed albatross, are regularly drowned by trawl fisheries and caught by longline vessels (Croxall and Gales 1998; Gales et al. 1998). Since population levels appear to be negatively correlated with fishing effort (Waugh et al. 1999b; Moore 2004), it is assumed that fisheries interactions pose a major threat to the species. Thus the aim of **Chapter 3** was to examine spatial and temporal overlap between fisheries vessels and the vulnerable Campbell albatross. Tracking and VMS data were originally interpolated at 10 minute intervals as I hoped to extract information regarding when and where changes in albatross foraging behaviours occurred and detect specialisation on fisheries discards. No spatio-temporal overlap was found; however this assumed that individuals (birds and boats) travelled in a straight line between locations. A new modelling technique (bivariate Gaussian Bridge movement models) became available which incorporated error estimates and thus was deemed more appropriate. Therefore I study the fine-scale interactions between fishing vessels and Campbell albatross using bivariate Gaussian Bridge movement models to

compute spatio-temporal utilisation distributions within New Zealand's Exclusive Economic Zone. I also explored differences in overlap as a function of the spatial scale over which the fishing vessel occurrence may affect bird behaviour as well as tested for differences in the extent of seabird-fisheries overlap between the sexes, stages of reproduction (incubation and chick-brooding) and between two years. Within the EEZ Campbell albatross only overlapped with fisheries vessels in a relatively small section in the southern portion of these waters. Within this area there was no evidence of spatio-temporal overlap between vessels and albatrosses suggesting Campbell albatross and fisheries vessels use the same areas but not necessarily at the same time. When accounting for the broader effects of fishing vessels, there were the low levels of overlap. Males trended to co-occur within the fishing vessel footprint more often than females. Overall, these results could be due to competitive exclusion by other species, or preference for foraging in areas without fishing activity.

Intrapopulation variation in foraging behaviour has been documented among many animal taxa, and this consistent individual-level variation is thought to play an important role in a wide variety of ecological, and evolutionary processes (see Estes et al. 2003; Bolnick et al. 2003; Araújo et al. 2011 for reviews). Individual foraging specialisation is often reported as a single metric that provides population level information on individual repeatability. However, because this metric combines two parameters that describe variation at different scales (i.e. individual- and population-level variation), it discards important information such as the extent to which an individual is consistent with respect to other individuals in the same population, or the distribution of specialisation within a trait or population. In **Chapter 4**, I examine temporal individual consistency in spatial foraging behaviour of Campbell albatross by

calculating both population- and individual-level metrics of specialisation during chick-rearing. I use bird-borne GPS loggers to reconstruct foraging behaviour and analyze six traits (maximum distance from the nest, terminal latitude, terminal longitude, total distance travelled, trip duration, and angle of departure) both within and between two years (2011 and 2012). The main findings of this chapter indicate that Campbell albatross demonstrate annual and inter-annual specialisation at both the population and individual level; the degree of specialisation was influenced by sex and year. Females, which foraged closer to the colony in neritic and shelf waters, showed more consistent behaviours than males which foraged in pelagic environments.

To put my results on Campbell albatross individual specialisation in context, I examined the literature and found that individual foraging specialisation is widely reported in seabirds (Estes et al. 2003; Bolnick et al. 2003; Araújo et al. 2011 for reviews). In **Chapter 5**, I provide the first review of the incidence and implications of individual foraging specialisation among seabirds. I also examine the spread of studies by region to see whether there are differences in specialisation as a function of latitude and more broadly between tropical, temperate, and polar regions. I hypothesised such differences may exist between regions because of differences in oceanography, which influence prey availability and predictability and in turn the likely benefits of individual specialisation. The main findings of this chapter were that 79.4% of the studies examining foraging specialisation found evidence of specialisation. Most evidence of foraging specialisation in seabirds comes from studies conducted between 40° and 60° latitude, where resources are predictable but patchy, suggesting a tentative link between regional area and specialisation.

Finally, **Chapter 6** summarises the main points within my thesis, compares my results to what is known for the black-browed albatross, and addresses the conservation implications of my findings as well as provide ideas for future directions.

CHAPTER 2: INFLUENCE OF SEX AND BREEDING STAGE ON THE FORAGING ECOLOGY OF CAMPBELL ALBATROSS

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¹ discussions, editing manuscript; ² statistical advice; ³ data collection

Abstract

Most albatross species are critically endangered, endangered or vulnerable. Foraging behaviour influences demography and alters risk from at-sea threats, such as fisheries and climate change, and is therefore central to applied albatross research. Campbell albatross (*Thalassarche impavida*) is endemic to Campbell Island, NZ and has recently been recognised as a distinct species from black-browed albatross (*T. melanophrys*). It is considered vulnerable because of its sole breeding location and population declines since the 1940s. We lack basic information on at-sea foraging behaviour during early and mid-breeding periods, which is necessary for understanding spatial use, ecosystem interactions and effective conservation and management. Here we investigated sex-specific foraging behaviour during incubation and chick brooding, using a combination

of GPS tracking and analysis of stable isotopes in blood. Campbell albatrosses are sexually dimorphic and segregate by sex in relation to foraging behaviour and habitat. During incubation, trip distance and duration decrease as hatch date approaches, but both increased again during chick brooding. These findings were also reflected in stable carbon and nitrogen isotopes. Average foraging trip duration for females and males during incubation are 9.9 ± 4.8 and 12.0 ± 5.9 days respectively, with individuals reaching a maximum distance of 3379 km from the colony. Trip duration shortens during chick brooding to 2.0 ± 1.1 and 2.4 ± 1.5 days for females and males, respectively with individuals reaching a maximum distance of 1594 km from the colony. Despite feeding at the same trophic level ($\delta^{15}\text{N}$), habitat use and terminal latitude showed significant sex differences. Females tended to forage on the Campbell Plateau and slope areas, whereas males travelled farther south into deeper waters of the Southern Ocean. Thus males and females may be vulnerable to different at-sea threats. Conservation and management strategies should consider sex-specific space use as well as breeding stage differences.

2.1. Introduction

Many seabirds are top predators in marine ecosystems that spend much of their lives at sea, only returning to land to reproduce. They are declining faster than any other group of birds, primarily due to the deleterious impact of fisheries, pollution, introduced species, habitat alteration, and climate change (Croxall et al. 2012). For example, 15 of 22 species of albatross are critically endangered, endangered or vulnerable, and the rest are near threatened (IUCN Red List 2014.2). Recently, much albatross research has focused on understanding their at-sea distribution and foraging behaviour. Foraging

behaviour is the essential link between prey availability and reproductive success, and ultimately impacts demography (Lack 1968).

Breeding stage, year or sex can greatly influence foraging behaviour and alter therefore population processes through differences in foraging success or interaction with threats. For example, while breeding, seabirds are constrained to a central place, yet these constraints differ between incubation, brooding, and chick rearing because of differing parental demands which, in turn, influences foraging behaviour (Shaffer et al. 2003). Moreover, annual alterations in foraging behaviour, distribution and reproductive success may arise in response to inter-annual variation in the environment, such as those due to climate change (e.g. Reid and Croxall 2001; Barlow and Croxall 2002; Pinaud et al. 2005). Foraging behaviours may also differ between sexes. Sexual segregation in habitat use, diet, and isotopic niche is found in a number of birds and is frequently associated with niche specialisation, size dimorphism, reproductive role, and competitive exclusion (Phillips et al. 2004; Catry et al. 2006; Phillips et al. 2011). For many albatross species, spatial segregation is associated with sexual dimorphism (Weimerskirch et al. 1993; Sagar and Weimerskirch 1996; Nel et al. 2000), although is also shown in some species with little or no dimorphism (Lewis et al. 2002; Hedd et al. 2014). Understanding the degree of variation in foraging behaviour between the sexes may have important implications understanding threats, such as those posed by fisheries bycatch (Ryan 1999).

Campbell albatrosses (*Thalassarche impavida*) are endemic to Campbell Island, New Zealand, a remote, uninhabited Sub-Antarctic island in the Southern Ocean (52°32'24"S 169°8'42"E). The population declined from 31,300 pairs in the 1940's to 21,648 pairs in

2012 (Waugh et al. 1999; Sagar 2014). This taxon was previously considered a subspecies of the black-browed albatross (*Thalassarche melanophrys*), but evidence from morphology, biometrics, behaviour, mitochondrial DNA and microsatellites indicate that they are best treated as two distinct species (Robertson and Nunn 1998; Sangster et al. 2013). While information exists about the at-sea distribution and foraging behaviour of black-browed albatross populations across much of their range (Weimerskirch et al. 1986; Weimerskirch et al. 1988; Gremillet et al. 1999; Cherel et al. 2000; Huin 2002; Wakefield et al. 2011), there are large gaps in the information available for Campbell albatrosses. We know that Campbell albatrosses travel to southern Australian waters, the Tasman Sea, and the southern Pacific Ocean during the non-breeding season (Waugh et al. 1999b). Moreover, during the post-guard chick rearing phase, two foraging strategies are present: short neritic trips (2.0-3.7 days) over the Campbell Plateau and longer (>5 days) oceanic trips to the Polar Front and in the southern Antarctic Zone (Waugh et al. 2000). However we do not know whether there are any sex-specific differences in foraging behaviour, nor how this varies during incubation and chick brooding. Therefore we used a combination of GPS loggers and stable isotopes of carbon and nitrogen to study the sex-specific foraging behaviour of Campbell albatross across two years (2011 and 2012) during incubation and chick brooding. We also provided updated information on Campbell albatross body measurements (previous assessments were based on small sample sizes that provide inconclusive; Moore et al. 2001) to establish the degree of sexual dimorphism, and relate this to sex-specific foraging.

2.2. Methods

Foraging information for this study was collected during incubation and chick-brooding (10 November 2011 to 29 December 2011, and 19 October 2012 to 27 December 2012; hereafter referred to as 2011 and 2012 respectively). Chicks hatched from late November through to mid-December (peak hatch during 2011 and 2012: 6-7 December, n=81 nests).

2.2.1. Data collection

To study at-sea distribution and behaviour, we attached modified GT-600 i-gotU GPS loggers (Mobile Action Technology, Taiwan) to the central back feathers of breeding adults using Tesa© tape under permit from the New Zealand Department of Conservation. The external plastic housing of the GPS loggers were removed to reduce weight and then sealed with heat shrink tubing (FiniShrink, UK) to waterproof each unit. GPS loggers weighed approximately 1.1% of body mass or ~33 g, and were set to record locations every 10 minutes. During handling, we took the following measurements: wing chord (relaxed), minimum bill depth, and bill length (tip to feathering). Bill depth and bill length were measured using vernier callipers to the nearest 0.1 mm. Wing chord was measured to the nearest mm. We weighed albatrosses (to the nearest 25 g) during deployment and retrieval of each GPS logger and took the average of mass measurements to account for changes during the breeding season. Blood (~0.3 ml) was taken from the medial tarsal vein at each capture event and kept cool until processing. Within six hours of sampling, blood samples were centrifuged for 6-10 minutes at 6,000 rpm. Serum and red blood cells (RBCs) were separately preserved in 70% ethanol and stored at room temperature until laboratory analysis. A

small aliquot (~0.05 ml) of RBC for each individual was sent for molecular sexing (Avian Biotech, Truro, Cornwall).

2.2.2. Tracking data and habitat use

Birds were re-captured on the nest following one or more foraging trips. All incomplete tracks, which were due to battery depletion, were removed from subsequent analyses. From the GPS data we reconstructed foraging trips and calculated the following nine metrics: (1) maximum distance from the nest (km), (2) terminal latitude (decimal degrees), (3) terminal longitude (decimal degrees), (4) total distance travelled (km), (5) trip duration (hours), (6) mean speed while flying (km hour^{-1}), (7) proportion of time spent flying (day and night), (8) angle of departure (degrees using circular statistics), and (9) proportion of time spent foraging on the plateau, slope, and oceanic waters (see definitions below). We assumed birds were in-flight when speeds exceeded $11.1 \text{ km hour}^{-1}$ based on minimum flight speed calculations of the closely related black-browed albatross (Pennycuik 1997). Total distance travelled and trip duration were calculated as the sum of the values from each point-to-point location. Mean speed was calculated as the average of the point-to-point speed exceeding $11.1 \text{ km hour}^{-1}$ (in-flight). Angle of departure was estimated as the mean of angle created by the first six locations (nest location as central point, North= 0°), representing approximately the first hour of the foraging trip using circular statistics to account for non-foraging behaviours, such as bathing or resting on the water.

Data on bathymetry was obtained from the National Oceanographic and Atmospheric Administration ETOPO1 Global Relief Model

<http://www.ngdc.noaa.gov/mgg/global/global.html>, which was then linked with

albatross movement data. These locations were categorized into three bathymetric classes: plateau (0-500 m), slope (500-2000 m), and oceanic (>2000 m), and we then calculated the proportion of time spent in each region. We classified foraging trips as using Campbell Plateau, Southern Ocean (all waters south of the Subtropical Front), or north of the Subtropical Front (NSF). The location of the Subtropical Front was estimated within our maps based on Heath (1985) and Orsi et al. (2014) (see Figure 2.1).

2.2.3. Stable isotope analysis

We used stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis to provide information on short and long-term space use and diet. We analysed stable carbon and nitrogen isotopes in lipid-extracted serum (turnover=4-5 days) and RBCs (turnover=4-5 weeks; Hobson and Clark 1992; Hobson and Clark 1993). Many studies reference plasma, which is obtained using anticoagulants (i.e. Hobson and Clark 1992; Hobson and Clark 1993); we assumed turnover rates for serum were similar to plasma because serum is plasma that has had the clotting factors (i.e. fibrinogens) removed. Carbon signatures ($\delta^{13}\text{C}$) largely reflect isotopic variation due to broad-scale gradients relating to water depth, temperature and distance to land and thus reveal variation in habitat use. Nitrogen signatures ($\delta^{15}\text{N}$) show consistent stepwise enrichment relating to differences in prey trophic status and variation in food-chain length, and thus serve as a proxy for dietary niches (Hobson et al. 1994; Cherel and Hobson 2007), although there may also be regional variation in nitrogen isotopes. Isotopic signatures range from 0‰ - 2‰ for carbon and 3‰ - 4‰ on average for nitrogen in each trophic step (Kelly 2000; Cherel et al. 2005). We limited the analysis of RBC to a single sample taken close to hatch per

bird each year as this would reduce temporal overlap within the samples and provided the best isotopic information during incubation.

Blood samples were dried in an oven at 55-60°C until constant weight was attained, before being homogenized. Lipids have depleted $\delta^{13}\text{C}$ values compared with proteins and carbohydrates in animals, and thus can introduce bias in stable isotope values depending on individual variation in lipid concentration (Post et al. 2007). Lipid content shows a strong relationship with carbon/nitrogen (C/N) mass ratios. The C/N mass ratios of our RBC samples did not exceed 4.0 indicating low lipid content, thus lipid extraction was not necessary (Cherel et al. 2005). In contrast, the C/N mass ratios of serum samples ranged from 4.38 to 5.43 and lipid extraction was necessary. Lipid extraction (see below) removed the problem of depleted $\delta^{13}\text{C}$ values in serum, and did not influence nitrogen (which can sometimes be an unforeseen consequence of lipid extraction, e.g. Sotiropoulos et al. 2004).

A subsample of dried serum (minimum of 2 mg) was lipid extracted applying the methods of (Belt et al. 2012) and (Brown et al. 2013) using dichloromethane (DCM) /methanol (MeOH) (2:1 v/v) solvent. Lipids were extracted by adding 6 mL of DCM / MeOH (2:1 v/v) solvent to the samples. Samples were then ultrasonicated (CamLab Transsonic T420; 34 kHz; ca. 5 min) to improve solvent penetration, before being spun in a centrifuge at 3,500 rpm for 20 minutes. A minimum of half the supernatant was removed using a glass pipette. An additional 3 mL of solvent was added to the sample, vortex stirred, then centrifuged (3,500 rpm; 20 min) and a minimum of half the supernatant was again removed. The process was repeated once more, but with a maximum amount of supernatant removed. The processed sample was left to air dry in a

fume hood until it appeared dry then moved to an oven at 55-60°C for 24 hours to evaporate any remaining solvent. Samples were then homogenized.

We analysed all serum samples as they represent short-term foraging and the RBC samples closest to the hatch date from each individual bird per year. Serum and RBC samples were weighed (~0.7 mg) with a microbalance and loaded into tin capsules for stable isotope analysis. Samples were analysed at the East Kilbride Node of the Natural Environment Research Council Life Sciences Mass Spectrometry Facility using continuous flow isotope ratio mass spectrometry using conventional elemental analyser interfaced with mass spectrometer. Stable isotopic values are reported in δ notation (‰) relative to international standards, namely Vienna PeeDee Belemnite and atmospheric N₂ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Isotopic measurement errors were less than 0.11 % and 0.14 % for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

2.2.4. Statistical analysis

For 36 females and 38 males, we tested for sexual dimorphism in mass, wing chord, bill length and bill depth using t-tests. To determine the influence of sex, year and stage of reproduction on foraging behaviour we modelled total distance, maximum distance, trip duration, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values using separate linear mixed-effects models (LMM: lme; R package: nlme). The LMMs included individual bird as a random effect (to control for repeat samples from the same bird) with sex and year as fixed-level factors and time to or since hatch date as a covariate. Instead of fitting the fully-saturated model (because of problems of overparameterization), models were fitted with the main effects and the two-way interaction between sex and year. We log transformed maximum distance, total distance and trip duration to obey the assumptions of homoscedasticity

prior to modelling. Time to or since hatch date was calculated as the absolute value (in days) of the start of the foraging trip minus the hatch date. In other albatrosses, breeding stages demonstrate distinct space use patterns with individuals travelling farther during incubation (Tickell 2000). Breeding stages were modelled separately because foraging behaviour during incubation and chick brooding may be influenced by different constraints. Full models including the interaction term were examined. If the interaction term was not significant, it was excluded to increase the power of our models to detect differences (Underwood 1996). We did not remove successive terms, as they explain some residual variance within the model (Burnham and Anderson 2002).

Terminal latitude and terminal longitude had non-normal residual distributions and could not be transformed to meet the model assumptions. We used non-parametric Mann-Whitney U test to investigate sex and year differences.

We also tested to see whether the sexes used different oceanic zones (i.e. Campbell Plateau, South Ocean, NSF), and therefore whether there might be differences in habitat choice rather than just foraging distance. We did this using two separate generalised linear mixed-effects models (GLMM; glmer; R package: lme4); one during incubation and one during chick brooding. A logit link function was used, with the individual bird identification as a random effect, sex as a fixed factor, and habitat type as a response variable.

We used multivariate, ellipse-based metrics in R (SIBER, Jackson et al. 2011) implemented in the SIAR package (Parnell et al. 2011) to calculate isotopic niche size and overlap between each oceanic zone classifications.

Alpha level of significance for all statistical tests was 0.05.

2.3. Results

2.3.1. Morphometric comparison

Male Campbell albatross were bigger than females for all measured traits, and statistically significantly different for all measures except wing chord (Table 2.1). On average males were 7.2% heavier, had 1.8% longer bills, 2.2% wider bills and 1.0% longer wings than females.

2.3.2. Foraging behaviour by reproductive stage and sex

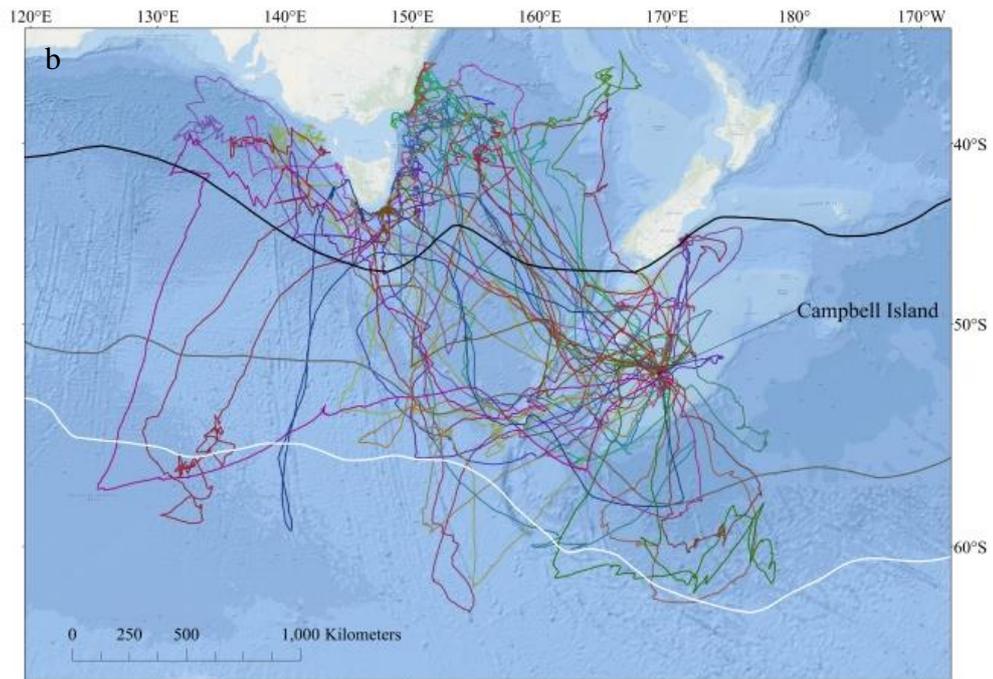
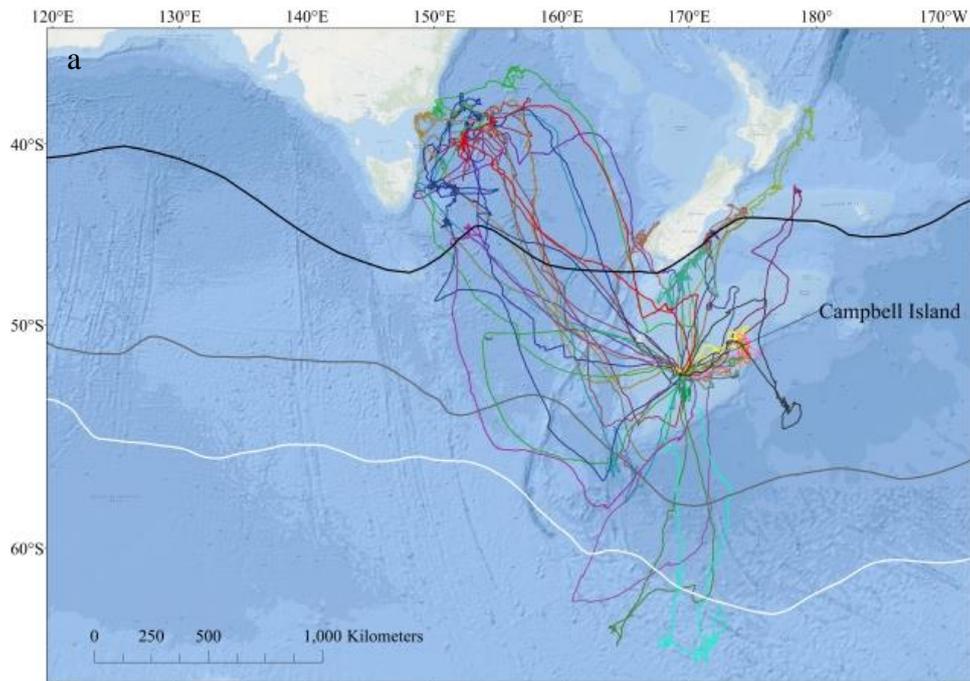
We reconstructed foraging trips yielding data from 29 individuals in 2011 (n=96 foraging trips) and 57 individuals in 2012 (n=195 foraging trips). Overall, Campbell albatross travelled in all directions from the colony, but the mean direction of initial travel ranged from 80° to 101° (North=0°; Table 2.1, Figure 2.1). During incubation, individuals travelled long distances to the Australian coast, Tasman Sea and Southern Ocean averaging 36 to 40 km hour⁻¹. By contrast, individuals travelled on the Campbell Plateau and to the Southern Ocean during chick brooding with an average speed of 32 to 36 km hour⁻¹.

Table 2.1. Morphometrics for Campbell albatross were tested for sexual dimorphism using t-test (n=36 females; n=38 males). Values reported as mean ± SD. Mean mass was calculated using the average mass for all instances measured on each individual. Measurements were pooled across the two years of sampling (2011/12).

	Females	Males	<i>t</i>	<i>P</i>
Mass (kg)	2.92 ± 0.25	3.13 ± 0.21	-3.84	<0.001
Bill Length (mm)	113.0 ± 3.8	115.1 ± 3.1	-2.56	0.01
Bill Depth (mm)	26.8 ± 1.0	27.4 ± 0.9	-2.72	0.01
Wing Chord (mm)	499 ± 12	505 ± 13	-1.73	0.09

Campbell albatrosses showed clear differences in foraging behaviour between incubation and chick brooding (Figure 2.1, Table 2.2). During incubation, maximum distance, total distance, and trip duration all decreased significantly closer to hatch date (Table 2.3, Figure 2.2). Incubation was characterized by longer foraging trips overall (ranging from 1-23 days). Mean trip duration was 9.9 ± 4.8 days for females and 12.0 ± 5.9 days for males (Table 2.2). Maximum distances for females and males were, on average, 1248 ± 709 km and 1768 ± 882 km, respectively. Total distance was 3.9 and 4.0 times the maximum distance travelled, on average, for females and males, respectively. Despite these trends, sex differences in distance and duration were not significant. There was a significant sex effect in terminal longitude ($W=446$, $p=0.02$) but not terminal latitude ($W=253$, $p=0.18$).

During chick brooding, sex differences and time since hatch (Time_{HD}) explained a significant portion of the variation in maximum distance (Sex: L-ratio=5.90, $p=0.02$; Time_{HD} L-ratio=6.14, $p=0.01$) and total distance (Sex: L-ratio=4.52, $p=0.03$; Time_{HD} L-ratio=5.69, $p=0.01$) within our LMM (Table 2.3). Mean maximum distance travelled was 337 ± 254 km for females and 499 ± 364 km for males during chick brooding. On average, males travelled 48.0% farther and 38% more than females (maximum and total distances, respectively). Trips during chick brooding were shorter than during incubation, averaging 47 ± 26 hours for females and 58 ± 36 hours for males. Trip duration, however, was only influenced by time since hatch (L-ratio=5.60, $p=0.02$, Table 2.3). During chick brooding terminal latitude was significantly associated with sex ($W=9120$, $p<0.001$); sex differences in terminal longitude were absent ($W=7809$, $p=0.25$).



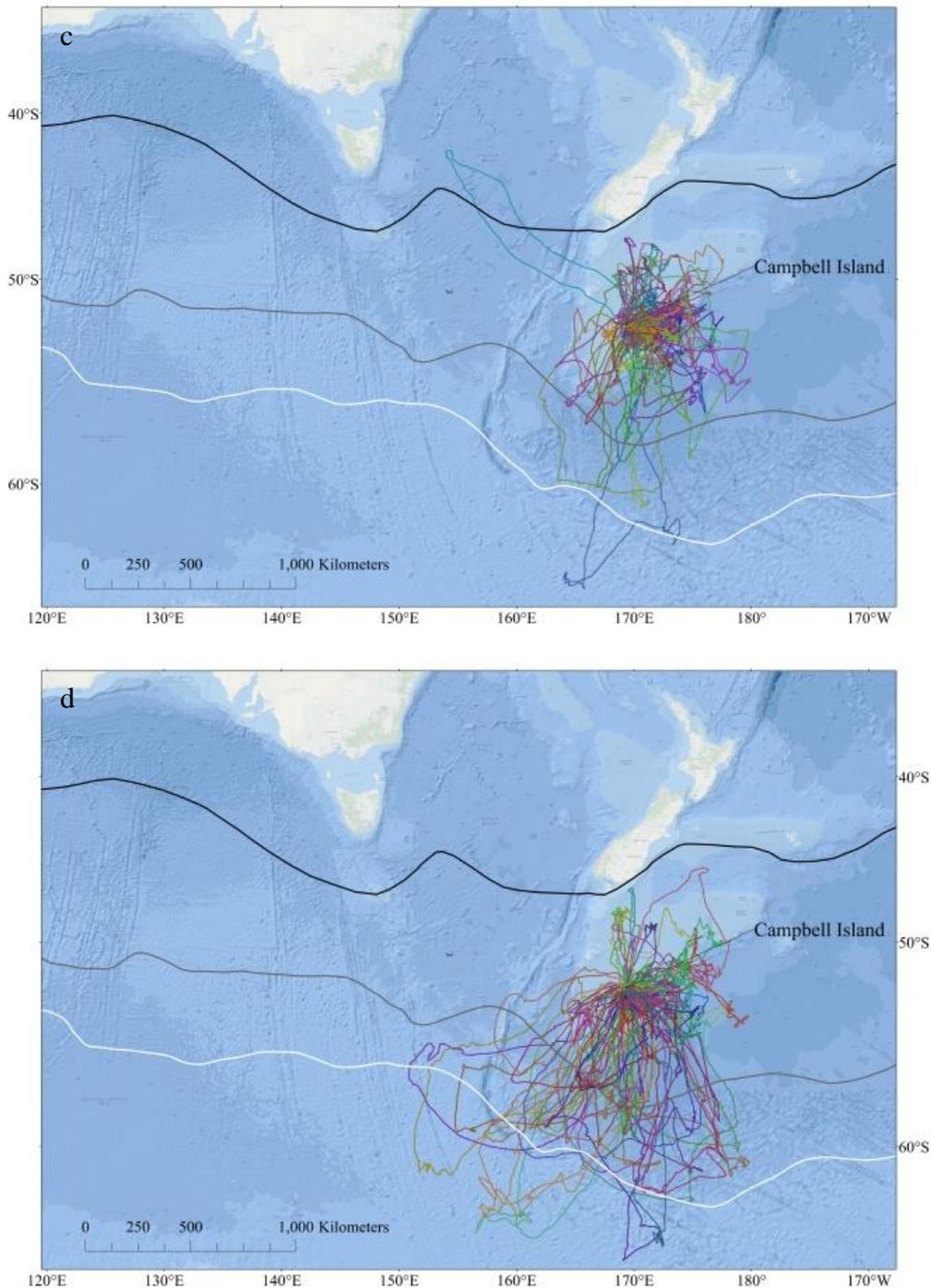


Figure 2.1. Sex and stage variation in Campbell albatross foraging distribution. Trip maps for a) females during incubation (n=26 trips); b) males during incubation (n=25 trips); c) females during chick brooding (n=124); d) males during chick brooding (n=116). Samples were pooled between years. Foraging trips are uniquely coloured by individuals. Subtropical Front (black); Subantarctic Front (grey); Polar Front (white). Front maps from Orsi et al. (2014).

