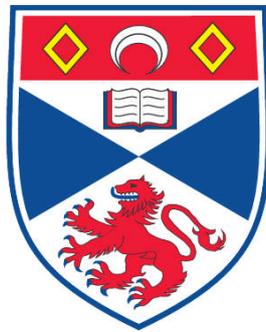


**ENVIRONMENTAL CONSTRAINTS ON THE FORAGING
BEHAVIOUR, SPATIAL USAGE AND POPULATION SIZES OF
ALBATROSSES**

Ewan D. Wakefield

**A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews**



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Environmental constraints on the foraging behaviour, spatial usage and population sizes of albatrosses

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BSc (Hons), MSc

A thesis submitted to the University of St. Andrews for the degree
of Doctor of Philosophy

School of Biology Sea Mammal Research Unit

12th August 2009

“..there is an infinite possibility about the sea; it may do what it has not been recorded to have done. It is not to be ordered; it may overleap the bounds human observation has fixed for it. It has a potency unfathomable. There is still something in it not quite grasped and understood – something still to be discovered – a mystery.”

Richard Jeffereies, *Nature near London*, 1883

Abstract

Satellite-tracking of wide-ranging, apex marine predators, combined with remote-sensing, can be used to test ecological hypotheses and to estimate spatial abundance. I used this approach to quantify the habitat usage of central place foraging black-browed albatrosses (BBA) from nine colonies, modelling population-level distribution as a function of habitat accessibility, habitat preference and conspecific competition. Throughout breeding, BBA preferred neritic waters, steeper bathymetry, and, during incubation, warmer sea surface temperatures. BBA from South Georgia also preferred highly dynamic oceanic waters. Foraging areas were partially spatially segregated with respect to colony and region, presumably to reduce intraspecific competition. Although such competition is often invoked to explain observed colony sizes, by accounting for travel costs, I demonstrate a strong relationship between the sizes of regional populations and the availability, accessibility and productivity of neritic waters, supporting the hypothesis that seabird populations are constrained by breeding season food availability. In response to this constraint, albatrosses have evolved to exploit energetically efficient gliding flight, allowing them to access prey 100-1000s of km from their colonies. Hence, I used satellite tracking and activity data to quantify the effects of relative wind speed on the flight speed of four albatross species. Groundspeed was linearly related to the wind speed in the direction of flight, its effect being greatest on wandering albatrosses, followed by BBA, light-mantled and grey-headed albatrosses, and airspeeds were higher in males than females. Commuting birds tended to encounter headwinds during outward trips and tailwinds on their return, such that return trips were faster. This supports the hypothesis that foraging upwind of the colony is more efficient but could also result from wind climate and the relative location of prey. The ability to use tracking data to estimate spatial usage is timely given the acute threat currently posed to albatrosses by incidental fisheries mortality.

I, Ewan David Wakefield, hereby certify that this thesis, which is approximately 53400 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in September 2005 and as a candidate for the degree of Doctor of Philosophy in September 2006; the higher study for which this is a record was carried out in the University of St Andrews between 2005 and 2009.

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I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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Acknowledgements

I embarked on this study in order to understand the natural world, both to appreciate its complexity more fully and in the hope that my findings might be used to protect nature from the ill-considered actions of man. Paradoxically, this meant using data that was collected by manipulating wild animals, for example by attaching small data loggers to them. While no albatrosses were injured during this process, I feel it is important to acknowledge that this did subject them to stresses that they would not experience in the course of their natural lives. For this reason, I would like to acknowledge, first and foremost, their contribution to my thesis. I hope I have done them justice.

As far as human animals go, I owe the success of my studies largely to my supervisors, to whom I would like to offer my sincerest thanks. As my primary supervisor at the British Antarctic Survey, Dr Richard Phillips has been unfailingly enthusiastic, supportive and resourceful, always ready to use his considerable ecological wisdom and intuition to develop my ideas and to guide me in a friendly way back onto the straight and narrow when my thoughts became too fanciful. In bringing a sympathetic humanity to bear in all aspects of his life, he sets a high standard to which I aspire. Similarly, during my visits to the University of St Andrews and in our correspondence, Dr Jason Matthiopoulos has taught me by example the value of rigorous thought and enquiry. Invariably, he has provided me with new insights into the problems I have been grappling with, pointing out the shortcomings of my approach when necessary but more often than not, casting things in new and far more illuminating light. My second supervisor at the British Antarctic Survey, Dr Phil Trathan, has always been ready to pass a seasoned eye over my work and has encouraged my studies in many ways.

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have been so much fun and support over the past four years. I would particularly like to mention the contribution made by Drs Angus Atkinson and Dave Barnes. Although neither of them was involved directly with my PhD, their thought-provoking conversation and kind advice they exerted a very positive influence on me and my studies.

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I am deeply indebted to my family, old and new, for their support during my studies and especially to my mother and father for fostering in me an enquiring nature and a love of the sea. Lastly and most deeply of all, I thank my wife, Melanie, for her forbearance, encouragement and love. In return I can only offer the prosaic gift of the dedication of this thesis.

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Explanatory note on the text

The first four chapters presented in the thesis were first prepared as manuscripts for submission to peer-reviewed journals. The publication status at the time of writing is indicated at the start of each chapter and proofs of those that are published or currently in press are presented in Appendix 5. Only minor alterations have been made to the text of these chapters in order to improve the readability and overall coherence of the thesis. For this reason, there is a small amount of repetition in some of the discursive sections of the thesis and the focus of the review presented in the introductory chapter is somewhat wider than might otherwise have been expected.

Chapter 1. Introductory review

This chapter is also published in Wakefield E.D., Phillips R.A. and Matthiopoulos J. (2009) Quantifying the habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series*, 391:165-182 (Appendix 5).

1.1 Introduction

Pelagic seabirds are large, long-lived and relatively easy to observe, capture, mark, and manipulate when they return to their colonies to breed. For these reasons, they have long been used as model organisms to address ecological questions, including those relating to: the regulation of population size (Lack 1954, Wynne-Edwards 1962, Ashmole 1963), the influence of the central place constraint on foraging behaviour (Orians & Pearson 1979, Costa 1991), the response of populations to inter and intraspecific competition (Croxall & Prince 1980, Furness & Birkhead 1984, Lewis et al. 2001), and environmental influences on life history traits (Lack 1968, Costa 1991, Weimerskirch 1992). Although providing partial answers to these questions, early studies were necessarily colony-based and therefore hampered by a lack of knowledge of the movements and behaviour of pelagic seabirds at sea (Ashmole 1971). Systematic observations from ships, which started in earnest in the 1970s (reviewed by Hunt et al. 1999, Ballance 2008), went some way to addressing this shortcoming. However, the spatiotemporal extent of such surveys was limited and it was not until the early 1990s, when it became possible to record the movements of individual seabirds using satellite-tracking devices (Jouventin & Weimerskirch 1990, Prince et al. 1992), that this aspect of the life styles of seabird could be investigated in detail. At the same time, in the field of oceanography, data provided by remote sensing technology has greatly improved our understanding of the effects of physical forcing on the marine environment (Longhurst 1998, Martin 2004). Furthermore, the development of auxiliary loggers for attachment to free-ranging birds is enabling the observation of an ever increasing range of behaviours (Ropert-Coudert & Wilson 2005).

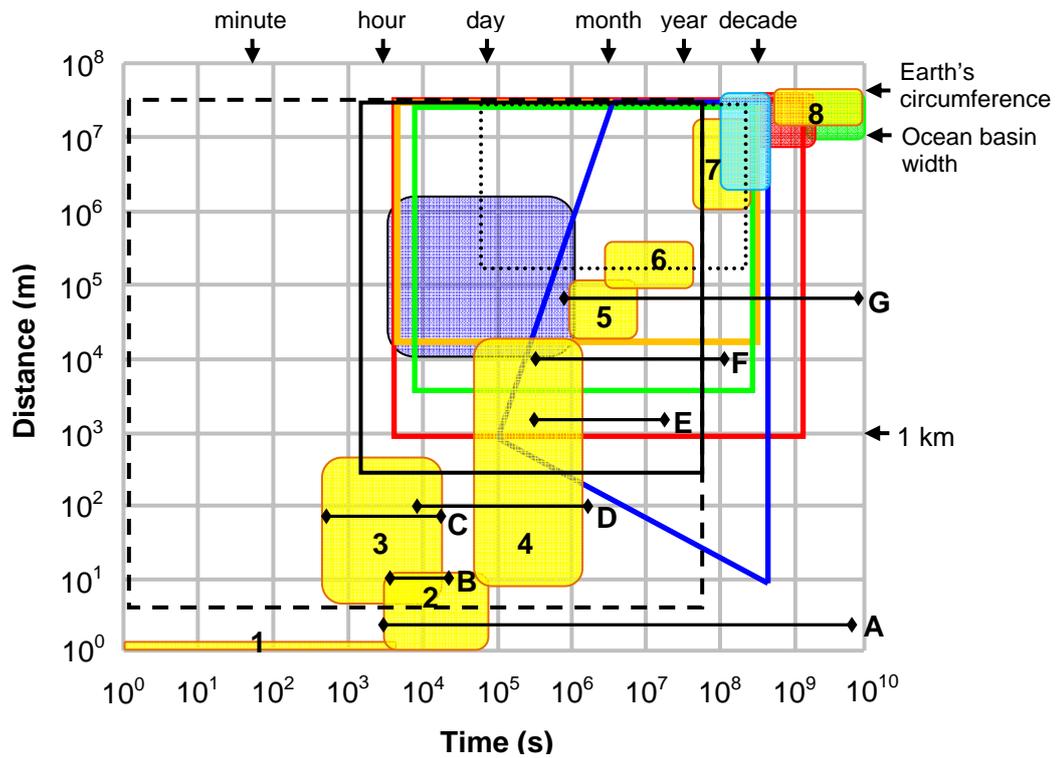
Intuitively, it might be supposed that by combining the ever-increasing volumes of data provided by these technologies, the study of pelagic seabirds would result in further, significant advances in ecological theory. However, although many seabird tracking studies have had widespread impact (Weimerskirch et al. 1993, Weimerskirch et al. 1997a, Fauchald & Tveraa 2003 are highly cited examples and many more are referred to in this review), I argue a lack of appropriate statistical techniques has hampered further progress. Fortunately, in recent years, significant innovations have been made in the analysis of individual movements and spatial modelling (e.g. Aebischer et al. 1993, Jonsen et al. 2003, Aarts et al. 2008), a process to which seabird ecologists have themselves contributed (e.g. Fauchald & Tveraa 2003, Pinaud & Weimerskirch 2005). It is timely, therefore, to review the state of the art and to make suggestions as to how these new and developing techniques might be more widely applied. In particular, I focus on quantifying and modelling habitat use and preferences of pelagic seabirds, using analogous approaches to those used frequently in the discipline of landscape ecology (Wiens et al. 1993, Lima & Zollner 1996, Scott et al. 2002).

In this review I use the term *habitat* to refer to a set of environmental conditions rather than to a geographical region (Hall et al. 1997), and *habitat use* to the proportion of time that an animal spends in a given habitat. Different habitats are rarely equally available, and *habitat preference* is defined as the disproportionality between usage and availability, commonly their ratio (Manly et al. 2002). I define pelagic seabirds as those which derive their nourishment from the sea but do not forage in the intertidal, benthic or demersal zones. Hence, this group, which includes albatrosses, petrels, frigatebirds, tropicbirds, boobies, some terns, etc. (c.f. Ashmole 1971) tends towards a single guild, i.e. wide-ranging, surface feeding and relatively shallow-diving predators. It excludes deep-diving birds, such as penguins, cormorants and alcids (which have greater functional affinities with pinnipeds), gulls and most terns (which tend to feed inshore). The studies reviewed are inevitably dominated by those on larger birds such as albatrosses and some petrels, which were the first to be fitted with tracking devices. However, continued miniaturization is allowing the tracking of ever smaller species, and hence analytical techniques discussed will be applicable to all pelagic seabirds. Before describing these approaches in detail, I discuss the context of their application

by considering issues of scale, measurement, behaviour, habitat availability, habitat accessibility and competition.

1.2 Scales of pelagic seabird-environment interactions

It has long been acknowledged that physical and biological processes result in patchy distributions of habitats and organisms (Dubois 1975, Wiens 1976, Haury et al. 1977). Time lags tend to increase with spatial scale, and so these patches can usefully be regarded as forming a spatiotemporal hierarchy (Kotliar & Wiens 1990). This approach is often seen in biological oceanography (Haury et al. 1977, Levin 1993), and has been applied more recently in studies of pelagic seabirds (Fauchald 1999, Fauchald et al. 2000, Pinaud & Weimerskirch 2005). The hierarchical patch distribution of the lower and mid-trophic level organisms that constitute the prey of pelagic seabirds, occurs as a consequence of both behaviour (e.g. shoaling/swarming and vertical and horizontal migration (Levin 1993, Folt & Burns 1999)) and physical forcing (e.g. Friedlaender et al. 2006, McGillicuddy et al. 2007, Sokolov 2008). Physical phenomena, such as wind and tide-induced overturning, currents, eddies, fronts and meanders (Fig. 1.1, Table 1.1) act, firstly, by transporting nutrients into the photic zone, stimulating new primary and secondary production (reviewed by Mann & Lazier 2006) and secondly, by advecting and aggregating biomass (Perry et al. 1993, Abraham 1998, Bertrand et al. 2008). These processes may be in a steady-state (e.g. geostrophic currents) or have a characteristic periodicity (e.g. tidal, diel, seasonal), whereas more episodic processes such as transient oceanic phytoplankton blooms tend to be predictably related to other events such as wind-driven mixing (Abbott & Barksdale 1991).



Tracking systems	Biophysical phenomena	
--- GPS	Turbulence	Regime shifts
— PTT	1. Micro scale	Long-term climate fluctuations
..... GLS	2. Fine scale	
	3. Langmuir convection	
	4. Submesoscale eddies	
	5. Mesoscale eddies	
	6. Warm/cold core rings	
	7. Ocean gyres	
	8. Thermohaline circulation	
Remote sensing	Horizontal variability in mixed layer depth	Width & lifetime of fronts associated with:
SST		A. Freshwater plumes
chl a and SLA		B. Density compensation
SSR		C. Internal waves
wind	El Niño Southern Oscillation	D. Topographic features
		E. Tidal mixing/shelf seas
		F. Shelf break
		G. Baroclinic currents

Figure 1.1 Spatiotemporal scales of climatic and oceanographic processes compared to the resolution and coverage of human observation in pelagic seabird habitat studies. Tracking systems shown are PTTs (Platform Terminal Transmitters), GPS (Global Positioning System tags) and GLS (geolocator tags). Remotely sensed variables include SST, chlorophyll *a* (chl *a*), Sea Level Anomaly (SLA), Sea Surface Roughness (SSR) and wind speed and direction. The spatiotemporal coverage achievable by ship-

based surveys is limited by maximum vessel speed (assumed here to be 15 knots). Adapted from Kaiser et al. (2005) and Haury et al. (1977).

Patches of habitat and prey occurring at different locations in this spatiotemporal hierarchy may be more or less profitable, or predictable, in their occurrence. For example, it is increasingly recognized that, at the mesoscale, the occurrence of the prey of temperate and polar pelagic seabirds is to some extent predictable, while that of tropical seabirds is less so (Hunt et al. 1999, Weimerskirch 2007, Weimerskirch et al. 2008) (to avoid ambiguity, I use the terms for spatial scale proposed by Haury et al. (1977) (Fig. 2.1)). Although the behaviour of pelagic seabirds themselves varies over timescales from seconds (Weimerskirch et al. 2005b) to years (Phillips et al. 2005b), and distances of metres (Pennycuik 1982) to tens of thousands of km (Shaffer et al. 2006), clear associations are often seen at scales corresponding to the various biophysical phenomena that lead to patchiness. For example, shearwaters *Puffinus* spp. forage at shelf sea tidal fronts that are 10s of km long (Begg & Reid 1997, Jahncke et al. 2005), and both large and medium-sized procellariiformes congregate at coarse to mesoscale shelf break fronts (Hoefler 2000, Pinaud & Weimerskirch 2002). A diverse range of pelagic seabirds associates with the edges of mesoscale eddies (Nel et al. 2001, Weimerskirch et al. 2004), and at coarse, meso- and macroscales, many pelagic seabird show affinities for either eutrophic, mesotrophic or oligotrophic waters (Hyrenbach et al. 2002, Awkerman et al. 2005, Pinaud & Weimerskirch 2005). In the equatorial Pacific, piscivorous seabirds prefer well-stratified waters, characterized by a deep and marked thermocline, whereas planktivores prefer areas with shallower, weaker thermoclines (Ribic et al. 1997, Spear et al. 2001, Vilchis et al. 2006). At the megascale, the global migratory movements of sooty shearwaters *Puffinus griseus* ensure that they are able to forage in highly productive upwelling areas year-round (Shaffer et al. 2006). Over decadal time scales, the association between sooty and pink-footed shearwaters *P. creatopus* with the California current system varies in parallel with the El Niño-Southern Oscillation (ENSO) (Oedekoven et al. 2001, Hyrenbach & Veit 2003), and over longer time scales still, changes in the size and distribution of seabird colonies occur in response to regime shifts and climate fluctuations (Olson & Hearty 2003, Jenouvrier et al. 2005, Lewis et al. 2009).

Table 1.1 Selected physical processes and marine phenomena, including: characteristic spatial and temporal scales; effects on primary production (PP), secondary production (SP) and biomass aggregation (AG), and; areas in which they occur.

Process/phenomenon	Scale		Effects ²			Areas/ examples	
	Horizontal (km) ¹	Temporal	PP	SP	AG		
Turbulence	Small scale turbulence caused by wind, currents, tides, etc.	0.00001 - 0.001	seconds - minutes	↓	↓	All	
	Large scale turbulence caused by wind, currents, tides, etc.	0.001 - 0.01	1 hour - 10 hours	↓	↓	All	
	Sub-mesoscale eddies/spiral eddies	0.01 - 20	days - weeks	?	?	✓	All
	Meanders, barotropic mesoscale eddies	20 - 100	weeks - months	↑	↑	✓	Margins of ocean currents
	Meanders, warm and cold core baroclinic rings	100 - 300	1 month - 1 year	↓	↑	✓	Margins of major ocean currents, Gulf Stream rings, ACC rings
	Langmuir convection cells	0.005 - 0.5	minutes - hours	?	?	✓	All
	Changes in mixed layer depth caused by wind, insolation, fresh water, currents, tides, upwelling, internal waves, fronts, etc.	10 - 1000	hours - weeks	↓	↓	✓	All. Spring and autumn blooms in temperate latitudes (only really marked in N Atlantic)
Fronts	Freshwater plumes and plume fronts	0.005 - 100	hours - months	↑	↑	✓	Coastal waters
	Compensation fronts	0.01 - 5	hours - days	↑	?	?	All areas with deep mixed layer and significant thermohaline variability
	Surface rips/slicks caused by internal waves/bores	0.1 - 1	minutes - hours	↑	?	✓	Neritic waters

Circulation	Fronts associated with geomorphic features	0.1 - 100	hours - weeks	↑	↑	✓	All areas except central ocean basins
	Shelf sea fronts caused by tidally induced mixing	2 - 10-100	days - months	↑	↑	✓	Neritic waters, Patagonian Shelf
	Coastal upwelling due to Ekman transport and upwelling fronts.	10 - 100-1000	5 days - years	↑	↑	✓	Eastern margins of ocean basins at sub-tropical latitudes, Humboldt and Benguela upwellings
	Shelf-break fronts	10 - 500	weeks - months	↑	↑	✓	All shelf breaks but more intense on western sides of ocean basins, Patagonian Shelf
	Fronts in baroclinic currents, shear fronts	50 - 21 000	weeks - years	↑	↑		Open ocean, Antarctic Polar Front
	Water masses	100 - 15 000	Months-decades	-	-		Antarctic surface water, sub Antarctic surface water, subtropical surface water
Sea ice	Marginal Ice Zone and polynyas	0.01 - 200	days - months	↑	↑	✓	Polar waters
Biogeochemical processes	Trace nutrient limitation	1000 - 10 000	weeks-years	↓	↓		Eastern equatorial Pacific, Southern Ocean, possibly South Pacific

Climatic fluctuations	El Niño - Southern Oscillation	15 000 - 40 000	4 years - 7 years	↑	↓	Eastern Pacific and worldwide
	Other climatic oscillations and regime shifts	15 000 - 40 000	10 years - 100 years	↓	↓	Antarctic Oscillation; Pacific Decadal Oscillation
	Medium/Long term climate fluctuations	40 000	>100 years	↓	↓	All

¹ Horizontal scale refers to diameter range of turbulent eddies; width range of Langmuir circulation and typical change in the mixed layer depth; typical width and length of fronts; width of polynyas and MIZ for sea ice and horizontal extent of other processes.

² Process tends to increase (↑), decrease (↓) or have both effects on production (↕),

✓ process tends to cause physical aggregation of biomass.

Based on (Lutjeharms et al. 1985, Moore et al. 1999, Eldevik & Dysthe 2002, Rudnick & Martin 2002, Kaiser et al. 2005, Mann & Lazier 2006).

That pelagic seabirds may express changes in habitat use and preference over such a wide range of scales raises a number of important analytical issues. Firstly, the observable window in the spatiotemporal spectrum is limited by the performance of both tracking and remote sensing systems (Fig. 1.1, discussed in detail below). This, in turn, limits the hypotheses that can currently be addressed using individual movement data. Similarly, the way that hypotheses are framed and tested may vary with scale (Levin 1992). If there is no *a priori* knowledge of the scale at which the phenomenon of interest occurs, then this can be determined either during exploratory data analysis using indirect techniques such as First Passage Time analysis (see Behaviour) or by adopting a multi-scale approach (e.g. Garcia & Ortiz-Pulido 2004, Suryan et al. 2006).

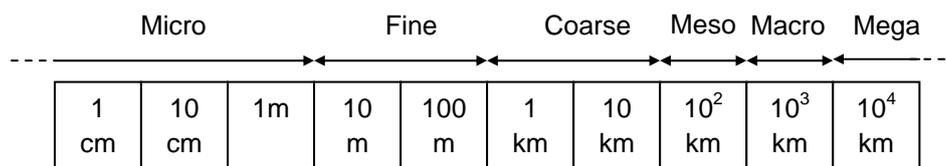


Figure 2.1 Definitions of terms used to describe spatial scale in habitat studies of pelagic seabirds (after Haury et al. 1977).

1.3 Measuring the marine environment

The spatiotemporal coverage and resolution of environmental data available to seabird ecologists is limited. Ship-based studies can record seabirds, prey and their environment simultaneously at high resolution (Fig. 1.1) (e.g. Pakhomov & McQuaid 1996). Similarly, environmental data can be collected by some animal tracking devices (e.g. Shaffer et al. 2006), auxiliary loggers (reviewed by Wilson et al. 2002), autonomous buoys, moorings, etc. However, these approaches do not provide the synoptic view of all potentially available foraging areas, which could extend over millions of km², that is necessary for habitat preference analyses. Hence, satellite remote sensing is generally the best source of environmental data.

Continuing innovation in satellite remote sensing is making more and higher resolution environmental variables available (Martin 2004). However, there are spatial and temporal limitations. Firstly, there is a trade-off which tends to prioritize global or near-global data collection at the expense of resolution, such that sub km phenomena remain poorly resolved (Table 1.2). Nevertheless, innovative instruments such as Synthetic Aperture Radars (SAR) can now detect sub-mesoscale eddies, freshwater plumes, sea ice, etc. with 10 m resolution (reviewed by Gens 2008). Secondly, only surface properties are measured by satellites. Although pelagic seabirds feed at or near the surface, their prey often include mesopelagic and deeper dwelling species (e.g. Croxall & Prince 1980, Cherel & Klages 1998). Inferences can be made about the three-dimensional structure of water masses using remotely sensed sea level and sea surface temperature (SST), especially by using these data to drive numerical oceanographic models (Thorpe et al. 2005), which can provide estimates of current velocity, temperature, salinity, etc, at horizontal resolutions as low as $1/8^\circ$ ($\sim 13\text{km}$) throughout the water column (Aksenov & Coward 2001). In addition, tags fitted to the animals themselves may be used to sample the water column (Wilson et al. 2002). Conductivity-temperature-depth tags, which are large, have only been deployed on large animals such as pinnipeds (Biuw et al. 2007, Boehme et al. 2008), but smaller temperature-depth recorders are deployed routinely on penguins. With continued miniaturization, these and similar instruments are likely to become more useful in the study of flying pelagic seabirds (Daunt et al. 2003, Garthe et al. 2007b). Thirdly, cloud cover renders many passive SST and chl-a sensors ineffective (Woodward & Gregg 1998). To achieve full spatial coverage, composite images (weekly or monthly) can be produced but this may result in poor resolution of dynamic mesoscale features (Uz & Yoder 2004). In the case of SST, this problem is increasingly circumvented by the use of interpolated datasets. These combine multi-satellite and *in situ* data (from ships, ARGO floats, etc.) to provide daily cloud free images at $1/20^\circ$ ($\sim 6\text{km}$) resolution, and are thus able to resolve all but very fine scale features (Stark et al. 2007). Lastly, there may be spatiotemporal lags between the measurement of biophysical processes (the recession of sea ice, the shedding of mesoscale eddies etc.) and their effects at higher trophic levels (see Mann & Lazier (2006) for examples). The magnitude of such lags depends on many factors, including: the rate at which primary production passes to

higher trophic levels, which varies between ecosystems (Verity & Smetacek 1996, Clarke 2003); the trophic level of the study species (Cherel et al. 2006); the rate of advection within the study area and movement capabilities of prey species themselves (e.g. Murphy et al. 2004). Although in some studies there may be enough information to determine likely lag times and/or distances *a priori*, potentially based on the relative timing of life history events and seasonal peaks in primary production (e.g. Laidre et al. 2008), it may be more pragmatic to investigate such effects on a study-by-study basis, by comparing the strength of relationships between spatial usage and biophysical covariates lagged at a range of plausible distances (e.g. Littaye et al. 2004, Croll et al. 2005).