Table 2.2. Campbell albatross foraging trip characteristics (n, mean \pm SD), which includes one to eight trips per individual across years and breeding stages.

	n	Incubation						Chick brooding				
		Female		Male		Female		Male				
	n	Value	SD	n	Value	SD	n	Value	SD	n	Value	SD
Maximum distance (km)	26	1248	709	25	1768	882	124	337	254	116	499	364
Total distance (km)	26	4898	2745	25	7034	3719	124	1155	765	35	1595	1074
Duration (hours)	26	238	114	25	288	142	124	47	26	116	58	36
Terminal latitude (2011)	12	-49.25	6.88	5	-45.44	6.89	44	-52.20	2.16	35	-54.14	3.08
Terminal latitude (2012)	14	-45.29	9.22	20	-44.05	9.32	80	-53.39	3.01	81	-54.90	4.30
Terminal longitude (2011)	12	165.25	12.00	5	156.04	16.62	44	171.90	3.46	35	170.87	4.46
Terminal longitude (2012)	14	162.36	10.99	20	155.09	13.22	80	171.66	3.21	81	170.30	5.85
Departure angle	26	93	32	25	80	33	124	97	24	116	101	31
Proportion of time flying (day)	26	0.66	0.1	25	0.7	0.11	124	0.74	0.14	116	0.76	0.13
Proportion of time flying (night)	26	2	0.05	25	0.14	0.06	124	0.12	0.09	116	0.12	0.08
Proportion of time on plateau	26	0.15	0.14	25	0.15	0.15	124	0.53	0.35	116	0.42	0.34
Proportion of time on continental slope	26	0.36	0.31	25	0.21	0.19	124	0.33	0.29	116	0.29	0.24
Proportion of time on oceanic waters	26	0.49	0.39	25	0.64	0.3	124	0.14	0.26	116	0.29	0.34

Table 2.3. Modelling Campbell albatross foraging distribution as a function of sex and stage of reproduction. Linear mixed-effects model results (Incubation: n=51; Chick Brooding: n=240). Time_HD: absolute value of the start date of a foraging trip to hatch date (days). Response variables were log normalized to meet model assumptions. Significant p-values indicate parameters that explain a significant amount of variation within the model (highlight in bold).

Incubation	Parameter	Value	SE	DF	L-ratio	p-value
Maximum distance (km, log)	Intercept	-296.78	391.72	43		
	Sex	0.07	0.18	43	1.43	0.23
	Year	0.15	0.19	4	0.85	0.36
	Time_HD	0.03	0.01	4	10.36	0.001
Total Distance (km, log)	Intercept	-490.43	326.42	43		
	Sex	-0.03	0.15	43	1.93	0.17
	Year	0.25	0.16	4	0.49	0.48
	Time_HD	0.04	0.01	4	21.51	<0.001
Duration (h, log)	Intercept	-400.11	295.59	43		
	Sex	-0.19	0.14	43	0.19	0.66
	Year	0.20	0.15	4	0.13	0.72
	Time_HD	0.04	0.01	4	32.30	<0.001

Chick Brooding	Parameter	Value	SE	DF	L-ratio	p-value
Maximum distance (km, log)	Intercept	-366.18	242.65	169		
	Sex	0.37	0.13	67	5.90	0.02
	Year	0.18	0.12	169	0.13	0.72
	Time_HD	-0.01	0.01	169	6.14	0.01
Total Distance (km, log)	Intercept	-442.84	230.11	169		
	Sex	0.32	0.12	67	4.52	0.03
	Year	0.22	0.11	169	1.10	0.29
	Time_HD	-0.01	0.01	169	5.69	0.01
Duration (h, log)	Intercept	112.16	186.23	169		
	Sex	0.23	0.10	67	2.42	0.12
	Year	-0.05	0.09	169	2.61	0.11
	Time_HD	-0.01	0.01	169	5.60	0.02

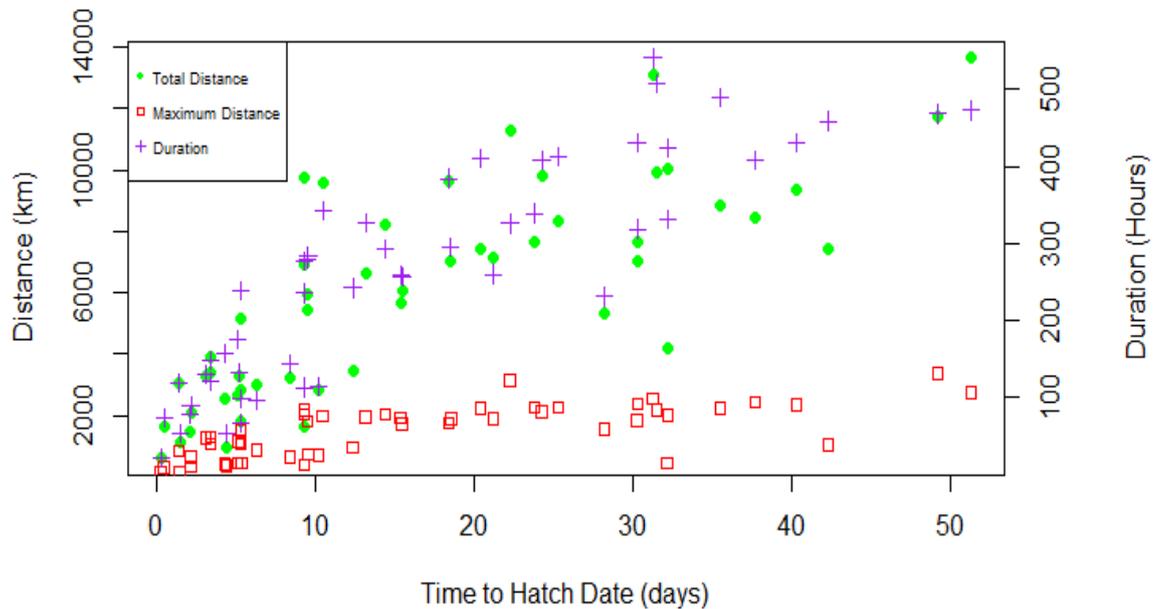


Figure 2.2. Effects of hatch date on maximum distance, total distance, and duration of foraging trips by Campbell albatross during incubation ($n=51$). Time to hatch date was calculated as the absolute value in days of the start of the foraging trip minus the hatch date.

The areas used by both sexes overlap (Figure 2.1); however, the frequency of use within the three oceanic zone classifications altered between sexes during chick brooding (Figure 2.3). During incubation, there was no significant sex effect, despite females frequently foraging on the Campbell Plateau and males tending to use the NSF ($z=1.71$, $n=51$, $p=0.09$). Females continued to use the Campbell Plateau more frequently than males during chick brooding. Males visited the Southern Ocean region more often than the NSF ($z=2.86$, $n=240$, $p<0.001$). These use characteristics were also reflected in the average proportion of time spent foraging in different bathymetry classes (Table 2.2). Both sexes spent, on average, 49% or more of their time over oceanic waters during

incubation, although females spent more time on the plateau and slope areas than males (51% vs. 36%). Males continued to use oceanic waters more frequently than females during the chick brooding period (29% vs. 14%).

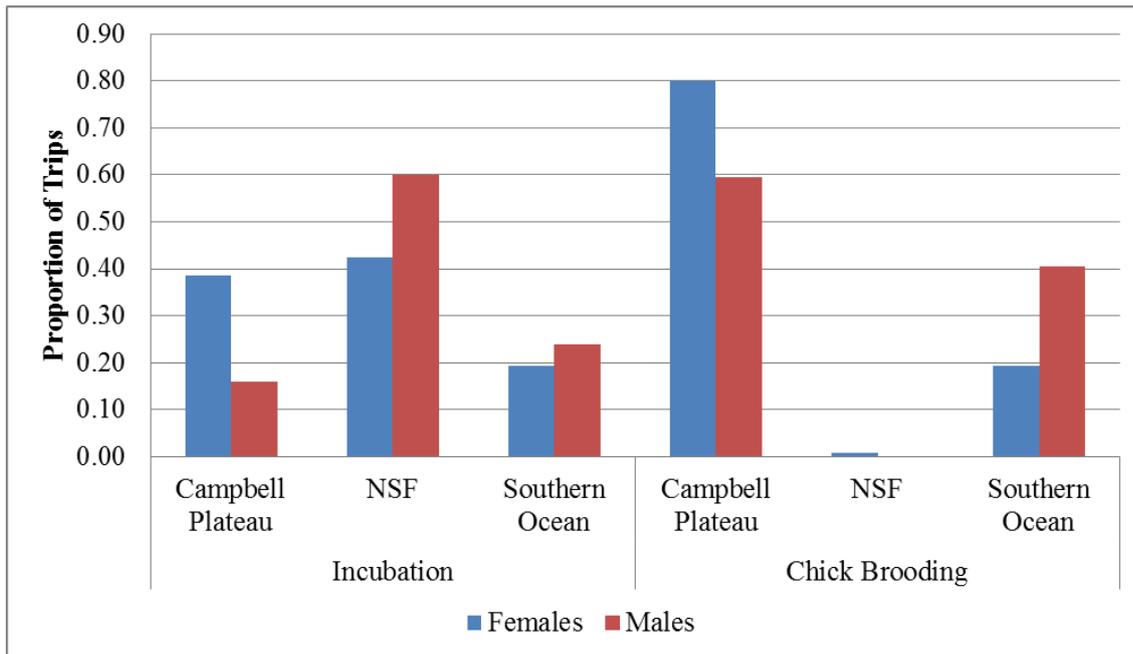


Figure 2.3. The proportion of trips within each habitat type used for incubation (n=26 females (blue) and 25 males (red) trips) and chick brooding (n=124 females (blue) and 116 males (red) trips). NSF: North of the Subtropical Front.

2.3.3. Annual variation

Annual variation in distance and duration were not found during incubation or chick brooding (Table 2.2). Annual differences in terminal latitude were marginally significant during incubation ($W=193$, $p=0.06$), and significant during chick brooding ($W=7676$, $p=0.01$). Individuals travelled further south in 2011 than 2012 during incubation whereas during chick brooding albatross travelled further south in 2012.

Terminal longitude was similar in both years during incubation and chick brooding (W=356, p=0.19 and W=7066, p=0.16, respectively).

2.3.4. Stable isotope signatures

To compare stable isotope and tracking results, we also assessed the effects of seasonal, annual and sex-specific interactions on stable isotope signatures from blood and sera samples. Blood samples were collected from 84 individuals over two years, resulting in 91 RBC samples and 173 serum samples with sex and hatch date information and of these, 127 serum samples had complete foraging trip data. Serum data was used to test for sex-specific differences in oceanic habitat use since this has a shorter turnover time and can therefore be better matched with tracking data compared with RBCs.

$\delta^{13}\text{C}$ values ranged from -21.9‰ to -18.2‰ (a 3.7‰ range) for RBCs and -22.5‰ to -17.6‰ (4.9) for sera (Table 4), which indicate broad-scale habitat use differences between individuals. $\delta^{15}\text{N}$ values, which provide information on trophic level and variation in food-chain length, ranged from 11.1‰ to 15.5‰ (4.4) for RBCs and 10.0‰ to 14.7‰ (4.7) for sera indicating that individuals may be foraging across trophic levels.

RBC $\delta^{13}\text{C}$ values (longer-term habitat use) showed sex, year and time from hatch date affects (Sex: L-ratio=9.07, p<0.01, Year: L-ratio=6.80, p=0.01, Time_{HD}: L-ratio=8.35, p<0.01, Table 5) whereas $\delta^{15}\text{N}$ signatures from RBCs (longer-term trophic level) were influenced by annual changes and time from hatch date (Year: L-ratio=17.29, p<0.001, Time_{HD}: L-ratio=8.02, p<0.01, Table 5). Sex differences in $\delta^{13}\text{C}$ values averaged 0.6-0.7 ‰. Differences between sexes and years for RBC $\delta^{15}\text{N}$ values averaged 0.1-0.3 ‰ and 0.6-1.0 ‰, respectively.

Table 2.4. Long-term (red blood cell) and short-term (delipidated serum) stable carbon and nitrogen signatures of breeding Campbell albatross (mean \pm SD).

	Female				Male			
	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C/N mass ratio	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C/N mass ratio
RBC 2011	14	-19.1 \pm 0.6	12.7 \pm 0.6	3.3 \pm 0.04	13	-19.9 \pm 1.0	12.8 \pm 1.1	3.3 \pm 0.05
RBC 2012	28	-18.8 \pm 0.5	13.7 \pm 0.4	3.3 \pm 0.03	36	-19.4 \pm 1.0	13.4 \pm 1.0	3.2 \pm 0.04
<i>Incubation</i>								
Serum 2011	15	-19.3 \pm 0.9	12.9 \pm 0.8	3.5 \pm 0.04	7	-19.7 \pm 1.0	13.0 \pm 1.0	3.6 \pm 0.04
Serum 2012	23	-18.7 \pm 0.6	13.7 \pm 0.8	3.5 \pm 0.05	31	-19.0 \pm 0.7	13.4 \pm 0.8	3.5 \pm 0.05
<i>Chick Brooding</i>								
Serum 2011	20	-20.3 \pm 0.8	11.1 \pm 0.7	3.6 \pm 0.05	12	-20.9 \pm 1.0	11.2 \pm 0.6	3.6 \pm 0.06
Serum 2012	31	-19.5 \pm 0.9	12.5 \pm 0.9	3.5 \pm 0.05	34	-20.2 \pm 1.1	11.7 \pm 0.8	3.5 \pm 0.05

Table 2.5. The effects of sex, year, time to or since hatch, and the interaction of sex and year on stable carbon and nitrogen signatures for red blood cell samples (RBC, n=91) and lipid-extracted serum during incubation (n=76) and chick brooding (n=97).

Time_HD: absolute value of the start date of a foraging trip to hatch date (days).

	Parameter	Value	SD	DF	L-ratio	p-value
$\delta^{13}\text{C}$ (RBC)	Intercept	-872.63	252.65	78		
	Sex (Male)	-0.63	0.19	78	9.07	<0.01
	Year	0.42	0.13	9	6.80	0.01
	Time_HD	0.00	0.00	9	8.35	<0.01
$\delta^{15}\text{N}$ (RBC)	Intercept	-1600.38	351.82	78		
	Sex (Male)	-0.22	0.18	78	0.10	0.76
	Year	0.80	0.17	9	17.29	<0.001
	Time_HD	0.00	0.00	9	8.02	<0.01
Incubation $\delta^{13}\text{C}$	Intercept	-1312.24	445.81	51		
	Sex (Male)	-0.31	0.22	51	0.84	0.35
	Year	0.64	0.22	21	6.77	0.01
	Time_HD	0.01	0.01	21	2.45	0.11
$\delta^{15}\text{N}$	Intercept	-1308.23	473.53	51		
	Sex (Male)	-0.12	0.22	51	0.91	0.34
	Year	0.66	0.24	21	6.22	0.01
	Time_HD	-0.01	0.01	21	7.45	0.01
Chick Brooding $\delta^{13}\text{C}$	Intercept	-1488.46	365.48	58		
	Sex (Male)	-0.48	0.22	58	3.13	0.07
	Year	0.73	0.18	35	13.32	<0.001
	Time_HD	0.00	0.00	35	1.52	0.22
$\delta^{15}\text{N}$	Intercept	-2607.38	457.19	58		
	Sex (Male)	1445.12	710.33	58	4.89	0.03
	Year	1.30	0.23	34	26.23	<0.001
	Time_HD	0.00	0.00	34	8.83	<0.01
	Sex*Year	-0.72	0.35	34	3.84	0.05

During incubation, $\delta^{13}\text{C}$ values from serum samples (short-term habitat use) showed a significant year effect (Year: L-ratio=6.77, $p=0.01$) whereas $\delta^{15}\text{N}$ signatures from serum (short-term habitat use) samples were affected by both year and time until hatch (Year: L-ratio=6.22, $p=0.01$, Time_{HD}: L-ratio=7.45, $P=0.01$, Table 5). Annual differences in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from serum were 0.6-0.7‰ and 0.4-0.8 ‰, respectively. Sera samples during chick brooding, $\delta^{13}\text{C}$ signatures (short-term habitat use) were affected by annual differences (L-ratio=13.32, $p<0.001$; difference 0.7-0.8‰) and $\delta^{15}\text{N}$ values (short-term habitat use) altered all parameters including the interactions of sex and year (Sex: L-ratio=4.89, $p=0.03$, Year: L-ratio=26.23, $p<0.001$, Time_{HD}: L-ratio=8.83, $p<0.01$, Sex*Year: L-ratio=3.84, $p=0.05$, Table 5). Sex and year differences in $\delta^{15}\text{N}$ values ranged from 0.1-0.8‰ and 0.5-1.4‰, respectively.

Male and female isotopic niches overlap, but females are slightly more enriched in $\delta^{13}\text{C}$. Serum $\delta^{15}\text{N}$ values were similar between the sexes in 2011, but are higher in females 2012, particularly during chick brooding (Table 2.4). Isotopic niche area was 2.6, 1.5, and 2.3 for Campbell Plateau, NSF, and Southern Ocean, respectively. NSF had minimal (<20%) isotopic overlap with Campbell Plateau and the Southern Ocean (area of overlap=0 and 0.3 respectively; Figure 2.4). During chick brooding, both sexes primarily foraged on the Campbell Plateau and in the Southern Ocean (Figure 2.3), but the isotopic signatures of these habitats are largely indistinguishable from one another with >60% overlap (area of overlap=1.6; Figure 2.4). Males spent more time foraging in oceanic waters than females (Table 2.2).

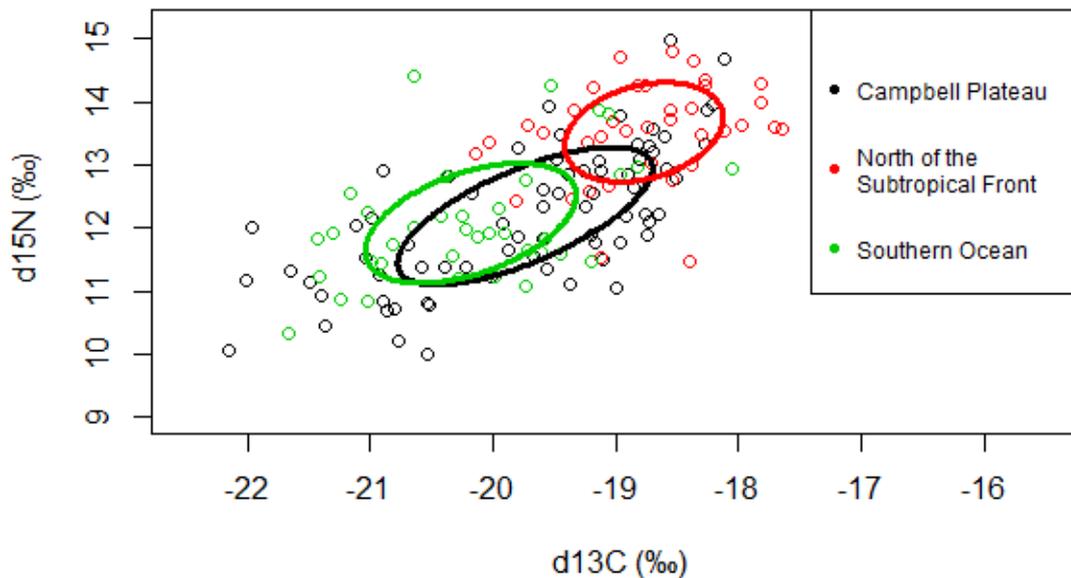


Figure 2.4. Stable isotopic niches for habitat classifications based on lipid extracted serum samples. CP: Campbell Plateau (n=66); SO: Southern Ocean (all waters south of the Subtropical Front; n=31); NSF: North of the Subtropical Front as estimated based on Heath (1985) and Orsi et al. (2014; n=30).

2.4. Discussion

Knowledge of foraging behaviour is critical to understanding interactions between predators, prey and their environment (e.g. Weimerskirch et al. 1994; Weimerskirch et al. 2005), its influence on demography (e.g. Weimerskirch et al. 2012), and how these behaviours alter population risks from at-sea threats (e.g. Torres et al. 2011). However to understand these influences and interactions, we must first have baseline information on foraging behaviour, which can alter with breeding stage, annual variability, and sexual segregation. Our study focused on providing this basic information during incubation and chick brooding on Campbell albatross.

As with other species of albatrosses (Tickell 2000), our results showed that the foraging behaviour of Campbell albatross changed between incubation and chick brooding; trip duration is longer during incubation when trip duration is limited by their partner's ability to fast and shorter trips are taken during chick brooding to meet self-maintenance and chick energetic needs (Weimerskirch et al. 1986; Weimerskirch 1995; Weimerskirch et al. 1997; Tickell 2000; Shaffer et al. 2003). Campbell albatross foraging behaviour also demonstrated annual variations and sexual segregation in trip parameters, oceanic region use and possibly diet, which provide information on the different roles of the sexes and can affect interactions with at-sea threats, such as fisheries interactions and climate change as well as impacting reproduction success and ultimately population abundance. For example, changes in wind patterns influenced foraging behaviour, breeding success and mass of wandering albatrosses (*Diomedea exulans*; Weimerskirch et al. 2012)

2.4.1. Breeding stage

Campbell albatrosses demonstrated at least three different foraging strategies that vary throughout the breeding season. Foraging during incubation was characterized by long trips with maximum trip distance that ranged from 171 to 3379 km with individuals mainly travelling to the southeast Australian coast, Tasman Sea and Southern Ocean. Foraging trips during chick brooding were shorter than during incubation (overall mean 2.2 days and 10.9 days, respectively) with birds primarily using the Campbell Plateau and Southern Ocean. Shifts in carbon stable isotope signatures, representing variation in foraging area used, were consistent with this pattern; however, birds appeared to feed at the same trophic level during incubation and brooding, as evidenced by similar nitrogen

isotope signatures. The duration of foraging trips in January and February, during post-brooding stage, was 1 to 9 days (mean 1.64; Waugh et al. 2000). At this stage, Campbell albatross switched between two foraging strategies, short neritic trips (2.0-3.7 days) and longer oceanic (>5 days) trips (Waugh et al. 2000). During short trips, individuals travelled 150 to 640 km away and on long trips individuals sometimes commuted in excess of 2000 km (Waugh et al. 2000).

Foraging strategies differ based on constraints imposed by offspring development during incubation and chick brooding. During incubation, distance and duration decreased as hatch date approaches. This has been documented in several seabird species and is likely associated with the need to feed chicks shortly after hatching (Weimerskirch et al. 1986; Weimerskirch et al. 1993; Tickell 2000). Hatch date also presents a switch in foraging behaviour as adults have limited foraging time between chick feedings. Similarly, foraging behaviour presumably alters due to the energy requirements of chicks accounting for changes in foraging trip characteristic during chick brooding (Weimerskirch et al. 1997; Waugh et al. 2000).

2.4.2. Annual variation

While foraging location (terminal latitude and longitude) were similar in both years during incubation, habitat shifts during chick brooding were more vertical than horizontal. Individuals used terminal latitude slightly farther south (~ 1 decimal degree) in 2012 during chick brooding. Short-term (serum) and long-term (RBC) carbon signatures during incubation and chick brooding support annual variations spatial use; the extent of these differences in habitat use depending on the species/site-specific

fractionation rates, which are currently unknown for this species. Inter-annual variation in stable isotopes could also be to do with shifts in the baseline values or diet switching in the same locations.

Campbell albatross spent most of their time over oceanic waters during incubation and on the plateau and slope during chick brooding suggesting the prey species may alter between stages; however these possible differences are not clearly demonstrated within the nitrogen signatures. Campbell albatross forage primarily on fish, particularly southern blue whiting (*Micromesistius australis*), but also consume cephalopods, crustaceans and carrion (Cherel et al. 1999; NIWA 1999). There is some indication that primary prey species differ between foraging areas; during chick-rearing, the diet of individuals using Campbell Plateau was dominated by fish whereas diet samples from individuals using oceanic waters and the polar front contained mostly squid (NIWA 1999). We do not know prey taken north of the Subtropical Front, but it is likely similar to the main prey taken in other areas- primarily fish (juvenile southern blue whiting *Micromesistius australis*) and squids (*Martialia hyadesi*). Our observed annual change in nitrogen of 0.8 ‰ to 1.4 ‰, while statistically significant, are within the average trophic step in nitrogen ranges (3‰ to 4‰; Kelly 2000; Cherel et al. 2005). Thus the variation within our nitrogen signatures is likely due to differences in the portion of prey types within the same trophic guild and the Campbell albatross diet was likely largely consistent through both years.

2.4.3. Sexual dimorphism and segregation

Sexual dimorphism occurs in many, but not all albatross species (Weimerskirch and Jouventin 1987; Prince et al. 1992; Salamolard and Weimerskirch 1993; Weimerskirch et al. 1993; Sagar and Weimerskirch 1996; Nel et al. 2000; Stahl and Sagar 2000a; Stahl and Sagar 2000b; Hedd et al. 2001). Campbell albatrosses are sexually dimorphic in mass and bill measurements, with slight but not statistically significant differences in wing length (Table 2.1). These differences in bill size and mass between sexes are less marked than in other albatross species, such as the black-browed albatross. Mass difference between male and female Campbell albatross average 7.2%, whereas the mass difference between sexes in black-browed albatross is 20.2% (Phillips et al. 2004). Previous work on Campbell albatross also indicated that males are larger than females, although the differences were not statistically significant (Moore et al. 2001).

Sexually dimorphic species are likely to demonstrate trophic and spatial segregation, but segregation can also differ between breeding stages (Phillips et al. 2004; Wearmouth and Sims 2008; Phillips et al. 2011; Mancini et al. 2013). Campbell albatross demonstrated sex differences in foraging behaviours during incubation and chick brooding. During incubation, males and females used the same latitudes, but males tended to travel farther west than females. The impacts of sex on foraging behaviour were more apparent during chick brooding as total and maximum distances were influenced by sex. Habitat use and terminal latitude showed significant sex differences as females tended to forage on the Campbell Plateau and slope areas, whereas males travelled farther south into deeper waters of the Southern Ocean. Carbon isotope signatures are generally negatively correlated with latitude in the Southern

Ocean (Cherel and Hobson 2007; Quillfeldt et al. 2008; Jaeger et al. 2010), thus we would expect sex differences in carbon, but our results were not significant. This is likely due to similar isotopic signatures of the Campbell Plateau and Southern Ocean (Figure 4) suppressing any latitudinal gradient. Nitrogen isotope values were influenced by sex, either suggesting dietary differences between sexes, or variation in baseline levels based on location or food chain length. Overall, the pattern of sexual segregation in which large Campbell albatross males travelled further than females during chick brooding is similar to that found in grey-head albatross (*T. chrysostoma*, Phillips et al. 2004) and magellanic penguins (*Spheniscus magellanicus*, Forero et al. 2002). However, this pattern of sexual segregation and sexual dimorphism appears less common than the reverse pattern. Generally the smaller sex forages further from the colony (Wearmouth and Sims 2008). Sexual segregation is generally considered to be result of social dominance, competitive exclusion, or niche specialization associated with breeding role or morphology (Peters and Grubb 1983; Petit et al. 1990; Marra 2000; Weimerskirch et al. 2009). However, flight proficiency, wing loading and wind speeds within habitats have been used to explain both the general pattern seen and that of grey-head albatross (Shaffer et al. 2001; Phillips et al. 2004).

2.5 Conclusions

Campbell albatross foraging behaviour varied between breeding stages and by sex; thus conservation and management strategies should consider sex-specific space use as well as breeding stage differences. Foraging areas of males and females overlap but sexes demonstrate distinct foraging behaviours and tend to use different oceanic regions during incubation and chick brooding. Thus sexes may experience different levels of

risk from threats, such as fisheries interaction, and climate change. For example, several fisheries report sex biases in bycatch mortality, which likely corresponds to either sexual exclusion or sexual segregation (i.e. Ryan 1999; Bugoni et al. 2011). In Campbell albatross, females use the Campbell Plateau more frequently than males; as this brings females closer to the New Zealand fisheries areas it may increase the risk of fisheries interactions. Sex biased mortality can lead to unequal sex ratios or removal of individuals attracted to vessels, which can impact population dynamics (Mills and Ryan 2005; Barbraud et al. 2013; Tuck et al. 2015). At the same time, males and females may be affected by local environmental changes based on bathymetry zone use, oceanic regional selection, and morphology, which can ultimately impact life history traits as seen in wandering albatross (Weimerskirch et al. 2012). However, more detailed examination of habitat selection is needed to comprehend what environmental factors might affect Campbell albatross demography.

CHAPTER 3: TRACKING REVEALS LIMITED INTERACTIONS BETWEEN CAMPBELL ALBATROSS AND FISHERIES

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¹ discussions, editing manuscript; ² data analysis /R coding

Abstract

The last century has seen a significant decline in global seabird populations that can, in part, be attributed to fisheries related mortality. Understanding the overlap between seabird and fisheries distribution is one important element of assessing the risk of seabird bycatch. Here we assess the spatio-temporal overlap between the vulnerable Campbell albatross *Thalassarche impavida* and large (>28m) commercial capture fisheries in New Zealand's Exclusive Economic Zone (EEZ). We used bivariate Gaussian bridge movement models to compute spatio-temporal utilisation distributions, both from high-resolution bird-borne GPS loggers and the Vessel Monitoring System (VMS), and estimated potential fisheries interactions for breeding albatrosses. During incubation and chick brooding, Campbell albatrosses spent 49.5% of their foraging trips within New Zealand's EEZ utilising 6.7% of EEZ. Within the EEZ they only

overlapped with fisheries vessels in a relatively small section in the southern portion of these waters (0.20% of the EEZ). Within this area there was no evidence of spatio-temporal overlap between vessels and albatrosses. When accounting for the broader effects of fishing vessels, which can influence a birds' behaviour for up to 30 km, we found albatross-vessel overlap in up to 8.4% of trips, typically lasting less than 10% of the time spent within the EEZ. Males trended to co-occur within the fishing vessel footprint more often than females. Overall, the low levels of overlap could be a result of competitive exclusion by other species, or preference for foraging in areas without fishing activity, but higher resolution data from both birds and vessels would be need to determine interactions. Campbell albatross spend most of their time foraging outside New Zealand waters. Thus conservation and fisheries management for this species needs to occur on a multi-national scale. Our results indicate the importance of a multi-scale approach to risk assessment, as results that rely solely on large-scale spatio-temporal overlap may overestimate risk associated with fisheries.

3.1. Introduction

Population declines in seabirds, particularly albatrosses and petrels, have been attributed to fisheries-related mortality from accidental bycatch (Brothers 1991; Nel et al. 2002; Sullivan et al. 2006; Rolland et al. 2010; Anderson et al. 2011). Globally, tens of thousands of seabirds are estimated to be killed every year, but these estimates vary greatly by location and among species (Lewison and Crowder 2003; Anderson et al. 2011). Risk of bycatch is also known to vary within species as a function of sex, age, or because of inter-individual differences in foraging site preference and behaviour (Nel et al. 2002; Votier et al. 2010, Tuck et al. 2015).

Conservation efforts to reduce seabird bycatch have been aided by identifying regions of seabird-fishery overlap to inform mitigation measures. Recently, bird-borne tracking has been used in tandem with spatially explicit fisheries data to better quantify the nature and extent of spatio-temporal overlap (Votier et al. 2010; Torres et al. 2011; Torres et al. 2013a; Votier et al. 2013; Bodey et al. 2014; Collet et al. 2015; Patrick et al. 2015). Various scales of analysis have been applied to seabird-fisheries overlap and have highlighted contrasting results in some cases due to the resolution of the data as well as our limited ability to distinguish between interactions and overlap events (e.g. (Torres et al. 2013a). Thus combining and contrasting multiple scales may provide complimentary information necessary to enhance our understanding of the true nature of seabird/fishery interactions.

In the present study, we examine the spatial and temporal overlap between fisheries vessels and the vulnerable Campbell albatross, *Thalassarche impavida*. This endemic species has declined from the 1940s to the present day, with a marked decline of 72% from 1966-1984. In common with other species of albatross, the steep population decline coincided with increased fisheries efforts in the Southern Ocean (Waugh et al. 1999b; Sagar 2014). Campbell albatross, and the closely related black-browed albatross, *T. melanophris*, are regularly drowned by trawl fisheries and caught by longline vessels (Murray et al. 1993; Croxall and Gales 1998; Gales et al. 1998). Thus, our goal was to estimate the degree of spatio-temporal overlap between fisheries and breeding Campbell albatross within New Zealand's Exclusive Economic Zone (EEZ) to provide an updated understanding of bycatch risk in these waters. We tested for differences in the extent of seabird-fisheries overlap between the sexes, stages of reproduction (incubation and chick-brooding) and between two years. Because albatrosses spend more time in the

EEZ during chick brooding (Chapter 2), we expected that there would be more interactions with fisheries during this stage. Furthermore, because female Campbell albatrosses tend to use areas that are closer to the New Zealand mainland than males (Chapter 2), we hypothesise that females are more likely to encounter fishing vessels within the EEZ. We also explored differences in overlap as a function of the spatial scale over which fishing vessel occurrence may affect bird behaviour. Recent work has shown the ecological footprint of fisheries is larger than previously thought (Bodey et al. 2014; Collet et al. 2015). Therefore, by examining albatross-fishery overlap as a function of variations in distance between entities we may increase our understanding of the factors, such as breeding stage and sex, that impact of interactions at various spatial scales.

3.2. Methods

3.2.1. Albatross tracking

Campbell albatross breed on the northern cliffs of Campbell Island, New Zealand (52°32'24"S, 169°8'42"E). To study foraging behaviour, we attached modified GT-600 i-gotU GPS loggers (Mobile Action Technology, New Taipei City, Taiwan) to the central back feathers of incubating and chick brooding adults using Tesa© tape during two breeding seasons (10 November 2011 to 29 December 2011 and 19 October 2012 to 27 December 2012; hereafter referred to as study years 2011 and 2012 respectively). GPS loggers were modified by removing the external plastic housing, and then sealed with heat shrink tubing (FiniShrink, UK) to waterproof each unit. The loggers weighed ~33 g, approximately 1.1% of body mass of albatrosses, and were set to record location every 10 minutes. Birds were re-captured on the nest following one or more complete foraging trips, as determined by nest attendance surveys. During capture, a small aliquot

(~0.05 ml) of blood was taken from each individual for molecular sexing (Avian Biotech, Truro, Cornwall) under licence from the New Zealand Department of Conservation.

3.2.2. Vessel monitoring system

We acquired data on the distribution and movement of fishing vessels via ship-borne GPS transponders provided by the New Zealand Ministry of Fisheries fishing vessel-monitoring system (VMS). Data were obtained for the same temporal period (i.e. 10 November 2011 to 29 December 2011 and 19 October 2012 to 27 December 2012) and spatial extent as the bird tracks. These data covered all fishing vessels >28 m in length operating within the EEZ. Additionally, smaller vessels fishing for orange roughy (*Hoplostethus atlanticus*) or New Zealand scampi (*Metanephrops challengeri*) were tracked. VMS transponders record vessel identification, speed, and location every 1 to 2 hours; gear type was not reported.

3.2.3. Data Analysis

Encounter probability

We used bivariate Gaussian bridge movement models to calculate the space use of both foraging Campbell albatrosses and fisheries vessels to examine their encounter probabilities (Kranstauber et al. 2014). The advantage of bivariate Gaussian bridges (BGB) over classic measures of utilisation distributions is that they track movement heterogeneity across time using two directional components instead of one to gain more precise estimates of the space utilised by individual animals/vessels. Moreover, space use between any two locations can be computed separately, allowing for temporally explicit estimates of the utilisation distribution (Kranstauber et al. 2014). To prepare the

tracking data, we split the VMS data into separate fishing trips with the same format as the albatross data; each fishing vessel trip was defined as a series of GPS fixes that were separated by a maximum of 24 hours. To prevent computational issues with birds and fishing vessels crossing the international dateline we shifted the dateline of the data by 180 degrees prior to all analyses.

Spatial overlap between albatross and fisheries

First, we calculated the total space use of birds and fishing vessels during each foraging/fishing trip. We did so by computing BGBs on the complete trips assuming a spatial error of the GPS-devices of 18m for both the albatross data loggers and the VMS system of the vessels (Duncan et al. 2013). From these, we extracted the 95% estimates of total space use with a spatial resolution of 5 km. We re-projected these 95% home ranges to the Lambert azimuthal equal area projection and calculated the total spatial overlap of each Campbell albatross and each fishing vessel during the entire study period. We then overlaid the resulting space use estimates for every combination of bird and fishing vessel (i.e. pooled data between years and individuals) and calculated the area that was shared.

Spatio-temporal overlap between albatross and fisheries

Secondly, we investigated whether birds and vessels shared areas during the same time, creating a potential for interactions. We calculated this fine resolution temporal overlap between albatrosses and fisheries vessels by splitting the BGBs. Using the estimates of motion variance from the full BGBs, we calculated the 95% utilisation distributions between every two consecutive GPS fixes (i.e. every ten minutes for albatrosses, every 2 hours for vessels) with a resolution of one square kilometre. For each potential

encounter (locations with overlapping time intervals), we calculated the spatial overlap of the distribution estimates to estimate the area that was shared in space and time.

Distance between albatross and fishing vessels

As fisheries vessels can alter the behaviour of foraging seabirds at a range of different spatial scales - ~11 kilometres for northern gannets (*Morus bassanus*; Bodey et al. 2014) and ~30 for wandering albatross (*Diomedea exulans*; Collet et al. 2015) - we additionally calculated the minimum spatial and temporal distances between foraging albatrosses and fishing vessels. First, we excluded all GPS fixes that did not have overlapping time intervals. We then calculated the rhumb line distance from every GPS-fix of a foraging albatross to every fishing vessel GPS-fix recorded within two hours (the temporal resolution of VMS tracks). Analyses used the full data set as well as the subset of the data where albatross and fishing vessel were less than 11 km apart, assuming a conservative effect of the fishing vessel (Bodey et al. 2014); for comparison we also examined the effect of 30 km footprint (Collet et al. 2015).

Sex, stage and year effects

We modelled spatio-temporal overlaps in foraging area and distance travelled by birds, and distance between albatross and vessels using linear mixed-effects models. The models included individual bird as a random effect (to control for repeat samples from the same bird) with year, sex and stage of reproduction (incubation and chick brooding) as fixed-level factors. We also fitted the two-way interaction between sex and stage of reproduction, to determine whether sex effects of fisheries associations varied as a function of breeding stage.

3.3. Results

Over the two breeding seasons, we collected data from 299 foraging trips made by 81 (43 males and 38 females) Campbell albatrosses (Table 3.1). Of the total space used by albatrosses (pooled), 32% was within the New Zealand EEZ. For the fishing vessels, a total of 320,510 VMS fixes were available to us in both years, of which 99.9 % were within the EEZ. Subsequent results are thus based upon the EEZ only.

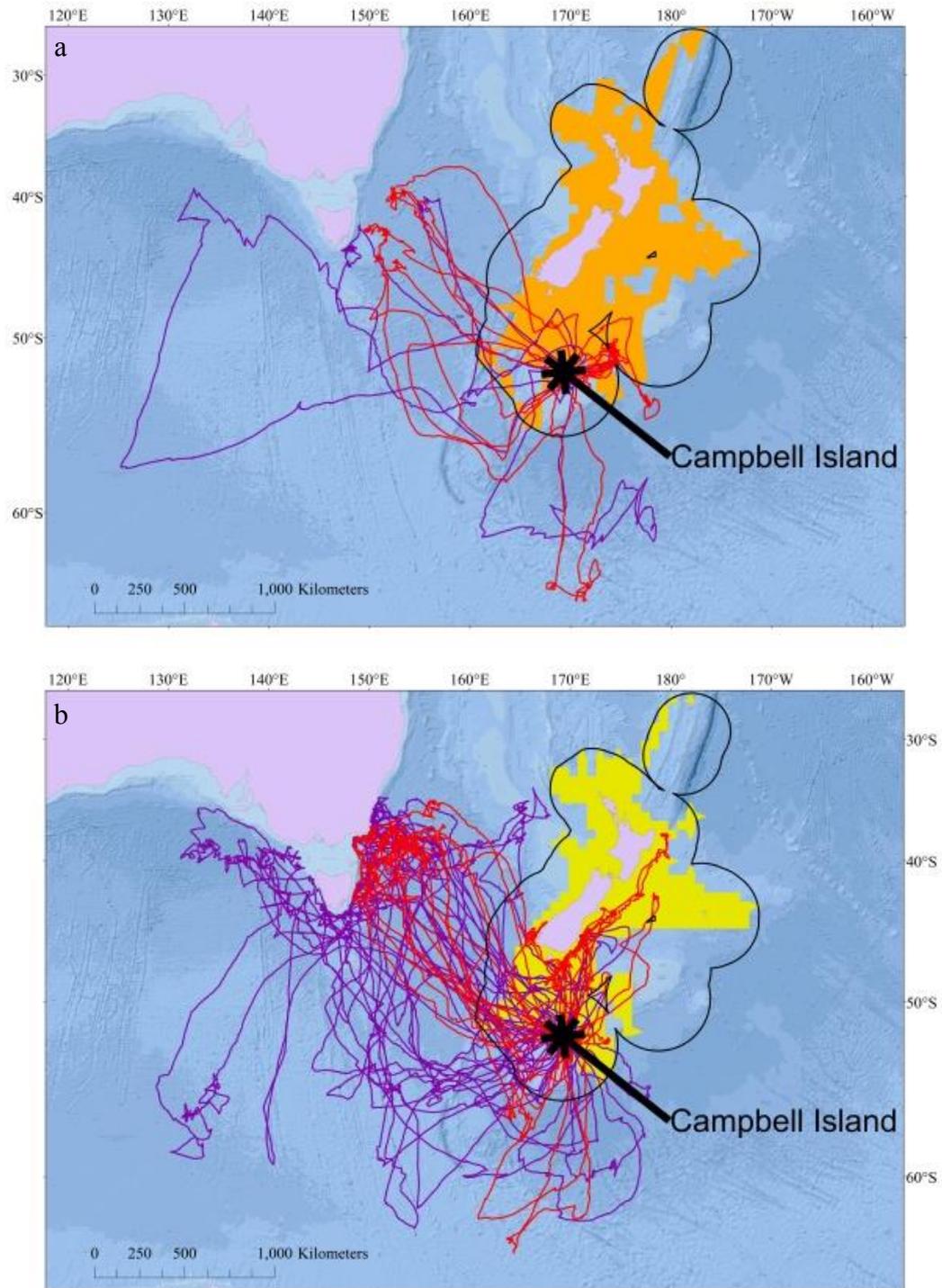
During their foraging trips, the albatrosses used a mean of $3,835.1 \pm 5,930.2$ km² (mean \pm standard deviation; 95% home range) and travelled over distances of $1,577.0 \pm 2,222.5$ km per trip (great-circle distances, see Table 3.1). Albatrosses spent $14,316.1 \pm 46.3$ of the $28,735.4 \pm 114.3$ hours within the EEZ (49.8 %).

3.3.1. Spatial overlap between albatross and fisheries

During the tracking period we found that Campbell albatrosses and vessels spatially overlapped across $8,748.0$ km² within the EEZ when overlaying the full 95% utilisation distributions (pooled data). This represents just 0.20% of the EEZ, mostly in the south (Figure 3.1).

3.3.2. Spatio-temporal overlap between albatross and fisheries

When calculating whether any of this shared space was used during the same time using the temporally explicit 95% utilisation distributions (resolution 1 km²), we found no overlap between vessels and birds despite albatrosses using a total of $8,748.0$ km² within the EEZ (Table 3.1).



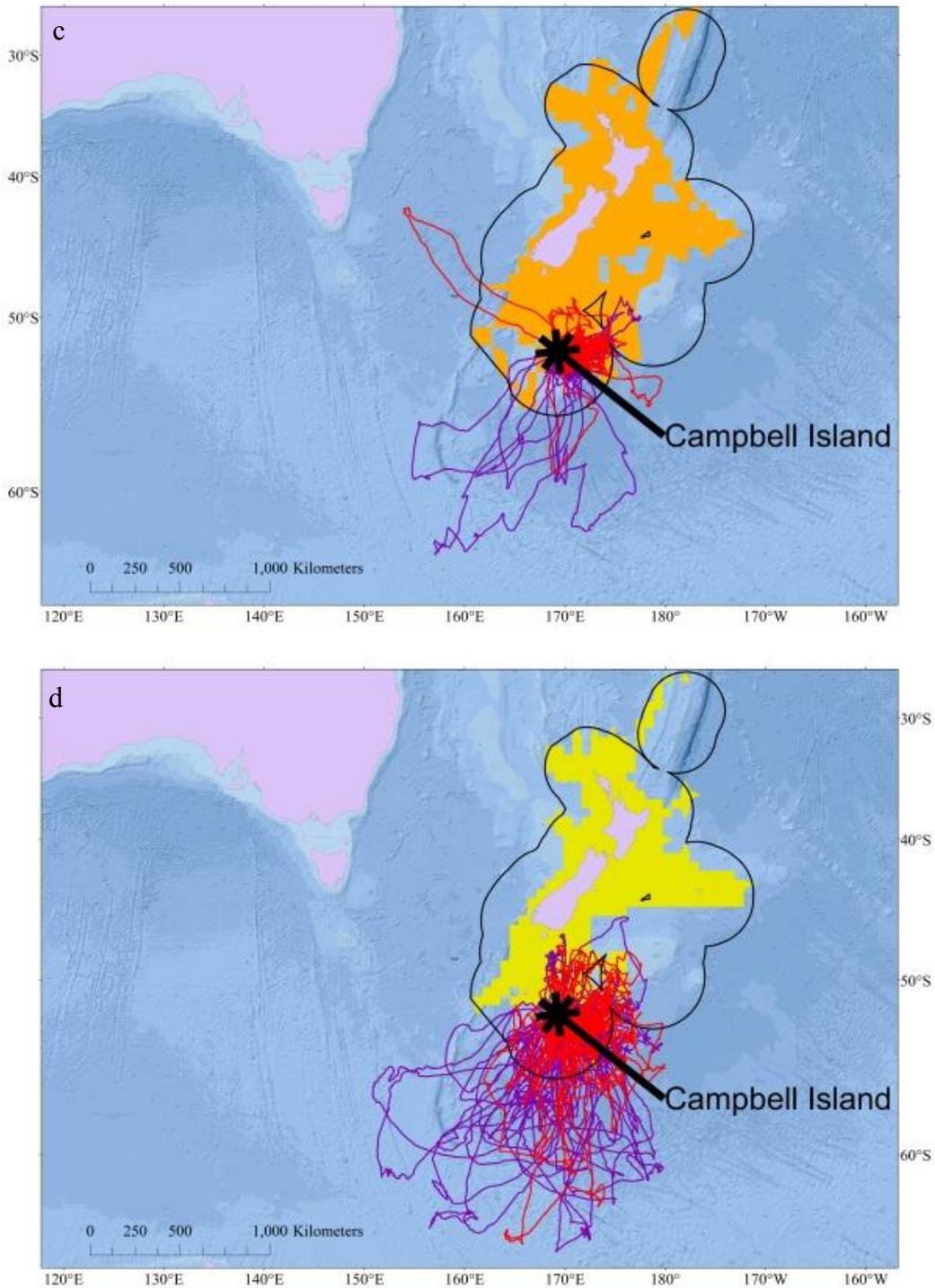


Figure 3.1. Spatial overlap between fishing vessels (2011: orange, 2012: yellow) and foraging trips within New Zealand's Exclusive Economic Zone (black) during: a) incubation in 2011 (n=18), b) incubation in 2012 (n=41), c) chick brooding during 2011 (n=79) and d) chick brooding during 2012 (n=161). Foraging trips were undertaken by females (red) and males (purple). Vessel monitoring data were transformed into a polygon.

Table 3.1. Distance travelled and spatial utilisation (area) per foraging trip (mean \pm standard deviation) for Campbell albatrosses within New Zealand's Exclusive Economic Zone.

Sex	Year	Stage	Number of Trips	Number of Individuals	Area (km ²)	Distance Travelled (km)	Time Inside EEZ (hours)	Time Outside EEZ (hours)
Female	2011	Incubation	12	11	2149.8 \pm 1222.7	2482.3 \pm 1858.5	23.4 \pm 33.5	48.7 \pm 100.2
Female	2012	Incubation	16	13	3048.7 \pm 2618.0	3892.9 \pm 3013.3	55.3 \pm 97.7	152.0 \pm 168.2
Female	2011	Brooding Chick	44	15	1172.7 \pm 737.2	639.4 \pm 602.8	35.1 \pm 19.1	17.0 \pm 28.6
Female	2012	Brooding Chick	80	27	1375.3 \pm 1088.3	843.6 \pm 784.8	23.2 \pm 18.5	15.4 \pm 22.0
Male	2011	Incubation	6	6	1570.7 \pm 870.4	3552.8 \pm 3441.1	25.3 \pm 20.3	166.2 \pm 101.7
Male	2012	Incubation	25	24	2466.5 \pm 1244.7	5558.9 \pm 4159.6	35.5 \pm 55.5	217.9 \pm 165.4
Male	2011	Brooding Chick	35	11	1112.6 \pm 656.5	805.0 \pm 875.9	35.8 \pm 31.9	27.0 \pm 28.5
Male	2012	Brooding	81	27	1372.9 \pm 935.1	1117.3 \pm 973.0	20.5 \pm 16.3	34.5 \pm 31.4

Table 3.2. The effects of sex, breeding stage, and year on the minimum distance between Campbell albatross and fishing vessels using linear mixed-effects models. Models included individual bird as a random effect (to control for repeat samples from the same bird).

Distance Between Albatross and Fishing Vessels (Full Dataset)				Distance Between Albatross and Fishing Vessels (Within 2 hours and ≤ 11 km)			
	DF	F-value	p-value		DF	F-value	p-value
Intercept	17659	3882.03		Intercept	21	23.94	
Sex	79	0.16	0.69	Sex	12	0.38	0.55
Stage	17659	572.41	1	Stage	21	0.019	0.92
Year	17659	6.57	0.01	Year	12	4.73	0.05
Sex*Stage	17659	2.28	0.13				

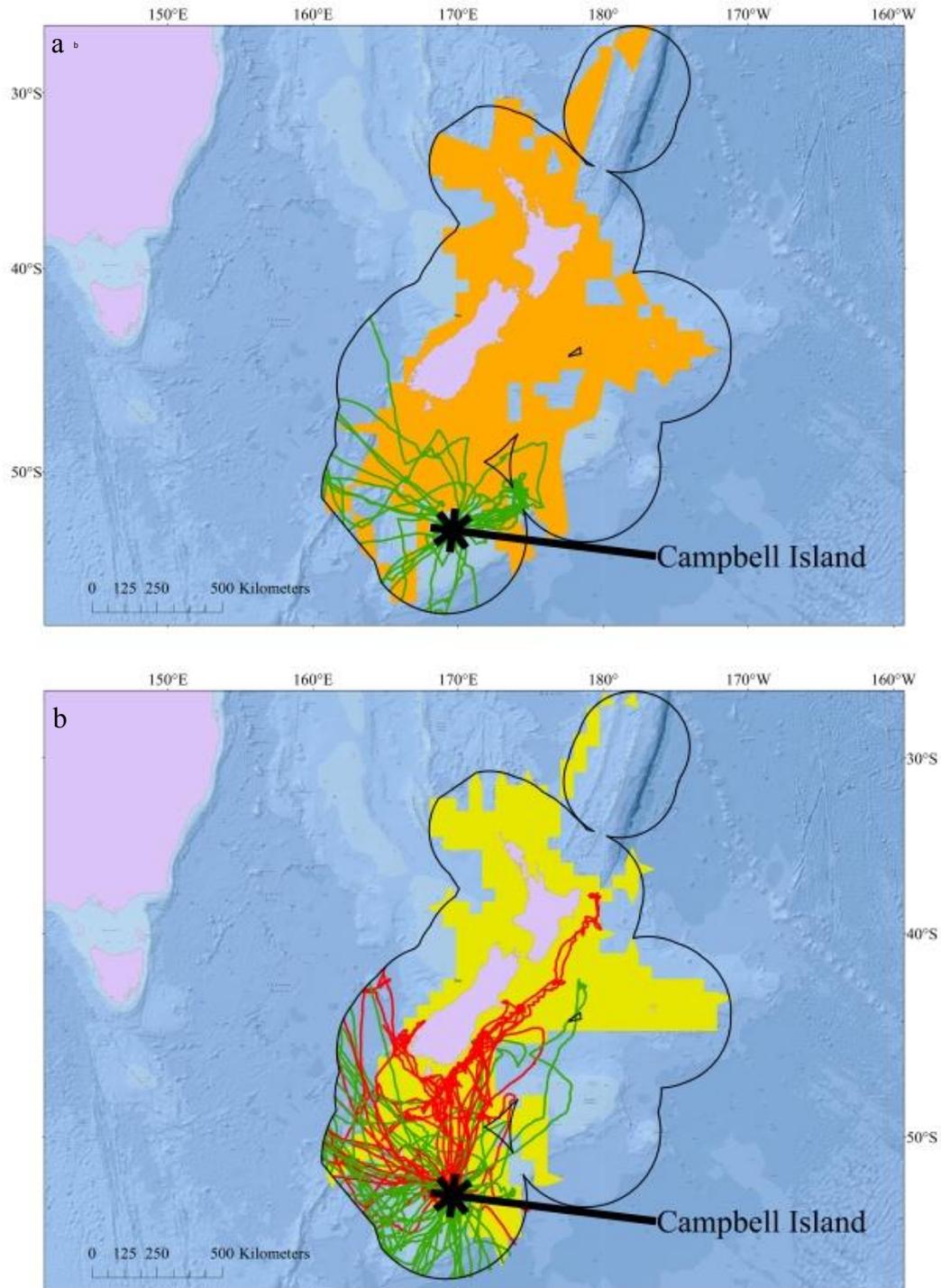
Distance Between Albatross and Fishing Vessels (Within 2 hours and ≤ 30 km)			
	DF	F-value	p-value
Intercept	55	59.39	
Sex	18	1.70	0.21
Stage	55	1.04	0.31
Year	18	0	0.98

3.3.3. Distance between albatross and fishing vessels

Sex, stage and year effects

The minimum distance between GPS-fix locations of albatrosses and fishing vessels on foraging trips was significantly affected by breeding stage and year (Table 3.2).

However, when using all spatial and temporal distances within 11 km and two hours of at least one vessel, albatrosses only overlapped during 17 of the 299 foraging trips (5.7%; Figure 3.2, Table 3.3). These 17 trips were performed by 15 unique individuals that were within 11 km and two hours of multiple vessels (range 1-8 vessels) during a single foraging trip. When considering the 11 km footprint of fishing vessels, year was marginally significant in the subset of foraging trips. All but one of these foraging trips



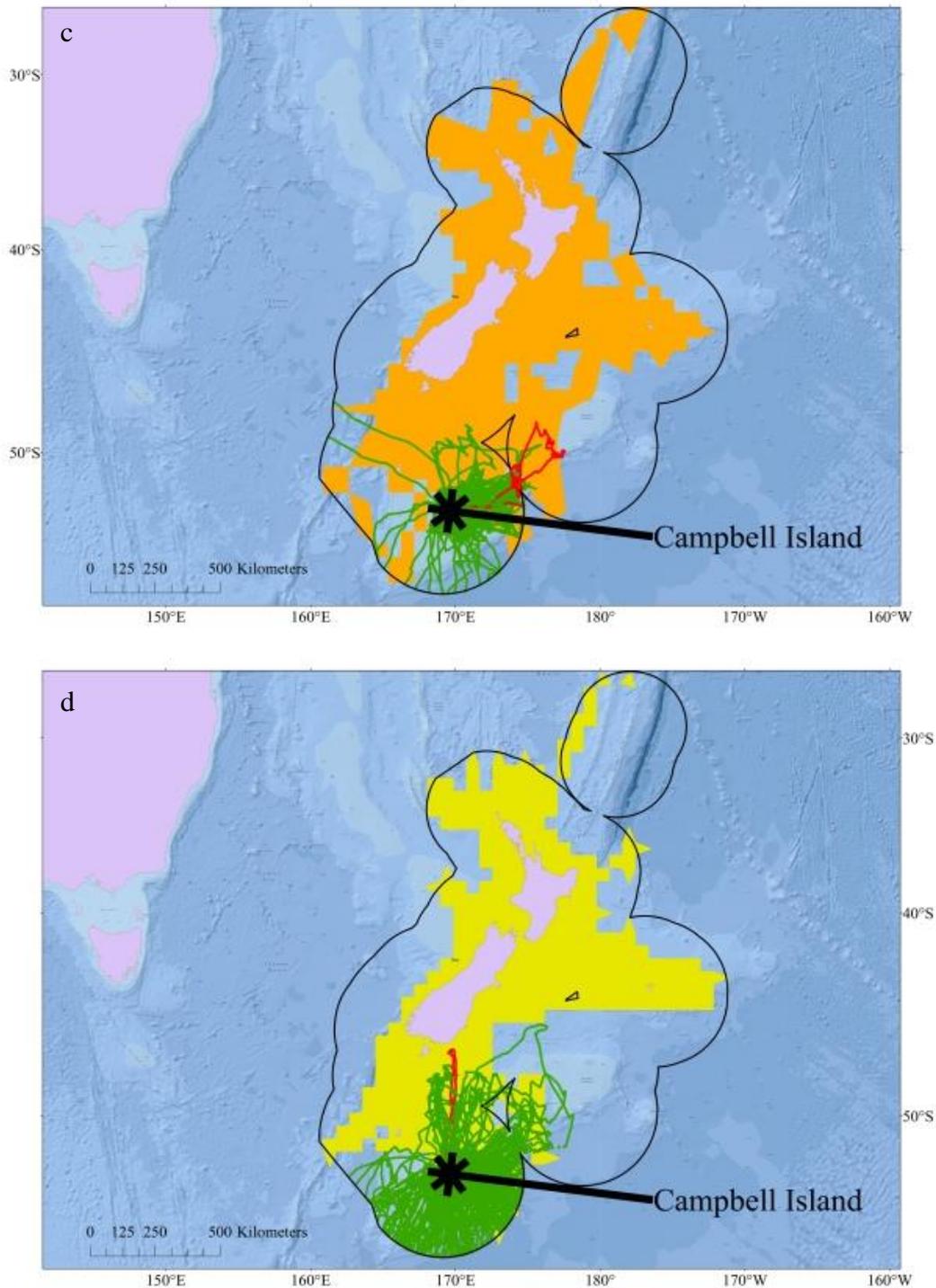


Figure 3.2. Spatio-temporal overlap of fishing vessels and Campbell albatross within the EEZ during a) incubation during 2011, b) incubation during 2012, c) chick brooding during 2011 and d) chick brooding during 2012 within New Zealand's Exclusive Economic Zone (black). Foraging trips (whole track) with locations within 11 km and two hours of fishing vessel location are indicated in red (n=17). All other trips showed no interaction (green; n=282).