Table 1.2 Measurements made using satellite-borne instruments and the oceanographic processes and phenomena that they can be used to identify (for references, see text).

Variable	Res. (km)	Revisit time (d)	Processes/phenomena detected in pelagic seabird tracking studies (other examples)
Sea surface temperature	1-4	0.25-3	Water mass, baroclinic currents & fronts (mesoscale eddies & meanders, shelf sea fronts, shelf-break fronts, coastal upwelling)
Sea surface colour	4	1	Primary production (suspended sediment and gelbstoffe concentration, coastal processes)
Sea level	4	1	Mesoscale eddies (meanders, shelf sea fronts, shelf-break fronts, baroclinic currents and fronts, coastal upwelling, El Niño)
Passive microwave	25	1	Sea ice (water masses, baroclinic currents & fronts)
Backscatter	25-50	1	Wind field (sea ice)
Sea surface roughness	0.01-1	3-35	(Sub-mesoscale eddies, internal waves, freshwater plumes and small scale fronts, sea ice concentration, polynyas)

Despite their limitations, remotely-sensed environmental data can describe habitats in a biologically meaningful way (Table 1.2), especially when multiple variables are used synergistically to derive other descriptors of habitat, such as the rate of primary production (Behrenfeld & Falkowski 1997a), mixed layer depth (Zawada et al. 2005), and measures of mesoscale activity (e.g. Eddy Kinetic Energy (Ducet et al. 2000), or to track the movement of fronts (Miller 2004). Finally, it can also be useful to consider indices of anthropogenic activity, especially fishing effort, in spatial usage/habitat studies. This is because some pelagic seabird species scavenge waste from, and/or target the same resources as fisheries (Petersen et al. 2008, Bugoni et al. 2009).

1.4 Tracking techniques and data preparation

The measurement of individual movement using tracking devices has been reviewed by Tremblay, Burger & Shaffer (2008) and Phillips et al. (2008). Briefly, Platform Terminal Transmitter (PTTs) were first deployed on large species: giant petrels *Macronectes* spp. (Parmelee et al. 1985) and wandering albatrosses *Diomedea exulans* (Jouventin & Weimerskirch 1990, Prince et al. 1992). Since then, almost all albatross species have been tracked (BirdLife-International 2004), as have a growing number of other pelagic seabird taxa, increasingly using Global Positioning System (GPS) tags. The species tracked vary from medium to large petrels, including *Procellaria* spp. (e.g. Freeman et al. 1997, Weimerskirch et al. 1999); *Fulmarus* spp. (e.g. Falk & Moller 1995), *Calonectris* spp. (e.g. Gonzalez-Solis et al. 2007, Magalhaes et al. 2008), and *Puffinus* spp. (e.g. Shaffer et al. 2006, Guilford et al. 2009), to sulids (e.g. Hamer et al. 2000, Weimerskirch et al. 2005b) and frigatebirds *Fregata* spp. (Weimerskirch et al. 2004). The relatively large size and mass of tracking devices initially prevented their deployment on smaller species (it is generally accepted that payloads of $> \sim 3\%$ of body mass can result in behavioural changes (Kenward 2001, Phillips et al. 2003)). Recently, however, species as small as the Cook's petrel *Pterodroma cookii* ($\sim 200\text{g}$) have been tracked using archival geolocators (Rayner et al. 2008), which can weigh as little as 1g (Mk.10, British Antarctic Survey, Cambridge, UK).

PTTs, geolocators and GPS tags have very different performance characteristics (Fig. 1.1), there being a general trade-off between temporal resolution, deployment duration and device mass. PTTs use the ARGOS (CLS, Toulouse, France) system to transmit location data via satellite to ground receiving stations, allowing animals to be tracked in near real time and without the need to recover the tag. PTTs can provide up to 40 locations/day. However, the accuracy and precision of these locations is degraded by poor satellite visibility, changes in temperature, erratic tag movements and high speeds (Brothers et al. 1998, Britten et al. 1999, Vincent et al. 2002, Nicholls et al. 2007, Soutullo et al. 2007), all of which are characteristic of deployments on pelagic seabirds. Hence, locations received from these species tend to be low quality, predominantly ARGOS location classes 0, A, and B (Nicholls et al. 2007, Soutullo et al. 2007). Trials on free-ranging birds indicate that these location classes have a median (and 90th percentile) accuracy of 7 (29), 13 (87) and 35 (209) km respectively, with accuracy being log-normally distributed (Soutullo et al. 2007). Transitions between behaviours such as resting, commuting, searching, diving, etc. may result in systematic changes in accuracy and precision, but these and many other aspects of errors associated with ARGOS locations for free-ranging seabirds have not been quantified (Nicholls et al. 2007). This shortcoming could be addressed by comparing PTT and GPS locations received from seabirds (Soutullo et al. 2007). Despite these issues, PTTs remain useful, especially for tracking small to medium-sized (~ 300-1000 g) species (Soutullo et al. 2007).

Given their considerably better accuracy (~ 95% of locations within 10 m of the true location, Steiner et al. (2000), Fukuda et al. (2004)), GPS tags are increasingly used in preference to PTTs (Weimerskirch et al. 2002, Gremillet et al. 2004, Awkerman et al. 2005). They also have the advantage that they can obtain locations at high temporal resolutions (up to 1 Hz, for periods of hours), allowing fine-scale behavioural information to be inferred from movement (Weimerskirch et al. 2007, Guilford et al. 2008). Initially, GPS units were archival and so had to be retrieved to obtain data. However, integration with the ARGOS system now allows data to be received via satellite (Yasuda & Arai 2005), and solar powered combined GPS-PTT devices have been deployed for >2 years (e.g. Urios et al. 2007).

Geolocators record ambient light levels, which, following tag retrieval, are used to derive two positions a day, with comparatively low mean accuracy of ~ 190 km (SD 110 km) (Phillips et al. 2004a). Although light-based geolocation cannot provide useable latitude estimates around the equinoxes, some loggers also record temperature, which in combination with remotely-sensed SST data can improve accuracy (Teo et al. 2004, Shaffer et al. 2005). Compared to PTTs and GPS loggers, geolocators are smaller, cheaper and can be attached to the bird's tarsus, allowing multiyear deployments and larger sample sizes (e.g. Phillips et al. 2005b).

Given the inaccuracies inherent, to a certain degree, in data provided by all tracking devices, improbable positions are often removed by filtering prior to detailed analysis (e.g. McConnell et al. 2002), and missing locations estimated by linear or curvilinear interpolation (e.g. Tremblay et al. 2006). Alternatively, by making the assumption that animals move in random walks, probabilistic estimates of locations can be made (Horne et al. 2007, Bost et al. 2009). However, the assumptions implicit in such preliminary procedures may bias further analysis. For example, albatross tracking data have been filtered such that locations resulting in speeds >80 km/h are flagged as erroneous. In reality, birds flying in strong tail winds have been shown to fly well in excess of this speed (Catry et al. 2004a). Ideally, therefore, observation error and movement biology should be dealt with simultaneously, as in the state-space modelling approach (SSM) (Patterson et al 2008).

1.5 Behaviour

Birds may engage in many different behaviours, including foraging, commuting, migrating, preening, resting, etc. These may be initiated by cues that are exogenous (e.g. a change in wind direction or moving into prey patch) or endogenous (e.g. physiological state). Hence, habitat use and preference is dependent on time-activity budgets, which in turn change with life history stage and environmental conditions, etc.

(Phalan et al. 2007, Guilford et al. 2009). As such, behavioural state is informative of habitat use and preference, and *vice versa*. During breeding, pelagic seabirds tend to commute to and from areas with more or less predictable resources (Weimerskirch 2007), so a key aim is often to distinguish between putative commuting (or taxis) and searching (or foraging) behaviour (Lima & Zollner 1996). Hence, many individual-based studies aim to infer behavioural state from measures of path geometry, such as speed and direction (Johnson et al. 2002, Jonsen et al. 2007). At all but the micro-scale, tracks tend to deviate from straight lines, and hence the divergence of the measured from the actual route increases with the time interval between locations (Alerstam et al. 1993). Very low speeds occur when the bird is not in flight, and are thus variously interpreted as foraging (Weimerskirch et al. 1997c, Weimerskirch & Guionnet 2002), resting (Nel et al. 2001), waiting for favourable winds (Murray et al. 2002), or rafting prior to entering a colony (Awkerman et al. 2005, Guilford et al. 2008). However, these behaviours have not yet been distinguished using path geometry alone.

It is assumed that during transit birds follow direct paths and move at high speeds at all scales of measurement, whereas, based on theoretical predictions and observations of birds at sea, regular changes in flight direction and low speeds are considered indicative of foraging - a behaviour termed Area-Restricted Search (ARS) (reviewed by Kareiva & Odell 1987). Hence, speed (Fernandez & Anderson 2000, Nel et al. 2001, Hyrenbach et al. 2002), turning angle (Fernandez et al. 2001, Huin 2002), coefficient of concentration (Hyrenbach et al. 2002, Hyrenbach & Dotson 2003), residence time (Prince et al. 1998), fractal dimension (Nams 2005, Tremblay et al. 2007) and First Passage Time (Fauchald & Tveraa 2003, Pinaud & Weimerskirch 2005) have all been used as indirect indices of ARS. Peaks in the variance of FPT, which is the time required for an animal to cross a circle of a given radius, indicate the spatial scales at which birds carry out ARS (Fauchald & Tveraa 2003, Pinaud & Weimerskirch 2005), making it a particularly useful tool for exploratory data analysis. However, the spatial resolution achievable with FPT and fractal dimension analyses is limited by that of the tracking data, such that results obtained from analyses of ARGOS locations may be unreliable at coarse to fine scales (Bradshaw et al. 2007, Pinaud 2008). Furthermore, although it may be intuitive to suppose that more tortuous tracks

indicate foraging, this assumption, and perhaps more importantly its corollary that birds engaged in direct movement are not foraging, has rarely been tested. Indeed, there is evidence to the contrary, in that grey-headed albatrosses *Thalassarche chrysostoma* are capable of foraging successfully even in very rapid ($>110 \text{ km h}^{-1}$), directed flight (Catry et al. 2004a), wandering albatrosses fitted with stomach temperature loggers do not capture prey at high rates during bouts of ARS (Weimerskirch et al. 2007), and tracks with ARS-like properties can arise due to location errors (Robinson et al. 2007, Pinaud 2008).

Auxiliary loggers are increasingly used to collect behavioural data (reviewed by Ropert-Coudert & Wilson 2005). Frequent landings and takeoffs recorded by activity loggers are regarded as indicative of foraging (Weimerskirch et al. 1997c), and time-depth recorders (Shaffer et al. 2006, Weimerskirch et al. 2008) and, particularly, stomach temperature loggers (Weimerskirch et al. 1994, Catry et al. 2004b) provide more direct measures. Accelerometers have been used to identify diving, feeding and flight behaviour (Ropert-Coudert & Wilson 2005, Weimerskirch et al. 2005b). However, regardless of whether behavioural state is measured directly or inferred from path geometry, it should be cautioned that although some behavioural states are inherently categorical (e.g. in flight vs. not in flight), others may fall on a continuous spectrum (e.g. commuting vs. ARS) and ideally, therefore, should be treated as continuous covariates during analyses.

1.6 Habitat availability and accessibility

The processes leading to patchiness in the distribution of pelagic resources also result in differences in the relative availability of habitats. Although incorporated in some recent studies of pelagic habitat preference (e.g. Pinaud et al. 2005, Louzao et al. 2006, Redfern et al. 2006), the geographical area under scrutiny is often defined arbitrarily by a boundary that broadly encompasses the known foraging range. A more biologically realistic approach would be to consider the area bounded by a species' maximum

foraging range from a particular colony (Awkerman et al. 2005). Furthermore, within this area, the energetic and temporal cost of moving to different habitats, termed habitat accessibility, may differ. Hence, during breeding, when birds act as central place foragers, accessibility varies inversely with distance from the colony (Orians & Pearson 1979, Matthiopoulos 2003). Furthermore, as with other marine central place foragers, such as pinnipeds and penguins (Thompson et al. 2003, Boersma & Rebstock 2009), the severity of the central place constraint, and therefore the potential foraging range, varies with life history stage (Weimerskirch et al. 1993, Shaffer et al. 2003). Although the majority of tracking studies have been carried out on breeding birds, analyses of habitat use have not generally accounted for these constraints. Yet, colony distance can be included as a candidate explanatory covariate in spatial usage models (Louzao et al. 2006), and an even more systematic approach is to compare observed spatial usage to a null model in which available habitats are sampled quasi-randomly, at a rate proportional to accessibility (Matthiopoulos 2003, Aarts et al. 2008). In the latter case, the apparent availability of habitats is then dependent not only on their spatial extents, but also on distance from the colony.

Recent research has highlighted the effects of wind on the energetic and temporal costs of flight incurred by seabirds (Weimerskirch et al. 2000b, Suryan et al. 2008, Wakefield et al. in press). Flight performance is dependent, in part, on wing loading, leading to suggestions that birds with higher wing loadings are better adapted to windier areas (Shaffer et al. 2001, Suryan et al. 2008). Migrating and breeding procellariiformes route their journeys and make behavioural decisions so as to exploit favourable winds at fine to mega-scales (Murray et al. 2003, Shaffer et al. 2006, Felicísimo et al. 2008). For example, using a grid-based mechanistic model, geolocator and remotely sensed wind data, Felicísimo et al. (2008) showed that Cory's shearwaters follow least cost paths during migration. Indeed, many pelagic seabirds may be constrained during non-breeding periods to use discrete migration corridors (Gonzalez-Solis et al. 2007, Guilford et al. 2009), and to windier areas in general, limiting habitat accessibility outside the breeding season. Furthermore, because adults gain mass when collecting prey for their chick, it has been hypothesized that prevailing winds can lead to asymmetry in the accessibility of areas up and downwind of colonies

(Pennycuik 1989). Hence, wind may affect accessibility during both breeding and non-breeding stages. However, the pelagic wind field is highly dynamic and modelling its effect on transport costs and accessibility is challenging.

1.7 Inter and intraspecific interactions

The spatial usage of animals may vary in response to both inter and intraspecific competition. The latter is often more intense because of a lack of niche partitioning between conspecifics (Begon et al. 2006). In central place foragers, such as colonial insects and land birds, direct intraspecific competition may result in the spatial partitioning of foraging areas (Dukas & Edelman-Keshet 1998, Adler & Gordon 2003). An analogous situation arises in seabirds foraging from adjacent colonies (e.g. Huin 2002, Ainley et al. 2003, Gremillet et al. 2004). As seabirds are not territorial at sea, indirect competition is thought to be the mediating factor (Furness & Birkhead 1984, Lewis et al. 2001). A hinterland model has been proposed (Cairns 1989), but this predicts absolute partitioning, whereas tracking data have shown partial partitioning, if any (Stahl & Sagar 2000, Huin 2002, Gremillet et al. 2004). This is probably because intensity of intraspecific competition varies with conspecific density and so decreases as a continuous function of distance from neighbouring colonies (Furness & Birkhead 1984). While direct competition with conspecifics and other species is detrimental to foraging success, other interactions between these groups may be beneficial. e.g. the presence or behaviour of other predators may indicate the location of prey, leading to local enhancement (Silverman et al. 2004), or network foraging (Au & Pitman 1986). Multi-species feeding associations, for example between dolphins or tuna and seabirds, may even be cooperative (Wittenburger & Hunt 1971). Few tracking studies have so far considered the response of pelagic seabirds to both competitors and habitat (Gremillet et al. 2004, Ford et al. 2007). However, this is now a realistic proposition given that conspecifics from neighbouring colonies and sympatric species from the same foraging guild can be tracked simultaneously.

1.8 Analyses and models

Early pelagic seabird tracking studies tended to describe habitat use qualitatively, often presenting either individual tracks (e.g. Weimerskirch et al. 1993, Prince et al. 1998) or locations from a number of animals overlaid on maps of environmental variables (e.g. Cherel & Weimerskirch 1995, Anderson et al. 1998). This was a pragmatic way of identifying likely macroscale preferences, such as those for neritic or oceanic waters (e.g. Huin 2002, Anderson et al. 2003). More recent analyses have tended to evolve from these approaches rather than from a theoretical base and the emphasis on hypothesis testing using conventional statistical techniques has various drawbacks (McCarthy 2007). For example ANOVA, Mann-Whitney tests and *t*-tests have been used to compare the amount of time spent by birds in regions that differed in bathymetry, SST, productivity and fishing effort (Waugh et al. 1999, Nel et al. 2000, Nel et al. 2002, Waugh & Weimerskirch 2003, Petersen et al. 2008). A weakness of this approach is that habitat categories perceived by humans may have little biological meaning (Aarts et al. 2008). Consideration should be given to the mechanisms through which covariates are hypothesized or known to affect spatial usage before deciding whether they should be treated as continuous or categorical (Hill & Binford 2002). For example, it is known *a priori* that neritic and oceanic waters are dominated by different suites of oceanographic phenomena (e.g. seasonally mixed vs. permanently stratified waters), so it may be appropriate in some cases to bin depth into these categories. It is less clear why productivity, SST, etc., should be classified into different regimes, other than to facilitate the use of conventional statistical tests. Differences in habitat use among trip types, breeding stages, sex, year, populations and species have also been shown through a hypothesis testing approach, using chi-squared tests, *t*-tests, ANOVA, Generalized Linear Models (GLMs) and mixed-effects models (Hyrenbach et al. 2002, Nicholls et al. 2002, Phillips et al. 2004b, Pinaud et al. 2005, Rayner et al. 2008, Shaffer et al. this issue).

Core areas of spatial usage are frequently identified using kernel density (KD) estimates (e.g. Wood et al. 2000, Hyrenbach et al. 2002). KD itself has been treated as

a response variable (Awkerman et al. 2005), and spatial correlations between KD and environmental variables have been used to infer habitat associations (Rayner et al. 2008). Habitat association has also been tested by comparing mean productivity (chl-a) in areas used by birds to an empirical distribution of productivity randomly resampled across the birds' range (Gonzalez-Solis et al. 2007). Differences in behaviour, such as the time spent searching or travelling, track straightness, FPT and flight speed with habitat have also been tested in order to identify which habitats are used more frequently for foraging (Weimerskirch et al. 1997c, Hyrenbach et al. 2002, Weimerskirch et al. 2002, Suryan et al. 2006, Pinaud & Weimerskirch 2007), and Discriminant Function Analysis has been used to test which environmental covariates best predict behavioural state (Awkerman et al. 2005, Pinaud & Weimerskirch 2007).

Most early studies treated individual telemetry locations as independent. This assumption is invalid because tracking devices collect many locations from one individual. As such, tracking data are increasingly analyzed using mixed-effects models, treating individual bird as a random effect (e.g. Hyrenbach et al. 2002, Garthe et al. 2007a). Tracking data also violate assumptions of independence because they tend to be serially and sometimes spatially autocorrelated (Aarts et al. 2008). A rather severe way of dealing with this is to delete locations sequentially until independence is achieved (e.g. Swihart & Slade 1985). A more economical approach would be to use spatiotemporally explicit techniques to model dependence due to autocorrelation (Dormann et al. 2007).

Methods often used to model the spatial usage of animals tracked in terrestrial environments, such as Resource Selection Functions (RSF) (Manly et al. 2002), have not found wide application in pelagic studies. Indeed, to date, the habitat preference *sensu* Manly (2002) of only one species of pelagic seabird has been quantified using individual movement data. Following Aebischer et al. (1993), Pinaud & Weimerskirch (2005) used compositional analysis to compare habitats used by breeding Indian yellow-nosed albatrosses *Thalassarche carteri* to those available on a 20 km grid, weighting the availability of each cell as a function of colony distance to account for

accessibility. Although the modelling of habitat preference using individual movement data is an active area of research, robust techniques are becoming widely available to ecologists, especially through the profusion of packages contributed to the R statistical computing project (e.g. Calenge 2006). Hence, there is a shift towards model selection and model averaging as a way of investigating habitat preference. Spatial usage models can be fitted to telemetry data at the level of individual (reviewed by Patterson et al. 2008, Schick et al. 2008), or population (reviewed by Moorcroft & Barnett 2008). The key problems facing population level modellers were discussed by Aarts et al. (2008) and Matthiopoulos & Aarts (2009). In addition to issues already mentioned, they include non-linearity in animals' response to the environment, which is increasingly being addressed using Generalized Additive Models (GAMs) (Guisan et al. 2002). Aarts et al. (2008) used mixed-effects GAMs to model the spatial usage of satellite-tracked grey seals *Halichoerus grypus* as a function of habitat accessibility and preference. A number of similar techniques may also be used to model habitat use with individual movement data (reviewed by Matthiopoulos & Aarts 2009). For example, Ecological Niche Factor Analysis has recently been used to model the spatial distribution of feeding northern gannets *Morus bassanus* (Skov et al. 2008). Although this technique is useful for identifying the environmental covariates to which birds respond, it provides no information on the shape of that response.

Increasingly, the behavioural response of animals to their environment is modelled at the individual level, using SSMs (Jonsen et al. 2003, Morales et al. 2004, Eckert et al. 2008) and it is hoped that SSMs will ultimately allow population level inferences to be drawn (Patterson & Fraser 2000). SSMs are able to account for uncertainty in location errors, a feature which makes them of particular utility in modelling geolocator data (Royer et al. 2005). Recently, Schick et al. (2008) proposed incorporating RSFs and SSMs in a hierarchical Bayesian framework, effectively modelling a moving animal's behavioural response to a habitat map centred on the present location (see also Christ et al. 2008). Although such techniques are complex and computationally demanding, they are becoming more practicable and look likely to play an important role in quantifying pelagic seabird habitat preferences.

Many other statistical techniques are also available for analyzing animal movement and spatial usage (see Turchin 1998, Kenward 2001, Scott et al. 2002). However, it should be cautioned that, historically, animal movement models and theory were developed for very different taxa to pelagic seabirds. For example, much effort has gone into modelling the spatial usage of endangered ungulates (Mladenoff et al. 1999, Johnson et al. 2002, Morales et al. 2005). However, unlike pelagic seabirds, these animals are not constrained to return to a central place, are slow moving and travel over a solid medium. Wide-ranging, higher marine predators, such as penguins, pinnipeds, fish and turtles, which have also been the subject of recent modelling studies (Jonsen et al. 2003, Royer et al. 2005, Jonsen et al. 2007, Aarts et al. 2008, Eckert et al. 2008, Gurarie et al. 2009) are more similar to pelagic seabirds, in that they travel through a fluid medium. This may have important consequences for the interpretation of observed movement patterns (Campagna et al. 2006, Gaspar et al. 2006, Cotte et al. 2007). However, unlike these animals, pelagic seabirds are almost unique, in that they travel in one fluid medium (the atmosphere) and forage in another (the sea), a trait that makes relating their movement to their environment somewhat more complex. Similarly, although there are many empirical and theoretical models of central place foragers, most of these relate to terrestrial taxa such as colonial insects, rodents and terrestrial birds (e.g. Giraldeau et al. 1994, Dukas & Edelstein-Keshet 1998, Brown & Gordon 2000, Olsson et al. 2008). Unlike the majority of pelagic seabirds, these groups usually suffer significant predation risk and may be territorial. In short, not all movement models are appropriate to pelagic seabirds. However, understanding the reasons for this is illuminating in itself.

1.9 Species considered in this study

The albatrosses (family Diomedidae, 21 species) are the largest of all seabirds and in this and many other traits they exhibit the most marked divergence of pelagic seabirds from other avian groups. As such, it may be expected that their response to the marine environment, both at the individual, population and evolutionary levels may be more marked than in smaller or less pelagic species. Their large size also makes it easier to

track their movements at sea using bird-borne devices and to record and manipulate them at their colonies. For these reasons, they are an apposite group within which to study pelagic seabird-environment interactions.