Table 3.3. Interaction characteristics of foraging trips within 11 km or 30 km and 2 hours of fishing vessel location

Individual	Foraging Trip	Sex	Stage	Year	Within 11 km and 2 hours			Within 30 km and 2 hours		
					Number of Vessels	Number of Locations	Proportion of Trip	Number of Vessels	Number of Locations	Proportion of Trip
1	1	Female	Incubation	2011	0	0	0	1	7	0.00
2	2	Female	Incubation	2012	0	0	0	4	8	0.00
3	3	Female	Incubation	2012	8	103	0.04	11	232	0.09
3	4	Female	Incubation	2012	6	246	0.14	6	506	0.30
3	5	Female	Chick Brooding	2012	0	0	0	3	6	0.02
4	6	Female	Incubation	2012	0	0	0	3	32	0.02
4	7	Female	Incubation	2012	1	7	0.01	1	18	0.02
5	8	Female	Incubation	2012	1	3	0.00	7	46	0.03
6	9	Female	Incubation	2012	1	2	0.00	1	30	0.01
7	10	Male	Chick Brooding	2011	1	2	0.00	1	11	0.01
8	11	Male	Incubation	2012	0	0	0.00	4	28	0.01
9	12	Male	Incubation	2012	6	962	0.49	7	1274	0.65
10	13	Male	Incubation	2012	1	5	0.01	1	53	0.10
10	14	Male	Chick Brooding	2012	2	17	0.05	3	71	0.20
11	15	Male	Incubation	2012	1	11	0.01	1	20	0.01
12	16	Male	Incubation	2012	1	21	0.01	5	50	0.02
13	17	Male	Chick Brooding	2012	1	39	0.14	1	65	0.23
14	18	Male	Incubation	2012	1	15	0.01	2	32	0.01
15	19	Male	Incubation	2012	1	53	0.02	3	122	0.04
16	20	Male	Incubation	2012	1	1	0.00	1	12	0.00
17	21	Male	Incubation	2012	0	0	0	2	22	0.01

18	22	Male	Incubation	2012	0	0	0	1	5	0.00
19	23	Male	Chick Brooding	2012	0	0	0	1	16	0.04
20	24	Male	Incubation	2012	3	23	0.02	6	107	0.07
21	25	Male	Incubation	2012	1	3	0.00	1	12	0.00

occurred in 2012. Fisheries overlap was most common during incubation (Table 3.3) and while sex had no significant effect, 12 of the 17 foraging trips with fisheries overlap were by males, which may be due to sample size (Table 3.3). When we expanded the footprint to 30 km, albatross foraging behaviour was potentially affected by fishing vessels on 25 foraging trips (8.4%) made by 21 individuals. Eighty percent of those foraging trips occurred during incubation with a sex ratio of 9:16 (female:male). The maximum number of vessels an individual potentially encountered within the 30 km footprint increased from 8 to 11. When testing the larger (30 km) footprint, sex, breeding stage and year were not significantly associated with the minimum distance between albatrosses and fishing vessels.

3.4. Discussion

We provide the first estimate of the degree of association between fisheries and the vulnerable Campbell albatross during the breeding season, using spatial and spatio-temporal overlap. Despite Campbell albatrosses utilising 6.7% of the EEZ, they only overlap with fishing vessels in a remarkably small section in the southern portion of the EEZ (0.20% of the area). Spatial area of overlap between albatross and vessels within the EEZ varied strongly depending upon the assumed vessel footprint and also showed variation by sex, and breeding stage. However we found very limited spatio-temporal overlap suggesting that albatrosses and boats may occupy the same areas, but seldom at the same time. Therefore risk assessments that rely solely on spatial overlap may overestimate interaction rates.

Information on bycatch rates for Campbell albatross are limited, as they were considered a subspecies of black-browed albatross until 1998 (Robertson and Nunn

1998; Sangster et al. 2013); thus bycatch rates prior to 1998 were often a combination of Campbell albatross and black-browed albatross. From 1989 to 1995, bycatch of all species of seabirds ranged from 0-0.6 birds per 1000 hooks in Southern Australia and Tasmania, areas used by Campbell albatrosses; 74% were albatrosses and a high proportion of those were reported as black-browed albatrosses (Gales et al. 1998). When subsamples of these were further examined, 52% were Campbell albatrosses, thus bycatch rates were estimated at 780 Campbell albatrosses per year (Gales et al. 1998). Bycatch rates were, however, higher (up to 1.26 birds per 1000 hooks) in summer than winter and skewed toward juveniles. Murray et al. (1993) reported declines in bycatch from 3662 seabirds in 1988 to 360 seabirds in 1992, suggesting mitigation measures may be reducing bycatch. Alternatively individuals that associate with fishing vessels could have been removed from the population limiting the number of albatross around vessels (Tuck et al. 2015). The most recent at-sea observations indicates that zero to three Campbell albatrosses per year were killed from 2004 to 2011 (Abraham E. R., Thompson F. N). These deaths were associated with fisheries for hoki (*Macruronus novaezelandiae*), arrow squid (*Nototodarus sloanii*, *N. gouldi*), New Zealand scampi and southern blue whiting (*Micromesistius australis*), and occurred outside the incubation and chick brooding stages (Abraham and Thompson 2012). Information is not yet available for our study year, but these low bycatch rates agree well with the low overlap rates and lack of spatio-temporal overlap we have recorded. However during our study period, Campbell albatross spent about half their time foraging within the EEZ; the rest of their foraging takes place in areas without fishing data, mostly the Tasman Sea or Australian waters. Thus our estimates are limited to the trip duration within the EEZ. It does appear that Campbell albatrosses may be more vulnerable to

fisheries related mortality in other regions, and at different ages and breeding stages (Murray et al. 1993; Gales et al. 1998; Waugh et al. 1999a).

There are also a number of factors that may impact the nature of fisheries interactions, including the presence and timing of discards, the use of mitigation measures, weather, inter-species competition and the availability of other resources (Dietrich et al. 2008; Jiménez et al. 2009; Favero et al. 2011; Croxall et al. 2013). On the Patagonia Shelf, the frequency of black-browed albatross-fisheries interactions was associated with wind conditions, season, time of day, and the presence of discards (Favero et al. 2011). Management of discards, such as offal mincing, reducing discharge to sump water, or waste holding/batch discharge, can reduce the abundance of seabirds around fisheries vessels, with concomitant reductions in mortality risk (Abraham et al. 2009; Pierre et al. 2010). Additionally, mitigation measures, such as weighted lines and Tori lines, have reduced bycatch rates and may also deter seabird-fisheries interactions (Løkkeborg 2003; Dietrich et al. 2008). While mitigation measures are becoming common practice, little is known of waste management and the timing of discard release in New Zealand's EEZ. Inter-species competition may also reasonably account for the low interaction rates as albatrosses larger than Campbell's are frequently killed by fishing vessels. For example, larger white-capped albatross (*Thalassarche steadi*) are frequently found behind fishing vessels and may be out-competing Campbell albatross (Bartle 1991; Torres et al. 2011). Annual variation in these factors combined with environmental variation could account for annual influences found in our models.

Research has demonstrated that the influence of fisheries vessels goes beyond the location of the boat itself and that the area of influence of vessels may extend up to 30

km (Bodey et al. 2014; Collet et al. 2015). When accounting for an 11 km ‘footprint’ as determined by Bodey et al. (2014), we found overlap in 5.7% of trips, in most cases lasting less than 10% of the trip within the EEZ. When we expanded this area to 30 km, assuming that Campbell albatrosses may behave like wandering albatrosses (Collet et al. 2015), we found the potential for interactions increased to 8.4% of foraging trips. While sex differences in spatial area overlap and distance between albatross and vessels were present, these differences disappeared when examining the ‘footprint’ affected by fishing activities. We expected females to have a higher risk of fisheries interactions based on time spent in proximity to the New Zealand mainland, and thus fishing activities; female Campbell albatrosses tend to use the Campbell Plateau and slope areas closer to the New Zealand mainland, while males travelled farther south into the Southern Ocean (Chapter 2). But, contrary to our expectations, 12 of the 17 foraging trips with fisheries overlap were by males. When these results are considered together, it suggests that size or social dominance, in addition to habitat use, influences the likelihood of overlapping with fishing vessels.

3.5. Conservation implications

Conservation and management efforts sometime take a multi-species population level approach to risk assessments. Such large scale approaches may use overlaps between global seabird distribution and fisheries activity, informed by additional information such as bycatch rates, and life history traits to highlight areas of concern (Nel et al. 2002; Xavier et al. 2004; Waugh et al. 2012). However, single-species and region-based analyses are also needed for mitigation plans and national policies. At these smaller scales, analysis of spatio-temporal overlap may both improve risk assessments and provide insight into foraging behaviour (Votier et al. 2010; Granadeiro et al. 2011;

Croxall et al. 2013; Torres et al. 2013a; Torres et al. 2013b). Thus, examining overlap at a finer resolution should be added to this ‘toolkit’ and incorporated into the development of management and conservation measures, particularly if dynamic ocean management, in which management areas change in response spatial and temporal alteration in the ocean or species movements to reduce bycatch (Howell et al. 2008; Hobday et al. 2010; Hobday et al. 2014), is evaluated for wide-ranging species.

In the case of breeding Campbell albatross, examining spatial overlap with fisheries may still provide an overestimate of risk if not accounting for temporal components which may be further reduced if behaviour state of the bird is added. During the incubation and chick brooding stages, overlap between fisheries and albatrosses occur in only a small percentage of trips; this may be due to mitigation measures reducing interactions, competition with other species or discard practices. However, as highlighted by Croxall et al. (2013), it is important to understand fisheries interactions at other times of the annual cycle and among other age classes. Current estimates suggest that the population of Campbell albatross is slightly declining or stable (Waugh et al. 1999b; Sagar 2014). If declines continue without an increase in bycatch, other factors such as food availability or environmental change should be assessed. More importantly, conservation and fisheries management for this species needs to occur on a multi-national scale as Campbell albatross spend much of their time foraging outside New Zealand waters.

More broadly, risk assessments should incorporate additional information when and where possible, and the addition of spatio-temporal overlap would be beneficial.

Current conservation practices, such as fixed marine conservation areas are problematic

in the face of environmental change and species with long-distance movements. In a few instances fisheries policies have employed dynamic ocean management. Unlike risk assessments based on distribution overlaps between seabirds and fishing vessel, which are largely static illustrations of distribution and account for only broad temporal change, examinations of fine scale resolution of seabird-fisheries overlaps can provide information on spatial and temporal variation (Torres et al. 2013a; Torres et al. 2013b). Thus, future conservation and management strategies should apply this information into dynamic models, in addition to current mitigation measures, to further reduce bycatch.

**CHAPTER 4: INDIVIDUAL FORAGING
SPECIALISATION OF THE VULNERABLE CAMPBELL
ALBATROSS (*THALASSARCHE IMPAVIDA*) VARIES BY
SEX AND YEAR**

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¹ discussions, editing manuscript; ² statistical advice

Abstract

Consistent inter-individual variations in behavioural traits have important implications for a wide range of evolutionary and ecological processes. Moreover, such differences may lead to variation in the risk of exposure to anthropogenic impacts such as fisheries bycatch. We tested for consistent inter-individual foraging site specialisation in chick-rearing Campbell albatross (*Thalassarche impavida*) – a vulnerable endemic impacted by longline fisheries. Using bird-borne GPS loggers we reconstructed foraging behaviour and analysed six foraging traits (maximum distance from the nest, terminal latitude, terminal longitude, total distance travelled, trip duration, and angle of departure) by studying repeat foraging trips both within and between two years. We

estimated individual foraging site specialisations by calculating metrics averaged across the population, as well as those at the individual level. Overall, Campbell albatrosses demonstrate annual and inter-annual specialisation at both the population and individual level; the degree of specialisation was influenced by sex and year. Individual level analyses revealed that a majority of individuals demonstrated consistent behaviours among successive trips. Consistent terminal latitude and longitude indicated high foraging area fidelity with a degree of flexibility in the fine-scale location. Females, which foraged closer to the colony in neritic and shelf waters, showed more consistent behaviours than males which foraged in pelagic environments. While the drivers of these patterns of habitat use are not fully understood, our results have important implications with respect to exposure to fisheries bycatch and thus are important in marine spatial planning.

4.1. Introduction

The incidence of inter-individual trait variation has important implications for conservation, ecology, and evolutionary processes. Consistent individual variation in foraging behaviour, also referred to as foraging specialisation, can impact on predator-prey interactions, parasitism risk, population and community dynamics and lead to disruptive selection and evolutionary divergence (Darimont et al. 2007; Johnson et al. 2009; Duffy et al. 2010). While intra-population variation in niche width has long been acknowledged (Van Valen 1965; Roughgarden 1972; Roughgarden 1974), its effects on these processes is often ignored. For example, individual-based life history models indicate that population growth rates are overestimated when no account is made of sex-biased mortality, disruption of breeding pairs, or uneven sex ratios (Mills and Ryan 2005).

Individual foraging specialisation has been reported in a wide range of taxa, particularly among marine vertebrates. For example, by 2011, foraging specialisation was documented in at least 28 marine mammals and seabirds, representing 26% of all taxa studied (Araújo et al. 2011). In marine species, individuals have been shown to specialise through studies of their diet (Newsome et al. 2009; Tinker et al. 2012), foraging behaviour (Woo et al. 2008; Torres and Read 2009; Baylis et al. 2012) and isotopic niche (Bearhop et al. 2006; Jaeger et al. 2009; Votier et al. 2010); tactics thought to increase foraging and digestion, the efficiency of which improve with age or experience with specific prey types (Werner et al. 1981; Sutherland and Ens 1987; Woodward and Laverty 1992; Laverty 1994a; Laverty 1994b; Dukas 1995). Individual foraging specialization has also been linked to reproductive success and population dynamics (Pierotti and Annett 1987; Pierotti and Annett 1990; Annett and Pierotti 1999; Votier et al. 2004) and therefore has an important role in conservation (Barbraud et al. 2013). The reasons for the apparently high frequency of individual foraging specialisations in marine vertebrates (Bolnick et al. 2003; Araújo et al. 2011) are unclear, but the predictable nature of large-scale oceanographic features which increase foraging site predictability and food availability (Weimerskirch 2007; Scales et al. 2014) may favour the emergence of specialized foraging strategies.

The methods used to test for foraging specialisation have been varied, making comparison across species or populations difficult. These inconsistencies stem, at least in part, from the type of foraging specialisation under scrutiny (e.g. diet, behaviour, spatial use and isotopic niche) as well as the nature of the data influencing the choice of statistical test (Bolnick et al. 2002; Layman et al. 2007; Nakagawa and Schielzeth 2010). When testing population level specialisation, a commonly used approach is to

generate repeatability estimates (Lessells and Boag 1987; Nakagawa and Schielzeth 2010). Specifically, these repeatability estimates indicate the variation among individuals, rather than within an individual, relative to the population level variance (Sokal and Rohlf 1995), and generates a single population level value for repeatability. This approach is useful in instances when the extent of individual specialisation between different populations is needed. However, because it combines two parameters that describe variation at different scales (i.e. individual and population level variation), it discards important information such as the extent to which an individual is consistent with respect to other individuals in the same population or the distribution of specialisation within a trait or population. When within population comparisons are of interest, such as a measure of individual consistency, then calculation of a metric such as the coefficient of relative plasticity (CRP; Réale and Dingemanse 2010) is preferred. This provides an index of the degree of specialisation for each individual and allows the testing of trait-specific responses (e.g. to determine if sex affects specialisation). Moreover, it provides information on individual variation within the population.

Though repeatability and consistency are similar concepts (uniformity of a behaviour), within this paper we have used repeatability when referring to population level analyses, consistency when discussing individual level results, and specialisation as an overarching term related to both terms and the overall concept within the published literature.

The endemic Campbell albatross (*Thalassarche impavida*) is listed as a vulnerable species due to its restricted breeding range, habitat degradation, and threats associated with fisheries (BirdLife International 2012). Therefore, improving trends in status and

the future prospects of this species requires a more detailed understanding of the way in which Campbell albatrosses use the marine environment and, in particular, how individual specialisation could affect this. The aims of this paper are to test for individual foraging site specialisation measured in two different ways: (1) by calculating an averaged value across the population (i.e. the intra-class coefficient) and, (2) by calculating a true individual level measure (i.e. the coefficient of relative plasticity). Based on fine-scale reconstruction of foraging during the chick brooding period, our goal is to answer two questions: (1) to what extent do Campbell albatross demonstrate individual foraging specialisation at the population level and, (2) does the degree of individual foraging specialisation vary as a function of sex and year at the individual level?

4.2. Methods

4.2.1. Ethics Statement

All scientific procedures and site access were conducted under permit issued by the New Zealand Department of Conservation and was approved by the animal ethics committee at the Plymouth University. Great care was taken to minimise stress to the animals during handling.

4.2.2. Instrumentation and tracking

Chick brooding Campbell albatrosses on Campbell Island, New Zealand (52°32'24"S 169°8'42"E) were temporarily captured and tagged during the 2011/2012 and 2012/2013 breeding seasons (hereafter referred to as 2011 and 2012, respectively). Modified GPS loggers (GT-600 i-gotU, Mobile Action Technology, Taiwan) were attached to the central back feathers of adult albatrosses using Tesa© tape. Modification

involved removing the external plastic housing of each logger then applying heat shrink tubing (FiniShrink, UK) to waterproof each unit. The mass of each GPS unit was ~33 g (~1.1% of body mass) and programmed to record its location every ten minutes (referred to as a 'point' hereafter). Birds were re-captured on the nest following two or more complete foraging trips determined from nest attendance surveys. Examination of loggers and birds on recapture revealed that a few devices had signs of pecking, and some birds had clipped/plucked feathers, but otherwise most devices had been preened into the plumage.

4.2.3. Analysis of tracking data

Foraging trips were reconstructed using the GPS data and six foraging traits were calculated to test for specialisation. These traits were: (1) maximum distance from the nest (km), (2) terminal latitude (decimal degrees), (3) terminal longitude (decimal degrees), (4) total distance travelled (km), (5) trip duration (hours), and (6) angle of departure (degrees). Terminal latitude and longitude was defined as the location at the furthest point from the colony as calculated as a straight line distance. Total distance travelled and trip duration were calculated as the sum of the values from each point-to-point location. Angle of departure (degrees) relative to nest location was calculated for the first 6 data points outside a 1 km buffer distance (North = 0°) and then averaged. This approach accounts for the occurrence of non-foraging behaviours during the first hour of the trip, such as bathing or resting on the water. Furthermore, the colony is located on the eastern side of the island so that a birds' initial angle of departure may not reflect its subsequent flight path.

4.2.4. Metrics of specialisation

Population level repeatability

We estimated an average population level repeatability (i.e. the proportion of variance in a character that occurs among rather than within individuals) for all foraging traits except angle of departure to test the null hypothesis that between-individual variance equals within-individual variance. Angle of departure was not assessed using the following methods due to the presence of circular statistical arguments (see below). Previous studies document sexual segregation in breeding albatrosses (Phillips et al. 2004; Xavier and Croxall 2005; Phillips et al. 2011) and sexual differences in specialisation in several shag species (*Phalacrocorax* spp.; Kato et al. 2000; Cook et al. 2005; Ratcliffe et al. 2013) and black-browed albatrosses (Patrick and Weimerskirch 2014). Thus, to account for possible confounding effects of sex at the individual level, we used sex as a factor within a linear mixed model (LMM) with restricted maximum likelihood (REML) and included the individual as a random factor to account for multiple observations of the same bird. 100 bootstrapping runs were performed (Nakagawa and Schielzeth 2010). All LMM analyses were undertaken using the “rptR” package in R. Traits of foraging behaviour were considered statistically repeatable if p-values were < 0.05 and the degree of specialisation increased as repeatability index values tend toward one.

Calculating angle of departure results in circular measurements, which are incompatible with the LMM method. Thus, we used the mean squares from a circular ANOVA (R package circular) to calculate repeatability, using equations from Lessells and Boag (1987) and Becker (Becker 1984) for standard errors. Circular ANOVAs cannot accommodate additional factors beyond accounting for individuals, and therefore we

cannot adjust for sex differences for angles of departure. P-values cannot be calculated for repeatability from circular statistics. Instead when the range of repeatability values (mean \pm standard error) does not include zero, the spatial foraging trait is considered repeatable. Again, the degree of repeatability increases as values approach one.

Individual level consistency: effects of sex and year

We estimated individual level of specialisation using CRP, which is the variation of the focal individual within a foraging trait (V_i) relative to the variation within the population (V_p) in that trait, i.e. $CRP = V_i/V_p$ (Dingemanse et al. 2010; Réale and Dingemanse 2010). CRP does not account for the number of trips per individual. While this may be problematic in some studies, in most instances our data represent all foraging trips taken by an individual during the chick brooding stage and therefore CRP is representative of the true variation throughout this period. To allow comparisons of specialisation across foraging metrics, CRP values were scaled between zero and one (scaled CRP = $(CRP - \text{minimum})/\text{range}$; minimum value =0, range=10). Once scaled, CRP values below 0.1 indicate that the variance of the focal individual was less than the population variance. The degree of specialisation increases as scaled values approach zero, which is the inverse of the population level repeatability metric.

We modelled scaled CRP values to examine patterns of specialisation within each of the foraging traits, between sex and years. Generalized linear mixed effects models (GLMM) with penalized quasi-likelihood and overdispersed Poisson distributions (glmmPQL; Zuur et al. 2009) were used to test for the effects of sex, year, and the interaction between sex and year on each of the foraging trip metrics. Individual bird identification was used as the random effect to account for individuals tracked in both

years. Full models including the interaction term were examined. If the interaction term was not significant, it was excluded to increase the power of our models to detect differences (Underwood 1996). We did not remove successive terms, as they explain some residual variance within the model (Burnham and Anderson 2002).

Comparing population-level and individual-level foraging specialisation

Finally, we also calculated the Spearman's rank correlation coefficient to compare population level repeatability estimates and individual level mean scaled CRP values.

4.3. Results

4.3.1. Foraging trip summary

Data were collected from 23 birds in 2011 (n=77 foraging trips) and 50 birds in 2012 (n=159 foraging trips), including ten individuals with data in both years (n=59 foraging trips; Figure 4.1). Degree of specialisation was calculated from 2 to 10 trips (Table 4.1). Total trip distances from the colony were, on average, longer in 2012 than 2011, with total trip distances 1517.8 ± 75.1 km in 2012 and 465.1 ± 26.6 km in 2011.

Unsurprisingly, maximum distances travelled from the colony were also greater in 2012 than 2011, with birds travelling 1119.9 ± 106.0 km and 338.0 ± 34.1 km respectively (mean \pm SE). Foraging trips averaged 2.2 days, but ranged from 6.9 hours to 9.9 days. A covariance matrix of foraging traits indicated that maximum distance, total distance, and trip duration traits are positively correlated ($R > 0.7$). However, we chose to include these variables as they provided different behavioural information and can vary independently in some cases.

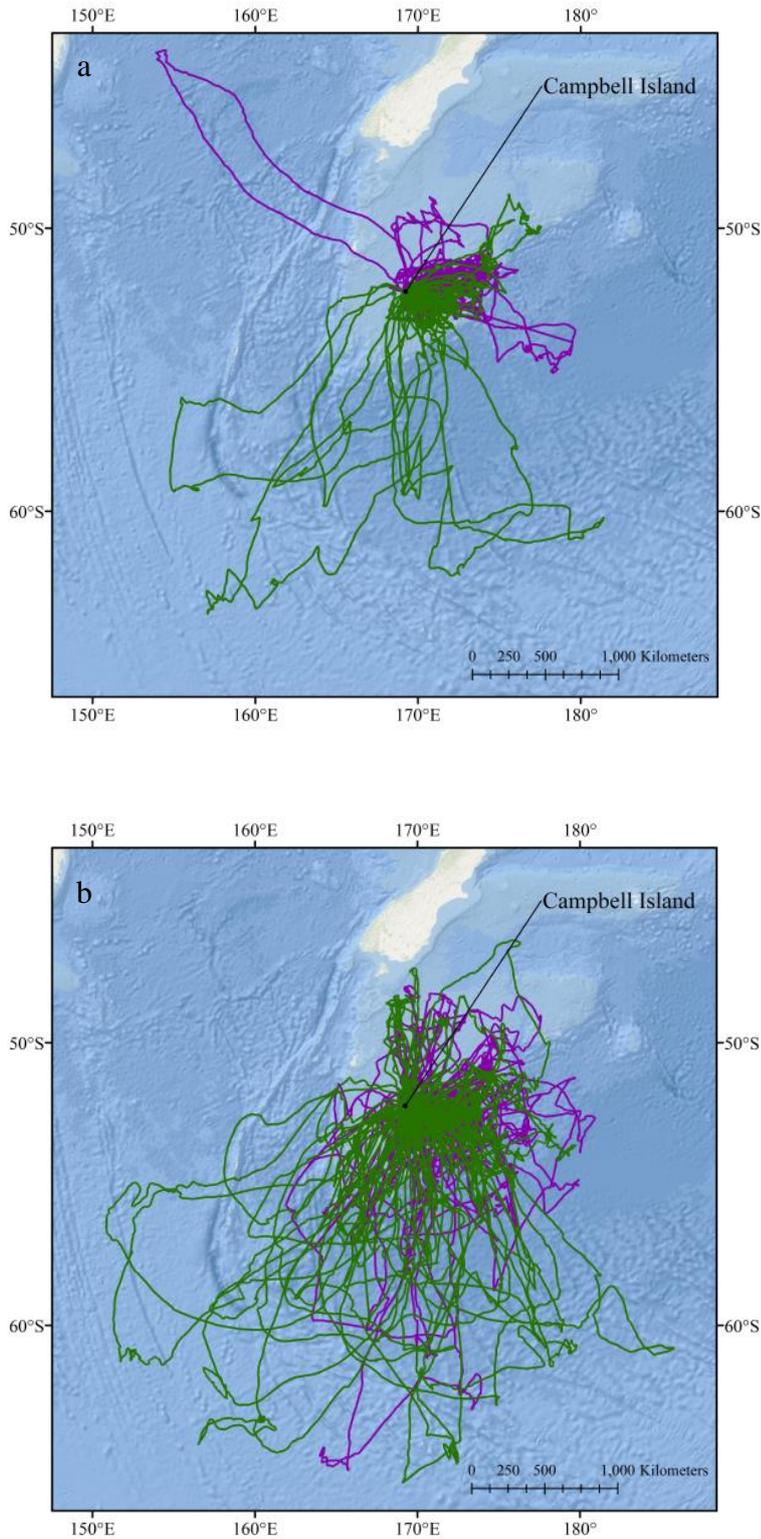


Figure 4.1. Foraging trips from Campbell albatross (*Thalassarche impavida*) (a) Foraging trips from males (green, n=35 foraging trips) and females (purple, n=42 foraging trips) during 2011. (b) Foraging trips from males (green, n=80 foraging trips) and females (purple, n=79 foraging trips) during 2012.

Table 4.1. Number of trips and individuals used for repeatability and coefficient of relative plasticity analyses for each breeding season and across both years.

Number of Trips	Individuals Tracked in 2011	Individuals Tracked in 2012	Individuals Tracked Across Both Years
Two	8	9	
Three	6	24	
Four	4	16	1
Five	3	1	4
Six	2		3
Seven			1
Ten			1

4.3.2. Population level repeatability

Population level repeatability (R_{adj}) for foraging traits ranged from -0.071 (low repeatability) to 0.569 (high repeatability; Table 4.2) within each year, as well as across two years, indicating that Campbell albatross specialise in some foraging behaviours, but not in others. All foraging metrics, with the exception of angle of departure across years, were significantly repeatable (Table 4.2), although there was considerable variation in repeatability (R_{adj}). Several foraging traits were highly repeatable ($R_{adj} \geq 0.3$), including terminal latitude in 2012, terminal longitude in both years, total distance travelled across years, and angle of departure in 2011. All other traits were repeatable, but to a lesser extent ($0.05 < R_{adj} < 0.3$). Angle of departure across years was the only spatial foraging trait where no evidence of repeatability was found.

Table 4.2. Population level repeatability (Radj±Standard Error) foraging behaviour during 2011 (n=23), 2012 (n=50) and for birds tracked in both years (n=10). Repeatability increases as values tend toward one. *p-value<0.05; **p-value<0.001; \$ indicates repeatability based on the absence of zero values.

Trait	2011	2012	Across Years
Maximum Distance	0.234±0.14**	0.295±0.089**	0.271±0.145**
Terminal Latitude	0.27±0.142*	0.434±0.077**	0.137±0.105*
Terminal Longitude	0.487±0.122**	0.569±0.062**	0.361±0.154**
Total Distance Travelled	0.263±0.153**	0.260±0.106**	0.354±0.138**
Trip Duration	0.185±0.134**	0.191±0.117**	0.172±0.126**
Angle of Departure	0.317±0.088 ^{\$}	0.181±0.125 ^{\$}	-0.071±0.062

4.3.3. Individual level consistency: effects of sex and year

When scaled CRP values were averaged, they ranged between 0.044 ± 0.010 (high repeatability) and 0.113 ± 0.048 (low repeatability; Figure 4.2) indicating consistent individual behaviour for several of the foraging traits (i.e. CRP < 0.1). CRP for maximum distance, terminal latitude and trip duration in 2011 were less consistent, as well as inter-annual trip duration and inter-annual angle of departure (scaled CRP > 0.1, Figure 4.2). The most consistent foraging traits were terminal longitude and angle of departure in 2012 (scaled CRP < 0.045).

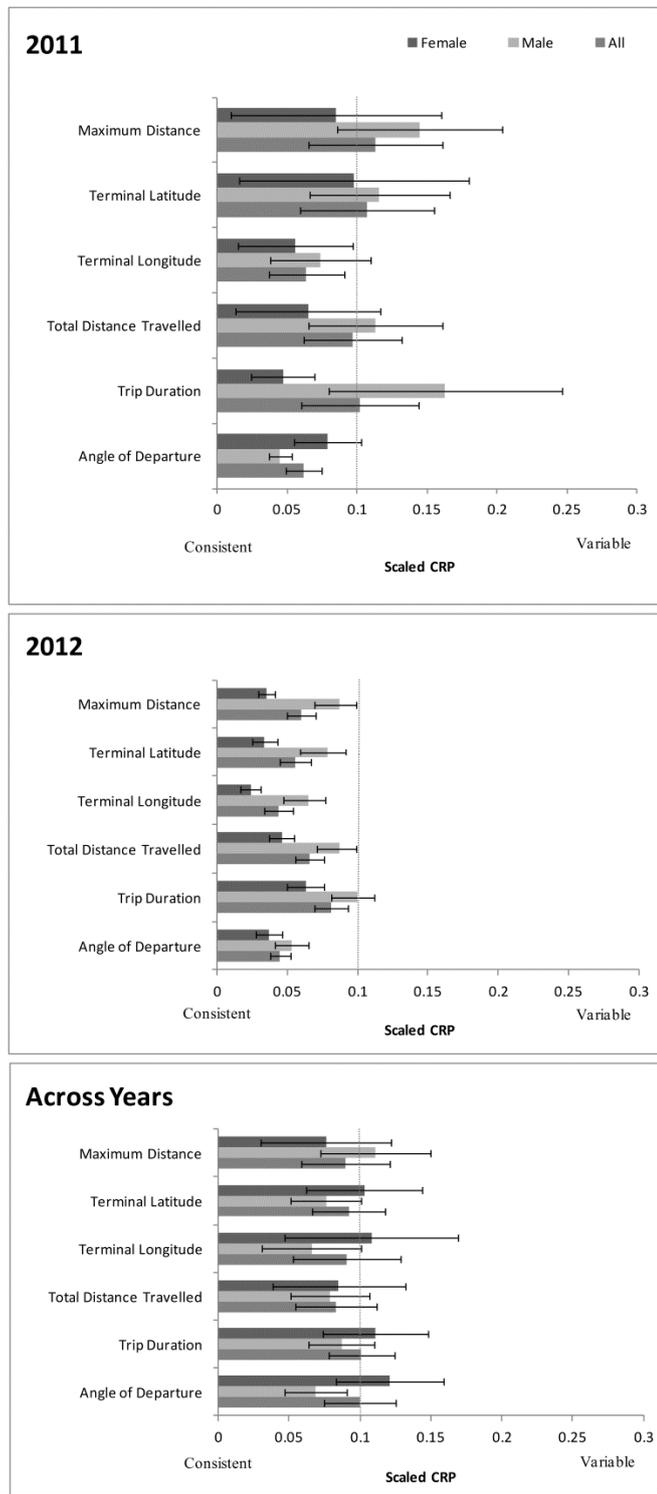


Figure 4.2. Mean \pm Standard Error of scaled coefficient of relative plasticity (CRP; the ratio of individual variance to population variance) for foraging behaviour of Campbell albatross (*Thalassarche impavida*) during 2011, 2012, and for individuals with tracks in both years. Scaled values enable cross trait and year comparisons. Consistent behaviours have values closer to zero and individual and population variation are equal when scaled CRP is 0.1 (dotted line).

There were sex-specific differences in individual foraging consistency for all foraging traits except angle of departure, and a significant effect of year on the consistency of maximum distance, terminal latitude and angle of departure traits (Table 4.3). Female Campbell albatrosses demonstrated the most consistent traits with terminal longitude, terminal latitude, maximum distance, and angle of departure in 2012 all with scaled CRP values of <0.04 . For male Campbell albatrosses, CRP values were higher than females. For example, angle of departure in 2011 and 2012, terminal latitude and longitude in 2012 and all inter-annual metrics except trip duration and maximum distance all had scaled CRP values of < 0.08 . The smallest scaled CRP value for males was 0.045 whereas for females, this value was zero for several individuals and traits indicating that within a given year, female foraging traits tend to be more consistent than males.

Because CRP values have a Poisson distribution, examining mean values may ignore overarching patterns and comparison amongst individuals. Most individuals within the population were consistent in their behaviours (Figure 4.3). Depending on the foraging trait and year examined, between 33 and 83% of females and 17-64% of males showed less than one quarter of the population trait variation. Despite mean values suggesting that Campbell albatross were more consistent in 2012 than 2011, a higher proportion of individuals used less than 25% of the population trait variation in 2011 than 2012. These differences may be related to a few individuals that showed highly variable behaviours (scaled CRP >0.4) in 2011. In 2012, the distribution of consistency was more evenly spread amongst the categories and had a smaller range of scaled CRP values (Figures 4.2 and 4.3).

Table 4.3. Results from generalized linear mixed effects models (glmmPQL with over-dispersed Poisson distributions (log scale)) which tested for the effects of sex, year, and the interaction between sex and year on the scaled coefficient of relative plasticity (CRP) behaviour traits. Individual bird identification was used as the random effect. Parameters with significant p-values are in bold.

Trait	Factor	Value	SE	DF	t-value	p-value
Maximum Distance	Intercept	-2.95	0.30	61	-9.72	0.00
	Sex	0.94	0.34	61	2.80	0.01
	Year	-0.66	0.25	9	-2.62	0.03
Terminal Latitude	Intercept	-2.88	0.32	61	-9.07	0.00
	Sex	0.80	0.36	61	2.24	0.03
	Year	-0.75	0.27	9	-2.73	0.02
Terminal Longitude	Intercept	-3.66	0.32	61	-11.58	0.00
	Sex	0.81	0.35	61	2.29	0.03
	Year	-0.32	0.25	9	-1.27	0.24
Total Distance Travelled	Intercept	-2.98	0.27	61	-10.99	0.00
	Sex	0.81	0.29	61	2.80	0.01
	Year	-0.37	0.23	9	-1.60	0.14
Trip Duration	Intercept	-3.07	0.25	61	-12.15	0.00
	Sex	0.70	0.27	61	2.62	0.01
	Year	-0.03	0.22	9	-0.14	0.89
Angle of Departure	Intercept	-2.94	0.24	61	-12.36	0.00
	Sex	0.16	0.28	61	0.57	0.57
	Year	-0.55	0.21	9	-2.61	0.03

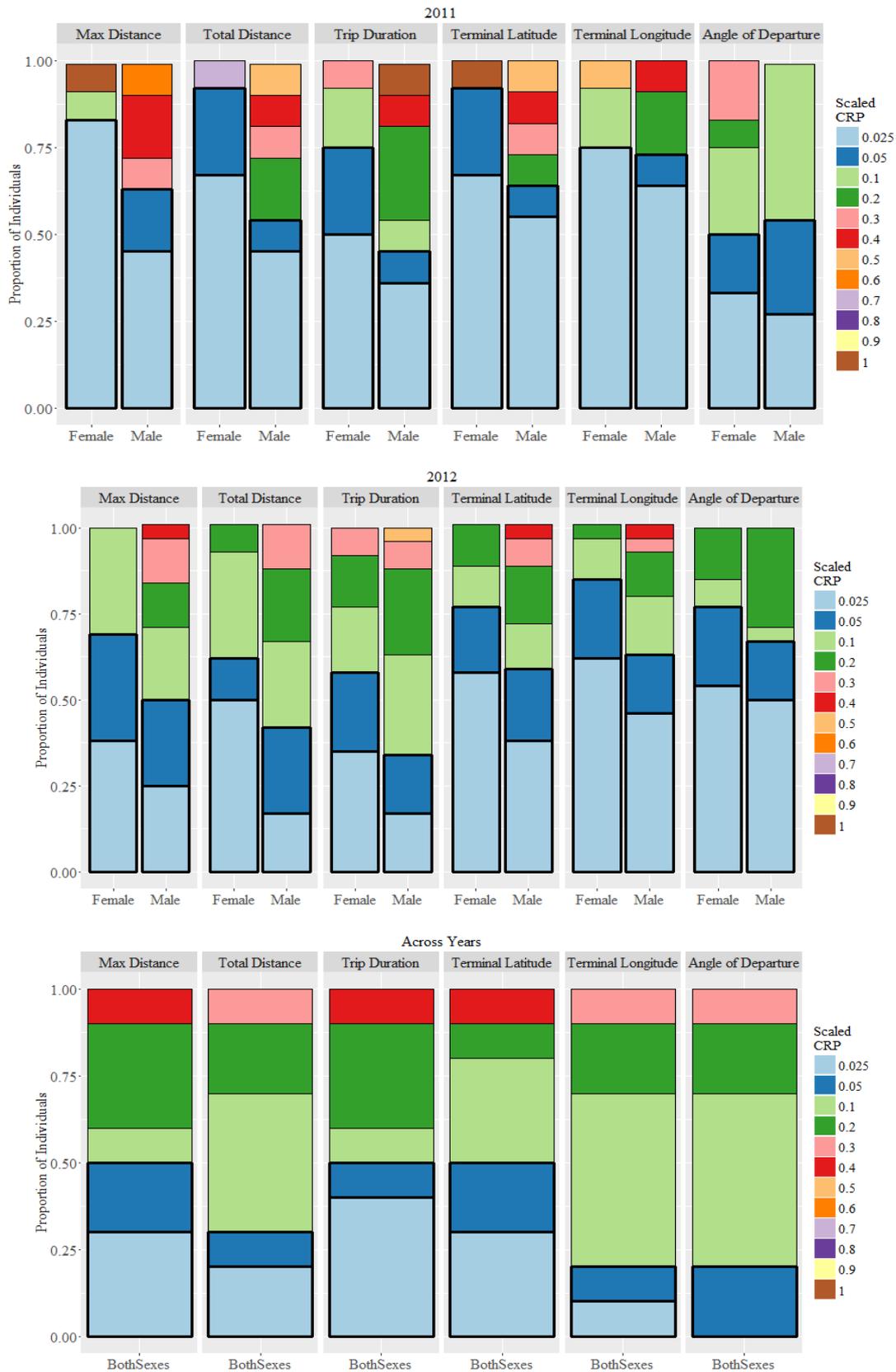


Figure 4.3. Proportion and distribution of individual foraging consistency of females and males in 2011 (n=12 and n=11, respectively) and 2012 (n=26 and n=24,

respectively), and inter-annual values for males and females together (n=10). Individual level specialisation represented coefficient of relative plasticity (CRP; the ratio of individual variance to population variance), scaled for comparisons between years and sexes. Individuals with values < 0.1 (outlined in bold) demonstrate less variation than the population.

4.3.4. Comparing population-level and individual-level foraging specialisation

Campbell albatross demonstrated individual foraging specialisation, but the most specialised foraging traits varied at the population and individual level. Population level repeatability estimates and individual-level scaled CRP were significantly correlated ($\rho = -0.53$, $df=16$, $P < 0.03$). When ranked, the most repeatable foraging traits at the population level ($R_{adj} \geq 0.3$) were terminal latitude in 2012, terminal longitude in all years, inter-annual total distance travelled, and angle of departure in 2011. The most consistent foraging traits at the individual level (CRP < 0.065) were terminal latitude and maximum distance in 2012, terminal longitude and angle of departure in 2011 and 2012.

4.4. Discussion

Behavioural alterations, foraging specialisation, and environmental changes have significant impacts on fitness (Pierotti and Annett 1987; Pierotti and Annett 1990; Annett and Pierotti 1999; Weimerskirch et al. 2012; Patrick and Weimerskirch 2014) and ultimately demography. Thus, a detailed understanding of how individual specialisation alters as a function of sex and year could have important implications for understanding population processes. Campbell albatross appear to be specialised for nearly all the foraging traits measured. The majority of individuals showed < 50% of the population trait variation, suggesting that the population can be broadly described as generalist in terms of foraging location, but with some specialists. However, the degree of specialisation varied by foraging trait, sex and year. Within a given year, female

foraging traits tended to be more consistent than males, but when aggregated across years, male foraging traits were generally more consistent, indicating that temporal scale may influence the degree of specialisation. This may be due to differences in how males and females respond to inter-annual environmental variation.

4.4.1. Sex-specific differences in foraging site specialisation

The degree of specialisation was influenced by sex in five of the six foraging traits. While sexual segregation in foraging habitats and behaviours are associated with niche specialisation, size dimorphism, reproductive role, and competitive exclusion (Phillips et al. 2004; Catry et al. 2006; Phillips et al. 2011), there are few studies investigating how sex affects specialisation (Kato et al. 2000; Cook et al. 2005; Ratcliffe et al. 2013; Patrick and Weimerskirch 2014). As with sex-specific patterns in specialisation in several shag species (Kato et al. 2000; Cook et al. 2005; Ratcliffe et al. 2013), female Campbell albatrosses were more consistent in their foraging behaviours than males. This is in contrast to black-browed albatross which show the opposite pattern (Patrick and Weimerskirch 2014). Factors driving variation in specialisation might include morphology, foraging range or competition (Pianka 1974). In South Georgia shags (*Phalacrocorax georgianus*), a substantial amount of inter-individual variation in dive depth was explained by sexual dimorphism: males were less affected by body mass than females when adopting different foraging strategies (Ratcliffe et al. 2013). Male Campbell albatross are on average 7.2% heavier than females (L. Sztukowski unpublished data), which could affect foraging energetics. Size may, therefore, influence sex-specific foraging specialisation or specialisation may be linked to competition through size dimorphism, reproductive role, or competitive exclusion (Phillips et al. 2004; Catry et al. 2006; Phillips et al. 2011). However, sex-specific

differences in specialisation may also be due to competition, sexual segregation in habitat use, and potential local environmental differences.

4.4.2. Inter-annual variation in foraging site specialisation

We found that the majority of birds demonstrated consistent behaviours and that the degree of specialisation was influenced by year in three of the six foraging traits measured. Most individuals were very consistent in their behaviours across foraging traits, with up to 83% of the population showing less than a quarter of the population trait variation. With the exception of departure angle, mean foraging metrics for Campbell albatross were more consistent during 2012 compared with 2011. These annual differences may be driven by environmental or resource-availability differences that were not measured. We found that specialisation was higher within years than between years for most foraging traits, consistent with the expectation that individual behaviours, like environmental conditions, are likely to be more predictable in the short-term (Catry et al. 1999). However, at the population level, total distance was more repeatable across years than within years. While it is possible that this reflects environmental conditions, total distance may be more influenced by intrinsic feeding rhythms related to chick age, and assimilatory capacity of chicks (Ricklefs 1987; Hamer and Hill 1994; Andersen et al. 1995; Weimerskirch et al. 1997). For example, albatross foraging effort is strongly correlated with stage of the breeding attempt (e.g. (Weimerskirch et al. 1997), which, in turn, is driven by the changing needs of the developing chick.

Highly repeatable terminal latitudes and longitudes indicate that Campbell albatross commute to consistent foraging locations, suggesting that individuals use previous

knowledge to inform foraging decisions. Despite this repeatability on large scales, foraging locations varied both within and between years, indicating a degree of flexibility in fine-scale foraging location. Thus, foraging site fidelity, in conjunction with fine-scale location adjustments within areas associated with predictable resources, may confer consistent energy intake (Bradshaw et al. 2004; Patrick et al. 2014).

4.4.3. Causes of individual foraging site specialisation

While cross-taxa drivers of specialisation have been identified as competition, predation, ecological opportunity, food predictability, and phenotype (see Estes et al. 2003; Bolnick et al. 2003; Araújo et al. 2011), factors that drive and maintain foraging specialisations in marine top predators are still poorly understood. In our study, females remained closer to the colony and demonstrated more consistent foraging behaviours than males. Additionally, during chick-brooding females tended to use neritic/shelf habitats whereas males frequented pelagic waters. This makes it difficult to disentangle the effects of habitat, environmental predictability, sexual segregation, and spatial scale on specialisation. We are left with questions such as (i) Does environmental predictability influence the degree of foraging specialisation? (ii) If species demonstrate sexual segregation, are they likely to show sex-specific trends in specialisation? (iii) How does territoriality or spatial use influence specialisation?

4.4.4. Implications

Whatever the determinants of foraging specialisation, foraging site fidelity and consistent sexual differences in spatial use have significant implications for management and conservation planning. Individuals that demonstrate foraging specialisation have increased fitness and success (Patrick and Weimerskirch 2014), but

any aspect that selectively impacts these individuals, such as fisheries or local environmental changes, could impact disproportionately on population success and alter site fidelity in the long-term. Thus management policies and conservation strategies, such as protected areas, should account for these changes and be reviewed periodically to ensure they meet the stated goals.

Declines in albatross populations, all of which are listed as vulnerable, near threatened, or endangered, have been attributed to changing climate, habitat loss, pollution and disease (Waugh et al. 1999; Lewison and Crowder 2003; Barbraud et al. 2011). But, perhaps the most pervasive threat to albatross is their interaction with fisheries (Gales and Robertson 1998; Anderson et al. 2011). Recent research revealed that threats posed by fisheries bycatch are not uniformly distributed across populations or individuals due to differences in reliance on fisheries waste (Votier et al. 2010; Torres et al. 2011; Barbraud et al. 2013; Torres et al. 2013). Fisheries interaction may also be affected by consistent sexual differences in spatial use. For example, male-biased fisheries mortality has been reported in grey-headed albatrosses (*Thalassarche chrysostoma*; Nel et al. 2002). Individual-based life history models indicate that population growth rates are overestimated when no account is made of sex-biased fisheries mortality, disruption of breeding pairs, or asymmetrical sex ratios (Mills and Ryan 2005). As most conservation policies or reserves do not encompass a population's entire range, they need to consider which segments of the population are most affected and how changes in population structure could affect management and conservation goals.

CHAPTER 5: INDIVIDUAL FORAGING SPECIALISATION IN SEABIRDS: A REVIEW

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Contribution: ¹ Editing and discussion

Abstract

Individual foraging specialisation plays an important role in a wide variety of ecological and evolutionary processes. Such consistent individual behaviours appear common across marine vertebrates, but there has been no systematic review. This review will provide the first synthesis of evidence for individual foraging specialisation among seabirds, and explores the potential drivers and implication of this strategy. Using standard literature searches, we found studies examining foraging specialisation for 34 species of seabird, with 27 (79.4%) providing evidence of consistent inter-individual differences (i.e. specialisation). When split into three parts, 47.1% of species show specialisation in choice of foraging location, 26.5% demonstrated specialised foraging behaviours, and more than half the species showed diet specialisation. Physical processes in the ocean appear to influence productivity, which interacts with previous experience, and competition to influence individual foraging specialisation. Current literature suggests a tentative link between regional area and specialisation; most

evidence of foraging specialisation in seabirds comes from studies conducted between 40° and 60° latitude, where resources are predictable but patchy. However, with limited data in tropical and polar regions, more studies are needed to test links between environmental predictability, competition, and specialisation.

5.1. Introduction

Intrapopulation variation in foraging behaviour has been documented among many animal taxa, and this consistent individual-level variation is thought to play an important role in a wide variety of ecological and evolutionary processes (see Estes et al. 2003; Bolnick et al. 2003; Araújo et al. 2011 for reviews). Individual foraging specialisation occurs when individual niche-width is narrower than the population niche, for reasons independent of age, sex or morphology (Bolnick et al. 2003). Since long-term diet studies are often difficult to obtain, individual foraging specialisation may be determined through proxies. For example, specialisation can be measured via longitudinal studies of foraging site fidelity (Patrick et al. 2014; Wakefield et al. 2014), other elements of foraging such as diving behaviour (Woo et al. 2008), diet (Votier et al. 2004ab, b) or through the analysis of stable isotope ratios in body tissues, which provide an integrated signal of habitat and diet (Bearhop et al. 2006; Inger and Bearhop 2008). While the causes of individual specialization are not fully understood, the primary drivers appear to be a combination of intra- and inter-specific competition, predator-prey interactions, and ecological availability which is influenced by a combination of prey availability, resource predictability and diversity (see Estes et al. 2003; Bolnick et al. 2003; Araújo et al. 2011 for reviews). Moreover, foraging specialisations appear to be more common in animals at higher trophic levels as it is inversely related to predation, suggesting that specialisation may be predicted by trophic

position (Werner and Sherry 1987; Estes et al. 2003; Matthews et al. 2010; Araújo et al. 2011).

Many of the apparent drivers of individual foraging specialisation are likely to influence marine vertebrates, particularly seabirds. These birds come to land to breed and >96% of seabirds breed in colonies (Wittenberger and Hunt 1985). These large aggregations of birds are constrained to return repeatedly to the nest and must therefore feed within a restricted area at sea, leading to high intraspecific competition (Furness and Birkhead 1984; Wakefield et al. 2013), which may favour inter-individual niche differentiation (i.e. Svanbäck and Persson 2004; Svanbäck and Bolnick 2005; Svanbäck and Bolnick 2007; Bolnick et al. 2010). Furthermore, predictable oceanographic processes such as upwelling and frontal activity greatly influence food availability and attract foraging seabirds (Weimerskirch 2007; Scales et al. 2014) – such consistent opportunities may lead to learning and the emergence of specialized foraging strategies. Given these considerations and the fact that many seabirds are close to the top of the marine food web, it is perhaps unsurprising that individual foraging specializations appear common among seabirds - between 2003 and 2010, 107 new examples of foraging specialization were identified in animals and plants; approximately 9% of those were in marine birds (Araújo et al. 2011).

Despite the circumstantial evidence suggesting that individual foraging specialisation may be widespread among seabirds, there has been no formal synthesis of this topic. The aim of the present study is, therefore, to provide the first review of the incidence and implications of individual foraging specialisation among this taxonomic diverse group of birds. An additional question is how physical processes in the sea influence

food and whether this may explain observed patterns in individual foraging behaviour. We examine the available studies to determine whether there are differences in specialisation as a function of latitude and more broadly between tropical, temperate, and polar regions. Inter-individual variation in foraging may also have a variety of consequences for conservation strategies. Top predators such as seabirds are declining sharply (Croxall et al. 2013) and intra-population variation in foraging may play a key role in understanding population changes. Consequently, we will consider the implications of such consistent individual foraging for the seabird conservation.

5.2. Incidence of Individual Foraging Specialisation

To assess the incidence of individual foraging specialisation, we split foraging behaviour into three parts: (1) choice of foraging location, (2) foraging behaviour (e.g. trip or diving parameters), and (3) diet. We used Google scholar to search all publications found prior to November 2014 for studies on seabirds using extensive keyword searches, such as individual foraging specialisation [specialization], intrapopulation variation, behaviour/diet repeatability, individual foraging site fidelity, seabirds. We also make reference to more recent articles on an *ad hoc* basis throughout the text; however they are not incorporated into the analysis or tables (November 2014).

5.2.1. Overall patterns of individual foraging specialisation

Our search returned results from 34 seabird species for which researchers have examined individual foraging specialisation. Of these, 27 (80%) of studies reported clear evidence of individual specialization in at least one aspect of foraging, and seven (20%) species showed no specialisation (Table 1).

Table 5.1. Summary of studies investigating individual foraging specialisation in seabirds. We split foraging into three incidence categories: choice of foraging location (location), foraging behaviour (behaviour), and diet. Method refers to the general methods used by the studies: stable isotope analysis (SIA), conventional dietary assessment techniques (diet sampling), bio-logging/tracking (logging), and other (e.g. avian yolk carotenoid deposition, mercury levels, selective culling).

Species	Common Name	Incidence Category	Specialisation	Method	References
<i>Aptenodytes patagonicus</i>	King penguin	Diet	No	SIA	(Cherel et al. 2007)
<i>Calonectris Diomedea</i>	Cory's shearwaters	Diet	Yes	SIA	(Ceia et al. 2014)
<i>Catharacta antarctica lonnbergi</i>	Brown skua	Diet	Yes	SIA, Diet sampling	(Anderson et al. 2009)
<i>Cephus Columba</i>	Pigeon guillemot	Diet	Yes	Diet sampling	(Golet et al. 2000)
<i>Cerorhinca monocerata</i>	Rhinoceros auklet	Diet	Yes	Other	(Hipfner et al. 2010)
<i>Diomedea exulans</i>	Wandering albatross	Diet, Location	Yes	SIA, Logging	(Weimerskirch et al. 1993; Jaeger et al. 2009; Jaeger et al. 2010; Ceia et al. 2012)
<i>Eudyptes chrysocome filholi</i>	Rockhopper penguin	Diet	No	SIA	(Cherel et al. 2007)
<i>Eudyptes chrysolophus</i>	Macaroni penguin	Location	Yes	SIA, Logging	(Barlow and Croxall 2002; Bearhop et al. 2006; Cherel et al. 2007)
<i>Eudyptula minor</i>	Little penguin	Behaviour	Yes	Logging	(Ropert-Coudert et al. 2003)
<i>Halobaena caerulea</i>	Blue petrel	Diet	No	SIA	(Cherel et al. 2006)
<i>Larus argentatus</i>	Herring gull	Diet	Yes	Diet sampling, Logging	(McCleery and Sibly 1986; Pierotti and Annett 1987; Pierotti and Annett 1991)
<i>Larus occidentalis</i>	Western gull	Diet, Location	Yes	Diet sampling	(Spear 1993; Annett and Pierotti 1999)
<i>Larus michahellis</i>	Yellow-legged gull	Diet	Yes	Diet sampling, Other	(Oro et al. 2005; Sanz-Aguilar et al. 2009)

Species	Common Name	Incidence Category	Specialisation	Method	References
<i>Morus bassanus</i>	Northern gannet	Behaviour, Diet, Location	Yes	Diet sampling, SIA, Logging	(Garthe et al. 2007; Hamer et al. 2007; Pettex et al. 2010; Votier et al. 2010b; Garthe et al. 2011; Soanes et al. 2013; Patrick et al. 2014),
<i>Pachyptila belcheri</i>	Thin-billed prion	Diet	No	SIA	(Cherel et al. 2006; Quillfeldt et al. 2008)
<i>Pachyptila desolata</i>	Antarctic prion	Diet	No	SIA	(Cherel et al. 2006)
<i>Pelecanoides georgicus</i>	South Georgian diving petrel	Diet	No	SIA	(Cherel et al. 2006)
<i>Pelecanoides urinatrix</i>	Common petrel	Diet	Yes	SIA	(Cherel et al. 2006)
<i>Phalacrocorax (atriceps) albiventer</i>	King cormorant	Behaviour	Yes	Logging	(Kato et al. 2000)
<i>Phalacrocorax (atriceps) georgianus</i>	South Georgia shag	Diet	Yes	SIA	(Wanless et al. 1992; Bearhop et al. 2006)
<i>Phalacrocorax (atriceps) verrucosus</i>	Kerguelen shag	Diet	Yes	SIA	(Bearhop et al. 2006)
<i>Phalacrocorax atriceps</i>	Imperial shag	Behaviour, Location	Yes	Logging	(Harris et al. 2014)
<i>Phalacrocorax filamentosus</i>	Japanese cormorant	Location	Yes	Logging	(Ishikawa and Watanuki 2002; Watanuki et al. 2004)
<i>Phalacrocorax melanogenis</i>	Crozet shag	Behaviour, Location	Yes	Logging	(Cook et al. 2005)
<i>Phalacrocorax pelagicus</i>	Pelagic cormorants	Behaviour, Location	Yes	Logging	(Kotzerka et al. 2011)

Species	Common Name	Incidence Category	Specialisation	Method	References
<i>Phalamocorax magellanicus</i>	Rock shag	Location	Yes	Logging	(Quintana 2001)
<i>Procellaria aequinoctialis</i>	White-chinned petrel	Diet, Location	Yes	Logging, SIA	(Catard et al. 2000; Jaeger et al. 2010)
<i>Rissa tridactyla</i>	Black-legged kittiwake	Location	Yes	Logging	(Irons 1998)
<i>Spheniscus magellanicus</i>	Magellanic penguin	Behaviour	Yes	Logging	(Radl and Culik 1999)
<i>Stercorarius skua/Catharacta skua</i>	Great skua	Diet, Location	Yes	Diet sampling, SIA, Logging, Other	(Bearhop et al. 2000; Votier et al. 2004a; Votier et al. 2004b)
<i>Sula sula</i>	Red-footed booby	Location	No	Logging	(Weimerskirch et al. 2005)
<i>Thalassarche cauta</i>	Shy albatross	Behaviour, Location	Yes	Logging	(Hedd et al. 2001)
<i>Thalassarche melanophrys</i>	Black-browed albatross	Location	Yes	SIA, Logging	(Phillips et al. 2005; Granadeiro et al. 2013; Patrick and Weimerskirch 2014)
<i>Uria lomvia</i>	Brünnich's guillemot or Thick-billed murre	Behaviour, Diet, Location	Yes	Diet sampling, SIA, Logging	(Mehlum et al. 2001; Woo et al. 2008; Elliott et al. 2008)

5.2.2. Foraging location

Specialising in foraging location (also referred to as foraging site fidelity or individual site fidelity in the literature) may influence foraging behaviour and diet consistency as well as life history traits. Foraging site fidelity has been found among a range of different taxa including several species of shag (*Phalacrocorax sp.*, Quintana 2001; Sapoznikow and Quintana 2003; Quintana et al. 2004; Watanuki et al. 2004; Cook et al. 2005; Michalik et al. 2013), black-legged kittiwakes (*Rissa tridactyla*, Irons 1998), common murrelets (*Uria aalge*, Regular et al. 2013), and northern gannets (*Morus bassanus*, Patrick et al. 2014; Table 5.1). Overall, fidelity to either general habitats or particular foraging sites was documented in 47.1% of all species studied (Table 5.1). Additionally, some individuals follow very similar routes during repeat foraging tracks, which may indicate an ability to predict the spatio-temporal distribution of prey (Pettex et al. 2010; Patrick et al. 2014). Studies have also suggested that there may be some fidelity to migration route and over-wintering locations (Croxall et al. 2005; Chérel et al. 2007); while this differs from foraging specialisation, it suggests that using known areas may be beneficial regardless of season.