The majority of the work presented in this thesis was carried out on black-browed albatrosses *Thalassarche melanophrys*. This species is among the most mobile and wide-ranging of marine predators, routinely commuting 100s-1000s of km from their subantarctic colonies to forage (Weimerskirch et al. 1997b, Huin 2002, Phillips et al. 2004b). Although they are polyphagous, during chick provisioning they show a marked preference for relatively few prey taxa (Croxall & Prince 1980, Cherel & Klages 1998), and spend the majority of their time in productive neritic, shelf-break and upper shelf-slope waters (Weimerskirch et al. 1997b, Gremillet et al. 2000, Wood et al. 2000, Huin 2002, Pinaud & Weimerskirch 2002, Phillips et al. 2004b, Terauds et al. 2006b). However, birds from some populations also forage in oceanic habitats, including the Antarctic Polar Frontal Zone (APFZ) (Phillips et al. 2004b, Pinaud & Weimerskirch 2007), and non-breeding birds associate with mesoscale eddies (Petersen et al. 2008). It is possible that the habitat preferences of black-browed albatrosses differ from those of their close relative, the Campbell albatross *T. impavida*, which is endemic to Campbell Island in the western Pacific (Burg & Croxall 2001). However, such differences have not been examined critically, because until recently the two species were regarded as conspecific (Roberson & Nunn 1998, Burg & Croxall 2001). Although black-browed albatrosses are the most abundant of the Southern Hemisphere albatrosses (current world breeding population ~ 601,000 pairs), increased incidental mortality since the mid 1980s in longline and trawl fisheries has caused widespread and unsustainable population declines (~ 8.5% over the past 10 years), such that they are now classified as Endangered (IUCN 2009).

1.10 Aims of the study

The overall aims of this study were to use individual movement data to determine how environmental constraints affect the foraging behaviour, spatial usage and population sizes of black-browed albatrosses and related species. Specifically, the aims were:

1. To determine how central place constraint affects the spatial usage of breeding albatrosses and how this changes with breeding stage.
2. To describe quantitatively the mesoscale oceanographic foraging habitat use and preferences of breeding albatrosses.
3. To determine whether foraging habitat use and preferences differ between breeding stages, populations and closely related species.
4. To model the effects of intraspecific competition and foraging habitat preference on the spatial usage of breeding albatrosses.
5. To estimate the spatial usage of albatrosses during the breeding season.
6. To determine whether prey availability and intraspecific competition during the breeding season regulate population size.
7. To determine how wind field affects flight performance and therefore limits foraging habitat accessibility.
8. To compare differences in flight performance between species and sexes and to determine whether these mitigate spatial segregation of foraging areas.

This thesis is structured as follows: In Chapter 2 I use individual movement data collected by tracking birds from their breeding colonies and remotely-sensed environmental data to model the population-level habitat preferences of black-browed and Campbell albatrosses. The effect of intraspecific competition between birds from neighbouring colonies is also considered before predictions of the birds' distribution at sea are made. In Chapter 3 I show that the size of black-browed albatross populations is limited by the availability and accessibility of preferred habitat. In Chapter four I use individual movement and wind data to quantify the effect of wind on the flight performance of this and three other species of albatross (wandering albatrosses *Diomedea exulans*, grey-headed albatrosses *T. chrysostoma* and light-mantled albatrosses *Phoebastria palpebrata*), representing three of the four extant genera of albatross. Finally, in Chapter 5 I present a synthesis and discussion of my results.

Chapter 2. Modelling the spatial usage of black-browed albatrosses as a function of habitat preference, accessibility and intraspecific competition

The data in this chapter also appear in Wakefield E.D., Phillips R.A., Matthiopoulos J., Trathan P., Arata J., Gales R., Huin N., Robertson G., Waugh S. and Weimerskirch H. (in review) Accessibility, habitat preference and conspecific competition limit the global distribution of breeding albatrosses. *Ecological Monographs*.

2.1 Introduction

Understanding how organisms use space is one of the primary aims of ecologists, and the capacity to identify key habitats and areas is fundamental to effective conservation (Guisan & Zimmermann 2000, Austin 2007). In order to achieve these goals, it may be necessary to model the factors that influence spatial usage, including habitat preference, competition, and accessibility (e.g. Lewis et al. 2001, Adler & Gordon 2003, Matthiopoulos 2003). While the effects of such factors on terrestrial animals, which are relatively straightforward to observe, have received much attention (Begon et al. 2006), there have, until recently, been few attempts to predict the spatial usage of long-ranging marine organisms (fish, cetaceans, pinnipeds and seabirds) in a similar way (Aarts et al. 2008). In the main, this reflects the difficulty of measuring the habitat characteristics and spatial usage of animals that range over wide areas of open ocean, remote from human observation. However, these problems can increasingly be overcome by a combination of satellite remote-sensing (Martin 2004, Mann & Lazier 2006), and improved instrumentation for animal tracking (Wilson et al. 2002). At the same time, advances in statistical modelling now make it possible to address ecological questions using the large volumes of individual movement and spatial data that these technologies provide (Guisan & Zimmermann 2000, Aarts et al. 2008, Patterson et al. 2008).

In this chapter I use satellite-tracking and remotely-sensed environmental data to identify environmental predictors, and to estimate the global distribution of this species

during the breeding season. In so doing, I address a number of ecological issues. Firstly, the accessibility of points in space is not equal - breeding seabirds are central place foragers, constrained to return periodically to their colonies (Orians & Pearson 1979). Therefore, the cost (in time or energy) of accessing different locations increases as a function of distance (Matthiopoulos 2003). In addition, in polar waters the seasonal retreat of sea ice considerably increases the area accessible to foraging albatrosses (Tickell 2000). Secondly, habitat preferences may vary with breeding stage. Breeding birds must first incubate their egg, then provision their chick until it fledges. In seabirds, the change of duties is often marked by a shift in spatial usage (Weimerskirch et al. 1993, Phillips et al. 2004b), either because of intrinsic factors, such as differences in the severity of the central place constraint (Shaffer et al. 2003) or differences in the dietary requirements of adult and chick (Williams et al. 2008), or extrinsic factors, such as seasonal changes in prey availability (Humphreys et al. 2006). Given that some populations of black-browed albatross switch foraging areas with breeding stage (Huin 2002, Phillips et al. 2004b), habitat preferences probably also change. Thirdly, competition may modify spatial usage: Because of niche overlap, competition between conspecifics is often more intense than that between species (Simberloff & Dayan 1991). In some central place foragers this is thought to result in spatial partitioning of animals from adjacent colonies (parapatric conspecifics) (Cairns 1989, Ainley et al. 2003, Ainley et al. 2004, Gremillet et al. 2004). Although it is not clear whether this is due to direct or indirect competition, it is generally believed that the intensity of competition varies with conspecific density (Ashmole 1963, Furness & Birkhead 1984, Lewis et al. 2001). A degree of spatial partitioning is exhibited by black-browed albatrosses in the Falkland Islands and Kerguelen but there remains some overlap in the foraging areas of birds from different colonies (Weimerskirch et al. 1988, Huin 2002).

Following Aarts et al. (2008), I used mixed-effects Generalised Additive Models (GAMMs), fitted to environmental and satellite-tracking data from 171 breeding black-browed and Campbell albatrosses, from nine colonies located throughout the subantarctic, to model spatial usage as a function of accessibility, habitat preference and intraspecific competition. This allowed me to quantitatively estimate the worldwide at-sea distribution of breeding black-browed albatrosses. In so doing, I

addressed a number of related hypotheses: (1) that spatial usage decreases at a rate proportional to distance from the colony; (2) that black-browed albatrosses express stage-dependent habitat preferences; (3) that closely related species (black-browed and Campbell albatrosses) have different habitat preferences; and (4) that spatial usage decreases with parapatric conspecific competition.

2.2 Methods

2.2.1 Conceptual framework

I adopted the analytical approach of Aarts et al. (2008), which defines a habitat as a point or cuboid in environmental space, the coordinates of which are the values of environmental covariates. The probability of an animal being recorded in the i^{th} habitat is defined by a binomial response variable \hat{u}_i . These locations (Fig. 2.1a) are assumed to be generated by a heterogeneous, spatial Poisson process, with a rate proportional to a spatial probability density function $f_1(X_s)$, where X_s is a vector of environmental covariates (Fig. 2.1c-h) at a given point s in geographical space. By adopting a case-control approach, I complemented each tracking location with three temporally matched, randomly generated pseudo-absence (control) locations, at which \hat{u}_i takes the value 0 (Fig. 2.1b). This framework permits the selection of control points from a biologically realistic null model. This null model expresses the expectation of where the animals might be if they had movement constraints but not preferences. In the case of central place foragers, a simple null model of usage assumes that the cost (in time or energy) of visiting a point in space is proportional to distance from the colony d_c , the inverse of which is termed accessibility α . (Matthiopoulos 2003). Hence, I selected control locations via a spatial Poisson process, at a rate $f_0(X_s)$ proportional to α . The response variable \hat{u}_i is then approximated by a Bernoulli process, with probability h_i . Aarts et al. (2008) show that at point s , the preference of the animal $h(X_s)$, for environmental conditions X_s , characteristic of the point s tends to:

$$h(X_s) = \frac{k_1 f_1(X_s)}{k_0 f_0(X_s) + k_1 f_1(X_s)} \quad (2.1)$$

where k_1 is the number of telemetry locations and k_0 the number of control locations. Rearranging equation 1, the probability of spatial usage at location s can be estimated by

$$f_1(X_s) = \frac{h(X_s)}{1 - h(X_s)} r f_0(X_s) \quad (2.2)$$

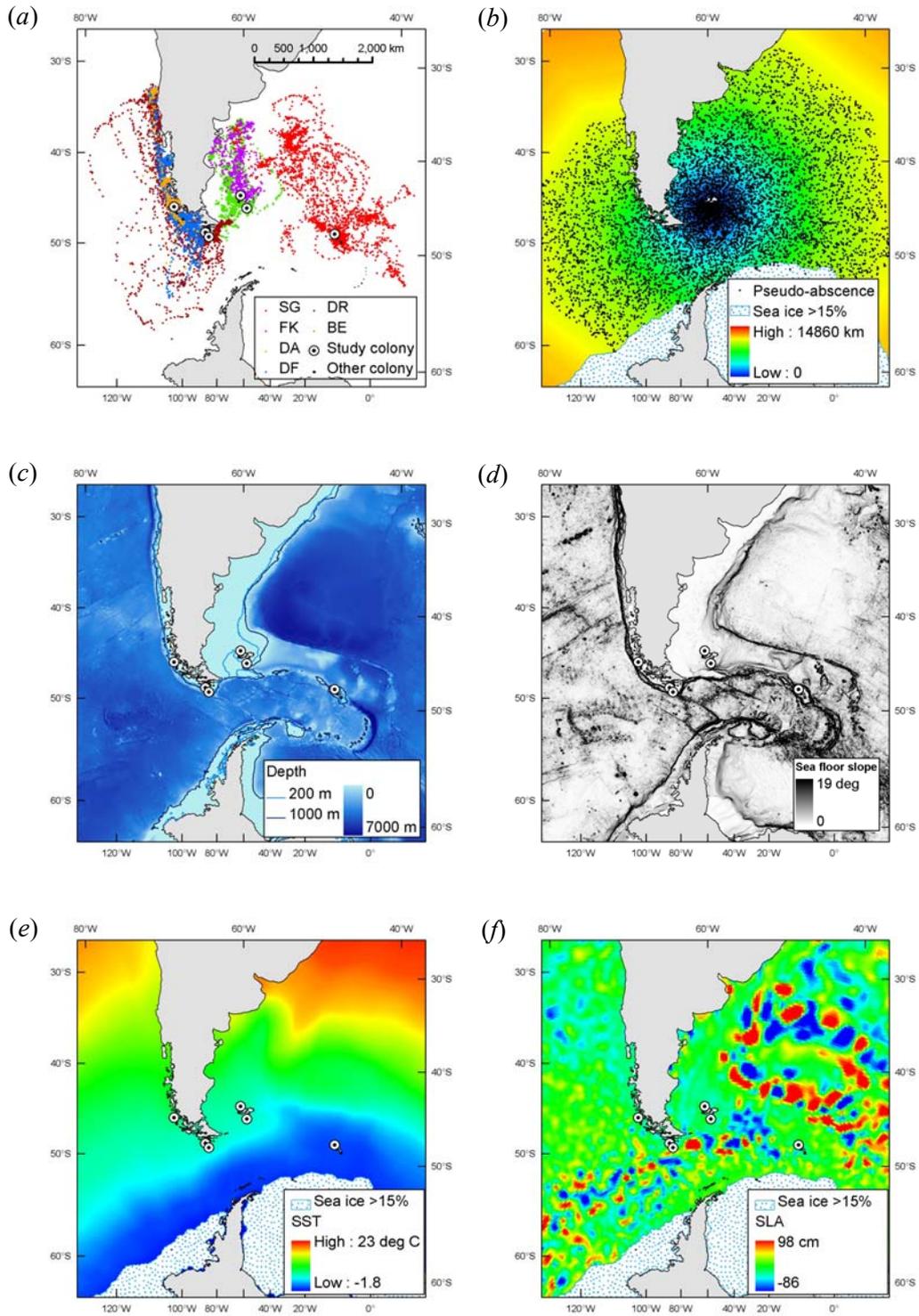
where $r = k_0/k_1$. The quantity h can be estimated empirically from the case-control data. To allow for the possibility of a non-linear response to environmental covariates, I modelled h_i as a GAMM:

$$h_i = g^{-1}(\eta_i) = \frac{e^{\eta_i}}{1 + e^{\eta_i}}$$

$$\eta_i = b_0 + s_1(x_{i,1}) + \dots + s_j(x_{i,j}) + \dots \quad (2.3)$$

where g^{-1} is the inverse of the logit link function and η_i is the linear predictor. I structured η_i such that it could include parametric smooths of single covariates, and to allow for the possibility of interactions, tensor product smooths of pairs of covariates (Wood 2006). Because tracked individuals are observed repeatedly, I treated individual as a random effect. I then assessed competing models by cross-validation, with forward selection, maximising log-likelihood. Although cross-validation is a somewhat conservative approach (Burnham & Anderson 1998), I adopted it because tracking data tend to be inherently spatially and serially autocorrelated, which are properties that can lead to over-parameterised models if information criteria (e.g. the AIC) are used for

model selection. Furthermore, parameters were estimated using penalized quasi-likelihood (Wood 2006), which also makes the use of model selection criteria, such as the AIC, inappropriate (Venables & Ripley 2002).



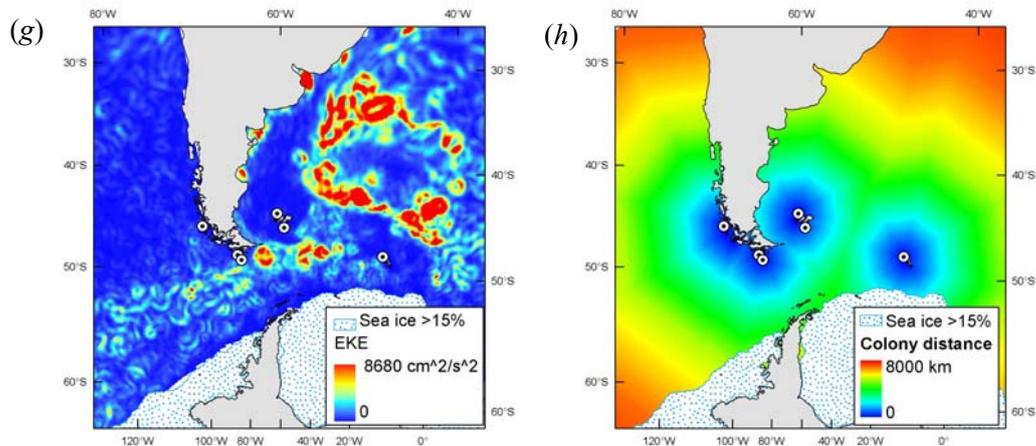


Figure 2.1 Examples of the data used to fit the spatial usage models (a) ARGOS locations of incubation stage black-browed albatrosses foraging from six colonies (SG = NW South Georgia, FK = NW Falklands Islands, DA = Isla Diego de Almagro, DF = Islas Ildefonso, DR = Islas Diego Ramirez, BE = Beauchêne Island); (b) minimum biological distance to all grid cells from the Beauchêne Island super-colony (d_c) and randomly generated control (pseudo-absence) locations, selected by a spatial Poisson process with a rate proportional to d_c^{-1} ; (c) depth; (d) depth slope; (e) mean Optimally Interpolated Sea Surface Temperature (SST); (f) mean Sea Level Anomaly (SLA); (g) mean Eddy Kinetic Energy (EKE); (h) minimum biological distance to the next nearest super colony to Beauchêne Island (d_n) (values of time-varying covariates are for November 2000).

2.2.2 Tracking data

Between 1994 and 2003, Platform Terminal Transmitters (PTTs) were used to record the spatial usage of foraging black-browed albatrosses breeding at eight colonies, located in southern Chile (Isla Diego de Almagro, Islas Ildefonso, Islas Diego Ramirez), the Falkland Islands (Beauchêne Island, Saunders Island), South Georgia (Bird Island), which together hold 96% of the world population, as well as Île Kerguelen in the southern Indian Ocean and Macquarie Island in the southwest Pacific (Fig. 2.2, Tables 2.1 and 2.2, for further details see Weimerskirch et al. 1997b, Phillips et al. 2004b, Terauds et al. 2006a, Pinaud & Weimerskirch 2007). In addition, Campbell albatrosses were tracked from Campbell Island (Waugh et al. 1999). Birds were tracked during the incubation or the post-brood chick-rearing stage (hereafter “chick-rearing”). During the former (late October-early January), parents incubate a single egg, taking turns to make long (~ 1 week) foraging trips. Once the chick hatches,

it is brooded and/or guarded continuously for ~ 3 weeks. During the chick-rearing stage (late January-mid May), when the chick can be left alone, parents forage simultaneously, returning to provision it after short (~ 2 d) or sometimes long trips. Birds were captured at the nest, either by hand or using a 1.5m pole fitted with a wire crook and equipped with a PTT (Microwave Telemetry PTT100, Telonics ST10, Toyocom T2038 or Kiwisat 101; mass 20-55g) attached to mantle feathers using Tesa[®] tape. PTT transmission rate was set to every 60 or 90 sec, providing ARGOS class 3, 2, 1, 0, A or B locations on average every 2.1 hrs. Birds were recaptured after one or more foraging trips and the devices recovered. Total instrument mass, including attachment materials and in some cases, an additional, small (5-10g) logger, was <2% of birds' body mass, which did not result in injury in any cases, and was well below the threshold likely to cause measureable changes in behaviour (Phillips et al. 2003). As errors associated with PTT locations are variable and sometimes large (Vincent et al. 2002), I filtered tracking data (McConnell et al. 2002), removing those locations that gave rise to unrealistically high average speeds (>80 m/s). In order to get a more balanced sample across individuals I used data from only one trip per bird, selecting trips randomly when multiple trips had been recorded. Given computational limitations, I then used only every fourth location to model spatial usage.

2.2.3 Colony grouping

To reduce computing time, I amalgamated colonies <50 km apart into 21 super-colonies, comprising all known black-browed and Campbell albatross breeding sites (Table 2.1). However, I excluded two of these from my analysis because they held <100 breeding pairs (i.e. <0.01% of the world population).

Table 2.1 Estimated size of all *Thalassarche melanophrys* (BBA) and *T. impavida* (CBA) breeding populations grouped into super-colonies (# refers to Fig. 2.2).

Super-colony (code)	Species	Latitude	Longitude	Pairs breeding annually ⁴
1. Eastern Îles Crozet	BBA	46° 24' S	052° 16' E	350
2. Western Îles Crozet	BBA	46° 11' S	050° 26' E	630
3. NW Kerguelen	BBA	48° 36' S	068° 32' E	2000
4. SE Kerguelen (KG)	BBA	49° 41' S	070° 14' E	1350
5. Heard Island ¹	BBA	53° 00' S	073° 20' E	600
6. Macquarie Island (MQ)	BBA	54° 46' S	158° 47' E	180
7. Snares Islands	BBA	48° 01' S	166° 30' E	1
8. Campbell Island (CB) ²	CBA	52° 33' S	169° 09' E	21000
9. Antipodes Islands	BBA	49° 25' S	178° 29' E	115
10. Isla Diego de Almagro (DA)	BBA	51° 25' S	075° 12' W	15594
11. Islas Evangelistas	BBA	52° 23' S	075° 05' W	4670
12. Islote Leonard	BBA	53° 23' S	074° 04' W	594
13. Islas Ildefonso (DF)	BBA	55° 48' S	069° 24' W	47000
14. Islote Albatros	BBA	54° 27' S	069° 01' W	50
15. Islas Diego Ramirez (DR)	BBA	56° 31' S	068° 42' W	55000
16. SW Falkland Islands ³	BBA	52° 00' S	061° 02' W	38117
17. NW Falklands Islands (FK) ³	BBA	51° 07' S	060° 34' W	272810
18. Beauchêne Is., Falklands Is. (BE) ³	BBA	52° 53' S	059° 12' W	103341
19. NW South Georgia (SG)	BBA	54° 01' S	038° 04' W	47294
20. Annakov Island, South Georgia	BBA	54° 30' S	037° 06' W	9398
21. SE South Georgia	BBA	54° 48' S	035° 54' W	16350
Total				636404

1. MacDonald Is. may hold c. 90 pairs but this is uncertain due to volcanic activity; 2. *T. impavida* is endemic to Campbell Is. and 30-100 pairs of *T. Melanophrys* also breed there; 3. Figures from year 2000 census; 4. (Gales 1998, Tennyson et al. 1998, Miskelly et al. 2001, Moore et al. 2001, Woehler et al. 2002, Aguayo et al. 2003, Arata et al. 2003, Moore 2004, Alderman et al. 2005, Huin & Reid 2006, Martin & Oehler 2006, Poncet et al. 2006, Robertson et al. 2007, Lawton et al. 2008, Robertson et al. 2008, Henri Weimerskirch, unpub. data).

Table 2.2 Spatial usage by black-browed and Campbell albatrosses satellite tracked during this study (Inc = incubation, PB = post-brood chick-rearing); area encompassing 75% of the kernel density of tracking locations (n = number birds tracked); area of neritic (<200 m deep) and neritic and upper shelf slope waters (<1000 m deep) within 800 km of the colony.

Code, population	Annual breeding population (pairs) ¹	Area encompassing 75% kernel density (km ² x 10 ⁵ , n)		Seasons tracked ²	Area within 800 km of colony (km ² x 10 ³)	
		Inc	PB		<200 m deep	<1000 m deep
4. (KG) SE Kerguelen	1350	2.1 (8)	1.3 (19)	1994, 1995, 2000	16.4	275.8
6. (MQ) Macquarie Island	180	5.1 (6)	-	2000, 2001	<0.1	58.5
8. (CB) Campbell Island ³	21,000	-	13.2 (8)	1997	8.4	408.6
10. (DA) Isla Diego de Almagro	15,594	1.6 (10)	-	2002	36.7	154.5
13. (DF) Islas Ildefonso	47,000	4.6 (25)	-	2002	32.0	325.1
15. (DR) Islas Diego Ramirez	55,000	6.4 (28)	2.7 (12)	1997, 2000, 2001, 2002	26.8	315.3
17. (FK) NW Falklands	27,2810	4.8 (11)	0.8 (7)	1999	67.0	754.5
18. (BE) S Falklands	103,341	4.2 (4)	0.6 (4)	2000, 2001	27.3	646.0
19. (SG) NW South Georgia	47,294	16.8 (17)	4.8 (12)	2002	13.2	50.0

1. (Gales 1998, Arata et al. 2003, Moore 2004, Huin & Reid 2006, Poncet et al. 2006, Robertson et al. 2007, Robertson et al. 2008, H.

Weimerskirch, unpub. data); 2. Chick-rearing year; 3. *T. impavida*.

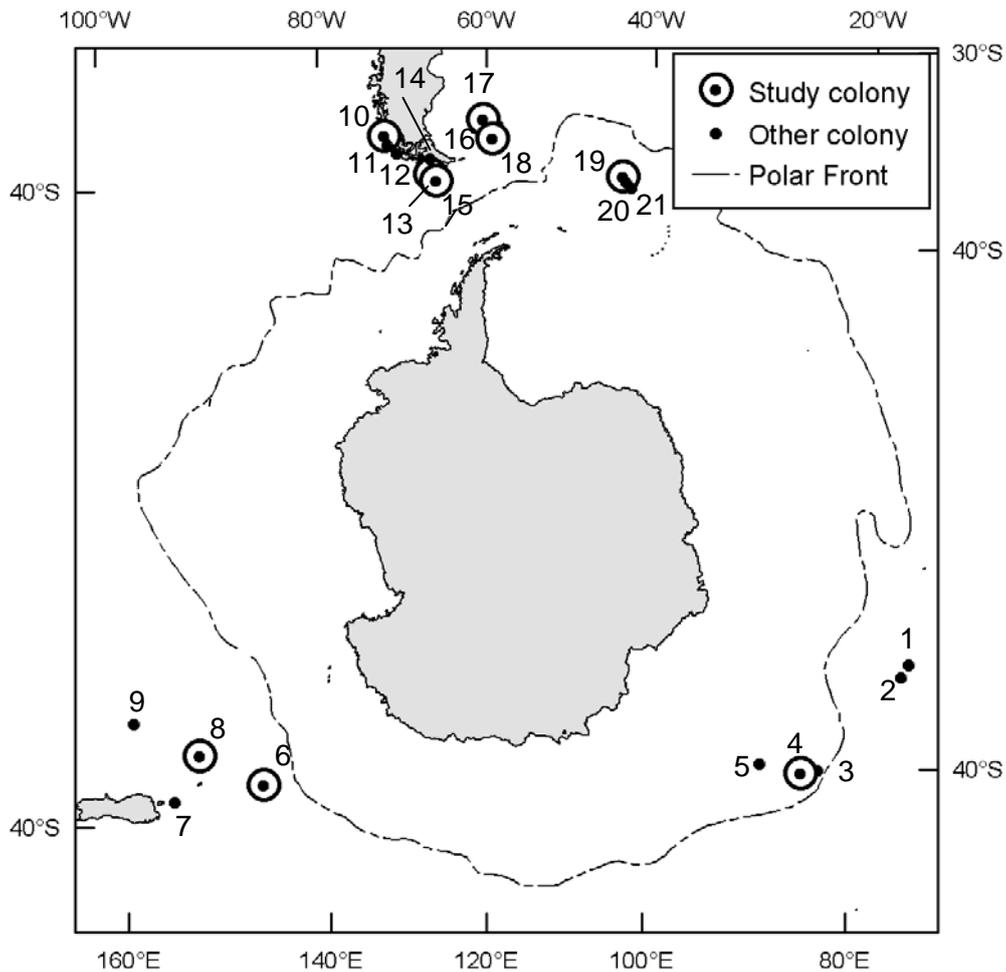


Fig. 2.2 Breeding locations of black-browed and Campbell albatrosses, indicating colonies from which birds were satellite-tracked. Super-colony numbers refer to Tables 2.1 and 2.2. Mean location of the Antarctic Polar Front from Moore et al. (1999).