While foraging site fidelity appears common, it may vary with scale, year, species, or study. Red-footed boobies, *Sula sula*, showed no site fidelity, adjusting foraging to the most productive zones during repeat trips (Weimerskirch et al. 2005), whereas Japanese cormorants (*Phalacrocorax filamentosus*) demonstrated site fidelity in some years but not others (Ishikawa and Watanuki 2002; Watanuki et al. 2004). Site fidelity may also vary in the scale examined and the definition used. For example, the site fidelity of black-legged kittiwakes to defined foraging sites where the scale varied by strength of the transmitters and the height that birds flew (Irons 1998) whereas Brünnich's

guillemots (*Uria lomvia*) were show site fidelity on the spatial scale of 1-20 km (Mehlum et al. 2001). Moreover, while a number of studies show site fidelity among northern gannets (Pettex et al. 2010; Patrick et al. 2014; Wakefield et al. 2014) when measured at the 50% kernel density of foraging areas, site fidelity appears low (Soanes et al. 2013). Therefore it is clear the differences in the degree of foraging site specialisation may vary both in terms of the scale and methods used.

The reasons for such a high degree of site fidelity are unclear, but they likely related to the predictability of food in the marine environment. Many seabirds respond to the patchiness yet predictability of marine resources (Weimerskirch 2007; Scales et al. 2014). Seabirds in temperate and polar regions frequently commute to known foraging areas which coincide with enhanced predictable, productivity zones, such as shelf edges, frontal zones, upwellings. In contrast, at least four tropical species showed low site fidelity or irregular commuting behaviour, instead using looping strategies associated with sparse prey densities and low predictability (Weimerskirch 2007) These physical features and processes occur at hierarchical scales driving predator densities, competition and thus specialisation (see Oceanography section below).

5.2.3. Foraging behaviour

Seabirds have morphological and physiological adaptations to exploit food resources based on prey behaviour such as bill morphology and physiological traits, which in-turn affects individual foraging behaviour (Schreiber and Burger 2001). Specialisation in feeding behaviour was found in 26.5% species. Definitions of foraging behaviour vary by study but include dive profiles, fidelity to specific depth ranges, search patterns, and trip parameters (departure angles, distance, range, duration, speed, time in flight, speed).

These behaviours are frequently, but not always, linked to foraging location or diet. While studies on shags, murres and gannets frequently link dive behaviour, activity patterns, and trip metrics with site location, other studies have found individuals that were consistent in foraging direction, distance and/or time spent foraging but vary their core foraging sites (Table 5.1). For example, shy albatrosses (*Thalassarche cauta*) maintained a constant heading from the colony but varied their core foraging sites (Hedd et al. 2001). Additionally, the proportion of the population that exhibits consistent behaviours and the degree of specialisation may change with behavioural trait and temporal scale measured. Campbell albatross (*Thalassarche impavida*), for example, demonstrated higher repeatability in total distance travelled than trip duration or departure angle (Chapter 4). The degree of specialisation varied by sex and year as well as showing higher specialisation within years than between years for most foraging traits.

Consistent behaviours may relate to preferred diet as foraging strategies change in relation to prey (Garthe et al. 2011). Dive depth and location are often used to infer diet differences. For example, thick-billed murres (*Uria lomvia*) demonstrate foraging strategies adapted to specific prey types, with individual specialisation in flight time, dive depth, and dive shape resulting in difference in diet (Woo et al. 2008; Elliott et al. 2008).

5.2.4. Diet

Overall, more than half of the species studied showed dietary specialisation (61.8%, Table 5.1). Six long-term studies (2-15 years of data) documented specific prey types and many of these are linked with reproductive success and survival suggesting an

adaptive advantage of specialisation (Pierotti and Annett 1987; Pierotti and Annett 1991; Annett and Pierotti 1999; Golet et al. 2000; Votier et al. 2004a; Votier et al. 2004b; Patrick and Weimerskirch 2014; see Fitness section below). Additionally, studies show that even if only a small portion of the population are specialist predators, they can exert a significant top-down effect on prey populations (Votier et al. 2004b).

The majority of studies examining diet consistency employed stable isotope analysis (15 of 21 species, Table 5.1), with specialisation indicated by variation in isotopic niche and a correlation between carbon and nitrogen signatures of tissue types with different turnover times (Hobson and Clark 1992a; Hobson and Clark 1993). Isotopic signatures provide a combined indication of both diet and habitat use (Hobson et al. 1994; Cherel and Hobson 2007), such that it may not always be possible to differentiate between the two. Some caution is required when examining isotopic variation as some prey items or spatial areas may have similar signatures, and thus underestimate differences in diets and habitat use. This technique is attractive, however, because it is repeatable, relatively non-invasive, and inference can be drawn from tissues with different turnover rates in a single sampling event (Hobson and Clark 1992a; Hobson and Clark 1992b; Hobson and Clark 1993; Bearhop et al. 2004). Stable isotope analysis can also provide information on behaviour during both breeding and non-breeding seasons; for example, isotopic signatures of wandering albatross (*Diomedea exulans*) demonstrate short-term consistency trophic level as well as long-term consistency in habitat use (Jaeger et al. 2009; Ceia et al. 2012). In six species, stable isotope analysis has indicated a lack of specialisation: four species were examined the non-breeding period when niche width expands (Cherel et al. 2006); one species-king penguin *Aptenodytes patagonicus* - examined values during the beginning of moult/reproductive cycle when no chicks were

present (Cherel et al. 2007); and one species-rockhopper penguin *Eudyptes chrysocome filholi* - had identical values to a sympatric species thus inter-specific competition may have limited specialisation (Cherel et al. 2007).

Combining stable isotope analysis with conventional diet studies and other approaches proves to be a powerful tool to address individual foraging specialisation as well as other research and conservation goals (e.g. Bearhop et al. 2001; Votier et al. 2010b). The use of both conventional diet sampling, stable isotope analysis and tracking has highlighted that some individuals specialise in fisheries discards (Votier et al. 2010a; Patrick et al. 2015).

5.2.5. Breeding vs. Non-breeding

Most species in this review (58.8%) were studied during the breeding season. Only nine species (26.4%) were examined during both breeding and non-breeding seasons and five species (14.7%) during the non-breeding season, most studies rely on stable isotope analysis to infer movement and diet during this period. All, but one, species examined during the non-breeding season showed no specialisation. However some of species studied during breeding and non-breeding, did show specialisation during the non-breeding season.

The energy requirements and constraints on seabirds differ between breeding and non-breeding seasons. Whilst breeding, individuals are central-place foragers with a limited foraging range, as they need to return to the nest to switch with their partner and/or feed young. Furthermore, the increased density of predators around the colony affects competition (Furness and Birkhead 1984; Wakefield et al. 2013), which would likely

influence the degree of specialisation. Cherel and others (2007) demonstrated that the variation in diet and habitat of five sympatric penguins and fur seals increased during the non-breeding season. Similarly, White-chinned petrels, *Procellaria aequinoctialis*, demonstrated specialisation during the breeding season that was lacking during the non-breeding season (Jaeger et al. 2010). Nevertheless, several seabird species show site fidelity during the non-breeding season (e.g. black-browed albatross and wandering albatross; Phillips et al. 2005; Jaeger et al. 2009; Ceia et al. 2012) – although it is not clear to what extent this leads to consistent differences in foraging behaviour. This hints that specialisation may still occur during non-breeding periods, although further work is required to understand foraging location, feeding behaviour and diet during this important part of the annual cycle.

5.2.6. Regional and Latitude Differences

To examine regional patterns, we constructed a table of the number of species and locations with information on specialisation (Table 5.2). When we looked at latitude, 87% of studies occurred at colonies located between 23.5° and 60° (temperate), with 11% in latitudes above 60° (polar) and 2% between latitudes 0° and 23.5° (tropical). Whether the limited data in the tropical and polar regions are due to a lack of specialisation, limited study, or an absence of specialisation is unclear. Due to the skewed nature of the data, we did not statistically test the association between specialisation and region or latitude. (See Oceanography and specialisation).

Table 5.2. Percentage and total number of species and locations with results on specialisation of seabirds occurring in tropical (latitude < 23.5°), temperate (23.5-60°) and polar regions (>60°). Note that species may be counted more than once if study colonies are in multiple regions.

Region	Specialisation Found (%)	Specialisation Not Found (%)	Total (n)
Tropical	0	100	1
Temperate	78.7	21.2	47
Polar	100	0	6

5.3. Implications of foraging specialisation

5.3.1. Fitness

Individual foraging specialisations have been shown to be adaptive; for example, successfully breeding black-browed albatross had narrower niche widths than unsuccessful individuals, (Patrick and Weimerskirch 2014). Individual foraging specialisation has also been linked to increased reproductive success and chick health in some, but not all, cases; the results may depend on prey composition or distance from foraging resources, as reproductive performance has been linked to lipid content, prey size, and species composition (Golet et al. 2000; Litzow et al. 2002; Wanless et al. 2005). For example, the location of great skua (*Stercorarius skua*) territories may influence specialisation in seabird prey, which has been linked to earlier hatch dates, larger clutch volumes and improved chick condition (Votier et al. 2004a; Votier et al. 2004b). In herring gulls (*Larus argentatus*), individuals with a diet based on intertidal animals laid eggs earlier, produced larger and heavier clutches, and had higher rates of hatching, however generalists and specialists on other food sources had similar breeding performance to one another (Pierotti and Annett 1991). These conflicting results may reflect the quality of each individual's diet, their foraging efficiency, and the interaction of the diets provided by both parents. It is clear therefore that more research is needed to

understand better the fitness consequences of individual foraging specialisation in seabirds.

5.3.2. Conservation

Population declines of numerous seabirds are attributed to fisheries-related mortality (Weimerskirch et al. 1997; Lewison et al. 2004; Rolland et al. 2010; Anderson et al. 2011), although such incidental by-catch may vary greatly by both sex and age (e.g. Ryan 1999, Mills & Ryan 2005). The risk of fisheries-related mortality may also be increased in some individuals if they consistently forage more extensively on discards than others (Votier et al. 2010b). Population models suggest that inter-individual variation in bycatch risk are directly linked with differences in survival probability and moreover that such individuals may have been removed from the population which may have significant phenotypic and population consequences (Barbraud et al. 2013; Tuck et al. 2015). Thus, the removal of those individuals specialised in foraging near fisheries vessels may shift selection to those individuals less likely to attend them or alter population growth, which may be overestimated when sex-biased mortality, disruption of breeding pairs, or uneven sex ratios are not taken into account (Mills and Ryan 2005; Tuck et al. 2015). However some species that forage around fishing boats do not specialise on discards, even if they are known to show other specialisations. For example, while black-browed albatross demonstrate site fidelity and increased reproductive success with specialisation, individuals did not specialise in fisheries discards (Granadeiro et al. 2013; Patrick and Weimerskirch 2014). Thus, each species of concern must be evaluated separately to assess the risks and impacts, but including individual heterogeneity and spatial components in conservation and management plans are important.

Research has documented changes in reproductive success and species distribution associated with alterations in environmental factors, such as sea ice and upwelling zones, and the associated changes in prey distribution and abundance (e.g. Fraser et al. 1992; Suryan et al. 2000; Forcada and Trathan 2009; Surman and Nicholson 2009). Since individual foraging specialization has also been linked to reproductive output (e.g. gulls: Pierotti and Annett 1987; Pierotti and Annett 1990; Annett and Pierotti 1999), we might expect long-term trends and changes in physical features to affect individual foraging specialization through reduced foraging efficiency and the need to switch primary prey species. For example, increases in reproductive success and adult mass of wandering albatross were linked to changes in wind and current conditions as environmental conditions increased foraging efficiency; however decreases in reproductive success and survival are expected if trends continue as foraging areas become less accessible (Weimerskirch et al. 2012). Thus, environmental changes in wind or oceanographic features could alter individual foraging tactics based on phenotypic traits (e.g. body size), competition, or prey availability. Gannets for example, demonstrate individual-based changes in search intensity under different environmental conditions (Patrick et al. 2014). This may alter life history traits as foraging effort changes, but predicting how seabird populations respond to future changes will require understanding the plasticity of individuals within the populations and the mechanisms affecting specialization within the marine environment.

An understanding of individual foraging specialisation is also important with respect to inter-specific interactions. For example, great skuas are major consumers of other seabirds and research has shown that some pairs specialize as seabird predators (Votier et al. 2004b) and, while these represent a small proportion of the population, they

consume a disproportionately large number of birds (Votier et al. 2004a). From a management perspective, control of such specialised predatory skuas could minimise their impact on prey populations, although it is unclear whether conspecifics may replace them, maintaining the high predation pressure (Votier et al. 2004a). Such specialisations also have relevance for other generalist predators like gulls, where studies hint at the effectiveness of removing a small number of highly predatory individuals. In Spain, the experimental removal of a small number of yellow-legged gulls (*Larus michahellis*) that specialise in feeding on European storm-petrels (*Hydrobates pelagicus*), has led to a significant reduction in predation with concomitant increase in storm-petrel demographics (Sanz-Aguilar et al. 2009). In these examples, management strategies that ignored such strong intra-population variation would be unlikely to achieve the desired reduction in predation pressure.

5.4. Discussion

Based on the available studies, individual foraging specialisation appears to be a common strategy among seabirds. Competition, prey availability, and resource predictability and diversity may all be influenced by oceanographic conditions that select for specialisation. Additionally, many seabirds show deferred sexual maturity (Weimerskirch 2002) and increased reproductive success with experience, which is attributed, at least in part, to learning and improving foraging efficiency which may be linked to specialisation (e.g. Greig et al. 1983; Weimerskirch 1990; Limmer and Becker 2010).

5.4.1. Oceanography

In the sea, food availability varies at a range of temporal and spatial scales with consequences for foraging among marine vertebrates (Palacios and Martin 2006; Yen et al. 2006), and ultimately foraging specialisations. Physical processes occur at hierarchical scales, ranging from tidal fronts at submesoscales (100 m-10 km) and may last hours or days, to mesoscale processes (10-1000 km), such as upwellings, eddies, currents and ocean fronts, which alter on the order of months, years or centuries (Haury et al. 1978; Hunt Jr et al. 1987). These oceanographic features can lead to conditions that increase levels of primary productivity, with bottom-up consequences for processes leading to an abundance of zooplankton and forage fish – food for higher trophic levels. For this reason, many seabirds forage at tidal fluctuations and fronts, eddies, bathymetric gradients, water mass boundaries and upwelling plumes (Holligan 1981; Owen 1981; Le Fevre 1986; Hunt Jr et al. 1987; Fiedler et al. 1998; Hunt Jr et al. 1998; Hunt Jr et al. 1999; Bost et al. 2009). An example is black-legged kittiwake which is known to associate with tidal fronts, suggesting that tidal features provide predictable foraging resources (Irons 1998). Thus, oceanographic features may produce predictable foraging resources that lead to increased predator densities and may facilitate specialisation through competition.

Competition is one of the primary drivers of foraging specialisation and may be influenced by persistent oceanographic features. Studies on fish and sea otters have shown an increase in specialisation when either population density increase or when resource abundance decreases as a result of increased competition (Svanbäck and Persson 2004; Svanbäck and Bolnick 2007; Svanbäck et al. 2008; Tinker et al. 2008; Svanbäck and Persson 2009; Yeakel et al. 2009; Svanbäck et al. 2011). Large predator

aggregations due to physical forcing (Gende and Sigler 2006; Yen et al. 2006; Scales et al. 2014) occur at persistent oceanographic features over predictable temporal scales. This results in increased competition at these predictable, productive areas suggesting a link between resource predictability and specialisation. These hierarchical scales of resource predictability are also evident in the degree of site fidelity found in seabirds (Weimerskirch 2007) supporting links between resource predictability and specialisation.

Tropical areas of the oceans are thought to be low productivity, less structured environment resulting in less predictable resources (Weimerskirch 2007). By contrast, high latitude waters tend to be characterised by patchy yet predictable resources influenced by oceanographic features. As a result, seabirds in the tropics use different foraging tactics, such as frequently foraging in flocks associated with underwater predators like tuna, than seabirds in higher latitudes (Ballance and Pitman 1999; Weimerskirch 2007). These behavioural differences along with the resource poor, low productivity environment (Cherel et al. 2008) suggest that the drivers of individual foraging specialisation in the tropics may be different from those at higher latitudes and individuals may forage more opportunistically.

If we note the pattern of specialisation (Table 2) and resource predictability, we find: (1) a high frequency of specialisation in temperate areas and 100% occurrence in studies conducted in polar regions; both of which are characterised by temporal and spatial predictability and (2) a lack of specialisation in the tropics-an area thought to be resource poor, low productivity environment. In concert, this suggests a tentative a link

between regional area and specialisation. However, more data is necessary to test this association.

5.4.2. Learning

The frequent use of persistent oceanographic features has been demonstrated in a broad array of taxa, including seabirds, showing that spatial distributions are associated with predictable physical features (e.g., McConnell et al. 1992; Hull et al. 1997; Reid and Croxall 2001; Campagna et al. 2006; Biuw et al. 2007; Weimerskirch 2007; Pinaud and Weimerskirch 2007; Cotté et al. 2007; Dragon et al. 2010; Scheffer et al. 2010). Thus, past experience and memory may influence predator movements when prey distributions are predictable and increase foraging efficiency (Hunt Jr et al. 1999; Pinaud and Weimerskirch 2005; Weimerskirch 2007). One aspect of these movements is to return repeatedly to the same foraging areas (i.e. site fidelity). Foraging site fidelity has also been shown to be higher in experienced individuals whereas inexperienced individuals were more exploratory; these differences in foraging fidelity were more pronounced when resources were scarce (Haug et al. 2015). Studies have also shown that foraging proficiency improves with age or previous experience with specific prey types (Heinrich 1976a; Heinrich 1976b; Heinrich 1979; Burger et al. 1980; Laverty 1980; Greig et al. 1983; Caldow et al. 1999). Thus, learning may lead to foraging specialisation based on past experience of different prey and locations.

5.4.3. Unresolved questions

Ultimately, our goal is to understand the mechanisms that affect individual foraging specialisation in the marine environment. To accomplish this we need: 1) published records of low variation or absence of specialisation; 2) data linking intra- and inter-

specific competition to individual specialisation in air-breathing marine vertebrates, and 3) to test the hypothesis that temporal and spatial consistency of oceanographic features interacts with competition, foraging behaviour and learning to affect the appearance of individual foraging specialization.

Absence of specialisation

There are only seven species for which research as documented low variation or the absence of individual foraging specialisation (Table 5.1). Whether this is due to the lack of published negative results or the near ubiquitous nature of specialisations is unclear. However, publishing studies where specialisation does not occur, or occurs at low frequency, is critical to the understanding of the mechanisms that drive specialisation, particularly in areas with limited data such as the tropics.

Linking competition and specialisation

While studies examining the link between competition and specialisation do exist, they offer conflicting results. Both intra- and inter-specific competition are identified as mechanisms of specialisation. However, only a few experimental studies on fish are available to test these associations. Generally, intra-specific competition for resources associated with high population densities promotes specialisation (Svanbäck and Persson 2004; Svanbäck and Bolnick 2005; Svanbäck and Bolnick 2007). Ecological release from interspecies competitors produced conflicting results suggesting the interactions are competitor-specific (Bolnick et al. 2010). The type of competition may affect the outcome and thus affect community dynamics.

Oceanographic features and specialisation

Our review suggests links between persistent marine features and specialisation, particularly in the temperate and polar regions. However, to test this hypothesis fully, we need more published studies examining specialisation, in particular at high and low latitudes. Specific studies could also examine the effect of environmental variability on the degree of specialisation found.

5.5. Concluding remarks and future directions

Individual foraging specialisation appears widespread among seabirds, and has been found in the majority of species that have been examined. The prevalence of consistent choice of foraging location, feeding behaviour, and diet suggest that environmental predictability interacts with previous experience, productivity, and competition to influence individual foraging specialisation. Current studies suggest a link between predictable resources and specialisation which results in increased fitness. Future work should study individual specialisation across a diverse range of taxa at a range of different locations, including tropical regions, to determine better how environmental conditions (including productivity and predictability) and competition (both intra- and inter-specific) drive the observed patterns. Moreover, once these underlying drivers are better understood, we will be better placed to understand the conservation implications of such inter-individual variation.

CHAPTER 6: GENERAL DISCUSSION

A wide variety of seabirds are experiencing population declines attributed to the deleterious impact of fisheries, pollution, introduced species, habitat alteration, and climate change (Croxall et al. 2012). Knowledge of the spatial and temporal dynamic of foraging behaviour is fundamental to understanding interactions between predators, prey and their environment (e.g. Weimerskirch et al. 1994; Weimerskirch et al. 2005), its influence on demography (Weimerskirch et al. 2012), and how these behaviours alter population risks (Torres et al. 2011).

Campbell albatross (*Thalassarche impavida*) is considered vulnerable because of its sole breeding location and dramatic population declines since the 1940s, which was correlated with fisheries effort. While we have data from the post-guard chick-rearing phase, we lacked basic information on at-sea foraging behaviour during early and mid-breeding periods, which is necessary for understanding spatial use, ecosystem interactions, and effective conservation and species management. I used a combination of fine resolution GPS tracking, Vessel Monitoring System data, and stable isotope analysis to study the basic foraging ecology, individual foraging specialisation, and to examine overlap with fisheries vessels.

6.1. Key Findings

- Campbell albatross shows similar broad-scale foraging strategies to other albatross species (Tickell 2000). Trip duration is longer during incubation when trip duration is limited by their partner's ability to fast and shorter trips are taken

during chick brooding to meet self-maintenance and chick energetic needs (Weimerskirch et al. 1986; Weimerskirch 1995; Weimerskirch et al. 1997b; Tickell 2000; Shaffer et al. 2003).

- The morphological and behavioural differences between Campbell and black-browed albatrosses (*T. melanophrys*, formerly one species) indicate that management and conservation strategies may need to be reviewed.
- Campbell albatross are sexual dimorphic and segregate by sex during both incubation and chick brooding. Contrary to what has been documented for many seabirds (Catry et al. 2006; Wearmouth and Sims 2008), larger males travelled further than females.
- Overlap between fishing vessels and Campbell albatross were remarkably low. However, a multi-national evaluation of fisheries interactions is needed as Campbell albatross spend much of their time foraging in Australian waters, Tasman Sea, and Southern Ocean.
- The multi-scale approach used in **Chapter 3** suggests Campbell albatross use some of the same habitats as fishing vessels, but not necessarily at the same time.
- Campbell albatross show high foraging area fidelity with a degree of flexibility in the fine-scale location and behaviour. A majority of individuals demonstrated consistent behaviours among successive trips, but there are generalists within the population. The degree of specialisation was influenced by sex and year.
- Individual foraging specialisation appears common in seabirds. Current literature suggests a tentative link between regional area and specialisation that may be influenced by environmental predictability.

Overall Campbell albatross demonstrate at least three foraging strategies during the breeding season. Similar to other albatross species (Tickell 2000), Campbell albatross travelled long distances during incubation and shorter trips during chick brooding (**Chapter 2**). Maximum trip distance during incubation ranged from 171 to 3379 km, with individuals mainly travelling to the southeast Australian coast, Tasman Sea, and Southern Ocean. Foraging trips during chick brooding were shorter than during incubation (overall mean 2.2 days and 10.9 days, respectively) with birds primarily using the Campbell Plateau and Southern Ocean. Previous studies during post-brooding stage found that Campbell albatross switched between two foraging strategies, short neritic trips (2.0-3.7 days) and longer oceanic (>5 days) trips (Waugh et al. 2000). During short trips, individuals travelled 150 to 640 km away and on long trips individuals sometimes commuted in excess of 2000 km (Waugh et al. 2000).

6.1.1. Comparison with Black-browed Albatross

Campbell albatross was previously considered a subspecies of the black-browed albatross (Robertson and Nunn 1998; Sangster et al. 2013). While information exists about the at-sea distribution and foraging behaviour of black-browed albatross populations across much of their range (Weimerskirch et al. 1986, Weimerskirch et al. 1988, Gremillet et al. 1999, Cherel et al. 2000, Huin 2002, Wakefield et al. 2011), data available for Campbell albatrosses were limited. However with the additional knowledge gain from my research, it may be beneficial to compare these findings with those for black-browed albatrosses, to highlight where conservation and management measures may need to account for differences in their ecology.

Comparisons of foraging behaviour between Campbell albatrosses and black-browed albatrosses have demonstrated niche segregation, which coincide with morphological and behavioural differences (Wakefield et al. 2011). While Campbell albatrosses are sexually dimorphic, the differences in bill size and mass between the sexes are less dramatic than those found within black-browed albatrosses on South Georgia (**Chapter 2**; Phillips et al. 2004). These differences in sexual dimorphism may influence behaviour as it has been linked to changes in distributions in seabirds (Spear and Ainley 1997).

Campbell and black-browed albatross demonstrate different patterns of sexual segregation during their prospective breeding seasons. Black-browed albatross demonstrate spatial segregation between sexes during incubation, not during chick brooding or chick-rearing (Phillips et al. 2004), in contrast, Campbell albatross demonstrate sexual differences in foraging during both incubation and chick brooding, but sex effects were more distinct during chick brooding (**Chapter 2**). Male Campbell albatross travelled further than females during incubation, whereas the opposite pattern is present in black-browed albatross (Phillips et al. 2004). These spatio-temporal dissimilarities between sexes of both species may influence the differential risks of threats to species, therefore applying uniform patterns between species is injudicious.

Trip durations of Campbell albatrosses were similar to many black-browed albatross colonies (Weimerskirch et al. 1988; Gremillet et al. 2000; Huin 2002; Phillips et al. 2004). However, Campbell albatrosses tend to travel farther from the colony than black-browed albatrosses (Weimerskirch et al. 1988; Gremillet et al. 2000; Huin 2002; Phillips et al. 2004). For example, while the trip durations are similar during chick brooding, Campbell albatrosses travelled a maximum distance of 4.6% to 5.4 % longer

than black-browed albatrosses (**Chapter 2**; Weimerskirch et al. 1988; Phillips et al. 2004). During chick brooding and post-guard stages, Campbell albatross also exploit oceanic habitats less commonly used by black-browed albatrosses (e.g. Weimerskirch et al. 1986; Weimerskirch et al. 1988; Cherel and Weimerskirch 1995; Weimerskirch et al. 1997; Cherel et al. 2000; Huin 2002; Phillips et al. 2004; Wakefield et al. 2011). These behavioural and habitat use differences between Campbell albatrosses and black-browed albatrosses likely influence energy budgets, and are probably a result of competition, oceanographic features, and colony location, as black-browed albatross behaviours range depending on colony location.