2.2.4 Null model and control locations

For each month I used the ArcGIS 9.2 Spatial Analyst package (ESRI Inc., Redlands, CA) to calculate the minimum biological distance d_c (Matthiopoulos 2003) from each super-colony to all points on a 10 km polar stereographic grid, assuming that albatrosses would not cross extensive land barriers or sea ice (Tickell 2000). I defined areas of sea ice ($\geq 15\%$ coverage) using monthly passive microwave data (Fetterer et al. 2002, updated 2008). I assumed birds would not travel beyond 3300 km (1.1 times

the maximum d_c reached by any bird during my study). Within this range, I then calculated accessibility α , as $\alpha = d_c^{-1}$ (c.f. Matthiopoulos 2003). Finally, I selected three control locations matched temporally to each tracking location, quasi-randomly, via a spatial Poisson process, with a rate proportional to α for the appropriate month (Fig. 2.1b). However, as the true relationship between α and d_c was unknown (the null model may over- or under-predict accessibility), following Aarts et al. (2008), I also included d_c as a candidate covariate in the spatial usage models.

2.2.5 Environmental covariates

I selected the following environmental covariates because, firstly, I had an *a priori* reason for supposing that they, or a phenomenon for which they are a proxy, would influence albatross spatial usage at my scale of interest (>50 km, months) (Austin 2007), and secondly, because their spatial coverage was uniform across my study area: *Depth*, which I obtained on a 0.1° grid from the GEBCO digital atlas (IOC 2003); *Depth slope*, which I calculated as the maximum rate of change of depth (re-sampled on a 10 km Cartesian grid, in polar stereographic projection) between each cell and its neighbouring 8 cells; monthly mean *Optimally Interpolated Sea Surface Temperature* (SST), which was supplied on a 1° grid from NOAA/OAR/ESRL PSD, Boulder, Colorado, via <http://www.cdc.noaa.gov/> - this dataset (NOAA_OI_SST_V2) combines satellite and in-situ observations to provide an estimate of SST in both cloud free and cloud obscured areas (Reynolds et al. 2002); seven day mean *Sea Level Anomaly* (SLA), which can be used to identify mesoscale phenomena such as eddies and meanders, were obtained on a 0.3° Mercator grid and then averaged by month; *Eddy Kinetic Energy* (EKE), which is another index of mesoscale activity, where $EKE = 1/2(u_a^2 + v_a^2)$ and u_a and v_a are the eastward and northward geostrophic current anomalies (Ducet et al. 2000). I obtained seven day mean values of u_a and v_a on a 0.3° Mercator grid, calculated EKE, and then averaged these values by month. Both u_a and v_a and SLA were produced by Ssalto/Duacs and distributed by Aviso, with support from CNES <http://atoll-motu.aviso.oceanobs.com/>.

2.2.6 Parapatric conspecific competition

To test hypothesis 4, I considered two covariates: (1) minimum biological distance to the next nearest super-colony (d_n), assuming that the accessibility of a point in space to parapatric conspecifics was $\propto 1/d_n$. I calculated d_n for each month and super-colony, in a similar manner to d_c ; (2) relative parapatric conspecific density (ρ_c), assuming that absolute parapatric conspecific density is proportional not only to the distance from the i th super-colony but also to the size of its breeding population (P_i). Hence, at the j^{th} location,

$$\rho_{c,j} = \sum \frac{P_i}{d_{n,i,j}} \quad (2.4)$$

For each super-colony, I calculated grids of d_n for all other super-colonies and then used estimates of the breeding population at those locations (Appendix 1) to calculate ρ_c . These density covariates formalise the notion of opportunity to use a location. Hence, if habitat preferences are captured by all the other covariates in the model, they offer the location in question to one colony or another.

2.2.7 Model fitting and selection

I modelled probability h_i (which is proportional to habitat preference) as a function of the covariates outlined above using GAMMs, implemented within the `mgcv` package (Wood 2004) in R (R-Development-Core-Team 2007). Hypothesis 2 could not be tested directly in a single model, because it proved computationally unfeasible to fit GAMMs containing interactions between categorical covariates (breeding stage) and smooths. Hence, I fitted a separate model for each breeding stage, deeming a difference in habitat preference to exist if different covariates were retained in one or other analysis. Habitat preference models fitted to data from one geographic area may perform poorly when applied to another geographical area because differences in the availability of habitats may lead to behavioural changes (Mysterud & Ims 1998, Boyce

et al. 2002). Hence, I tested the ability of global models to explain the spatial usage of individual populations. If the global model explained spatial usage of a population poorly, I also fitted a separate model for that population.

I structured candidate covariates either as parametric variables or smooths of single variables. In order to improve the spread of the data, I double square root transformed depth slope and \log_e transformed EKE and ρ_c (Wood 2006). As the shelf-break is often located close to deep-water trenches, my models initially predicted spuriously high spatial usage in distant abyssal areas. To avoid this issue, and with the justification that bathymetric variability does not directly give rise to surface biological variability in these areas, I truncated depth at 4000 m. To allow for plausible, biologically interpretable interactions between terms, I considered tensor product smooths of the following pairs of variables: Depth and depth slope; depth and SLA; depth and EKE; SST and EKE; and d_c and d_n . I determined minimum adequate models by forward selection, using K -folds cross validation, where K = number colonies, maximising the log-likelihood L ,

$$L = \frac{\log_e \sum_{i=1}^n h_i^{\hat{u}_{m,i}} (1 - h_i)^{(1 - \hat{u}_{m,i})}}{n} \quad (2.5)$$

where $\hat{u}_{m,i}$ is the i th observation from the m th colony and n is the number of locations from that colony (c.f. Aarts et al. 2008). I proceeded with model selection as follows: Firstly, I fitted all possible models containing a single covariate or tensor product smooth and ranked them according to L . I then selected the highest ranked model, to which I added each of the remaining terms in turn, retaining the resulting model if L increased. I continued this process until no further increase in L occurred. To reduce the chances of over fitting, I replaced smooths with parametric terms at each stage and, again, retained the resultant model if L increased. As an additional measure against over parameterisation, smooths were produced using cubic regression splines with

shrinkage, allowing covariates to be penalised out of the model entirely during fitting (Wood 2006).

2.2.8 Estimating spatial usage

Spatial predictions were made using the models' fixed effects. Following eq. 2, for each super-colony, I calculated the probability density $f_i(X_s)$ across a regular 0.1° grid centred on each super-colony. I then normalised this to one and multiplied the resulting values by P_i (Appendix 1), assuming that during incubation only half the breeding population would be at sea, while during chick-rearing, birds would spend a negligible amount of time at the nest.

2.3 Results

2.3.1 Observed spatial distribution and habitat use

A total of 109 birds were satellite-tracked from eight colonies during incubation, and a further 62 birds, from six colonies, during chick-rearing (Table 2.2). In the former stage, black-browed albatrosses tended to forage in areas either near or to the north of their colonies, ranging throughout neritic, shelf-break, upper shelf-slope and, to a lesser extent, adjacent oceanic waters. These included Chilean coastal waters and the Humboldt Current Upwelling south of 34° S, the Patagonian Shelf south of 40° , the eastern Bass Strait and the peri-insular shelves of South Georgia, Kerguelen and Macquarie Island (Fig. 2.3). In addition, birds from NW South Georgia foraged in the deep oceanic waters of the APFZ and the Brazil Malvinas Confluence during incubation and during both incubation and chick-rearing birds from the Chilean colonies entered coastal fjords and channels. During chick-rearing, black-browed albatrosses similarly spent the majority of their time in neritic, shelf-break, upper shelf-slope waters but tended to have a more southerly distribution, with birds from NW South Georgia and the Islas Diego Ramirez foraging in ice-free neritic areas around the Antarctic Peninsula and South Orkney Islands. Campbell albatrosses spent the majority of their time on and at the margins of the Campbell Plateau, especially in the vicinity of the Subantarctic Front, but they also ranged widely in oceanic waters between 37°

and 68° S, especially in the APFZ. Segregation of black-browed albatross foraging areas occurred at two scales. At the super-colony level, birds from the south and northwest Falkland Islands tended to be absent from the immediate vicinity of the neighbouring super-colony, especially during chick-rearing (Fig. 2.3, Fig 2.1a). In contrast, the foraging zones utilised by black-browed albatrosses from adjacent Chilean colonies overlapped considerably. At the regional scale, birds from Chile, the Falkland Islands and South Georgia foraged in mutually exclusive areas. There was no correlation between foraging area, as defined by the size of the 75% kernel density contour (Table 2.2), and colony size (incubation $r^2 = 0.17$, $F_{1,6} < 0.01$, $p = 0.98$; chick-rearing $r^2 = -0.02$, $F_{1,6} 0.92$, $p = 0.39$).

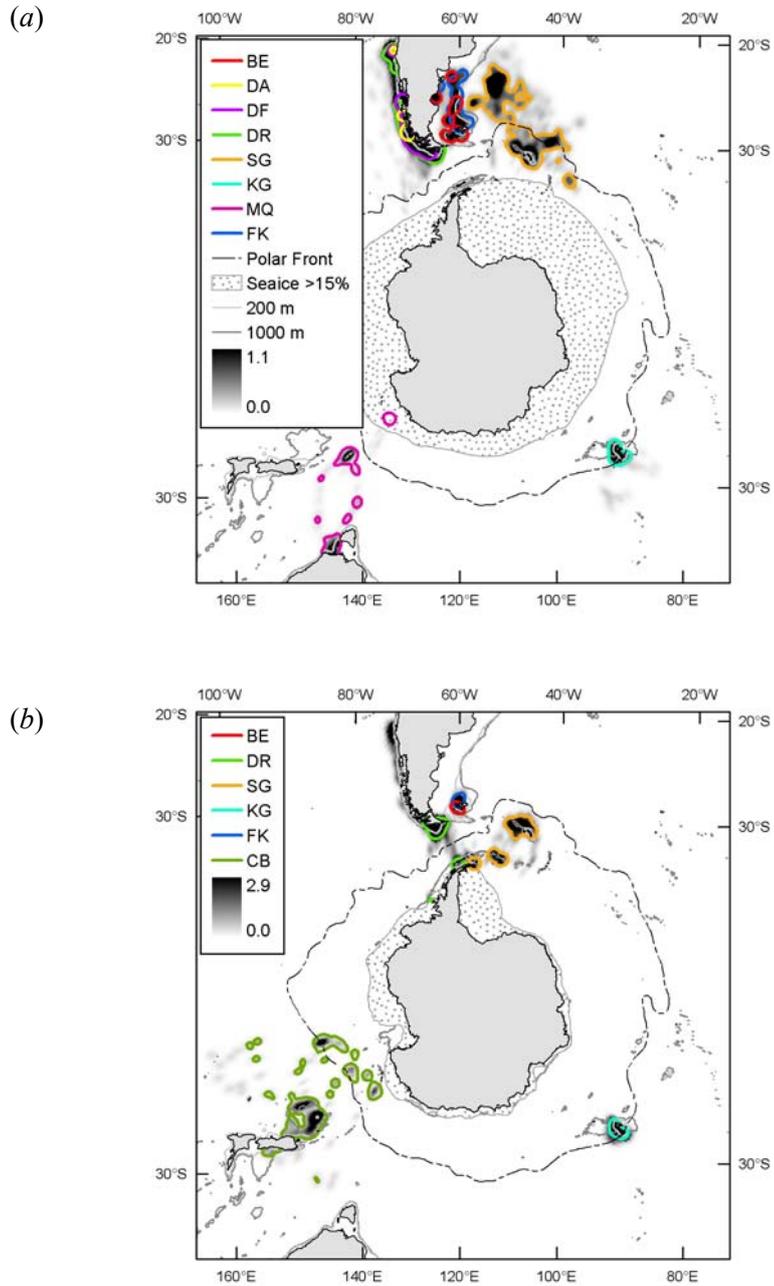


Figure 2.3 Kernel density of black-browed and Campbell albatross satellite-tracking locations recorded during (a) incubation ($n = 109$), and (b) post-brood chick-rearing ($n = 62$). Coloured lines = 75% kernel density contours; for population codes see table 2.2; mean sea ice extent ($\geq 15\%$ cover) for Nov. and Feb. Kernel density estimated following Phillips et al. (2005b) with a cell size of 20 km and a search radius of 100 km.

Spatial usage decreased with d_c , the rate of decrease being greater during chick-rearing than incubation (Fig. 2.4). During the latter stage, albatrosses made long trips, with a median duration of 8.3 days (range 0.9-24.2 days), reaching a median maximum d_c of 987 km (20-3039 km). Birds from some populations (e.g. NW South Georgia and Macquarie Island) visited one or more discrete, distant areas, giving rise to multimodal distributions of d_c , whereas the spatial usage of birds from the Falkland Islands tended to decline more uniformly with d_c . Large areas of oceanic waters were accessible to all populations but the amount of accessible neritic and upper shelf-slope waters (<1000 m deep) differed (Fig. 2.5a and e, Table 2.2), being greatest for the population at the Falkland Islands, and least for that at Macquarie. Typically, foraging black-browed albatrosses spent a disproportionately large amount of time in neritic waters, compared to the amount of such habitat available. The exception was birds from NW South Georgia which during incubation spent more time in the deep (> ~ 4500 m) oceanic waters of the Brazil-Malvinas Confluence. During chick-rearing, black-browed albatrosses made shorter trips (median 2.0, range 0.4-23.8 days), closer to their colonies (median max. d_c 298, range 10-2949 km). Birds from the Falklands and SE Kerguelen remained in neritic and slope waters, adjacent to their colonies (d_c < ~1000 km), and those from Islas Diego Ramirez and NW South Georgia also travelled to distant oceanic, neritic, shelf-break and shelf-slope areas.

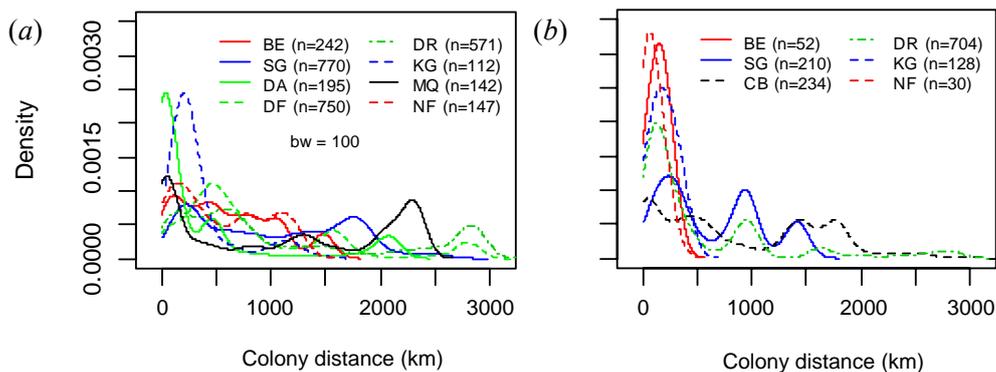
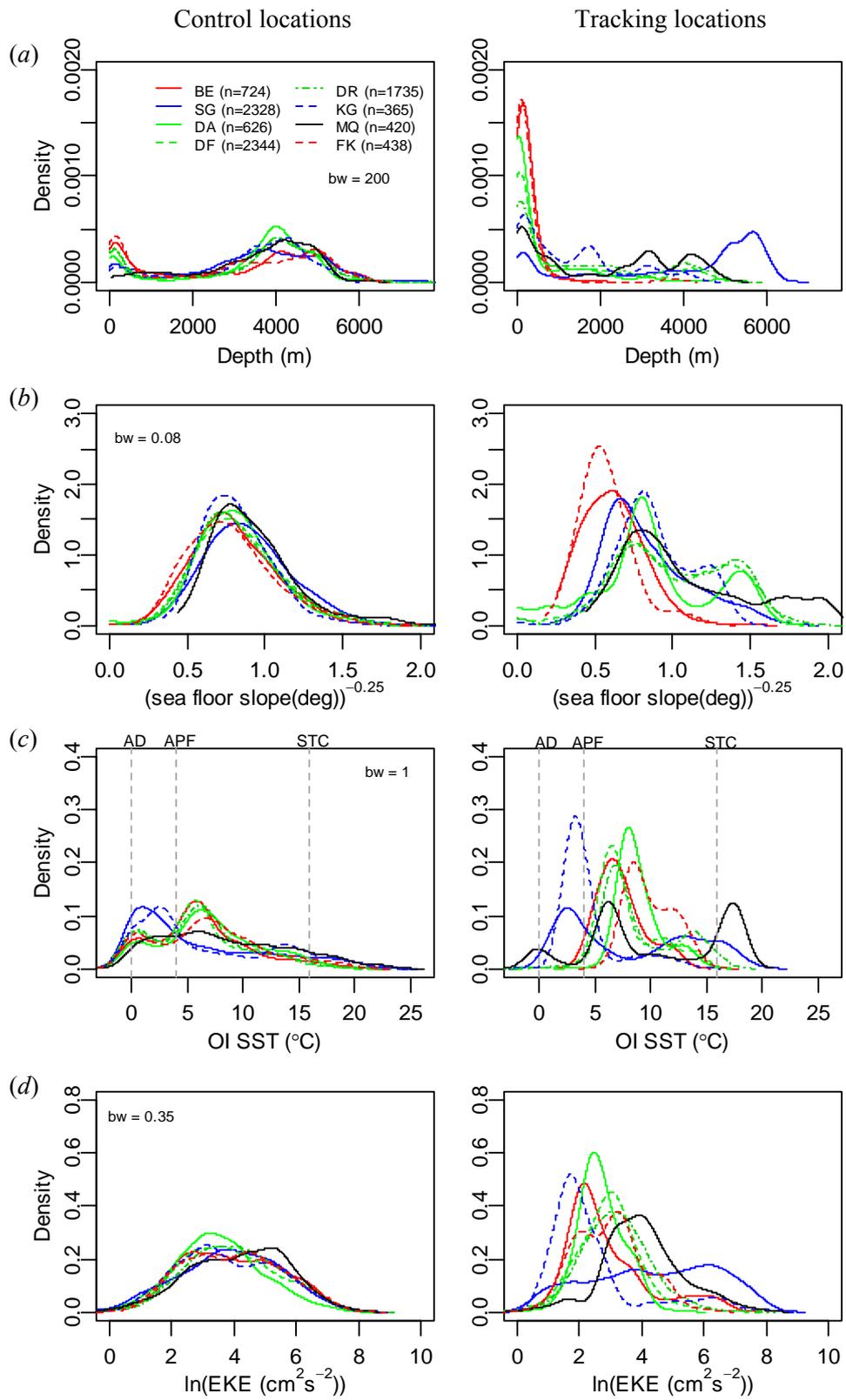


Figure 2.4 Kernel density of colony distance (d_c) to black-browed and Campbell albatross satellite-tracking locations recorded during (a) incubation ($n = 109$) and (b) post-brood ($n = 62$), from Beauchêne Island (BE), NW South Georgia (SG), Isla Diego de Almagro (DA), Islas Ildefonso (DF), Islas Diego Ramirez (DR), SE Kerguelen (KG), Macquarie Island (MQ) and NW Falkland Islands (FK); n = number of locations, bw = band-width.



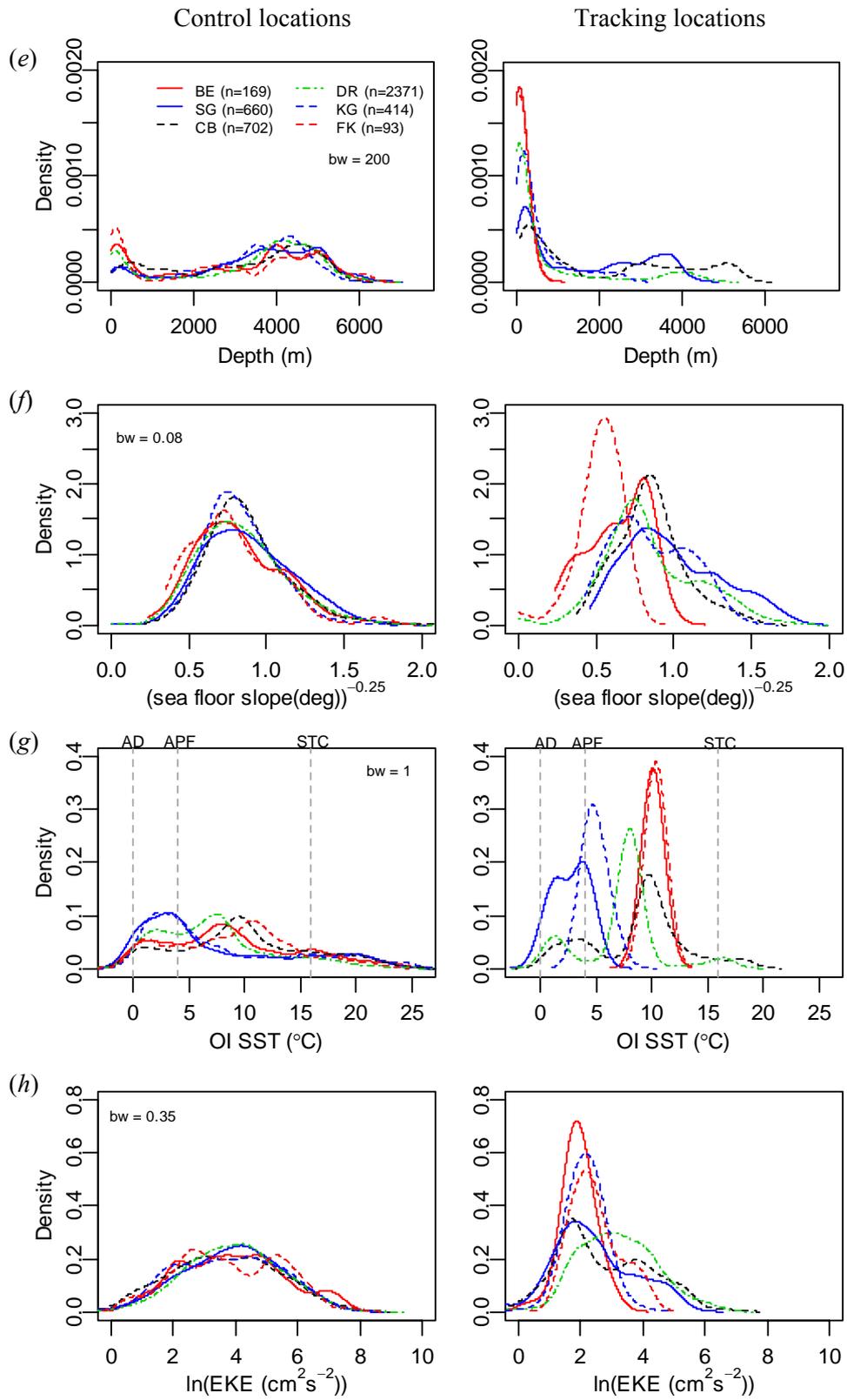


Figure 2.5 [previous pages] Kernel density of environmental covariates at black-browed and Campbell albatross satellite-tracking and control locations during (a-d) incubation and (e-h) post-brood chick-rearing. For population codes, see table 2.2; n = number of control locations (number of tracking locations = $n/3$), bw = band-width. Approximate summertime values of Optimally Interpolated SST are marked for the Antarctic Divergence (AD), Antarctic Polar Front (APF) and the Subtropical Convergence (STC).

Table 2.3 Summary of covariates retained in the most parsimonious models of spatial usage of black-browed and Campbell albatrosses.