Overall, these morphological and behavioural differences suggest that basing management and conservation plans on assumptions of similarity between these species may be inappropriate.

6.1.2. Overlap with Fisheries

Population declines in many species of seabird have been attributed to fisheries-related mortality from accidental bycatch (Brothers 1991; Nel et al. 2002; Sullivan et al. 2006; Rolland et al. 2010; Anderson et al. 2011). Following this pattern, the steep population decline of Campbell albatross coincided with increased fisheries efforts in the Southern Ocean (Waugh et al. 1999; Sagar 2014). Thus, I estimated the degree of spatial and spatio-temporal overlap between fisheries and breeding Campbell albatross within New Zealand's Exclusive Economic Zone (EEZ) to provide an updated understanding of bycatch risk, as well as testing for differences in the extent of seabird-fisheries overlap between the sexes, stages of reproduction (incubation and chick-brooding), and between two years (**Chapter 3**). Despite Campbell albatrosses utilizing 6.7% of the EEZ, they only overlap with fishing vessels in a small section in the southern portion of the EEZ

(0.20% of the area) and showed limited spatio-temporal overlap. When accounting for the broader ecological footprint of fishing vessels, which can influence a birds' behaviour for up to 30 km, we found albatross-vessel overlap in up to 8.4% of trips. This may be due to mitigation measures reducing interactions, competition with other species, discard practices, or the limited amount of time spent within the EEZ. Further investigation is needed to determine if this occurs throughout the year and their range as well as examining behavioural responses to assess if Campbell albatross are attracted to vessels, avoid them, or co-occur/use the same habitat. While my results correspond to the relatively low bycatch rates during the timeframe I examined (Murray et al. 1993; Gales et al. 1998; Abraham and Thompson 2012), it is important to note that these results are confined to the New Zealand EEZ and that Campbell albatross spend much of their time foraging in the Southern Ocean, the Tasman Sea and Australian waters for which I did not have fisheries data. Thus, investigating overlap in these additional areas is needed and conservation and fisheries management for this species needs to occur on a multi-national scale.

6.1.3. Individual Foraging Specialisation

Individual foraging specialisations are widespread among seabirds suggesting specialisation provides an adaptive advantage (**Chapter 5**; Annett and Pierotti 1999; Votier et al. 2004; Patrick and Weimerskirch 2014). Intra-population variation in foraging may play a key role in understanding population changes as well as playing role in a wide variety of ecological, and evolutionary as well as management and conservation strategies (see Bolnick et al. 2003, Estes et al. 2003, Araújo et al. 2011 for reviews).

Campbell albatrosses demonstrate annual and inter-annual specialisation at both the population and individual level; the degree of specialisation was influenced by sex and year (**Chapter 4**). Individual level analyses revealed that a majority of individuals demonstrated consistent behaviours between successive trips, with high foraging area fidelity. Females, which foraged closer to the colony in neritic and shelf waters, showed more consistent behaviours than males, which foraged further offshore in pelagic environments. While the drivers of these patterns of habitat use are not fully understood, our results have important implications with respect to potential exposure to threats, such as fisheries activities, and thus are important for marine spatial planning.

6.2. Overall Conclusions

Throughout this dissertation the data show that Campbell albatross demonstrate sexual differences in foraging behaviour and individual foraging specialisation as well as potential differences in rates of overlap with fishing vessels (**Chapter 2-4**). Sex effects were found in both trip distance and duration. Additionally, females tended to forage on the Campbell Plateau and slope areas, whereas males travelled farther south into deeper waters of the Southern Ocean. Campbell albatrosses also frequently specialised in foraging behaviours suggesting site fidelity. While I did not find significant sex differences in fisheries overlap, likely due to the small number of overlapping foraging trips, males tended to overlap with fisheries more than females (9 female:16 male, **Chapter 3**). However despite these spatial use patterns, diet (based on stable isotope analysis) was largely similar (**Chapter 2**).

Sexual segregation, which is sometimes associated with sexual dimorphism, is widespread in seabirds; generally the smaller sex travels further from the colony, which may affect foraging efficiency and diet in some species (Catry et al. 2006; Wearmouth and

Sims 2008). Campbell Albatrosses are sexually dimorphic and segregate by sex in relation to foraging behaviour, oceanic region use, and individual foraging specialisation. Contrary to the overall pattern of sexual dimorphism and segregation (Wearmouth and Sims 2008), the large Campbell Albatross males travelled further than females during chick brooding. However, there are species with similar results, namely Grey-head Albatross (*T. chrysostoma*, Phillips et al. 2004) and Magellanic Penguins (*Spheniscus magellanicus*, Forero et al. 2002); both species are sexually dimorphic with the large sex travelling further than the smaller sex. (Wearmouth and Sims 2008).

Sexual segregation is generally considered to be result of social dominance, competitive exclusion, breeding role or niche specialization associated with breeding role or morphology (Peters and Grubb 1983; Petit et al. 1990; Marra 2000; Weimerskirch et al. 2009). Additionally, variation in regional wind speed, flight proficiency, and wing loading have been used to explain both the general pattern seen and that of Grey-head Albatross (Shaffer et al. 2001; Phillips et al. 2004) as well as the latitudinal sexual segregation of albatross during the non-breeding season in the Benguela system (Phillips et al. 2005). While I do not have wing area to calculate wing loading, wing to mass ratios for male and female Campbell Albatrosses are significantly different ($F=11.77$ $p<0.001$); thus if wind velocities are higher in the Southern Ocean than on the Campbell Plateau, then the theory on flight proficiency may be a plausible. A similar comparison between the wing to mass ratio of greater albatrosses (*Diomedea spp.*) was used to explain the use of sub-tropical waters by Amsterdam albatross (*Diomedea amsterdamensis*; Waugh and Weimerskirch 2003). However further study is needed to determine whether flight proficiency, social dominance, competitive exclusion, or niche/breeding role specialization explain my results.

Several species of marine birds, including Campbell albatross, demonstrate both sexual segregation and individual foraging specialisation (e.g. black-browed albatross, wandering albatross, shag:*Phalacrocorax spp.*). However, there are few studies investigating how sex affects specialisation (Kato et al. 2000; Cook et al. 2005; Ratcliffe et al. 2013; Patrick and Weimerskirch 2014). Factors driving variation in specialisation might include morphology, foraging range or competition (Pianka 1974). In South Georgia shags (*Phalacrocorax georgianus*), a substantial amount of inter-individual variation in dive depth was explained by sexual dimorphism: males were less affected by body mass than females when adopting different foraging strategies (Ratcliffe et al. 2013). Male Campbell albatross are on average 7.2% heavier than females (**Chapter 2**), which could affect foraging energetics. However foraging range or spatial extent could also explain patterns for Campbell albatross. Female Campbell albatrosses were more consistent in their foraging behaviours during chick brooding than males and also remained closer to the colony, on average. This is in contrast to black-browed albatross which show the opposite pattern (Patrick and Weimerskirch 2014). Thus future studies may need to account for spatial extent to determine the causes of these patterns. However, both sexual segregation and individual foraging specialisation may be related to competition through size dimorphism, social dominance, competitive exclusion or niche/breeding role specialization (Phillips et al. 2004; Catry et al. 2006; Araújo et al. 2011; Phillips et al. 2011).

6.3. Conservation Implications

Spatial use by individuals or sexes affects their interaction with the environment, and anthropogenic influences, such as interactions with fisheries or environmental changes. Changes in habitat use have been shown to have fitness consequences (**Chapter 5**;

Marra 2000; Marra and Holmes 2001), which ultimately change population dynamics of the species. The behavioural and morphological differences between Campbell albatross and black-browed albatross previously discussed highlight the need to revisit conservation and management plans implemented prior to the taxonomic split. More specifically, examining how sexual differences in spatial use influences risk from threats, such as local climate shifts.

Sex biased mortality can lead to unequal sex ratios, such as removal of individuals attracted to vessels, which can impact population dynamics (Murray et al. 1993; Gales et al. 1998; Ryan 1999; Mills and Ryan 2005; Bugoni et al. 2011; Barbraud et al. 2013; Tuck et al. 2015). For example, female grey-headed albatross spent a higher proportion of their time within longline fishing areas than males, thus had a higher risk of incidental mortality. Female wandering albatross distribution also overlapped more often with tuna long-line fisheries; however in this case males interacted more with the Toothfish long-line fishery (Nel et al. 2002). While both sexes interacted with fisheries, males and females could show differences in the survival probabilities as was shown at other colonies (e.g. Weimerskirch et al. 1997a; Tuck et al. 2001). Additionally, individuals that specialise in fisheries discards show reduced survival, which had significant phenotypic and population consequences (Barbraud et al. 2013; Tuck et al. 2015). While I did not find sex differences in fisheries overlap, sex may still affect bycatch rates in other times of year or areas outside the New Zealand EEZ. Additionally, more advanced population models that employ spatial use and individual behaviour should be examined to test if, like wandering albatross (*Diomedea exulans*), individuals that specialise or were susceptible to fisheries related mortality were removed from the population and are thus affecting the current population dynamics and

the patterns documented in **Chapter 3** (Barbraud et al. 2013; Tuck et al. 2015). My results also highlight the advantages of a multi-scale approach to assess foraging ecology and distribution. Similar to the results on Buller's albatross (*Thalassarche bulleri*, (Torres et al. 2013), my multi-scale analysis suggests albatrosses and fishing vessels may occupy the same areas, but seldom at the same time. Thus spatial overlap between birds and vessels may overestimate the level of interaction if the temporal aspect is not assessed. This knowledge is critical especially where this can lead to inter-population variation, with concomitant conservation and management implications.

Much of the literature on sexual segregation focuses on the conservation implications of spatial overlap with fisheries. However, male and females may also be affected by local environmental changes. Segregation in habitat use and diet can ultimately impact life history traits. For example, changes in wind patterns shifted the northern range of wander albatross poleward affecting the distribution of females to a greater extent than males (Weimerskirch et al. 2012). Females tended to forage on the Campbell Plateau and slope areas, whereas males travelled farther south into the waters of the Southern Ocean (**Chapter 2**). Thus changes to one area or the other could impact energetic costs, reproductive success or survival. However, more detailed examination of habitat selection is needed to comprehend what environmental factors might affect Campbell albatross demography.

Current conservation practices, such as fixed marine conservation areas are problematic in the face of environmental change and species with long-distance movements. Thus, examining fine-scale interactions should be incorporated into the development of management and conservation measures, particularly if dynamic ocean management, in which management areas change in response spatial and temporal alteration in the ocean

or species movements to reduce bycatch (Howell et al. 2008; Hobday et al. 2010; Hobday et al. 2014; Maxwell et al. 2015), is evaluated for wide-ranging species. The advantage to dynamic assessment and management is that it can better match changing conditions at appropriate scales and can refine/reduce the extent of the management area (Maxwell et al. 2015).

6.4. Future Directions

It is unclear if sexual segregation occurs during egg laying, early incubation (prior to my study), chick-rearing or non-breeding seasons. Campbell albatross demonstrate two foraging strategies during chick-rearing, but sex differences were not examined.

Tracking data are limited or non-existent during other periods. Perhaps most critical to conservation needs are spatial data during the non-breeding stage and for juveniles.

Similar to other species, life history characteristics and spatial use by juveniles is largely unknown.

My study of foraging behavior highlighted broad spatial use and differences between sexes. However, more detailed examinations of habitat use are needed to assess what environmental characteristics are preferred so that we can predict key conservation areas and impacts of environmental or management changes.

More broadly, we need to understand how limited fine-scale seabird-vessel overlap relates to mortality and interaction rates. Our results on Campbell albatross is similar to the situation for black-browed albatross in the Falkland Islands, where fisheries have only limited influence on albatross distribution (Granadeiro et al. 2011; Catry et al. 2013). However in waters around the Falklands, hundreds of black-browed albatross gather behind fishing boats, indicating that scavenging is still common at the

population-level. It is not clear whether this apparent discrepancy is because of non-breeders are more reliant on scavenging than breeders, or because of inter-individual differences in discard use. Further work is required to better understand such patterns, which could be achieved by increasing the sample of tracked birds and by studying other age-classes.

The patterns of species specialisation in my literature review (**Chapter 5**) suggested a tentative link between specialisation and regional areas where resources are predictable but patchy. While more data is needed to test this on a broader scale, moving forward I would like to examine whether specialisation in Campbell albatross is associated with particular environmental variables or the variation within them. To reach this goal, there are several analyses that may reveal more about their foraging ecology and habitat selection. As a first step, area restricted search could be used to: (1) test for individual foraging specialisation at the foraging sites and the scale at which individual forage, (2) define habitat selection variables, and (3) determine the spatial scale in which to test links between specialisation and environmental factors. Additionally, if the data are available, I would like to examine how specialisation influences survival and reproductive success in albatross. A comparative study on a tropical species would also be beneficial.

REFERENCES

- Abraham ER, Pierre JP, Middleton DA, Cleal J, Walker NA, Waugh SM (2009) Effectiveness of fish waste management strategies in reducing seabird attendance at a trawl vessel. *Fish Res* 95:210–219
- Abraham ER, Thompson FN (2012). Captures of birds in trawl fisheries, in the New Zealand Exclusive Economic Zone, during the 2010–11 fishing-year. Retrieved from <http://data.dragonfly.co.nz/psc/v20121101/explore/>, Apr 15, 2013."
- Andersen R, Sæther B-E, Pedersen HC (1995) Regulation of parental investment in the Antarctic petrel *Thalassoica antarctica*: an exchange experiment. *Polar Biol* 15:65–68
- Anderson ORJ, Phillips RA, Shore RF, McGill RAR, McDonald RA, Bearhop S (2009) Diet, individual specialisation and breeding of brown skuas (*Catharacta antarctica lonnbergi*): an investigation using stable isotopes. *Polar Biol* 32:27–33
- Anderson O, Small C, Croxall J, Dunn E, Sullivan B, Yates O, Black A (2011) Global seabird bycatch in longline fisheries. *Endanger Species Res* 14:91–106
- Annett CA, Pierotti R (1999) Long-term reproductive output in western gulls: consequences of alternate tactics in diet choice. *Ecology* 80:288–297
- Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. *Ecol Lett* 14:948–958
- Ballance LT, Pitman RL (1999) Foraging ecology of tropical seabirds. In: Proceedings of the 22nd International Ornithological Congress, Durban. BirdLife South Africa, Johannesburg.p 2057–2071
- Barbraud C, Rivalan P, Inchausti P, Nevoux M, Rolland V, Weimerskirch H (2011) Contrasted demographic responses facing future climate change in Southern Ocean seabirds. *J Anim Ecol* 80:89–100
- Barbraud C, Thomson R, Tuck G, Delord K, Weimerskirch H (2013) Fisheries bycatch as an inadvertent human-induced evolutionary mechanism. *PLoS ONE*:epub ahead of print
- Barlow KE, Croxall JP (2002) Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. *Mar Ecol Prog Ser* 232:291–304
- Bartle JA (1991) Incidental capture of seabirds in the New Zealand subantarctic squid trawl fishery, 1990. *Bird Conserv Int* 1:351–359

- Baylis AM, Page B, McKenzie J, Goldsworthy SD (2012) Individual foraging site fidelity in lactating New Zealand fur seals: continental shelf vs. oceanic habitats. *Mar Mammal Sci* 28:276–294
- Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73:1007–1012
- Bearhop S, Phillips RA, McGill R, Cherel Y, Dawson DA, Croxall JP, others (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Mar Ecol Prog Ser* 311:157–164
- Bearhop S, Phillips RA, Thompson DR, Waldron S, Furness RW (2000) Variability in mercury concentrations of great skuas *Catharacta skua*: the influence of colony, diet and trophic status inferred from stable isotope signatures. *Mar Ecol Prog Ser* 195:261–268
- Bearhop S, Thompson DR, Phillips RA, Waldron S, Hamer KC, Gray CM, Votier SC, Ross BP, Furness RW (2001) Annual variation in great skua diets: the importance of commercial fisheries and predation on seabirds revealed by combining dietary analyses. *The Condor* 103:802
- Becker WA (1984) *Manual of quantitative genetics*. McNaughton and Gunn. Ann Arbor MI
- Belt ST, Brown TA, Rodriguez AN, Sanz PC, Tonkin A, Ingle R (2012) A reproducible method for the extraction, identification and quantification of the Arctic sea ice proxy IP25 from marine sediments. *Anal Methods* 4:705–713
- BirdLife International (2012) *Thalassarche impavida*. The IUCN Red List of Threatened Species. Version 2014.2
- Biuw M, Boehme L, Guinet C, Hindell M, Costa D, Charrassin J-B, Roquet F, Bailleul F, Meredith M, Thorpe S (2007) Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. *Proc Natl Acad Sci* 104:13705–13710
- Bodey TW, Jessopp MJ, Votier SC, Gerritsen HD, Cleasby IR, Hamer KC, Patrick SC, Wakefield ED, Bearhop S (2014) Seabird movement reveals the ecological footprint of fishing vessels. *Curr Biol* 24:R514–R515
- Bolnick DI, Ingram T, Stutz WE, Snowberg LK, Lau OL, Paull JS (2010) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proc R Soc B Biol Sci* 277:1789–1797
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28
- Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R (2002) Measuring individual-level resource specialization. *Ecology* 83:2936–2941

-
- Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar Syst* 78:363–376
- Bradshaw CJ, Hindell MA, Sumner MD, Michael KJ (2004) Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Anim Behav* 68:1349–1360
- Brothers N (1991) Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. *Biol Conserv* 55:255–268
- Brown TA, Bicknell AWJ, Votier SC, Belt ST (2013) Novel molecular fingerprinting of marine avian diet provides a tool for gaining insights into feeding ecology. *Environ Chem Lett*:1–6
- Bugoni L, Griffiths K, Furness RW (2011) Sex-biased incidental mortality of albatrosses and petrels in longline fisheries: differential distributions at sea or differential access to baits mediated by sexual size dimorphism? *J Ornithol* 152:261–268
- Burger J, Olla BL, Winn HE (1980) *Marine birds*.
- Burger AE, Shaffer SA (2008) Application of tracking and data-logging technology in research and conservation of seabirds. *The Auk* 125:253–264
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer
- Caldow RWG, Goss-Custard JD, Stillman RA, Durell SEALV, Swinfen R, Bregnballe T (1999) Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. *J Anim Ecol* 68:869–878
- Campagna C, Piola AR, Rosa Marin M, Lewis M, Fernández T (2006) Southern elephant seal trajectories, fronts and eddies in the Brazil/Malvinas Confluence. *Deep Sea Res Part Oceanogr Res Pap* 53:1907–1924
- Catard A, Weimerskirch H, Cherel Y (2000) Exploitation of distant Antarctic waters and close shelf-break waters by white-chinned petrels rearing chicks. *Mar Ecol Prog Ser* 194:249–261
- Catry P, Phillips RA, Croxall JP (2006) Sexual segregation in birds: patterns, processes and implications for conservation. *Sex Segreg Vertebr Ecol Two Sexes*:351–378
- Catry P, Ruxton GD, Ratcliffe N, Hamer KC, Furness RW (1999) Short-lived repeatabilities in long-lived great skuas: implications for the study of individual quality. *Oikos*:473–479
- Ceia FR, Paiva VH, Garthe S, Marques JC, Ramos JA (2014) Can variations in the spatial distribution at sea and isotopic niche width be associated with

- consistency in the isotopic niche of a pelagic seabird species? *Mar Biol* 161:1861–1872
- Ceia FR, Phillips RA, Ramos JA, Cherel Y, Vieira RP, Richard P, Xavier JC (2012) Short- and long-term consistency in the foraging niche of Wandering Albatrosses. *Mar Biol* 159.7: 1581-1591
- Cherel Y, Corre M Le, Jaquemet S, Ménard F, Richard P, Weimerskirch H, others (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. *Mar Ecol Prog Ser* 366:281–291
- Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar Ecol Prog Ser* 329:281–287
- Cherel Y, Hobson KA, Guinet C, Vanpe C (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *J Anim Ecol* 76:826–836
- Cherel Y, Hobson KA, Hassani S (2005) Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. *Physiol Biochem Zool* 78:106–115
- Cherel Y, Phillips RA, Hobson KA, McGill R (2006) Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biol Lett* 2:301–303
- Cherel Y, Waugh S, Hanchet S (1999) Albatross predation of juvenile southern blue whiting (*Micromesistius australis*) on the Campbell Plateau.
- Cherel Y, Weimerskirch H (1995) Seabirds as indicators of marine resources: black-browed albatrosses feeding on *ommastrephid* squids in Kerguelen waters. *Mar Ecol Prog Ser* 129:295–300
- Cherel Y, Weimerskirch H, Trouvé C (2000) Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. *Mar Ecol Prog Ser* 207:183–199
- Collet J, Patrick SC, Weimerskirch H (2015) Albatrosses redirect flight towards vessels at the limit of their visual range. *Mar Ecol Prog Ser* 526:199–205
- Cook TR, Cherel Y, Tremblay Y (2005) Foraging tactics of chick-rearing Crozet shags: individuals display repetitive activity and diving patterns over time. *Polar Biol* 29:562–569
- Cotté C, Park Y-H, Guinet C, Bost C-A (2007) Movements of foraging king penguins through marine mesoscale eddies. *Proc R Soc B Biol Sci* 274:2385–2391
- Croxall JP, Butchart SH, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv Int* 22

- Croxall JP, Gales R (1998) An assessment of the conservation status of albatrosses. *Albatross Biol Conserv*:46–65
- Croxall JP, Silk JRD, Phillips RA, Afanasyev V, Briggs DR (2005) Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science* 307:249–250
- Croxall J, Small C, Sullivan B, Wanless R, Frere E, Lascelles B, Ramirez I, Sato M, Yates O (2013) Appropriate scales and data to manage seabird-fishery interactions: comment on Torres et al.(2013). *Mar Ecol Prog Ser* 493:297–300
- Darimont CT, Paquet PC, Reimchen TE (2007) Stable isotopic niche predicts fitness of prey in a wolf–deer system. *Biol J Linn Soc* 90:125–137
- Dietrich KS, Melvin EF, Conquest L (2008) Integrated weight longlines with paired streamer lines – Best practice to prevent seabird bycatch in demersal longline fisheries. *Biol Conserv* 141:1793–1805
- Dingemanse NJ, Kazem AJN, Réale D, Wright J (2010) Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol Evol* 25:81–89
- Dragon A-C, Monestiez P, Bar-Hen A, Guinet C (2010) Linking foraging behaviour to physical oceanographic structures: southern elephant seals and mesoscale eddies east of Kerguelen Islands. *Prog Oceanogr* 87:61–71
- Duffy MA, Cáceres CE, Hall SR, Tessier AJ, Ives AR (2010) Temporal, spatial, and between-host comparisons of patterns of parasitism in lake zooplankton. *Ecology* 91:3322–3331
- Dukas R (1995) Transfer and interference in bumblebee learning. *Anim Behav* 49:1481–1490
- Duncan S, Stewart TI, Oliver M, Mavoja S, MacRae D, Badland HM, Duncan MJ (2013) Portable global positioning system receivers: static validity and environmental conditions. *Am J Prev Med* 44:e19–e29
- Elliott K, Woo K, Gaston A, Benvenuti S, Dall’Antonia L, Davoren G (2008) Seabird foraging behaviour indicates prey type. *Mar Ecol Prog Ser* 354:289–303
- Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. *J Anim Ecol* 72:144–155
- Favero M, Blanco G, García G, Copello S, Seco Pon JP, Frere E, Quintana F, Yorio P, Rabuffetti F, Cañete G, Gandini P (2011) Seabird mortality associated with ice trawlers in the Patagonian shelf: effect of discards on the occurrence of interactions with fishing gear. *Anim Conserv* 14:131–139
- Fiedler PC, Reilly SB, Hewitt RP, Demer D, Philbrick VA, Smith S, Armstrong W, Croll DA, Tershy BR, Mate BR (1998) Blue whale habitat and prey in the California Channel Islands. *Deep-Sea Res Part II* 45:1781–1801

- Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. *Glob Change Biol* 15:1618–1630
- Forero MG, Hobson KA, Bortolotti GR, Donázar JA, Bertellotti M, Blanco G (2002) Food resource utilisation by the Magellanic penguin evaluated through stable-isotope analysis: segregation by sex and age and influence on offspring quality. *Mar Ecol Prog Ser* 234:289–299
- Fraser WR, Trivelpiece WZ, Ainley DG, Trivelpiece SG (1992) Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biol* 11:525–531
- Furness RW, Birkhead TR (1984) Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature* 311:655–656
- Gales R, Brothers N, Reid T (1998) Seabird mortality in the Japanese tuna longline fishery around Australia, 1988–1995. *Biol Conserv* 86:37–56
- Gales R, Robertson G (1998) Albatross biology and conservation. Surrey Beatty & Sons
- Garthe S, Montevecchi WA, Davoren GK (2007) Flight destinations and foraging behaviour of northern gannets (*Sula bassana*) preying on a small forage fish in a low-Arctic ecosystem. *Deep Sea Res Part II Top Stud Oceanogr* 54:311–320
- Garthe S, Montevecchi WA, Davoren GK (2011) Inter-annual changes in prey fields trigger different foraging tactics in a large marine predator. *Limnol Oceanogr* 56:802
- Gende SM, Sigler MF (2006) Persistence of forage fish hot spots' and its association with foraging Steller sea lions (*Eumetopias jubatus*) in southeast Alaska. *Deep Sea Res Part II Top Stud Oceanogr* 53:432–441
- Golet GH, Kuletz KJ, Roby DD, Irons DB (2000) Adult prey choice affects chick growth and reproductive success in pigeon guillemots. *The Auk* 117:82–91
- Granadeiro JP, Brickle P, Catry P (2013) Do individual seabirds specialize in fisheries' waste? The case of black-browed albatrosses foraging over the Patagonian Shelf. *Anim Conserv*
- Granadeiro JP, Phillips RA, Brickle P, Catry P (2011) Albatrosses following fishing vessels: how badly hooked are they on an easy meal? *PLoS ONE* 6:e17467
- Greig SA, Coulson JC, Monaghan P (1983) Age-related differences in foraging success in the herring gull (*Larus argentatus*). *Anim Behav* 31:1237–1243
- Gremillet D, Wilson RP, Storch S, Gary Y (1999) Three-dimensional space utilization by a marine predator. *Mar Ecol Prog Ser* 183:263–273
- Gremillet D, Wilson RP, Wanless S, Chater T (2000) Black-browed albatrosses, international fisheries and the Patagonian Shelf. *Mar Ecol Prog Ser*:269–280

-
- Guilford TC, Meade J, Freeman R, Biro D, Evans T, Bonadonna F, Boyle D, Roberts S, Perrins CM (2008) GPS tracking of the foraging movements of Manx shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis* 150:462–473
- Hamer KC, Hill JK (1994) The regulation of food delivery to nestling Cory's shearwaters *Calonectris diomedea*: the roles of parents and offspring. *J Avian Biol* 25:198
- Hamer KC, Humphreys EM, Garthe S, Hennicke J, Peters G, Grémillet D, Phillips RA, Harris MP, Wanless S (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Mar Ecol Prog Ser* 338:295–305
- Harris S, Raya Rey A, Zavalaga C, Quintana F (2014) Strong temporal consistency in the individual foraging behaviour of imperial shags *Phalacrocorax atriceps*. *Ibis* 156:523–533
- Haug FD, Paiva VH, Werner AC, Ramos JA (2015) Foraging by experienced and inexperienced Cory's shearwater along a 3-year period of ameliorating foraging conditions. *Mar Biol*:1–12
- Haury LR, McGowan JA, Wiebe PH (1978) Patterns and processes in the time-space scales of plankton distributions. In: *Spatial pattern in plankton communities*.p 277–327
- Hedd A, Gales R, Brothers N (2001) Foraging strategies of shy albatross *Thalassarche cauta* breeding at Albatross Island, Tasmania, Australia. *Mar Ecol Prog Ser* 224:267–282
- Hedd A, Montevecchi WA, Phillips RA, Fifield DA (2014) Seasonal sexual segregation by monomorphic sooty shearwaters *Puffinus griseus* reflects different reproductive roles during the pre-laying period.
- Heinrich B (1976a) Bumblebee foraging and the economics of sociality: how have bumblebees evolved to use a large variety of flowers efficiently? Individual bees have specialized behavioral repertoires, and the colony, collectively, can harvest food from many different resources. *Am Sci* 64:384–395
- Heinrich B (1976b) The foraging specializations of individual bumblebees. *Ecol Monogr*:105–128
- Heinrich B (1979) Resource heterogeneity and patterns of movement in foraging bumblebees. *Oecologia* 40:235–245
- Hipfner JM, Dale J, McGraw KJ (2010) Yolk carotenoids and stable isotopes reveal links among environment, foraging behavior and seabird breeding success. *Oecologia* 163:351–360