Model	Stage	Population	Covariates retained						
			d_c	depth	slope	SST	EKE	SLA	d_n
I	Incubation	All	x	x	x	x			
II		NW South Georgia	x	x	x	x	x		
III	Chick-rearing	All	x	x	x				x
IV		Campbell Island	x	x				x	x

The availability of different bathymetric slope habitats was very similar between colonies (Fig 2.5b and f). During both incubation and chick-rearing, birds from the NW Falklands spent most time in areas of shallow slopes ($\sim 0.1^\circ$), typical of the continental shelf, whereas birds from other populations utilised both shallow ($\sim 0.3^\circ$) and in some cases steep ($\sim 4^\circ$) slopes, the latter typically around the shelf-break. The SST regime in accessible waters depended on whether colonies were either south (SE Kerguelen and NW South Georgia), or north of the Polar Front (all other colonies, Fig. 2.5c and g). During incubation, birds from the latter group spent the majority of time in waters with SSTs of 5 - 15°C, which in oceanic areas are classified as subtropical (Mann & Lazier 2006). Birds from the southerly colonies also foraged in warm water areas but spent some (SE Kerguelen) or much (NW South Georgia) time in polar ($<5^\circ\text{C}$) waters. During chick-rearing, black-browed albatrosses foraged in waters with a more restricted range of SSTs. All populations, with the exception of those from the Falklands, spent some time in oceanic areas with high mesoscale turbulence (and therefore variability in SLA), including the APFZ (SST $\sim 5^\circ\text{C}$). However, only black-

browed albatrosses from NW South Georgia, and Campbell albatrosses exploited these areas extensively, so EKE values at tracking locations were generally low (Fig 2.5d & h).

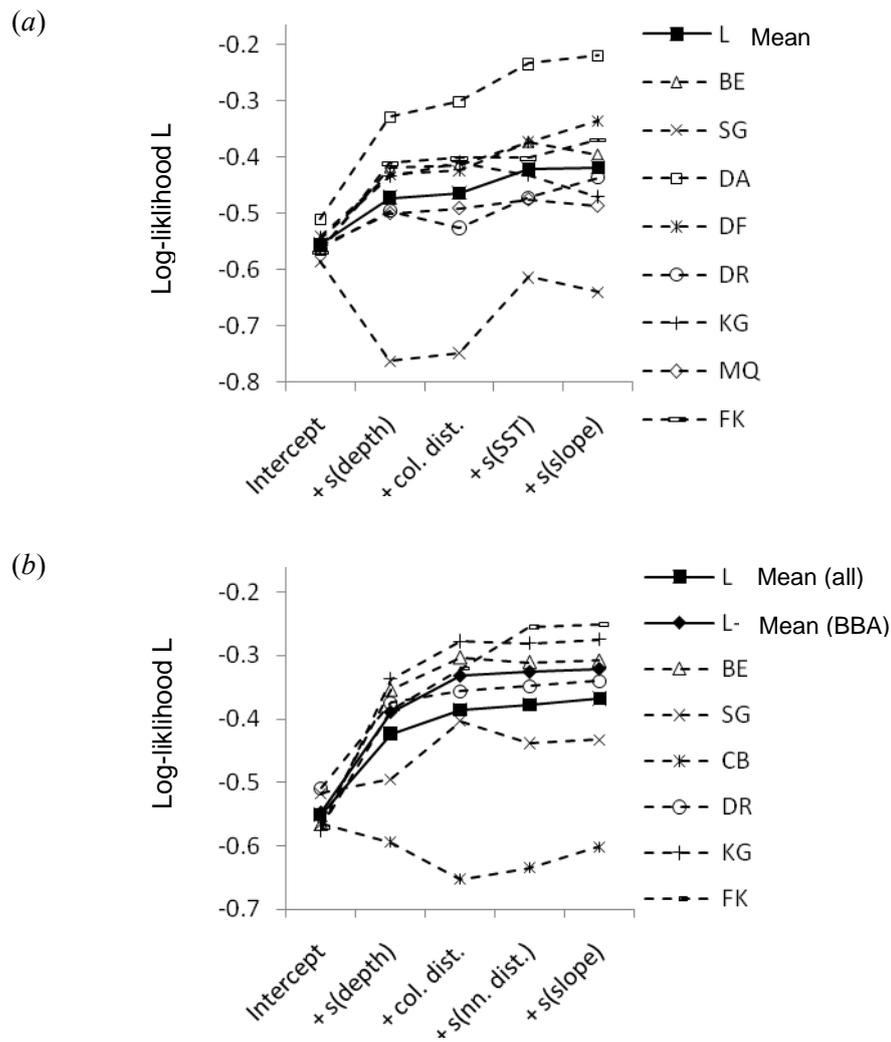


Figure 2.6 Log-likelihood (L) of models fitted to data from (a) black-browed albatrosses during incubation (model I), and (b) black-browed and Campbell albatrosses during post-brood chick-rearing (model III), the latter showing the mean log-likelihood for all populations and for black-browed albatross (BBA) populations only.

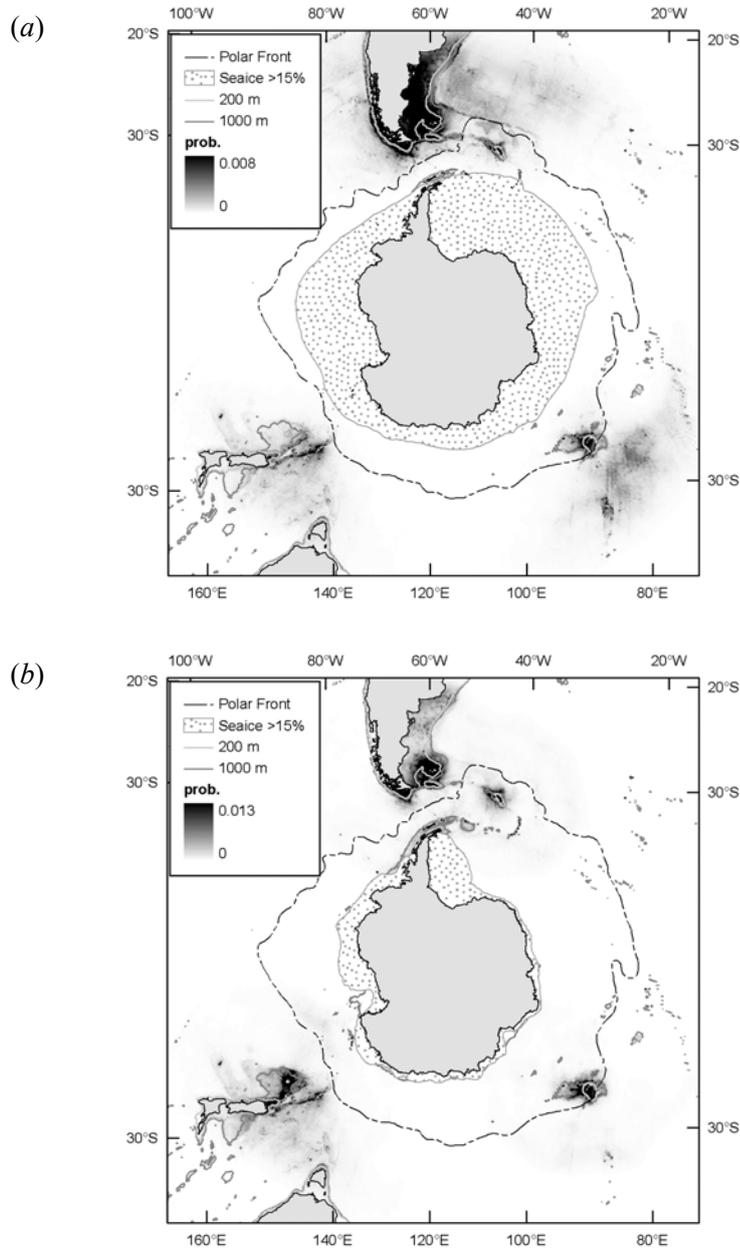


Figure 2.7 Probability of the presence (h) of satellite-tracked black-browed albatrosses predicted using the fixed-effects part of (a) model I, fitted to all data from incubation, and (b) model III, fitted to all data from post-brood chick-rearing.

2.3.2 Model selection and validation

Of the single covariate models considered, that including depth best described both the incubation and chick-rearing data. Including further covariates, the most parsimonious model fitted to data from incubation (model I) contained four covariates, with no interactions: depth, d_c , SST and depth slope (Table 2.3, Figs. 2.6a). With the addition of covariates, population specific variations in L indicated that the habitat preferences of the NW South Georgia population differed from all others (Fig. 2.6a). A second model (II), fitted to incubation data from this population alone, included an additional covariate, EKE. The minimum adequate model fitted to the chick-rearing data (III) had four covariates, with no interactions: depth, d_c , d_n and depth slope (Figs. 2.6b). The habitat preferences of Campbell albatrosses differed from those of black-browed albatrosses (Fig. 2.6b). A separate model (IV), fitted to the Campbell albatross data included the covariates depth, d_c , d_n and SLA. All terms retained in all models were highly significant ($p \leq 0.001$), except SLA in model IV ($p = 0.002$). Spatial predictions show that both global models (I & III) performed well, reproducing most of the large-scale features of observed spatial usage (c.f. Figs. 2.3 & 2.7). For example, predicted usage decreased with d_c around the study colonies, was greatest in neritic, shelf-break and shelf-slope waters, and became more southerly during the chick-rearing stage. However, model I under-predicted spatial usage in the Humboldt Upwelling region and Chilean coastal waters between ~ 36 and 42°S and in the Brazil-Malvinas Confluence, and over-predicted it on the northern Patagonian Shelf between ~ 38 and 42°S , in subtropical waters to the north of Kerguelen and on the eastern side of the Campbell Plateau. Model II reproduced the spatial usage of birds from South Georgia more satisfactorily, predicting high usage in both peri-insular shelf waters and the Brazil-Malvinas Confluence (Fig. 2.8). Model III (global chick-rearing), captured the shift to foraging in more southerly waters, especially around the Antarctic Peninsula, and the partial spatial segregation of birds from neighbouring populations. However, it under-predicted usage on the central Chilean coast and Humboldt Upwelling (at $36\text{-}46^\circ\text{S}$) and over-predicted it on the Patagonian Shelf in areas distant from the Falklands. Model III did not predict the oceanic spatial usage of Campbell albatrosses as well as model IV (Fig. 2.11).

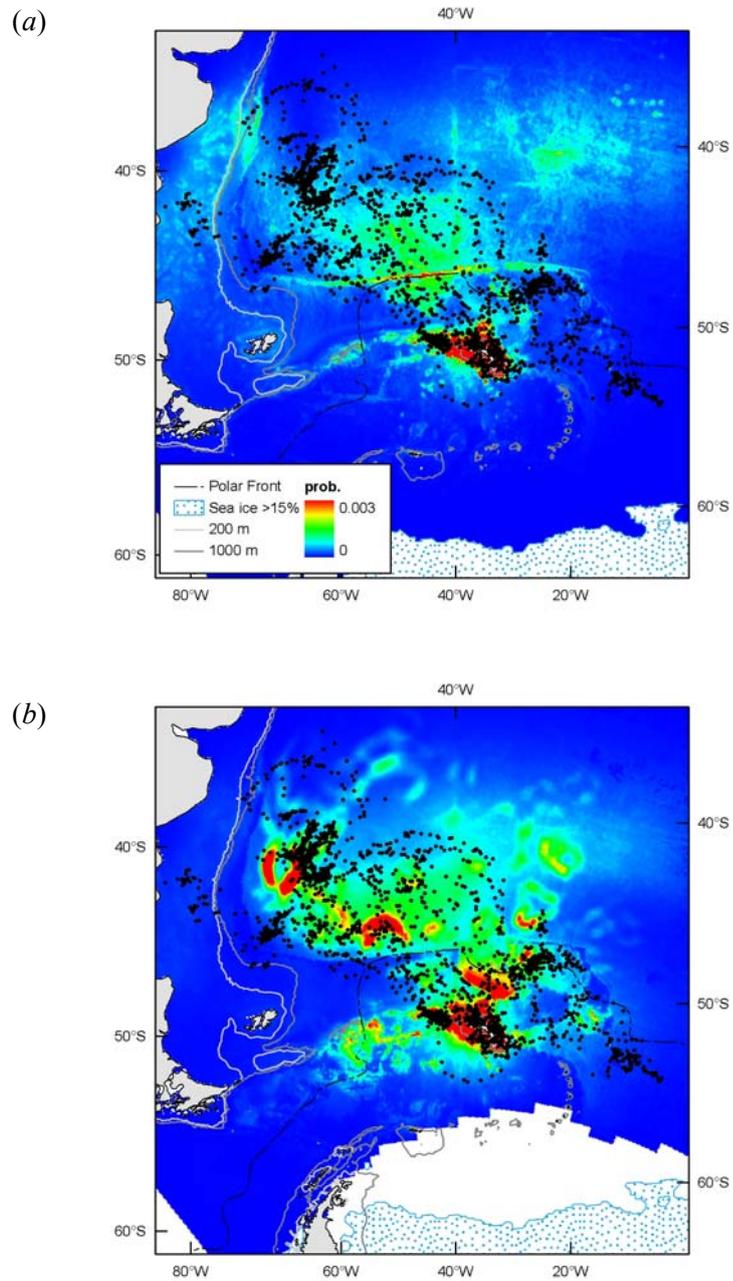


Figure 2.8 Probability of the presence (h) of black-browed albatrosses satellite-tracked from NW South Georgia during incubation, predicted using the fixed effects part of (a) model I, fitted to data from all populations and (b) model II, fitted to data from NW South Georgia alone.

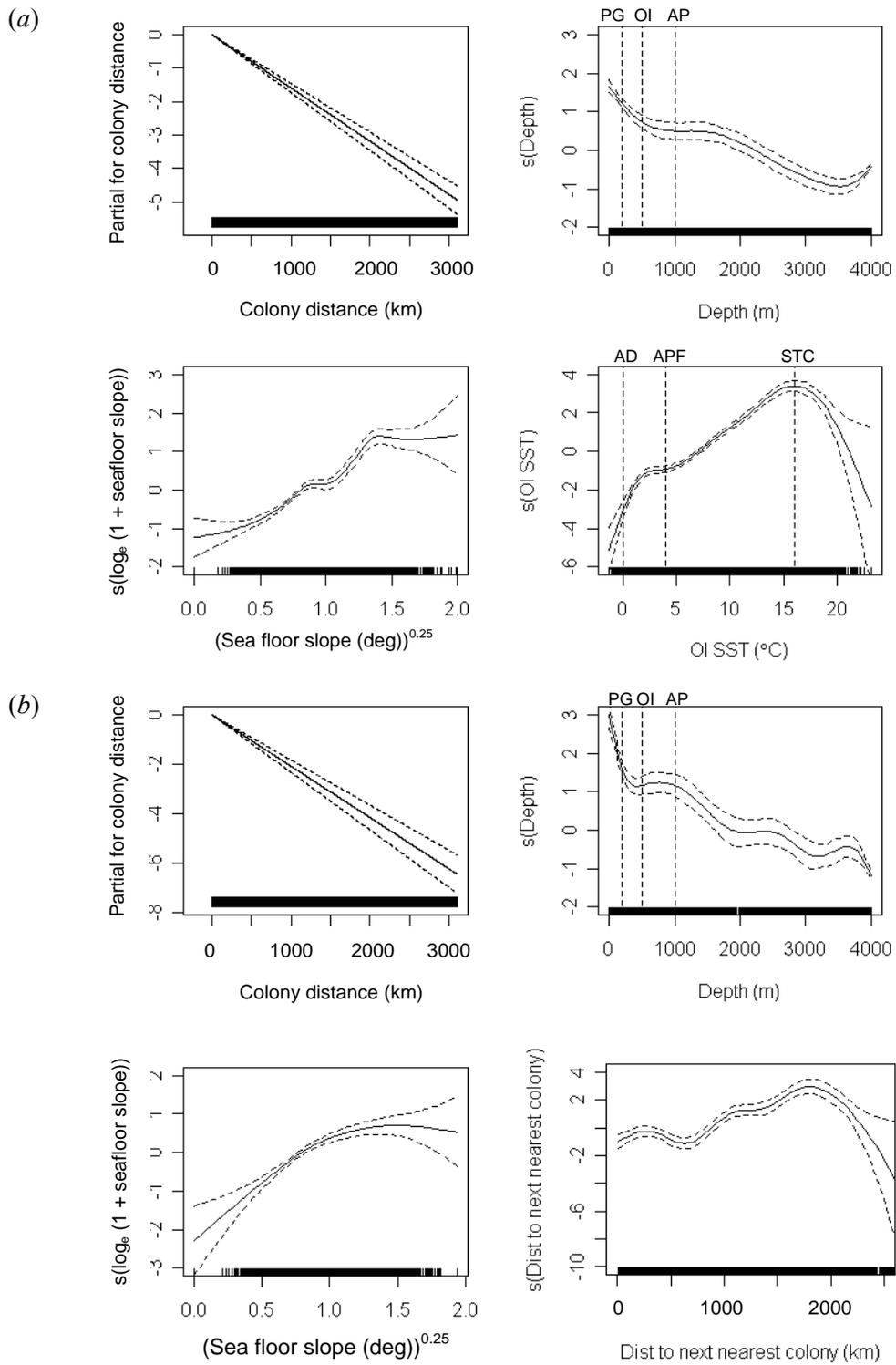


Figure 2.9 Fixed-effects covariates retained in (a) model I, fitted to spatial usage data from incubation, and (b) model III, fitted to all data from post-brood chick-rearing,

showing the effect of each covariate at the population level on the response variable (y-axis) at the scale of the linear predictor (dashed lines = estimated 95% CIs). The approximate depth of the shelf-break bounding Patagonia (PG), oceanic island colonies (OI) and the Antarctic Peninsula (AP), as well as the approximate summertime SST of the Antarctic Divergence (AD), Antarctic Polar Front (APF) and Subtropical Convergence (STC) are also shown.

2.3.3 Habitat preference

All covariates included in the two global spatial usage models (I and III) were retained as smooths, except colony distance, d_c , which was retained as a linear term (Fig. 2.9). In both cases d_c had a negative slope, implying that, counter to hypothesis 1, spatial usage decreases at a greater rate than $1/d_c$. On the scale of the linear predictor, the gradient of d_c vs. the response was greater for model III ($-2.07 \times 10^{-3} \pm 0.25 \times 10^{-3}$) than model I ($-1.61 \times 10^{-3} \pm 0.14 \times 10^{-3}$), confirming that spatial usage declined more sharply with d_c during chick-rearing than incubation. Model I shows that during the latter stage, black-browed albatrosses prefer shallow, neritic waters. Preference decreases with depth to ~ 500 m (encompassing South American continental and most peri-insular shelf waters), is similar from ~ 500 -1600m (further encompassing deeper peri-insular waters, such as those around Kerguelen) and decreases thereafter. Furthermore, areas with steeper ($>3^\circ$) sea floor slopes are most preferred, with preference decreasing with slopes shallower than this value. SST preference peaked at $\sim 16^\circ\text{C}$, this temperature being indicative in oceanic areas of the Subtropical Convergence Zone (STCZ). Above and below this value, preference decreases, but is constant from ~ 3 - 5°C (i.e. in the S part of the APFZ). Model II indicated that the habitat preference of birds from NW South Georgia were similar to the global mean, but also showed an increase in preference with EKE above values of $\sim 250 \text{ cm}^2/\text{s}^2$ (Fig. 2.10). Although chick-rearing birds showed no preference for particular SSTs, model III shows their depth and depth slope preferences were very similar to those of incubation stage birds (Fig. 2.9b). Model IV shows that although chick-rearing Campbell albatrosses also prefer shallower waters, depth was most parsimoniously structured as a linear covariate (Fig. 2.11). Campbell albatrosses also exhibit a weak preference for positive SLA, peaking at ~ 9 cm.

2.3.4 Parapatric conspecific competition

Parapatric conspecific density (ρ_c) was not retained in any model. However, the minimum biological distance (i.e. not over-land) to the next nearest super-colony (d_n), was retained in model III, indicating that during chick-rearing, black-browed albatross preference increases with d_n up to ~ 250 km from the nearest colony, decreases again to a minimum at ~ 700 km, before increasing again to a maximum at ~ 1800 km (Fig. 2.9b).

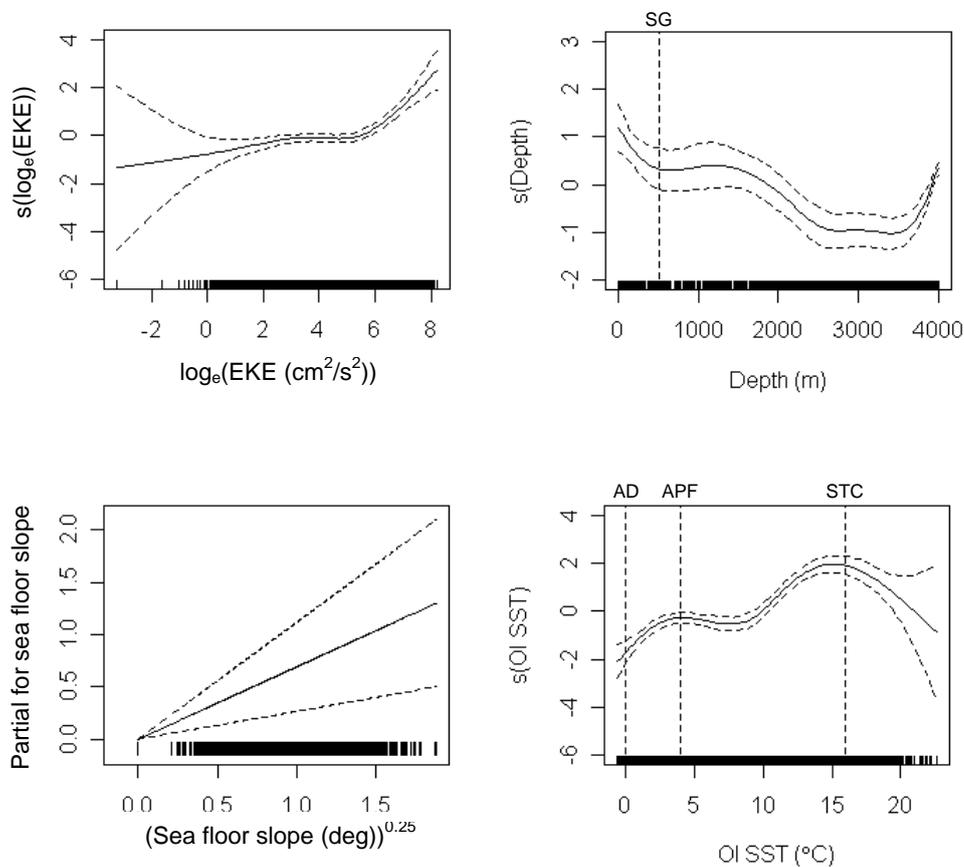


Figure 2.10 Fixed-effects covariates retained in model II, fitted to spatial usage data from black-browed albatrosses from NW South Georgia during incubation, showing the effects of the covariates at the population level on the response variable (y-axis), at the scale of the linear predictor (dashed lines = estimated 95% CIs, colony distance was also retained but is not illustrated).

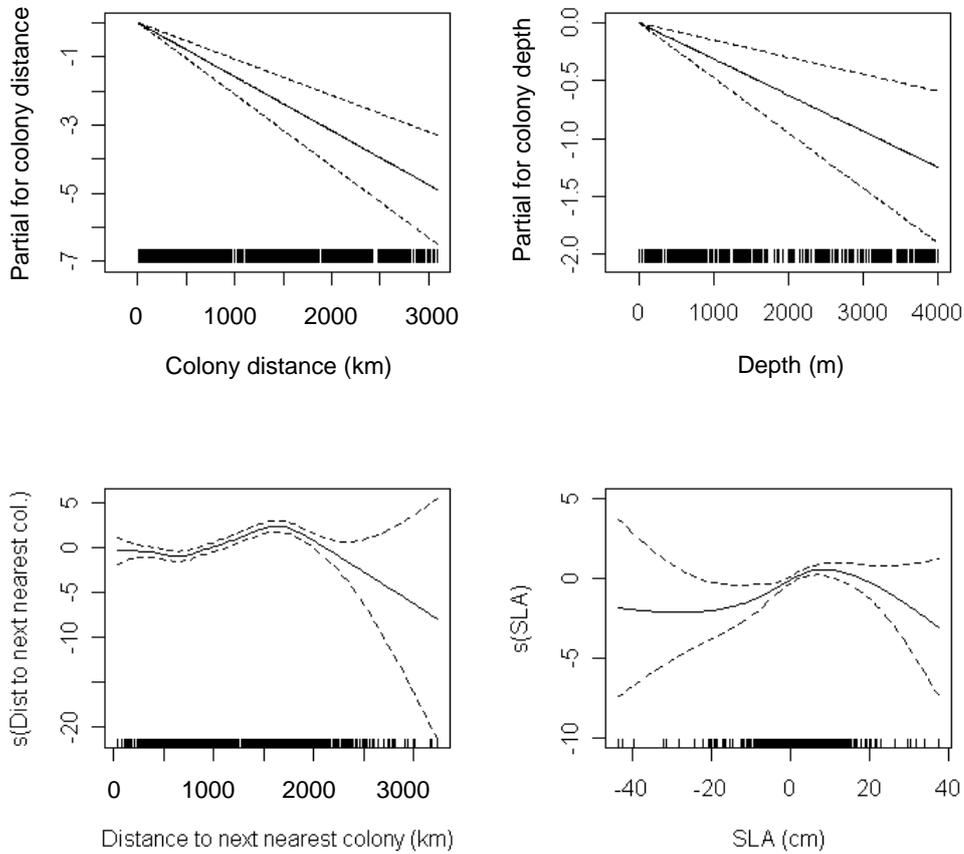


Figure 2.11 Fixed-effects covariates retained in model IV, fitted to spatial usage data from Campbell Albatrosses tracked during post-brood, showing the effects of the covariates at the population level on the response variable (y-axis), at the scale of the linear predictor (dashed lines = estimated 95% CIs).

2.3.5 Estimated usage

Monthly plots of predicted mean spatial usage show that the majority of the world's breeding black-browed albatrosses are confined to the SW Atlantic, southern Chilean coastal waters and the Humboldt Current (Fig. 2.12a-b). During incubation, they are predicted to range from ~ 31 - 60°S , whereas during chick-rearing their range extends southward, to 75°S on the Antarctic Peninsula. During incubation, estimated densities are highest (max. $15\text{ birds}/\text{km}^2$) in waters $< \sim 1500\text{ m}$ deep on the Patagonian Shelf,

south of the Rio de la Plata (36°S), and around Cape Horn, the Chilean coast, and Humboldt Current Upwelling south of Chiloe Island (42°S). Smaller areas of high density are predicted in the Brazil Malvinas Confluence (~ 42°S 053°W), the APFZ to the north of South Georgia, and on the South Georgia peri-insular shelf. Birds are predicted to occur at lower densities in oceanic waters bounding these areas, especially in the APFZ and STCZ in the SW Atlantic. During chick-rearing, the maximum predicted density is higher (73 birds/km²), with birds concentrated in the same neritic areas as during incubation, but at lower densities in oceanic areas. The ice-free, neritic waters of the western Antarctic Peninsula and the South Orkney islands are also expected to hold high large numbers of black-browed albatrosses during chick-rearing. During both stages, black-browed albatrosses are also predicted to occur at relatively low densities in neritic waters close to breeding colonies in the southern Indian and Pacific Oceans (Fig. 2.12a-b).

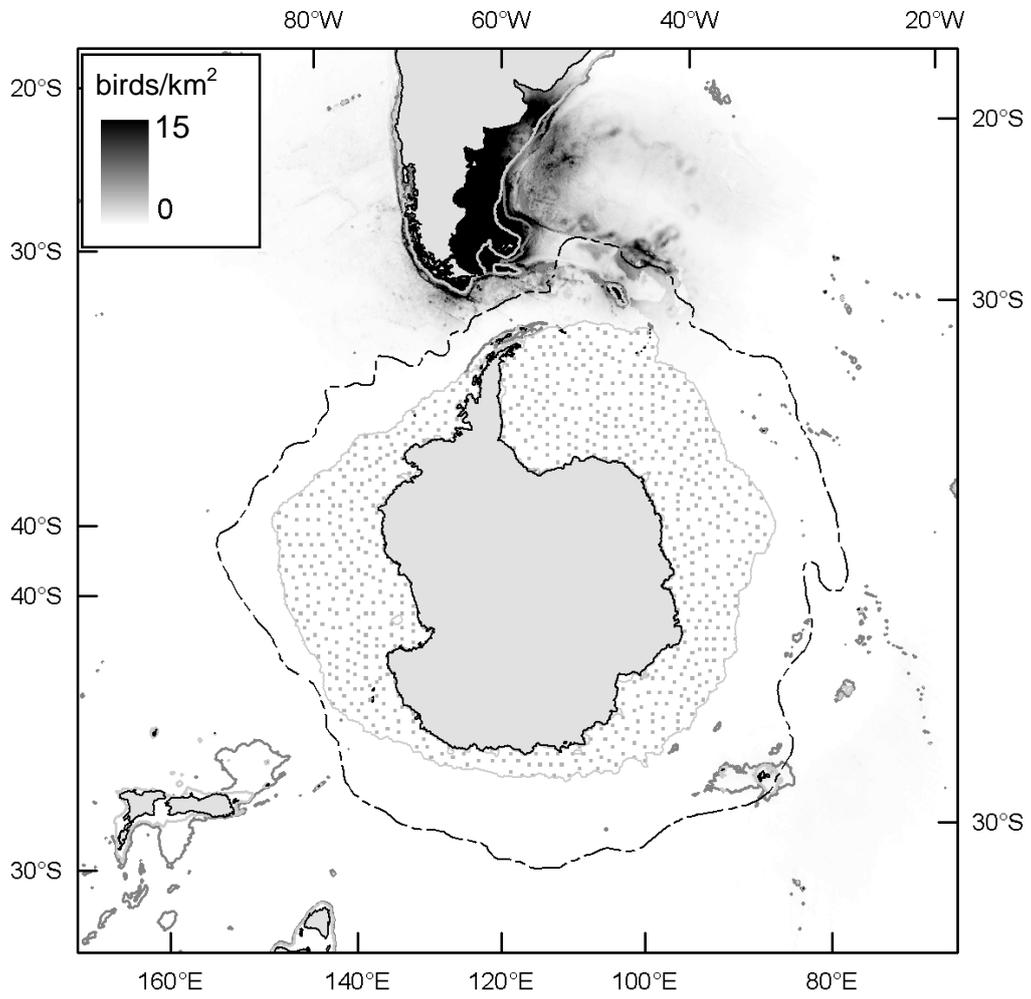
2.4 Discussion

2.4.1 Model performance and limitations

I used a combination of satellite-tracking, bathymetric, and remotely-sensed oceanographic data to model the spatial usage of breeding black-browed albatrosses as a function of habitat preference, accessibility and parapatric conspecific density. In so doing I was able to estimate, with unprecedented accuracy, the worldwide distribution at sea of an abundant, long-ranging, pelagic seabird. My models performed satisfactorily, as shown by the high congruity between predicted spatial usage by black-browed albatrosses from Heard Island during chick-rearing, and recently published satellite-tracking data that were not available for my analysis (c.f. Fig. 2 in Lawton et al. (2008) with Fig. 2.13c in this study). Nonetheless, there were some apparent limitations to the predictive capacity of my models. For example, spatial usage on the northern Patagonian Shelf was over-predicted, and that on the coast of central Chile was under-predicted. This result, and a small amount of residual spatial autocorrelation evident in model I, suggests that an important covariate such as the wind field (see Chapter 4) may not have been considered in my analysis (Aarts et al. 2008).

Although the spatiotemporal resolution of the models was limited by that of the environmental data, (min 33 km, 1 month) I was able to detect responses to mesoscale phenomena such as eddies and meanders. Since locations with missing environmental data are effectively treated as inaccessible, any systematic pattern in the occurrence of missing values results in a spurious null model. In consequence, I was unable to incorporate remotely-sensed chlorophyll-a or conventional SST because cloud cover causes a reduction in satellite acquisition of these data at high latitudes (Woodward & Gregg 1998). Also, as the first tracking dataset was collected in 1994 (Table 2.2), the only contemporaneous cloud-free SST dataset available (NOAA_OI_SST_V2) had a relatively low spatial resolution (1°) so I was only able to detect responses to water masses at large scales (>100 km). More recent studies would be able to exploit SST data with higher spatial (25 km) and temporal (daily) resolution to examine interactions with oceanic frontal systems, such as the Antarctic Polar Front (Boehme et al. 2008). In addition, GPS loggers (which can be accurate to < 10m) are now readily available, and enable more detailed investigations of factors limiting spatial usage at the submesoscale level (Awkerman et al. 2005). Such data might have improved my capacity to model the hot-spots of spatial usage in central Chilean coastal waters, which I suspect occur in response to high levels of primary production associated with the Humboldt Current Upwelling (Longhurst 1998). A higher resolution spatial model, fitted at regional or colony level, could also resolve the response of black-browed albatrosses to topographically constrained fronts on the Patagonian Shelf (Acha et al. 2004), and spatial usage in the complex channels of the Chilean fjords. In addition, my models could be extended to consider time-lagged biological responses to physical processes, such as phytoplankton blooms induced by mixing or ice recession (Ainley et al. 1993, Hunt et al. 1999, Gremillet et al. 2008). Furthermore, the inclusion of individual characteristics (sex, age, experience, quality etc.) would have been an appropriate refinement (Aarts et al. 2008), particularly as male and female black-browed albatrosses from at least one population exhibit different spatial usage patterns (Phillips et al. 2004b). However, such characteristics were not known for the majority of birds tracked. Finally, anthropogenic activities (i.e. fishing) may affect spatial usage of black-browed albatrosses in relation to the physical environment (Thompson 1992, Waugh et al. 2005).

(a)



[cont.]

(b)

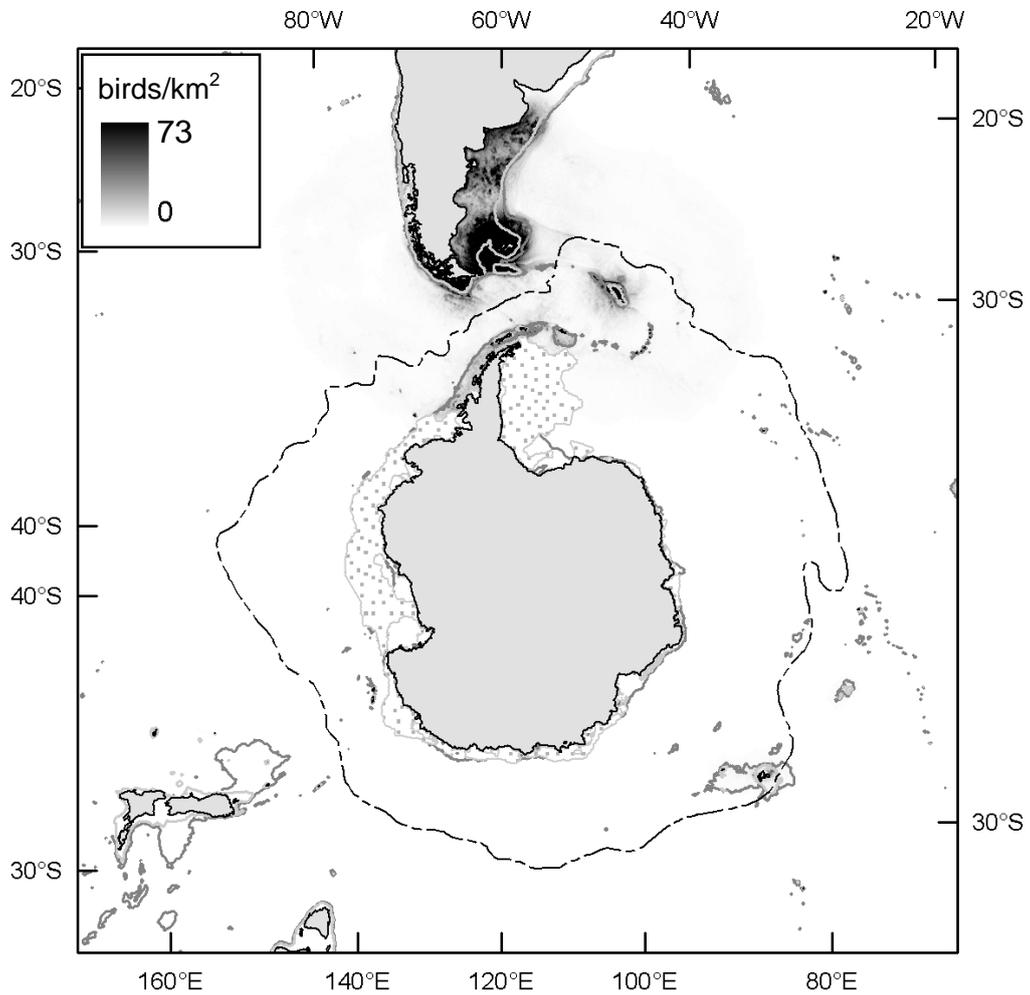


Figure 2.12 Estimated at-sea distribution (birds/km²) of breeding black-browed albatrosses, (a) world-wide during incubation (November, 2000) predicted using model II for South Georgia and model I for all other populations (b) world-wide during post-brood chick-rearing (February, 2001) predicted using model III.

2.4.2 Accessibility

My data support hypothesis 1, that the spatial usage of breeding black-browed and Campbell albatrosses decreases with d_c , confirming that these species act as typical central place foragers (Orians & Pearson 1979). Although pelagic seabirds are widely acknowledged to conform to this paradigm, few studies of habitat preference make this explicit (Pinaud & Weimerskirch 2005, Louzao et al. 2006). Colony distance (d_c) was retained as an explanatory covariate in my usage models, indicating that α declines at a greater rate than $1/d_c$, as in other colonial breeders (Nemeth et al. 2005). Further refinement of the null usage model could be achieved firstly by determining whether energetic (intrinsic) or time (extrinsic) costs ultimately limit α (Ydenberg et al. 1994, Hedenström & Alerstam 1995). During incubation, the time available for foraging trips is determined by the partner's ability to fast on the nest, whereas during chick-rearing, it is the endurance of the chick that is limiting (Shaffer et al. 2003, Humphreys et al. 2006). In order to fledge successfully, a chick requires a high rate of energy delivery; hence, its parent returns much more frequently than during incubation. The rate of decline in α with d_c is greater during chick-rearing than incubation, suggesting that extrinsic factors limit α - a conclusion further supported by the low energetic cost of flight in albatrosses (Bevan et al. 1995, Arnould et al. 1996). Secondly, both the temporal and energetic costs of albatross flight also vary with relative wind speed (Weimerskirch et al. 2000b, Wakefield et al. in press). As wind field is a highly dynamic variable, its relationship to α is potentially complex. However, could this relationship be modelled, it would further refine models of spatial usage (Felicisimo et al. 2008, Wakefield et al. in press). Finally, α alters dramatically in polar regions due to seasonal changes in the extent of sea ice. Although I allowed this to restrict accessibility on a monthly time scale, sea ice cover may change more rapidly (Heil & Allison 1999), and therefore a higher temporal resolution might improve model fit.

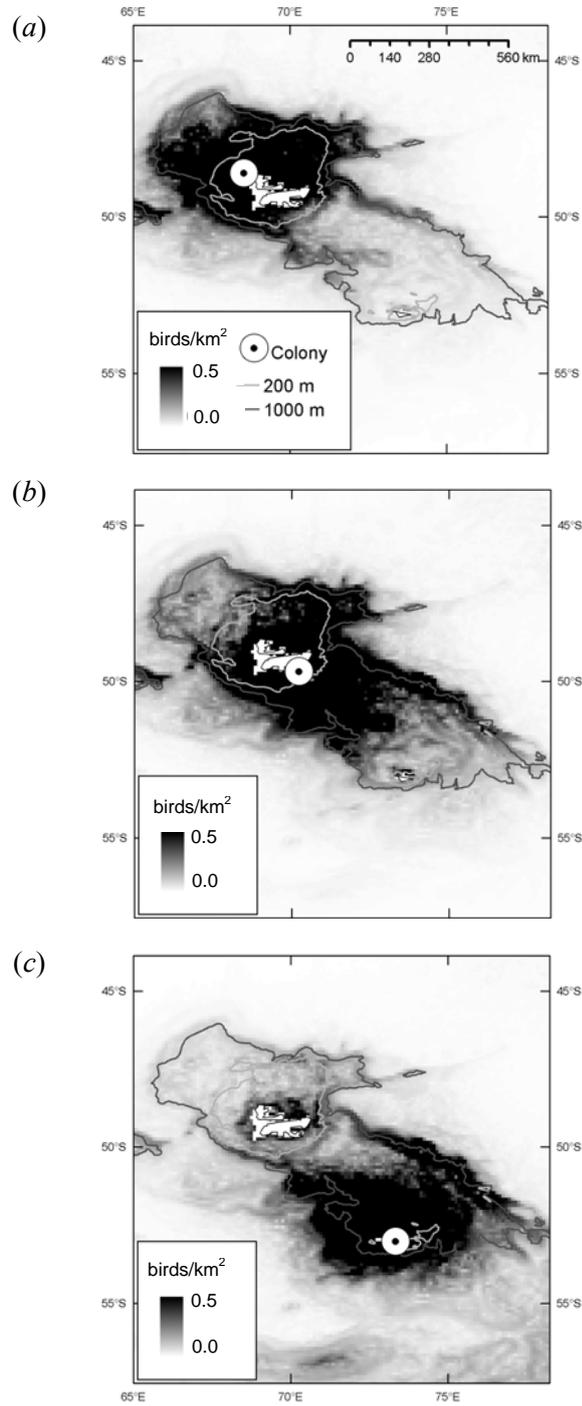


Figure 2.13 Estimated at-sea distribution (birds/km²) of breeding black-browed albatrosses during post-brood chick-rearing from (a) NW Kerguelen (b) SE Kerguelen and (d) Heard and MacDonal Island predicted using model III.

2.4.3 Black-browed albatross habitat preferences

Previous studies have described habitat *use* of breeding black-browed albatrosses (Weimerskirch et al. 1997b, Gremillet et al. 2000, Wood et al. 2000, Huin 2002, Pinaud & Weimerskirch 2002, Phillips et al. 2004b, Terauds et al. 2006b, Pinaud & Weimerskirch 2007) and Campbell albatrosses (Waugh et al. 1999) but this is the first study to quantify habitat *preferences*. By comparing habitat use with availability (Manly et al. 2002), my study confirms that, in all populations, habitat preference decreases with depth; birds prefer, in order, neritic (0-500 m), shelf-break and shelf-slope (500 – 1000 m) and oceanic waters (>1000 m). Habitat preference also increases with sea floor slope, to a maximum of $\sim 3^\circ$. Although such slopes are typical of the shelf-break, the interaction between depth and depth slope was not retained in my models, indicating that areas with steeper relief are preferred *per se*, regardless of depth. Data collected over multiple breeding seasons suggests that this preference varies little between years (Prince et al. 1998, Wood et al. 2000, Pinaud & Weimerskirch 2002, Phillips et al. 2004b).

Primary production in neritic and shelf-break waters is often strongly seasonal, peaking in spring, summer and autumn, when albatrosses are breeding. Hence, prey density is predictable at large temporal and spatial scales (months, 100s km) (Longhurst 1998). Furthermore, prey aggregate predictably at smaller scales (days, 10s km) due to the presence of tidal and shelf-break fronts. As these and other shallow water processes are topographically constrained, they occur at similar depths in different regions (Lefevre 1986, Acha et al. 2004). Consequently, physical forcing may explain why bathymetric preferences are expressed similarly by birds from widely-separated colonies, despite considerable variation in the depths of different continental and peri-insular shelves (e.g. Patagonian Shelf ~ 200 m; Antarctic Peninsula Shelf ~ 500 m; Kerguelen Shelf ~ 1000 m). Given that black-browed albatrosses prefer neritic waters and that, in biological terms, the transition between neritic and oceanic regimes, which occurs in the vicinity of the shelf-break, is often abrupt, one might expect a step in the preference function (Fig. 2.9) at the shelf-break depth. That this does not occur may be because at some spatial scales, depth increases with d_c (i.e. shallow habitats are more accessible),

although the form of this relationship is highly variable with location (c.f. the bathymetry around Macquarie with that of the Falklands). Hence, it could be hypothesized that black-browed albatrosses utilize neritic waters more frequently simply because their breeding islands lie on continental or peri-insular shelves. Although it is difficult to separate the ultimate and proximate causes of specialisation, this seems unlikely: firstly, because black-browed albatrosses also forage in distant neritic waters (e.g. during chick-rearing, birds from northwest South Georgia and Isla Diego Ramirez travel >1600 km to forage on the shelf of the west Antarctic Peninsula) and secondly, because sympatric congeners, such as the grey-headed albatross *T. chrysostoma*, which is morphologically very similar to the black-browed albatross, forage more frequently in oceanic waters (Nel et al. 2001, Phillips et al. 2004b).

In common with the majority of seabirds, black-browed albatrosses are long-lived, have low fecundity, locate patchily dispersed prey by searching, and have a catholic diet, which includes carrion (Croxall & Prince 1994, Cherel & Klages 1998). Although these are all traits typical of generalists (Begon et al. 2006), I have shown that the same habitats are preferred in all but one population, suggesting a degree of habitat specialization. This exception was exhibited by black-browed albatrosses from NW South Georgia during incubation, which foraged not only in neritic, shelf-break and shelf-slope habitats but also in the distant oceanic waters of the Brazil-Malvinas Confluence. This was manifested as an increase in habitat preference with EKE above $\sim 250 \text{ cm}^2/\text{s}^2$. EKE in the Brazil-Malvinas Confluence exceeded $3600 \text{ cm}^2/\text{s}^2$, indicating intense mesoscale activity. In the subtropical Southern Hemisphere such activity occurs only in this region, the Agulhas Current Extension off the Cape of Good Hope, and on the east coast of Australia (Ducet et al. 2000). Notably, the latter two areas are exploited by non-breeding black-browed albatrosses (Tickell 2000, Phillips et al. 2005b, Petersen et al. 2008). Mixing and advection at the edges of mesoscale meanders and eddies, where EKE values are highest, may lead to enhanced primary and secondary production, as well as the aggregation of prey (Mann & Lazier 2006). Numerous studies have demonstrated associations with mesoscale eddies by long-ranging higher predators, including southern elephant seals *Mirounga leonine* in the Brazil-Malvinas Confluence (Campagna et al. 2006), and grey-headed albatrosses in the APFZ (Nel et al. 2001).

2.4.4 Stage-specific habitat preferences

Although bathymetric preferences were similar across breeding stages, the spatial usage of birds during incubation also varied with SST, supporting hypothesis 2, that black-browed albatrosses express stage-specific habitat preferences. During incubation, birds from some populations also made occasional, or in the case of birds from northwest South Georgia, frequent, trips into distant oceanic waters. This can be interpreted in a number of ways. For example, during incubation, black-browed albatrosses have sufficient time to make longer trips, allowing them to access oceanic subantarctic waters between the APF and the STCZ. This may be profitable because complex fronts, meanders and eddies give rise to comparatively high levels of primary and secondary production in these areas (Lutjeharms et al. 1985). Alternatively, the preference for warmer SSTs may be spurious, arising because black-browed albatrosses have a more northerly distribution during incubation for other reasons, e.g. if black-browed albatrosses were broadly tracking resources, because primary production peaks during November in the mid southern latitudes and two months later in high latitudes (Yoder et al. 1993). If this is the explanation, any causal link between SST and spatial usage would be indirect. However, Pinaud & Weimerskirch (2002) have shown that, over an 18-year period, breeding success of black-browed albatrosses at Kerguelen is positively correlated with the mean monthly SST anomaly in core foraging areas, implying a more direct link between SST and foraging success. During chick-rearing, black-browed albatrosses showed no SST preference. However, 21 of the 54 black-browed albatrosses I tracked in this stage visited areas covered by sea ice earlier in the season, whereas during incubation, only one of 109 birds visited the marginal ice zone. This shift to foraging in marginal sea ice was synchronised with recession of pack ice, which is followed by a period of high productivity (El Sayed & Taguchi 1981). Alternatively, black-browed albatrosses may simply be exploiting previously inaccessible neritic, shelf-break and shelf-slope areas, which are preferred *per se* (Ainley et al. 1993). Indeed, the extent of open water <1000m deep within 3200 km of the Islas Diego Ramirez increases on average by 230 000 km² as the sea ice retreats between December and February, and such areas are often replete with Antarctic krill, *Euphausia superba* (Murphy et al. 2007). Finally, changes in dietary

requirement with breeding stage may play a role in habitat selection. Although there is a wealth of data on the diets of seabirds during chick-rearing, very little is known about the diet of incubating, or indeed non-breeding, birds (e.g. Croxall & Prince 1980, Cherel & Klages 1998). However, fatty acid analysis has shown recently that diet may differ between breeding stages (Williams et al. 2008). Such a shift is likely to occur in some populations of black-browed albatross, because they forage south of the PF (which marks the biogeographical limit of the Southern Ocean) only during chick-rearing (Fig. 2.3). Hence, the differences in black-browed albatross habitat preference I observed could be interpreted in terms of stage-dependent foraging niches, mediated by intrinsic factors such as the dietary or energetic requirements of adults and chicks (Charrassin et al. 1998, Humphreys et al. 2006), or by extrinsic factors.

2.4.5 Campbell albatross habitat preferences

Closely-related species often occupy different niches. As such, it may be unsurprising that the chick-rearing stage habitat preferences of Campbell and black-browed albatrosses differ. However, differences in habitat preferences can also arise due to differences between the relative availability of habitats to different (allopathic) populations (Mysterud & Ims 1998, Boyce et al. 2002). The oceanographic regime in waters surrounding Campbell Island differs in a number of respects from that in waters bounding black-browed albatross colonies. Firstly, although the Campbell Plateau is extensive, it is also deep (600 – 1000 m) in comparison to typical continental or peri-insular shelves (usually < 200 m deep). Hence, although Campbell albatrosses have access to comparatively small areas of neritic waters close to their colony, there are large areas of waters of intermediate depth (Table 2.2). Secondly, topographic steering of the Antarctic Circumpolar Current around the plateau gives rise to intense mesoscale eddy activity in the subantarctic and subtropical frontal zones, in very predictable areas close to the island (Morris et al. 2001). Hence, because of the paucity of truly neritic waters around Campbell Island, Campbell albatrosses may have a general preference for shallower waters similar to black-browed albatrosses but also exploit predictable oceanic frontal zones (Waugh et al. 1999), as indicated by their preference for positive SLAs. As such, the habitat preferences of Campbell albatrosses during incubation may be similar to those of black-browed albatrosses from South Georgia. The questions of

whether observed differences in chick-rearing stage habitat preferences of Campbell and black-browed albatrosses arise due to specialisation or are simply differences in the relative availability of habitats could be addressed by tracking and modelling the habitat preferences of the small population of black-browed albatrosses which breed sympatrically with Campbell albatrosses on Campbell Island.