-
- Hobday AJ, Hartog JR, Timmiss T, Fielding J (2010) Dynamic spatial zoning to manage southern bluefin tuna (*Thunnus maccoyii*) capture in a multi-species longline fishery. *Fish Oceanogr* 19:243–253
- Hobday AJ, Maxwell SM, Forgie J, McDonald J, Darby M, Seto K, Bailey H, Bograd SJ, Briscoe DK, Costa D, others (2014) Dynamic ocean management: integrating scientific and technological capacity with law, policy and management. *Stanf Environ Law J* 33:125–165
- Hobson KA, Clark RG (1992a) Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. *Condor*:181–188
- Hobson KA, Clark RG (1992b) Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. *Condor*:189–197
- Hobson KA, Clark RG (1993) Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. *The Auk* 110:638–641
- Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol*:786–798
- Holligan PM (1981) Biological implications of fronts on the northwest European continental shelf. *Philos Trans R Soc Lond Ser Math Phys Sci* 302:547–562
- Howell EA, Kobayashi DR, Parker DM, Balazs GH, Polovina JJ (2008) TurtleWatch: a tool to aid in the bycatch reduction of loggerhead turtles *Caretta caretta* in the Hawaii-based pelagic longline fishery. *Endanger Species Res* 5:267–278
- Huin N (2002) Foraging distribution of the black-browed albatross, *Thalassarche melanophris*, breeding in the Falkland Islands. *Aquat Conserv Mar Freshw Ecosyst* 12:89–99
- Hull CL, Hindell MA, Michael K (1997) Foraging zones of royal penguins during the breeding season, and their association with oceanographic features. *Mar Ecol Prog Ser* 153:217–228
- Hunt Jr GL, Mehlum F, Russell RW, Irons D, Decker MB, Becker PH (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. In: *Proceedings of the International Ornithological Congress*.p 2040–2056
- Hunt Jr GL, Russell RW, Coyle KO, Weingartner T (1998) Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Mar Ecol Prog Ser* 167:241–259
- Hunt Jr GL, Schneider DC, others (1987) Scale-dependent processes in the physical and biological environment of marine birds. In: *Seabirds: feeding ecology and role in marine ecosystems*.p 7–41
- Inger R, Bearhop S (2008) Applications of stable isotope analyses to avian ecology. *Ibis* 150:447–461

-
- Irons DB (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79:647–655
- Ishikawa K, Watanuki Y (2002) Sex and individual differences in foraging behavior of Japanese cormorants in years of different prey availability. *J Ethol* 20:49–54
- Jaeger A, Blanchard P, Richard P, Cherel Y (2009) Using carbon and nitrogen isotopic values of body feathers to infer inter- and intra-individual variations of seabird feeding ecology during moult. *Mar Biol* 156:1233–1240
- Jaeger A, Connan M, Richard P, Cherel Y, others (2010) Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialisation in seabirds. *Mar Ecol Prog Ser* 401:269–277
- Jiménez S, Domingo A, Brazeiro A (2009) Seabird bycatch in the Southwest Atlantic: interaction with the Uruguayan pelagic longline fishery. *Polar Biol* 32:187–196
- Johnson CK, Tinker MT, Estes JA, Conrad PA, Staedler M, Miller MA, Jessup DA, Mazet JAK (2009) Prey choice and habitat use drive sea otter pathogen exposure in a resource-limited coastal system. *Proc Natl Acad Sci* 106:2242
- Jouventin P, Weimerskirch H (1990) Satellite tracking of wandering albatrosses.
- Kato A, Watanuki Y, Nishiumi I, Kuroki M, Shaughnessy P, Naito Y (2000) Variation in foraging and parental behavior of king cormorants. *The Auk* 117:718–730
- Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can J Zool* 78:1–27
- Kotzerka J, Garthe S, Hatch SA (2010) GPS tracking devices reveal foraging strategies of black-legged kittiwakes. *J Ornithol* 151:459–467
- Kotzerka J, Hatch SA, Garthe S (2011) Evidence for foraging-site fidelity and individual foraging behavior of pelagic cormorants rearing chicks in the Gulf of Alaska. *The Condor* 113:80–88
- Kranstauber B, Safi K, Bartumeus F (2014) Bivariate Gaussian bridges: directional factorization of diffusion in Brownian bridge models. *Mov Ecol* 2:5
- Lack D (1968) Bird migration and natural selection. *Oikos*:1–9
- Laverty TM (1980) The flower-visiting behaviour of bumble bees: floral complexity and learning. *Can J Zool* 58:1324–1335
- Laverty TM (1994a) Costs to foraging bumble bees of switching plant species. *Can J Zool* 72:43–47
- Laverty TM (1994b) Bumble bee learning and flower morphology. *Anim Behav* 47:531–545

-
- Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48
- Le Fevre J (1986) Aspects of the biology of frontal systems. *Adv Mar Biol* 23:163–299.
- Lessells CM, Boag PT (1987) Unrepeatable repeatabilities: a common mistake. *The Auk*:116–121
- Lewis S, Benvenuti S, Dall–Antonia L, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC (2002) Sex-specific foraging behaviour in a monomorphic seabird. *Proc R Soc Lond B Biol Sci* 269:1687–1693
- Lewison RL, Crowder LB (2003) Estimating fishery bycatch and effects on a vulnerable seabird population. *Ecol Appl* 13:743–753
- Lewison R, Crowder L, Read A, Freeman S (2004) Understanding impacts of fisheries bycatch on marine megafauna. *Trends Ecol Evol* 19:598–604
- Limmer B, Becker PH (2010) Improvement of reproductive performance with age and breeding experience depends on recruitment age in a long-lived seabird. *Oikos* 119:500–507
- Litzow MA, Piatt JF, Prichard AK, Roby DD (2002) Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia* 132:286–295
- Løkkeborg S (2003) Review and evaluation of three mitigation measures—bird-scaring line, underwater setting and line shooter—to reduce seabird bycatch in the north Atlantic longline fishery. *Fish Res* 60:11–16
- Mancini PL, Bond AL, Hobson KA, Duarte LS, Bugoni L (2013) Foraging segregation in tropical and polar seabirds: testing the intersexual competition hypothesis. *J Exp Mar Biol Ecol* 449:186–193
- Marra PP (2000) The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behav Ecol* 11:299–308
- Marra PP, Holmes RT (2001) Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. *The Auk* 118:92–104.
- Matthews B, Marchinko KB, Bolnick DI, Mazumder A (2010) Specialization of trophic position and habitat use by sticklebacks in an adaptive radiation. *Ecology* 91:1025–1034
- Maxwell SM, Hazen EL, Lewison RL, Dunn DC, Bailey H, Bograd SJ, Briscoe DK, Fossette S, Hobday AJ, Bennett M, Benson S, Caldwell MR, Costa DP, Dewar H, Eguchi T, Hazen L, Kohin S, Sippel T, Crowder LB (2015) Dynamic ocean management: defining and conceptualizing real-time management of the ocean. *Mar Policy* 58:42–50

-
- McCleery RH, Sibly RM (1986) Feeding specialization and preference in herring gulls. *J Anim Ecol*:245–259
- McConnell BJ, Chambers C, Fedak MA (1992) Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarct Sci* 4:393–393
- Mehlum F, Watanuki Y, Takahashi A (2001) Diving behaviour and foraging habitats of Brünnich's guillemots (*Uria lomvia*) breeding in the high-Arctic. *J Zool* 255:413–423
- Michalik A, McGill RA, Noordwijk HJ van, Masello JF, Furness RW, Eggers T, Quillfeldt P (2013) Stable isotopes reveal variable foraging behaviour in a colony of the imperial shag *Phalacrocorax atriceps*: differences between ages, sexes and years. *J Ornithol* 154:239–249
- Mills MS, Ryan PG (2005) Modeling impacts of long-line fishing: what are the effects of pair-bond disruption and sex-biased mortality on albatross fecundity? *Anim Conserv* 8:359–367
- Moore PJ (2004) Abundance and population trends of mollymawks on Campbell Island. Department of Conservation
- Moore PJ, Burg TM, Taylor GA, Millar CD (2001) Provenance and sex ratio of black-browed albatross, *Thalassarche melanophrys*, breeding on Campbell Island, New Zealand. *Emu* 101:329–334
- Murray TE, Bartle JA, Kalish SR, Taylor PR (1993) Incidental capture of seabirds by Japanese southern bluefin tuna longline vessels in New Zealand waters, 1988–1992. *Bird Conserv Int* 3:181–210
- Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev* 85:935–956
- Nel DC, Nel JL, Ryan PG, Klages NT, Wilson RP, Robertson G (2000) Foraging ecology of grey-headed mollymawks at Marion Island, Southern Indian Ocean, in relation to longline fishing activity. *Biol Conserv* 96:219–231
- Nel D, Ryan PG, Nel JL, Klages NT, Wilson RP, Robertson G, Tuck GN, others (2002) Foraging interactions between wandering albatrosses *Diomedea exulans* breeding on Marion Island and long-line fisheries in the southern Indian Ocean. *Ibis* 144:E141–E154
- Nel DC, Ryan PG, Watkins BP (2002) Seabird mortality in the Patagonian toothfish longline fishery around the Prince Edward Islands, 1996–2000. *Antarct Sci* 14:151–161
- Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA (2009) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology* 90:961–974

-
- NIWA P (1999) Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. *Mar Ecol Prog Ser* 117:243–254
- Oro D, León A de, Minguéz E, Furness RW (2005) Estimating predation on breeding European storm-petrels (*Hydrobates pelagicus*) by yellow-legged gulls (*Larus michahellis*). *J Zool* 265:421–429
- Owen RW (1981) Fronts and eddies in the sea: mechanisms, interactions and biological effects. *Anal Mar Ecosyst*:197–233
- Palacios MG, Martin TE (2006) Incubation period and immune function: a comparative field study among coexisting birds. *Oecologia* 146:505–512
- Patrick SC, Bearhop S, Bodey TW, Grecian WJ, Hamer KC, Lee J, Votier SC (2015) Individual seabirds show consistent foraging strategies in response to predictable fisheries discards. *J Avian Biol*
- Patrick SC, Bearhop S, Grémillet D, Lescroël A, Grecian WJ, Bodey TW, Hamer KC, Wakefield E, Nuz M Le, Votier SC (2014) Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* 123:33–40
- Patrick SC, Weimerskirch H (2014) Consistency pays: sex differences and fitness consequences of behavioural specialization in a wide-ranging seabird. *Biol Lett* 10:20140630
- Peters WD, Grubb TC Jr (1983) An experimental analysis of sex-specific foraging in the downy woodpecker, *Picoides Pubescens*. *Ecology* 64:1437–1443
- Petit LJ, Petit DR, Petit KE, Fleming WJ (1990) Intersexual and temporal variation in foraging ecology of Prothonotary warblers during the breeding season. *The Auk*:133–145
- Pettex E, Bonadonna F, Enstipp MR, Siorat F, Grémillet D (2010) Northern gannets anticipate the spatio-temporal occurrence of their prey. *J Exp Biol* 213:2365–2371
- Phillips RA, McGill RAR, Dawson DA, Bearhop S (2011) Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Mar Biol* 158:2199–2208
- Phillips RA, Silk JR, Croxall JP, Afanasyev V, Bennett VJ (2005) Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology* 86:2386–2396
- Phillips RA, Silk JRD, Phalan B, Catry P, Croxall JP (2004) Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proc R Soc B Biol Sci* 271:1283–1291

-
- Pianka ER (1974) Niche overlap and diffuse competition. *Proc Natl Acad Sci* 71:2141–2145
- Pierotti R, Annett C (1987a) Reproductive consequences of dietary specialization and switching in an ecological generalist. In: Kamil AC, Krebs JR, Pulliam HR (eds) *Foraging Behavior*. Springer US, p 417–442
- Pierotti R, Annett CA (1990) Diet and reproductive output in seabirds. *BioScience* 40:568–574
- Pierotti R, Annett CA (1991) Diet choice in the herring gull: constraints imposed by reproductive and ecological factors. *Ecology*:319–328
- Pierre JP, Abraham ER, Middleton DA, Cleal J, Bird R, Walker NA, Waugh SM (2010) Reducing interactions between seabirds and trawl fisheries: responses to foraging patches provided by fish waste batches. *Biol Conserv* 143:2779–2788
- Pinaud D, Chereil Y, Weimerskirch H (2005) Effect of environmental variability on habitat selection, diet, provisioning behaviour and chick growth in yellow-nosed albatrosses. *Mar Ecol Prog Ser* 298:295–304
- Pinaud D, Weimerskirch H (2005) Scale-dependent habitat use in a long-ranging central place predator. *J Anim Ecol* 74:852–863
- Pinaud D, Weimerskirch H (2007) At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *J Anim Ecol* 76:9–19
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189
- Prince PA, Wood AG, Barton T, Croxall JP (1992) Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. *Antarct Sci* 4:31–36
- Quillfeldt P, Bugoni L, McGill RAR, Masello JF, Furness RW (2008) Differences in stable isotopes in blood and feathers of seabirds are consistent across species, age and latitude: implications for food web studies. *Mar Biol* 155:593–598
- Quillfeldt P, McGill RAR, Masello JF, Weiss F, Strange IJ, Brickle P, Furness RW (2008) Stable isotope analysis reveals sexual and environmental variability and individual consistency in foraging of thin-billed prions. *Mar Ecol Prog Ser* 373:137–148
- Quintana F (2001) Foraging behaviour and feeding locations of rock shags *Phalacrocorax magellanicus* from a colony in Patagonia, Argentina. *Ibis* 143:547–553
- Quintana F, Yorrio P, Lisnizer N, Gatto A, Soria G (2004) Diving behavior and foraging areas of the Neotropic cormorant at a marine colony in Patagonia, Argentina. *Wilson Bull* 116:83–88

- Radl A, Culik BM (1999) Foraging behaviour and reproductive success in Magellanic penguins (*Spheniscus magellanicus*): a comparative study of two colonies in southern Chile. *Mar Biol* 133:381–393
- Ratcliffe N, Takahashi A, O’Sullivan C, Adlard S, Trathan PN, Harris MP, Wanless S (2013) The roles of sex, mass and individual specialisation in partitioning foraging-depth niches of a pursuit-diving predator. *PloS One* 8:e79107
- Réale D, Dingemanse NJ (2010) Personality and individual social specialisation. *Soc Behav Genes Ecol Evol*:417–441
- Regular PM, Hedd A, Montevecchi WA (2013) Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. *Anim Behav*
- Reid K, Croxall JP (2001) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proc R Soc Lond B Biol Sci* 268:377–384
- Ricklefs RE (1987) Response of adult Leach’s storm-petrels to increased food demand at the nest. *The Auk*:750–756
- Robertson CJR, Nunn GB (1998) Towards a new taxonomy for albatrosses. *Albatross Biol Conserv Surrey Beatty Sons Chipping Nort Aust* 23:13–19
- Rolland V, Weimerskirch H, Barbraud C (2010) Relative influence of fisheries and climate on the demography of four albatross species. *Glob Change Biol* 16:1910–1922
- Ropert-Coudert Y, Kato A, Naito Y, Cannell BL (2003) Individual diving strategies in the little penguin. *Waterbirds* 26:403–408
- Ropert-Coudert Y, Wilson RP (2005) Trends and perspectives in animal-attached remote sensing. *Front Ecol Environ* 3:437–444
- Roughgarden J (1972) Evolution of niche width. *Am Nat*:683–718
- Roughgarden J (1974) Niche width: biogeographic patterns among *Anolis* lizard populations. *Am Nat*:429–442
- Rutz C, Hays GC (2009) New frontiers in biologging science. *Biol Lett* 5:289–292
- Ryan PG (1999) Consistent male-biased seabird mortality in the Patagonian toothfish longline fishery. *The Auk* 116:851–854
- Sagar PM (2014) Population estimates and trends of Campbell and grey-headed albatrosses at Campbell Island. NIWA
- Sagar PM, Weimerskirch H (1996) Satellite tracking of southern Buller’s albatrosses from The Snares, New Zealand. *The Condor* 98:649–652

-
- Salamolard M, Weimerskirch H (1993) Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. *Funct Ecol*:643–652
- Sangster G, Collinson JM, Crochet P-A, Knox AG, Parkin DT, Votier SC (2013) Taxonomic recommendations for Western Palearctic birds: ninth report. *Ibis* 155:898–907
- Sanz-Aguilar A, Martínez-Abraín A, Tavecchia G, Mínguez E, Oro D (2009) Evidence-based culling of a facultative predator: efficacy and efficiency components. *Biol Conserv* 142:424–431
- Sapoznikow A, Quintana F (2003) Foraging behavior and feeding locations of imperial cormorants and rock shags breeding sympatrically in Patagonia, Argentina. *Waterbirds* 26:184–191
- Scales KL, Miller PI, Embling CB, Ingram SN, Pirotta E, Votier SC (2014) Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *J R Soc Interface* 11:20140679
- Scales KL, Miller PI, Hawkes LA, Ingram SN, Sims DW, Votier SC (2014) On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *J Appl Ecol*:n/a–n/a
- Scheffer A, Trathan PN, Collins M (2010) Foraging behaviour of king penguins (*Aptenodytes patagonicus*) in relation to predictable mesoscale oceanographic features in the Polar Front Zone to the north of South Georgia. *Prog Oceanogr* 86:232–245
- Schreiber EA, Burger J (2001) *Biology of Marine Birds*. CRC Press
- Shaffer SA, Costa DP, Weimerskirch H (2003) Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Funct Ecol* 17:66–74
- Shaffer SA, Weimerskirch H, Costa DP (2001) Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. *Funct Ecol* 15:203–210
- Soanes LM, Atkinson PW, Gauvain RD, Green JA (2013) Individual consistency in the foraging behaviour of northern gannets: Implications for interactions with offshore renewable energy developments. *Mar Policy* 38:507–514
- Sokal RR, Rohlf FJ (1995) *Biometry: The principles and practice of statistics in biological research*, 3rd edn Freeman. N Y NY
- Sotiropoulos MA, Tonn WM, Wassenaar LI (2004) Effects of lipid extraction on stable carbon and nitrogen isotope analyses of fish tissues: potential consequences for food web studies. *Ecol Freshw Fish* 13:155–160
- Spear LB (1993) Dynamics and effect of western gulls feeding in a colony of guillemots and Brandt's cormorants. *J Anim Ecol*:399–414

-
- Spear LB, Ainley DG (1997) Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis* 139:221–233
- Stahl JC, Sagar PM (2000a) Foraging strategies and migration of southern Buller's albatrosses *Diomedea b. bulleri* breeding on the Solander Is, New Zealand. *J R Soc N Z* 30:319–334
- Stahl JC, Sagar PM (2000b) Foraging strategies of southern Buller's albatrosses *Diomedea b. bulleri* breeding on The Snares, New Zealand. *J R Soc N Z* 30:299–318
- Sullivan BJ, Reid TA, Bugoni L (2006) Seabird mortality on factory trawlers in the Falkland Islands and beyond. *Biol Conserv* 131:495–504
- Surman CA, Nicholson LW (2009) The good, the bad and the ugly: ENSO-driven oceanographic variability and its influence on seabird diet and reproductive performance at the Houtman Abrolhos, Eastern Indian Ocean. *Mar Ornithol* 37:129–138
- Suryan RM, Irons DB, Benson J (2000) Prey switching and variable foraging strategies of black-legged kittiwakes and the effect on reproductive success. *The Condor* 102:374–384
- Sutherland WJ, Ens BJ (1987) The criteria determining the selection of mussels *Mytilus edulis* by oystercatchers *Haematopus ostralegus*. *Behaviour*:187–202
- Svanbäck R, Bolnick DI (2005) Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. *Evol Ecol Res* 7:993–1012
- Svanbäck R, Bolnick DI (2007) Intraspecific competition drives increased resource use diversity within a natural population. *Proc R Soc B Biol Sci* 274:839–844
- Svanbäck R, Eklöv P, Fransson R, Holmgren K (2008) Intraspecific competition drives multiple species resource polymorphism in fish communities. *Oikos* 117:114–124
- Svanbäck R, Persson L (2004) Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *J Anim Ecol* 73:973–982
- Svanbäck R, Persson L (2009) Population density fluctuations change the selection gradient in Eurasian Perch. *Am Nat* 173:507–516
- Svanbäck R, Rydberg C, Leonardsson K, Englund G (2011) Diet specialization in a fluctuating population of *Saduria entomon*: a consequence of resource or forager densities? *Oikos* 120:848–854
- Tickell WLN (2000) Albatrosses. Pica Press.

- Tinker MT, Bentall G, Estes JA (2008) Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proc Natl Acad Sci* 105:560
- Tinker TM, Guimarães PR, Novak M, Marquitti FMD, Bodkin JL, Staedler M, Bentall G, Estes JA (2012) Structure and mechanism of diet specialisation: testing models of individual variation in resource use with sea otters. *Ecol Lett* 15:475–483
- Torres LG, Read AJ (2009) Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. *Mar Mammal Sci* 25:797–815
- Torres LG, Sagar PM, Thompson DR, Phillips RA (2013a) Scaling down the analysis of seabird-fishery interactions. *Mar Ecol Prog Ser* 473:275–289
- Torres LG, Sagar PM, Thompson DR, Phillips RA (2013b) Scale-dependence of seabird-fishery data analysis and management: Reply to Croxall et al.(2013). *Mar Ecol Prog Ser* 493:301–304
- Torres L, Thompson D, Bearhop S, Votier S, Taylor G, Sagar P, Robertson B (2011) White-capped albatrosses alter fine-scale foraging behavior patterns when associated with fishing vessels. *Mar Ecol Prog Ser* 428:289–301
- Tremblay Y, Bertrand S, Henry RW, Kappes MA, Costa DP, Shaffer SA (2009) Analytical approaches to investigating seabird–environment interactions: a review. *Mar Ecol Prog Ser* 391:153–163
- Tuck GN, Polacheck T, Croxall JP, Weimerskirch H (2001) Modelling the impact of fishery by-catches on albatross populations. *J Appl Ecol* 38:1182–1196.
- Tuck GN, Thomson RB, Barbraud C, Delord K, Louzao M, Herrera M, Weimerskirch H (2015) An integrated assessment model of seabird population dynamics: can individual heterogeneity in susceptibility to fishing explain abundance trends in Crozet wandering albatross? *J Appl Ecol*
- Underwood AJ (1996) *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press
- Valen L Van (1965) Morphological variation and width of ecological niche. *Am Nat*:377–390
- Votier SC, Bearhop S, Ratcliffe N, Furness RW (2004) Reproductive consequences for great skuas specializing as seabird predators. *The Condor* 106:275
- Votier SC, Bearhop S, Ratcliffe N, Phillips RA, Furness RW (2004) Predation by great skuas at a large Shetland seabird colony. *J Appl Ecol* 41:1117–1128
- Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *J Appl Ecol* 47:487–497

- Votier SC, Bicknell A, Cox SL, Scales KL, Patrick SC (2013) A bird's eye view of discard reforms: bird-borne cameras reveal seabird/fishery interactions. *PLoS One* 8:e57376
- Votier SC, Furness RW, Bearhop S, Crane JE, Caldow RW, Catry P, Ensor K, Hamer KC, Hudson AV, Kalmbach E (2004) Changes in fisheries discard rates and seabird communities. *Nature* 427:727–730
- Votier SC, Grecian WJ, Patrick S, Newton J (2010) Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Mar Biol* 158:355–362
- Wakefield ED, Bodey TW, Bearhop S, Blackburn J, Colhoun K, Davies R, Dwyer RG, Green JA, Gremillet D, Jackson AL, Jessopp MJ, Kane A, Langston RHW, Lescroel A, Murray S, Nuz M Le, Patrick SC, Peron C, Soanes LM, Wanless S, Votier SC, Hamer KC (2013) Space partitioning without territoriality in gannets. *Science* 341:68–70
- Wakefield ED, Cleasby IR, Bearhop S, Bodey TW, Davies R, Miller PI, Newton J, Votier SC, Hamer KC (2014) Long-term individual foraging site fidelity – why some gannets don't change their spots. *Ecol Monogr*
- Wakefield ED, Phillips RA, Trathan PN, Arata J, Gales R, Huin N, Robertson G, Waugh SM, Weimerskirch H, Matthiopoulos J (2011) Habitat preference, accessibility, and competition limit the global distribution of breeding black-browed albatrosses. *Ecol Monogr* 81:141–167
- Wanless S, Harris MP, Morris JA (1992) Diving behaviour and diet of the blue-eyed shag at South Georgia. *Polar Biol* 12:713–719
- Wanless S, Harris MP, Redman P, Speakman JR (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar Ecol Prog Ser* 294:8
- Watanuki Y, Ishikawa K, Takahashi A, Kato A (2004) Foraging behavior of a generalist marine top predator, Japanese cormorants (*Phalacrocorax filamentosus*), in years of demersal versus epipelagic prey. *Mar Biol* 145:427–434
- Waugh SM, Filippi DP, Kirby DS, Abraham E, Walker N (2012) Ecological risk assessment for seabird interactions in Western and Central Pacific longline fisheries. *Mar Policy* 36:933–946
- Waugh SM, Sagar PM, Cossee RO (1999) New Zealand black-browed albatross *Diomedea melanophrys impavida* and grey-headed albatross *D. chrysostoma* banded at Campbell Island: recoveries from the South Pacific Region. *Emu* 99:29–35
- Waugh SM, Weimerskirch H, Chérel Y, Prince PA (2000) Contrasting strategies of provisioning and chick growth in two sympatrically breeding albatrosses at Campbell Island, New Zealand. *The Condor* 102:804–813

-
- Waugh SM, Weimerskirch H, Moore PJ, Sagar PM (1999) Population dynamics of black-browed and grey-headed albatrosses *Diomedea melanophrys* and *D. chrysostoma* at Campbell Island, New Zealand, 1942–96. *Ibis* 141:216–225
- Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Adv Mar Biol* 54:107–170
- Weimerskirch H (1990) The influence of age and experience on breeding performance of the Antarctic fulmar, *Fulmarus glacialisoides*. *J Anim Ecol*:867–875
- Weimerskirch H (1995) Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia* 102:37–43
- Weimerskirch H (2002) Seabird demography and its relationship with the marine environment. In: Schreiber, EA and Burger, J.(eds), *Biology of marine birds*. CRC Press, pp. 115–135
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res Part II Top Stud Oceanogr* 54:211–223
- Weimerskirch H, Bartle JA, Jouventin P, Stahl JC (1988) Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor*:214–219
- Weimerskirch H, Brothers N, Jouventin P (1997) Population dynamics of wandering albatross *Diomedea exulans* and Amsterdam albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: conservation implications. *Biol Conserv* 79:257–270
- Weimerskirch H, Corre M Le, Gadenne H, Pinaud D, Kato A, Ropert-Coudert Y, Bost CA (2009) Relationship between reversed sexual dimorphism, breeding investment and foraging ecology in a pelagic seabird, the masked booby. *Oecologia* 161:637–649
- Weimerskirch H, Corre M Le, Jaquemet S, Marsac F, others (2005) Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. *Mar Ecol Prog Ser* 288:251–261
- Weimerskirch H, Doncaster CP, Cuenot-Chaillet F (1994) Pelagic seabirds and the marine environment: foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proc Biol Sci*:91–97
- Weimerskirch H, Gault A, Cherel Y (2005) Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology* 86:2611–2622
- Weimerskirch H, Jouventin P (1987) Population dynamics of the wandering albatross, *Diomedea exulans*, of the Crozet Islands: causes and consequences of the population decline. *Oikos*:315–322

-
- Weimerskirch H, Jouventin P, Stahl JC (1986) Comparative ecology of the six albatross species breeding on the Crozet Islands. *Ibis* 128:195–213
- Weimerskirch H, Louzao M, Grissac S De, Delord K (2012) Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335:211–214
- Weimerskirch H, Mougey T, Hindermeier X (1997) Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behav Ecol* 8:635–643
- Weimerskirch H, Salamolard M, Sarrazin F, Jouventin P (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *The Auk*:325–342
- Werner EE, Mittelbach GG, Hall DJ (1981) The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology*:116–125
- Werner TK, Sherry TW (1987) Behavioral feeding specialization in *Pinaroloxias inornata*, the “Darwin’s finch” of Cocos Island, Costa Rica. *Proc Natl Acad Sci* 84:5506
- Wittenberger JF, Hunt GL (1985) The adaptive significance of coloniality in birds. *Avian Biol* 8:1–78
- Witt MJ, Godley BJ (2007) A step towards seascape scale conservation: using vessel monitoring systems (VMS) to map fishing activity (R Thompson, Ed.). *PLoS ONE* 2:e1111
- Woodward GL, Laverty TM (1992) Recall of flower handling skills by bumble bees: a test of Darwin’s interference hypothesis. *Anim Behav* 44:1045–1051
- Woo KJ, Elliott KH, Davidson M, Gaston AJ, Davoren GK (2008) Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *J Anim Ecol* 77:1082–1091
- Xavier JC, Croxall JP (2005) Sexual differences in foraging behaviour and diets: a case study of wandering albatrosses. In: *Sexual segregation in vertebrates: ecology of the two sexes*. Cambridge University Press, Cambridge, p 74–91
- Xavier JC, Trathan PN, Croxall JP, Wood AG, Podesta G, Rodhouse PG (2004) Foraging ecology and interactions with fisheries of wandering albatrosses (*Diomedea exulans*) breeding at South Georgia. *Fish Oceanogr* 13:324–344
- Yeakel JD, Patterson BD, Fox-Dobbs K, Okumura MM, Cerling TE, Moore JW, Koch PL, Dominy NJ (2009) Cooperation and individuality among man-eating lions. *Proc Natl Acad Sci* 106:19040–19043
- Yen PPW, Sydeman WJ, Bograd SJ, Hyrenbach KD (2006) Spring-time distributions of migratory marine birds in the southern California Current: Oceanic eddy associations and coastal habitat hotspots over 17 years. *Deep Sea Res Part II Top Stud Oceanogr* 53:399–418

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science & Business Media