2.4.6 Parapatric conspecific competition

My null model assumes that spatial usage decreases with d_c (Matthiopoulos 2003). A corollary of this is that the capacity of individuals to compete for resources declines with d_c , because energetic reserves and/or the time available to locate and capture prey also diminish with d_c . Direct competition between black-browed albatrosses can be intense, with frequent agonistic encounters between birds during foraging (Cherel et al. 2002). Hence, in order to minimise intraspecific competition, locations should be preferred if they are both close to the nest and distant from other colonies. If prey is uniformly distributed, this would give rise to a partial spatial segregation along colony lines, perhaps enhanced by cultural effects and wind patterns (Gremillet et al. 2004). Such segregation has been noted between some adjacent populations of black-browed albatrosses (Weimerskirch et al. 1988, Huin 2002), and in other colonial central-place foragers, including seabirds (e.g. Giraldeau et al. 1994, Brown & Gordon 2000, Ainley et al. 2003, Gremillet et al. 2004). However, if colonies were far enough apart, the decrease in usage with d_c alone may be sufficient to give rise to an apparent exclusivity in foraging areas (Lea et al. 2008). The hinterland model (Cairns 1989) proposes a similar mechanism to explain spatial segregation in seabirds. However, the tracking data presented here show that this model is inappropriate for black-browed albatrosses firstly, because it predicts that the foraging zones of birds from adjacent colonies are entirely mutually exclusive, whereas foraging black-browed albatrosses from the three main Chilean colonies, which are located 100-700 km from one another, overlap extensively (Fig. 2.3a) and secondly, because the predicted positive correlation between foraging area and colony size does not hold true for black-browed albatrosses. Similarly, contrary to Lewis et al. (2001), black-browed albatrosses from larger colonies do not necessarily travel further to forage (Fig. 2.4), a mechanism by which it was proposed birds could avoid indirect competition with sympatric conspecifics.

Indeed, birds from Beauchêne Island, which is the second largest black-browed albatross colony in the world, forage relatively close to their colony (Fig. 2.3). This is perhaps unsurprising, as it seems reasonable to assume that, on average, the fitness of two birds from the same colony diminishes at the same rate with d_c (see also Forero et al. 2002).

During model selection, I rejected parapatric conspecific density (ρ_c) as an explanatory variable. Distance to the next nearest colony (d_n) was, however, retained in my post-brood model (III). Black-browed albatrosses apparently responded to d_n at two scales. At the mesoscale, they showed a preference for areas ~ 200 km from the next nearest colony while at the macroscale (1000s km) they preferred areas ~ 1800 km away. I interpret this as a behavioural response to an increased need to avoid direct competition with parapatric congeners during chick-rearing. During this stage, encounters with parapatric conspecifics in the vicinity of neighbouring colonies would be more likely, both because foraging ranges contract and twice as many adults are at sea (during incubation, one parent from each breeding pair must remain on the nest). Hence, black-browed albatrosses either make short trips in the vicinity of the home colony but far from neighbouring colonies (such as in the Falklands populations), and/or longer trips to areas remote from both the home and neighbouring colonies. The latter strategy is exhibited by black-browed albatrosses from South Georgia and Islas Diego Ramirez, which also travel to the South Orkneys Islands and the west Antarctic Peninsula during chick-rearing (Fig. 2.3). Hence, while hypothesis 4 is supported, it should be emphasised that spatial usage is a function not just of intraspecific competition but also of accessibility and habitat preference, factors which may mitigate against spatial segregation.

Chapter 3. The limiting effects of habitat availability and accessibility on population size

The data in this chapter have also been submitted to Nature as Wakefield E.D., Phillips R.A. and Matthiopoulos J., Marine habitat availability and accessibility regulate seabird population size.

3.1 Introduction

It has long been suspected that populations of pelagic seabirds are regulated by the availability of food during the breeding season (Ashmole 1963). This is demonstrated, indirectly, by correlations between breeding success and proxies of food abundance (Pinaud & Weimerskirch 2002, Weimerskirch 2002). If this is the case, it follows that population size, and therefore the environment's carrying capacity ought to be predictable from some measure of prey availability. However, this apparently simple supposition belies a number of problems: firstly, population units perceived by humans (individual colonies, birds foraging at sea, etc.) may not function independently (Furness & Birkhead 1984, Lewis et al. 2001) and models of seabird populations often invoke density-dependent food limitation and intraspecific competition to explain observed colony sizes (Ashmole 1963, Furness & Birkhead 1984, Lewis et al. 2001); secondly, it is not generally feasible to measure the abundance and distribution of pelagic seabirds' prey directly and thirdly, the cost to seabirds of accessing available food is not uniform, but increases with distance from the colony (Chapter 2). Taking the black-browed albatross as an example of a wide-ranging, abundant pelagic seabird, I addressed these problems and tested the hypothesis that population size is regulated by habitat, and therefore food, availability and accessibility during the breeding season. The black-browed albatross is an apposite model because firstly, all of its known colonies have been censused in the past ten years (Appendix 1); and secondly, as shown in Chapter 2, satellite-tracking from colonies throughout its range has allowed its foraging habitat preferences (which are primarily for neritic waters, <1000 m deep) to be quantified.

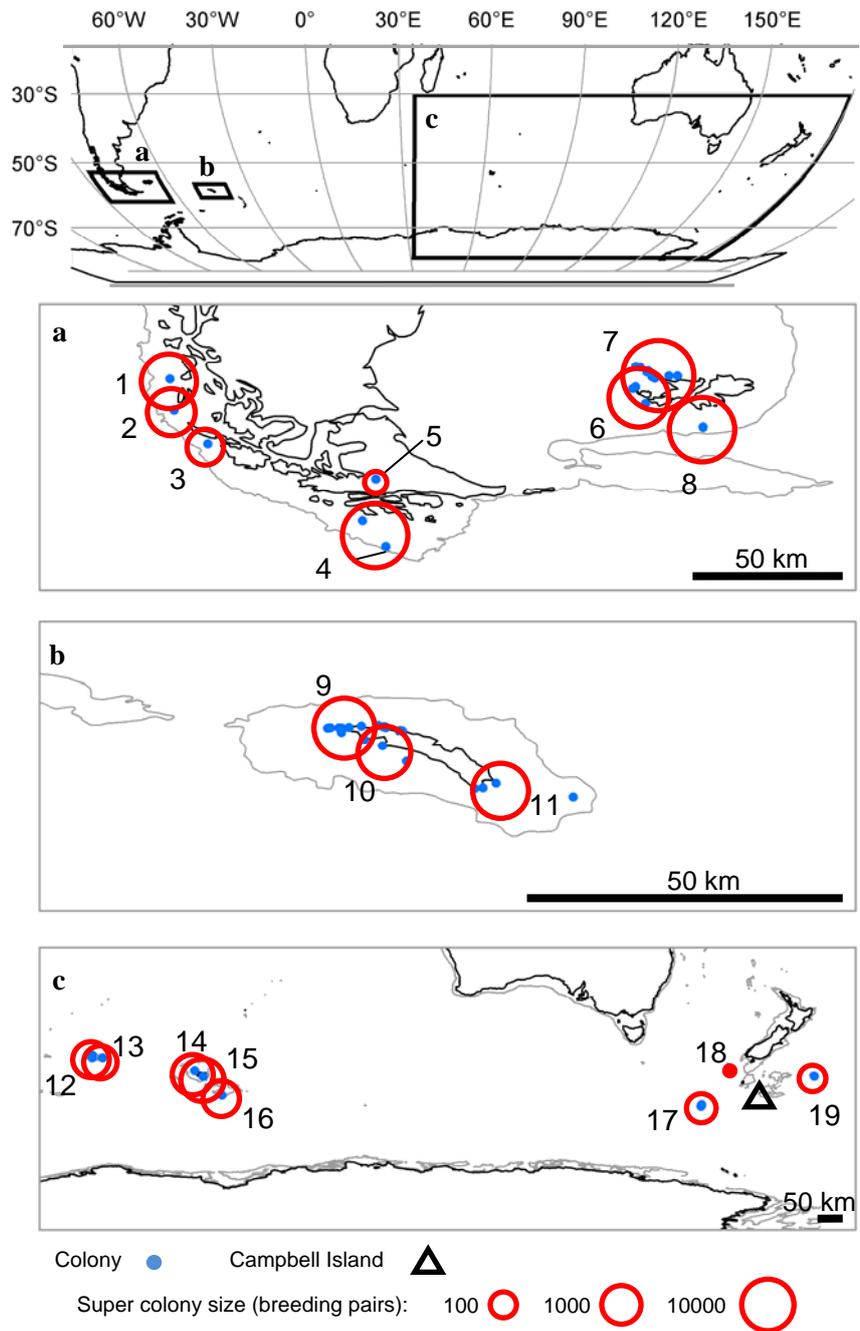


Figure 3.1 Location and size of black-browed albatross colonies. All known colonies ($n = 48$) were grouped into regional super-colonies by cluster analysis such that the maximum distance by sea between colonies i and j within super-colonies d_{ij} was $\leq 50, 100, 200, 400$ and 800 km. For illustration, red circles indicate the number of pairs of birds breeding annually in super-colonies defined by $d_{ij} \leq 100$ km.

Black-browed albatrosses breed during the austral spring and summer on isolated islands in the subantarctic, which are inherently distributed in clusters, separated by long distances (Fig. 3.1). Depending on the breeding stage, birds from nearby colonies exploit either overlapping or exclusive foraging areas (Huin 2002, Chapter 2). Such behaviour, in this and other species, is regarded as evidence of intraspecific competition between birds from adjacent colonies (Cairns 1989, Gremillet et al. 2004) - a mechanism frequently invoked to explain apparent negative correlations between colony size and the number of parapatric conspecifics within foraging range (Furness & Birkhead 1984, Lewis et al. 2001). However, this and other processes thought to limit colony size are not fully understood (Weimerskirch 2002) and it is not clear how far apart colonies of different sizes should be in order to function independently. Furthermore, it may be hypothesised that while colony sizes vary, the combined population within an area remains constant, being a simple function of available resources. For these reasons, and because of the difficulty of assessing spatial autocorrelation with small samples of point data (Cliff & Ord 1981, Fortin & Dale 2005), I adopted a multi-scale approach aimed at defining populations as functional units, i.e. all birds relying on the resources of a given region. In order to test the hypothesis that black-browed albatross populations are regulated by food availability during the breeding season (Ashmole 1963), I used preferred habitat and depth-integrated Net Primary Production (NPP) climate data as a proxies for food abundance. In addition, because the spatial usage models presented in Chapter 2 indicate that this species prefers not to forage close to neighbouring colonies during chick-rearing, I tested the hypothesis that population size is also limited by the total accessibility-weighted null density of conspecifics from neighbouring populations sharing the same potential foraging area. This approach builds upon empirical models of the effect of intraspecific competition on the size of corvid colonies (Griffin & Thomas 2000, Olea 2009).

3.2 Methods

3.2.1 Colony size and grouping

Colony size estimates (numbers of breeding pairs) were obtained for all known extant black-browed albatross colonies from published and unpublished sources. In almost all

cases, apparently occupied nest sites were censused during incubation, using direct or photographic counts or density estimation (for details and sources see Appendix 1). Where data were available from more than one breeding season, colony size measured during the period in which NPP was estimated (1998-2007) was used in the analysis.

The minimum distance by sea $d_{i,x}$ from the i th colony to each grid cell x at sea, as well as the distances $d_{i,j}$ between all pairs of colonies i and j , were calculated on a $1/6^\circ$ regular grid (Fig. 3.2). A complete-linkage clustering algorithm (Kauffman & Rousseeuw 2005) was then used to join adjacent colonies hierarchically into super-colonies, based on the distances between them. Complete-linkage minimises the maximum d_{ij} within clusters, resulting in compact, circular clusters (Kauffman & Rousseeuw 2005), appropriate to the central place paradigm. Clustering was implemented using the `hclust` function in R (R-Development-Core-Team 2007) at spatial scales $d_{i,j}$ ranging from 50 to 800 km, (Fig. 3.3).

3.2.2 Habitat availability, accessibility and competition

Grid cells accessible from each colony were defined as those lying within d_{\max} , the maximum foraging range observed during the breeding season. This was regarded as 3200 km, which is 1.1 x the maximum observed foraging range of 163 black-browed albatrosses, satellite-tracked from 8 colonies (Chapter 2). Bathymetric data were obtained from the ETOPO2 Global Relief 2v2 data set (U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Geophysical Data Center, 2006), and re-sampled on a $1/6^\circ$ grid.

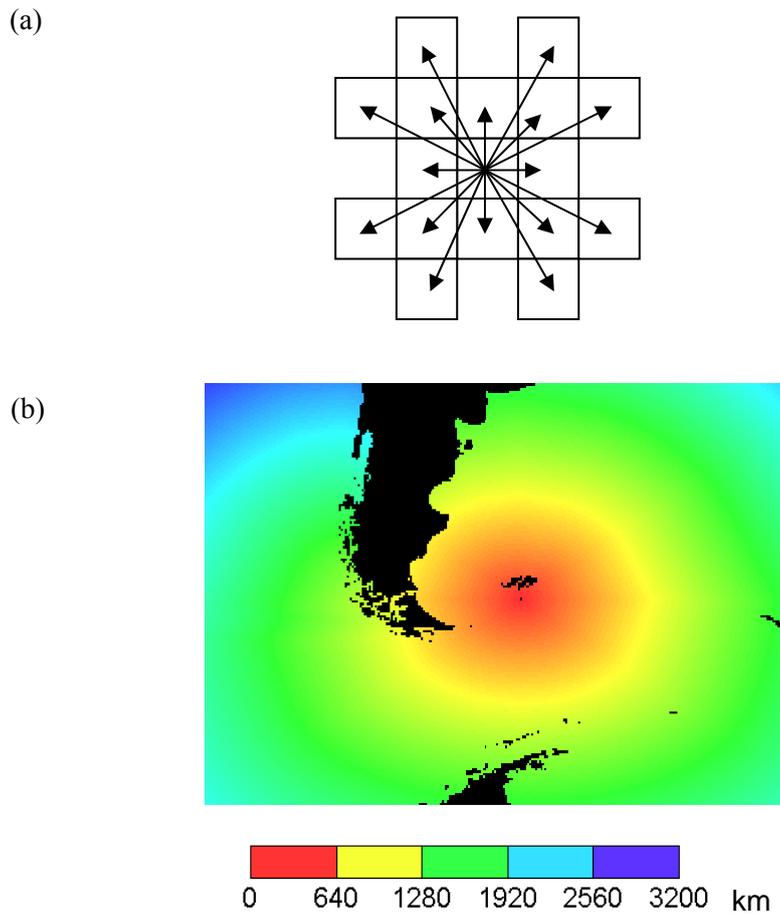


Figure 3.2 Calculation of distance by sea. Albatrosses do not usually cross large land masses. Hence, I used the by-sea distance d in my analysis. I calculated d between colonies and points in space on a regular $1/6^\circ$ grid. Starting at the colony, the minimum greater circle distance to all accessible cells in a 16 cell neighbourhood (a) were calculated. Proceeding to the cell with the minimum d , the minimum cumulative d to each cell in the 16 cell neighbourhood was then calculated. This process was repeated until the minimum distance by sea to all accessible cells (b) within d_{\max} (3200 km) had been calculated.

Cells were flagged as preferred if they contained neritic waters (i.e. if the depth Z_x was less than Z_p , where Z_p was defined successively as 250, 500 and 1000 m). H , the total area of preferred habitat available to birds from each population, was then:

$$H_i = \sum_{\text{All } x} A_x \delta_{i,x} \xi_x \quad \text{where} \quad \delta_{i,x} = \begin{cases} 1 & \text{if } d_{i,x} < d_{\max} \\ 0 & \text{otherwise} \end{cases} \quad \text{and} \quad \xi_x = \begin{cases} 1 & \text{if } z_x < z_p \\ 0 & \text{otherwise} \end{cases} \quad (3.1)$$

where A_x is the area of grid cells. The relative accessibility (Chapter 2) of grid cells was defined as:

$$\alpha_{i,x} = \left(\frac{d_{i,x} + 1}{d_{\max}} \right)^{-1} \quad (3.2)$$

The total preferred accessibility-weighted habitat available to each population was then:

$$H_i^* = \sum_{\text{All } x} A_x \delta_{i,x} \xi_x \alpha_x, \quad (3.3)$$

Monthly NPP climatology data ($\text{mg C m}^{-2} \text{ day}^{-1}$) estimated using a Vertically Generalised Production Model (Behrenfeld & Falkowski 1997b, Behrenfeld et al. 2006) for the period 1998-2007, were provided by Robert O'Malley and the Ocean Productivity website <http://science.oregonstate.edu/ocean.productivity> (2009) on a $1/6^\circ$ grid for the black-browed albatross breeding period (September – April). For each month, I then calculated total NPP available to each population:

$$P_i = \sum_{\text{All } x} A_x \text{NPP}_x \delta_{i,x} \quad (3.4)$$

and the total accessibility-weighted NPP available:

$$P_i^* = \sum_{\text{All } x} A_x \text{NPP}_x \delta_{i,x} \alpha_x . \quad (3.5)$$

The null distribution of birds C_x from each population (Matthiopoulos 2003, Aarts et al. 2008) was defined as:

$$C_{i,x} = \frac{\alpha_{i,x} N_i \delta_{i,x}}{\sum_{\text{All } x} \alpha_{i,x} \delta_{i,x}} . \quad (3.6)$$

where N_i is the number of pairs of birds in the i th population (Fig. 3.4). The total null density of conspecifics C_i^* within the foraging range of population i , one of the set of all other populations ($j = 1, 2 \dots, n, j \neq i$), was then:

$$C_i^* = \sum_{\text{All } x} \delta_{i,x} \alpha_{i,x} \sum_{\text{All } i \neq j} C_{j,x} \quad (3.7)$$

The null distribution of birds C_x from each population is that which would be observed if the spatial usage was dependent solely on accessibility (Matthiopoulos 2003). Hence, null density of conspecifics C_i^* is a measure of the intensity of competition from conspecifics from other populations, which is regarded as being proportional to the size of populations and inversely proportional to distance from colonies within those populations.

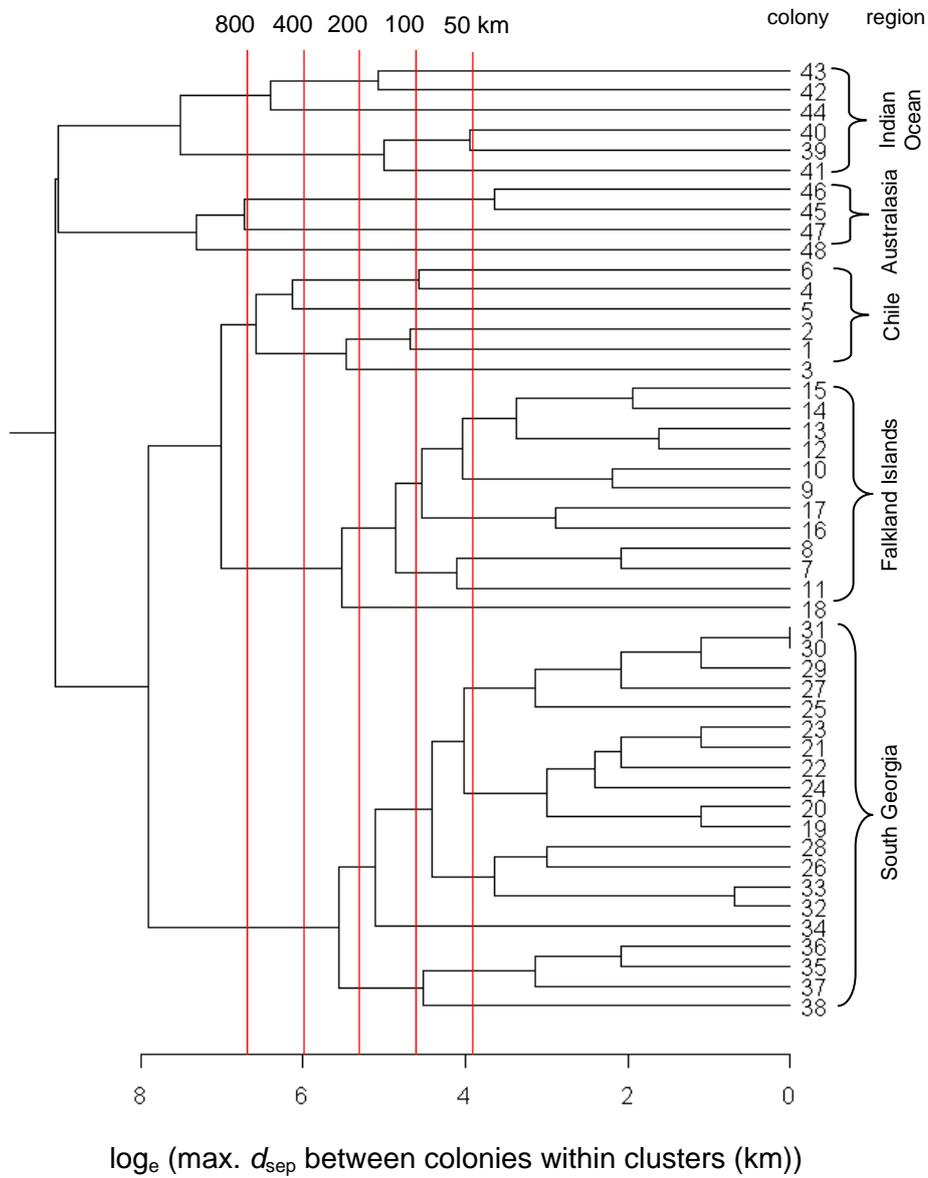


Figure 3.3 Distance by sea between black-browed albatross colonies. Clustering was carried out on untransformed values, but for clarity \log_e transformed distances are presented here (see Appendix 2 for details of colony clusters).

3.2.3 Models

For each clustering scale, N was modelled as a function of H , H^* , P , P^* and C^* using linear and quadratic regression. Seabirds colony sizes tend to be log-normally distributed (Jovani et al. 2008). Hence, all covariates were \log_e transformed to approximate normality, which was assessed using Anderson-Darling tests. Preliminary analysis showed that modelling $\log_e N$ using linear and quadratic regression resulted in better performing models than Poisson GLMs fitted to the untransformed data. Relative model fit was determined using AIC_c (second order AIC (Burnham & Anderson 1998)), R^2 and residual plots. Residual spatial autocorrelation was assessed using semivariograms (Cliff & Ord 1981).

3.3 Results

Black-browed albatross colony sizes were log-normally distributed (Anderson-Darling test \log_e colony size, $A = 0.25$, $p = 0.711$, $n = 48$). Cluster analysis showed that colonies were naturally distributed in spatial clusters, identifiable at a number of scales (Fig. 3.3, Appendix 2). For example, by clustering the 48 known black-browed albatross colonies such that $d_{ij} \leq 100$ km, 19 super-colonies were defined (Fig. 3.1). When considered as the number of pairs breeding annually in each colony or super-colony, population size N correlated positively with the total preferred neritic habitat H (i.e. waters < 500m deep, Chapter 2) within maximum foraging range (Fig. 3.5a, Table 3.1). However, irrespective of the scale at which colonies were clustered, the total accessibility-weighted area of preferred habitat H^* was a better predictor of N than H (Table 3.1, Fig. 3.5b). This pattern was clearest when colonies were clustered using d_{ij} values greater than 100 km (at $d_{ij} \leq 200$ km, $\log_e N = -45.0 + 3.5 \times \log_e H^*$, $F_{1,9} = 63.13$, $p < 0.001$). At this scale and above, over 87% of the variability in $\log_e N$ was explained by habitat availability and accessibility. Similar but weaker correlations were found between N and H when preferred habitat was defined either as waters < 250 m or < 1000 m deep.

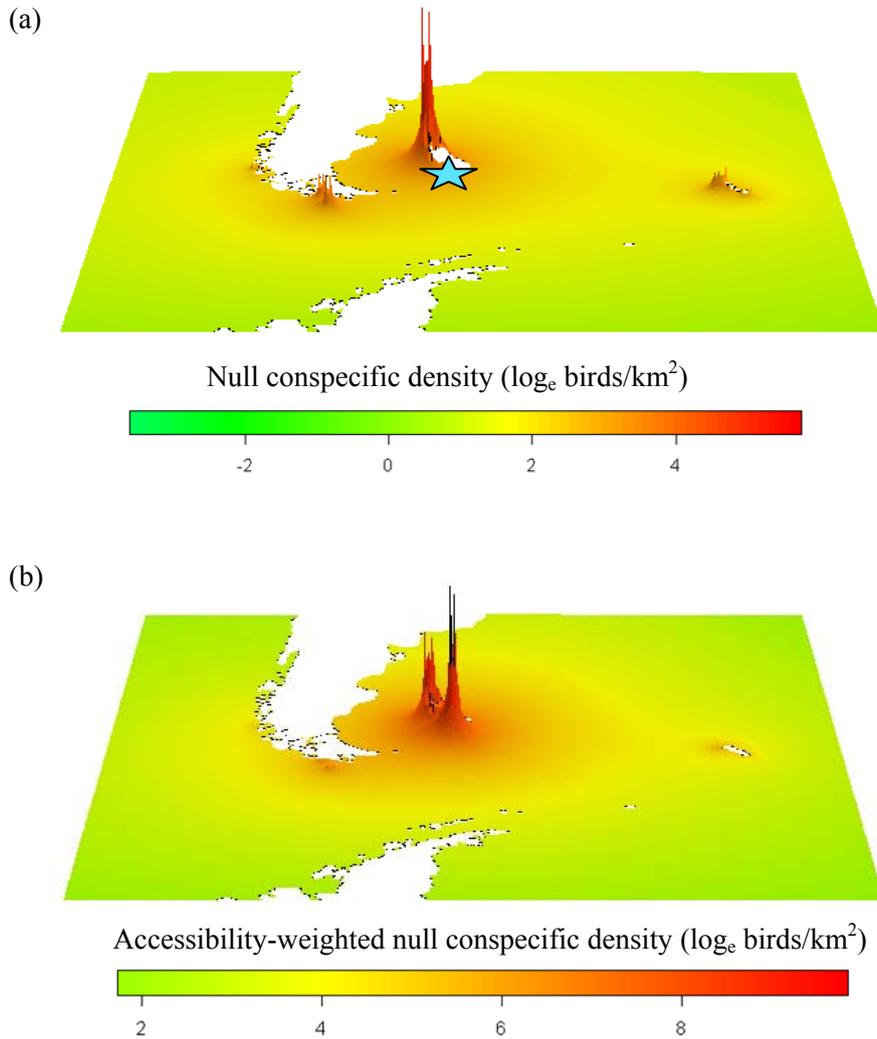


Figure 3.4 Estimation of the null conspecific density. The example is for population #12, defined at $d_{max} \leq 50$ km (Beauchêne Is., blue star). The null density of conspecifics, in each grid cell x , from each colony i , is the product of the population size N_i and accessibility $\alpha_{x,i}$. This value is summed for all populations except #12 to arrive at the null density of conspecifics from all other populations $C_x = \sum_{i \neq 12} C_{x,i}$.

Thus (a) is the density of conspecifics that would be observed if spatial usage were dependent upon accessibility alone. C_x is then weighted by the accessibility of population #12, $\alpha_{x,12}$ to give (b) the accessibility-weighted null conspecific density. The total density C_{12}^* is the volume under this surface. The area shown corresponds to that encompassed by in Fig.3.1a.

NPP available to foraging birds varied with season, peaking in December-January (Fig. 3.6a). In these months, there was a strong relationship between population size and total NPP weighted by accessibility, P^* (Fig. 3.5c and 3.6b). However, only at the largest grouping scale considered ($d_{ij} \leq 800$ km) did P^* explain variability in N as effectively as H^* (Table 3.1, $\log_e N = -211.7 + 11.8 \times \log_e P^*_{\text{January}}$, $F_{1,5} = 33.23$, $p = 0.002$). H^* and P^* explained N most effectively when colonies were clustered at regional scales (Table 3.1). The addition of C^* (the total accessibility-weighted null density of conspecifics from neighbouring populations sharing the same potential foraging area) did not improve models of population size, either at the colony or super-colony scale (Table 3.2).

Table 3.1 Goodness of fit of linear models of \log_e population size vs. habitat availability and accessibility.

d_{ij} between colonies (km)	n	AIC _c , R ²			
		$\log_e H$	$\log_e H^*$	$\log_e P$	$\log_e P^*$
0	48	216.4, 0.13	204.2 , 0.33	218.5, 0.09	212.9, 0.19
50	24	89.3, 0.55	78.3 , 0.72	95.3, 0.42	90.2, 0.54
100	16	61.8, 0.64	52.8 , 0.79	64.7, 0.57	59.6, 0.68
200	11	47.6, 0.61	35.0 , 0.88	48.9, 0.56	45.4, 0.68
400	9	42.3, 0.58	31.3 , 0.87	42.8, 0.55	39.7, 0.68
800	7	36.8, 0.55	27.9 , 0.88	35.3, 0.64	28.2, 0.87

Values in **bold** indicate minimum AIC_c for each super-colony grouping.

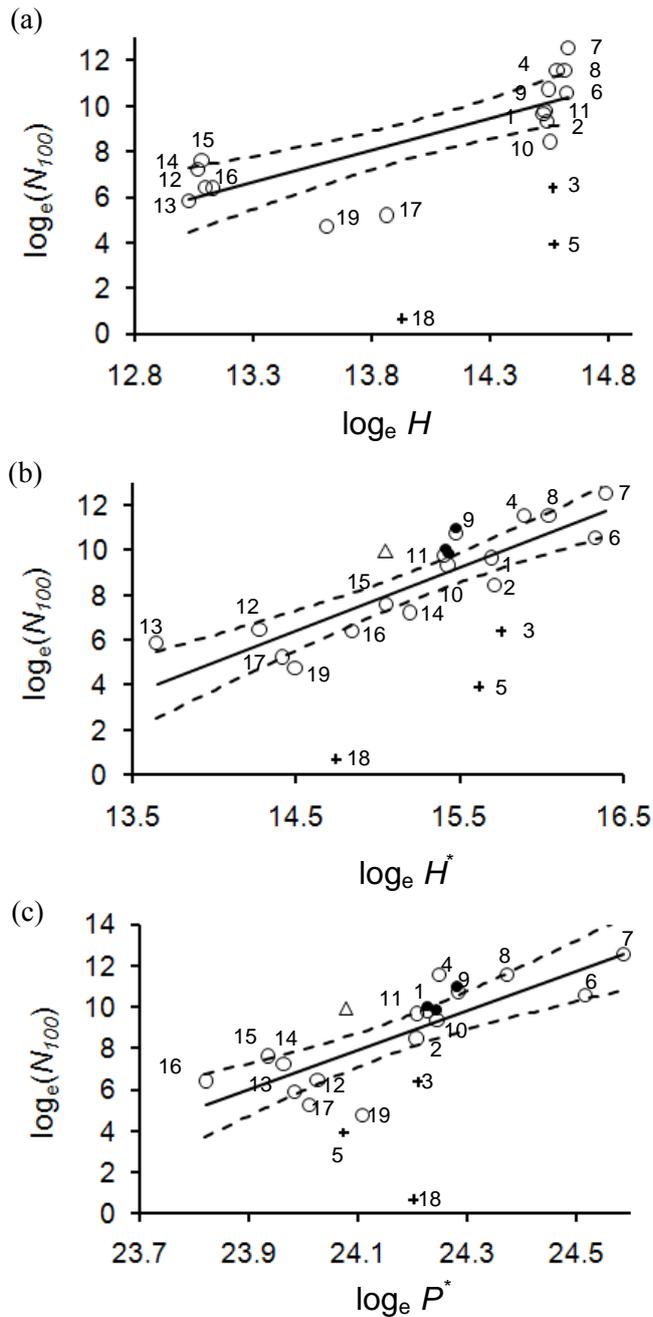


Figure 3.5 Black-browed albatross population size vs. (a) the total area (in km^2) of preferred habitat (neritic waters, <500 m deep, H) within max. foraging range (3200 km), (b) the total preferred habitat weighted by accessibility ($1/\text{distance}$ from the colony) H^* and (c) the total NPP (in $\text{mg C km}^{-2} \text{ day}^{-1}$) weighted by accessibility, P^* . Open circles indicate colonies used to fit models, closed circles South Georgia super-colonies censused in 1986, and crosses known outliers (see Discussion). The triangle indicates the world population of Campbell albatross, a single-island endemic. Super-colony numbers refer to Figure 3.1 and Appendix 2. Dotted lines indicate estimated 95% prediction CIs.

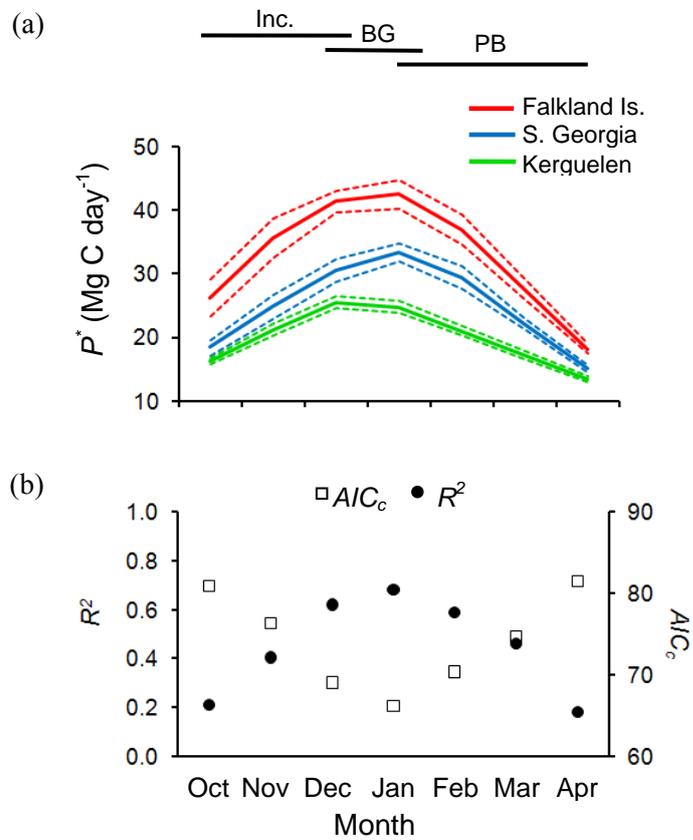


Figure 3.6 (a) Accessibility-weighted NPP (in $\text{mg C km}^{-2} \text{ day}^{-1}$) available to breeding black-browed albatrosses, indicating that P^* peaks in December or January, depending on the region. (b) The goodness of fit of models of super-colony size as a function of P^* (monthly averages, 1997 – 2007) is also best at this time. Horizontal bars indicate the temporal extent of incubation (Inc.), brood-guard (BG) and post-brood chick-rearing (PB) periods. Colonies were grouped at $d_{ij} \leq 100 \text{ km}$, but the trend was similar at all colony clustering scales.

3.4 Discussion

Although it was hypothesised almost half a century ago that seabird populations are regulated by the prey availability during the breeding season (Ashmole 1963) surprisingly few studies have attempted to relate available resources to population sizes. Furthermore, those that have, have made the unrealistic assumption that all locations within foraging range are equally accessible (Laidre et al. 2008). For example, Weimerskirch (2002) noted that the size of regional black-browed albatross populations was related to the amount of neritic habitat in the vicinity of colonies. In reality, time and energy costs increase and accessibility α declines with distance from the colonies (Orians & Pearson 1979). To account for this I weighted habitat units by α , and then modelled N as a function of the total accessibility-weighted area of preferred habitat H^* . At all scales, this was a better predictor of N than the un-weighted habitat availability H (Table 3.1, Fig. 3.5b), implying that population size is regulated by habitat accessibility as well as availability (Matthiopoulos 2003). Indeed, the large amount of variability in N explained by H^* for colonies clustered at $d_{i,j} > 100$ km suggests that these are the main factors regulating population size at the regional scale. The size of the world's only colony of Campbell albatross *T. impavida*, which is closely related to the black-browed albatross, was significantly greater than predicted by my models (Fig. 3.5b), in accordance with the findings presented in Chapter 2 that Campbell albatrosses have different bathymetric preferences to black-browed albatrosses. This is further ecological evidence in support of the view that these taxa should be regarded as separate species (Roberson & Nunn 1998, Burg & Croxall 2001).

My analysis assumed in accordance with optimal foraging theory that black-browed albatrosses prefer particular foraging habitats because they provide the most favourable conditions and resources (Parker & Stuart 1976). Hence, I interpret the strong relationship between population size and the availability of preferred habitat as an indication that black-browed albatross populations are regulated by food availability during the breeding season (Ashmole 1963). This is shown more directly by using NPP as a proxy for food abundance. Although diet composition varies among populations, black-browed albatrosses tend to consume middle to upper trophic level prey, such as

nototheniid and channichthyid fish, Antarctic krill *Euphasia superba* and ommastrephid squid (Cherel & Klages 1998). At large scales, the distribution and abundance of such organisms is determined by NPP (Iverson 1990, Atkinson et al. 2004, Jennings et al. 2008). In the latitudes at which black-browed albatrosses breed and forage, NPP is markedly seasonal, peaking in December-January (Fig. 3.6a). At this time of year, there was a strong relationship between population size and total NPP weighted by accessibility, P^* (Fig. 3.5c). However, P^* only explained population size as well as H^* at the largest clustering scale. This may be partly because NPP was estimated using SeaWiFS Chl-a and AVHRR SST data, which are prone to inaccuracies due to cloud interference at mid to high latitudes (Woodward & Gregg 1998).

Black-browed albatrosses, like most pelagic seabirds, are highly philopatric and therefore the number of recruits to a colony depends largely on its breeding productivity in previous years (Tickell 2000). As P^* in December-February was the best predictor of N (Fig 3.6b), and abundance of higher trophic level prey lags behind NPP, it would appear that black-browed albatross population sizes are regulated to a large extent by food availability during chick-rearing (Fig. 3.6a). This is presumably because chicks that are better provisioned show higher survival. Although the NPP time series available is too short (1998-2007) to carry out a detailed analysis, this is further supported by a positive correlation between the breeding success of black-browed albatrosses from Bird Island, South Georgia and P^* in January ($r = 0.65$, $n = 10$, $p = 0.041$, British Antarctic Survey, unpublished data), the month in which breeding attempts on the island are most likely to fail (Prince et al. 1994b). In contrast, at Kerguelen, failures occur most often during incubation (Pinaud & Weimerskirch 2002), which ties in with the observed peak in P^* in that region in December, at the end of which chicks start to hatch. However, because shallower waters are more productive, summer P^* is inevitably positively correlated with H^* (Weimerskirch 2002) (correlation with January P^* when $d_{ij} = 100$ km, $r = 0.80$, $n = 19$, $p < 0.001$), and hence the inferences I draw from the correlation between P^* and N are tentative. Nevertheless, it is noteworthy that other recent studies of colonial species in terrestrial and marine environments have also demonstrated the limiting effect on population size

of habitat and food availability during the breeding season (Griffin & Thomas 2000, Laidre et al. 2008).

At the level of individual colonies only 33% and 19% of the variance in N was explained by H^* and P^* respectively. Hence, other factors must account for the majority of variability in individual colony size. Unlike other seabird studies (Furness & Birkhead 1984, Lewis et al. 2001, Forero et al. 2002), my results indicate that intraspecific competition is unlikely to account for much of this variability. Another potential candidate is suggested by the outliers in the data. At $d_{ij} \leq 100$ km, the population size of super-colonies 3, 5, 18 and, to a lesser extent, 19 lie well below N predicted by either H^* or P^* (Fig. 3.5b and c). The first two of these are small islets (Isote Leonard and Isote Albatros, approximate area 0.15 and <0.5 km² respectively (Aguayo et al. 2003, Martin & Oehler 2006)), indicating that land area *per se* may be limiting. Indeed, as nesting black-browed albatrosses require steep slopes or cliffs from which to take off, the area of suitable breeding habitat may be limited even on large islands. The remaining two outliers, The Snares and Bollons Is. (Antipodes Islands), are thought to be newly established populations in a region currently being colonised by the black-browed albatross (Moore et al. 2001). As such, they may not yet have reached their potential carrying capacities, which the P^* model suggests are ~ 7300 and 3000 pairs (~ 95% CIs 3400-15800 and 1300-6600). Colony size could be further regulated by natural processes occurring outside the breeding season (Cairns 1992, Rolland et al. 2008) but it is unlikely that such processes would impact on colonies within a regional population differentially.

Table 3.2 Goodness of fit (AIC_c) of linear models of \log_e black-browed albatross population size vs. habitat availability and accessibility (H^*), productivity ($tNPP^*$) and intraspecific competition (C^*).

Model	Maximum by sea distance between colonies					
	d_{sep} (km) \leq					
	0	50	100	200	400	800
$\log_e H^*$	204.2	78.3	52.8	35.0	31.3	27.9
$\log_e tNPP^*$	212.9	90.2	59.6	45.4	39.7	28.2
$\log_e C^*$	210.2	91.4	61.2	42.8	42.6	36.3
$\log_e H^* + \log_e C^*$	206.2	80.7	54.7	35.1	35.1	33.0
$\log_e H^* * \log_e C^*$	208.6	82.6	56.9	40.0	41.8	46.5
$\log_e tNPP^* + \log_e C^*$	212.4	92.1	60.7	42.3	40.9	34.1
$\log_e tNPP^* * \log_e C^*$	214.8	91.4	62.4	47.4	48.1	45.9

Values in **bold** indicate minimum AIC_c for each super-colony grouping.

Adult black-browed albatrosses have few natural predators and very high survival rates (Prince et al. 1994b, Nevoux et al. 2007). However, over the past two decades, major declines have occurred in some populations as a consequence of incidental mortality in longline and trawl fisheries (Phillips et al. 2005b, Sullivan et al. 2006, Rolland et al. 2008). In particular, the South Georgia population declined by *ca.* 30% over this period (Poncet et al. 2006), and the Falkland Islands population by 1% per annum between 2000 and 2005 (Huin & Reid 2006). Conversely, discards from fishing operations provide supplementary food for some black-browed albatross populations, which may enhance productivity (Thompson 1992, Cherel et al. 2000, Rolland et al. 2008). As a consequence, current population sizes may, in some cases, be above or below their natural carrying capacity, introducing unexplained variability into my analyses. However, because of the log-normal nature of the colony size distribution (Jovani et al. 2008), in practise the relationships between N , and H^* and P^* are rather insensitive to variation in the size of the larger populations, which are those most affected by fisheries (cf. population estimates for South Georgia in 1984 and 2004 against Fig. 3.5b and c). Indeed, the strong relationship between black-browed

albatross population size, and habitat availability, accessibility and productivity across the entire Southern Ocean, including several disparate biogeographical regions (the Humboldt upwelling, Patagonian Shelf, Antarctic margin, etc.), suggests that the equilibrium population sizes of central place foragers are predictable using my approach. Moreover, it emphasises that the relative proximity of suitable breeding sites and areas of foraging habitat are fundamental to a thorough understanding of seabird ecology. By quantifying these and other factors regulating population size (Weimerskirch 2002), we can improve predictions of the impacts of bycatch, overfishing and climate change (Pinaud & Weimerskirch 2002, Nevoux et al. 2007, Rolland et al. 2008). Furthermore, the potential role of seabirds as indicators of the state of marine ecosystems (Boyd et al. 2006) may be more fully realised.

Chapter 4. Wind imposed constraints on flight performance

The data in this chapter are also published in Wakefield E.D., Phillips R.A., Matthiopoulos J., Fukuda A., Higuchi H., Marshall G.J. and Trathan P. (in press) Wind field and sex constrain the flight speeds of central place foraging albatrosses. *Ecological Monographs* (Appendix 5).

4.1 Introduction

During the breeding season, pelagic seabirds have to return to their colonies at regular intervals and thus act as central-place foragers. One of the most extreme examples of this behaviour is manifest in albatrosses (family Diomedidae), whose foraging trips may take them hundreds or thousands of km from their colonies, to remote patches of habitat, which are preferred due to high productivity or niche specialization (Nel et al. 2001, Hyrenbach et al. 2002, Phillips et al. 2005a, Pinaud & Weimerskirch 2005). Due to the great distances involved, the success of this strategy lies in maintaining relatively low transport costs while ensuring that trips, particularly those to provision chicks, can be completed within given time constraints. During flight, the metabolic rates of albatrosses are exceptionally low (Bevan et al. 1995, Arnould et al. 1996). This is because they proceed almost exclusively by gliding, which is the least energetically demanding form of flight (Pennycuick 1982, Norberg 1986). Although the exact mechanisms that albatrosses use to glide are still under debate, they are thought to rely predominantly on exploiting wind velocity gradients close to the surface of the sea ('gust' or 'dynamic soaring', Tickell 2000, Pennycuick 2002).

Wind also plays a major role in dictating flight patterns at larger spatial scales. Satellite tracking has shown that some species tend to direct their flight paths relative to synoptic-scale wind patterns, avoiding headwind flight (Weimerskirch et al. 2000b, Murray et al. 2003). However, many areas traversed by albatrosses are subject to strong, persistent prevailing winds. In such areas birds travelling to and from foraging

patches may be more constrained in their choice of flight directions. This is of considerable consequence, because albatrosses rarely resort to flapping flight (Pennycuick 1982) so their groundspeeds, and hence transport costs, are likely to be affected by their orientation with respect to the wind at several spatial scales.

The ability to regulate flight speed may be particularly important for breeding birds (Hedenström & Ålerstam 1995). Albatrosses, like all seabirds, experience changes in the severity of the central-place constraint as the breeding season advances (Shaffer et al. 2003). During incubation, which is carried out alternately by both parents, foraging trips may be long, their duration limited only by the fasting capability of the bird left on the nest (Weimerskirch 1995). After hatching, the chick is brooded or guarded for a few days or weeks (depending on the species) alternately by one parent while the other forages. Thereafter, it is left unattended and provisioned by both parents. During these latter stages, the length of foraging trips is usually much shorter because adults must satisfy both their own and their chicks' energetic requirements (Weimerskirch et al. 1997b). Although several studies have shown that albatrosses contract their foraging ranges in response to these changing time constraints (Shaffer et al. 2003, Phillips et al. 2004b), the hypothesis that they also regulate groundspeeds in order to reduce time costs during more constrained stages, by changing flight direction with respect to wind direction, has not been tested. Furthermore, within individual foraging trips it is likely that groundspeeds measured at the scale of hours will vary with behaviour. For example, birds en route to and from foraging areas are likely to travel faster than those engaged in prey search and capture (Houston 2006).

The airspeed, and therefore groundspeed, of gliding birds is also constrained by their morphology. Theoretical airspeed is proportional to the square root of a bird's wing loading (defined as the weight per unit wing area (Pennycuick 1989)). Wing loadings are greater in the larger species of albatross (Shaffer et al. 2001, Phillips et al. 2004b), in theory resulting in greater airspeeds. Furthermore, because albatrosses are sexually size dimorphic, theoretical airspeeds of females are lower than those of males. This prediction has led to the hypothesis that, females have concomitantly lower stall speeds due to adaptation to flight in light winds, which explains the pattern of spatial sexual segregation observed in some species (Shaffer et al. 2001, Phillips et al. 2004b).

However, empirical relationships between groundspeeds of males and females and wind speed and direction have not hitherto been tested.

In this chapter I examine several factors that may influence flight speeds of foraging albatrosses: Firstly, I use a combination of satellite telemetry and immersion logger data to quantify groundspeeds of wandering albatrosses *Diomedea exulans*, black-browed albatrosses *Thalassarche melanophrys*, grey-headed albatrosses *T. chrysostoma* and light-mantled sooty albatrosses *Phoebastria palpebrata* at the scale of hours. I chose these species because they breed sympatrically and reflect the range of sizes and life history traits expressed by albatrosses. By careful selection of tracking locations, I minimize errors in groundspeed estimates, allowing me to model the response to relative wind speed. I compare observed interspecific and sexual differences in groundspeeds with those predicted by aerodynamic theory, testing the hypotheses that larger species fly faster than smaller ones. For each species I then model groundspeed in response to relative wind speed in more detail, considering the effects of breeding- and trip-stage, and testing the hypothesis that males fly faster than females. As albatrosses are more active during the day and on moonlit nights (Weimerskirch & Guionnet 2002, Phalan et al. 2007), I also consider whether diel or lunar phase could influence my estimates of groundspeed. I then test the hypothesis that male birds frequent windier habitats than females. Finally, I compare observed flight directions with respect to wind during the outward and inward stages of foraging trips, when birds are more constrained in their choice of flight directions, and between species during the comparatively unconstrained middle stages of trips.

4.2 Methods

4.2.1 Instrumentation

Albatrosses were tracked from Bird Island, South Georgia (54°00' S, 38°03' W) during the austral breeding seasons of 2000/01-2003/04 (Table 4.1). A total of 52 black-browed albatrosses, 47 grey-headed albatrosses and 4 light-mantled sooty albatrosses were equipped with PTT 100 Platform Terminal Transmitters (either 20g, 54x18x17 mm or 30g, 63x18x17 mm, Microwave Telemetry, Columbia, MD, USA) set to transmit *ca.* every 90 s. Locations were received from these devices on average every

1.13 hrs. A further 54 wandering albatrosses were equipped with BGDL-II GPS loggers (67g, 42x71x31 mm, Fukuda et al., 2004) set to log positions at intervals of 0.5 to 2 hrs. All birds were of known sex, except the light-mantled sooty albatrosses, and approximately equal numbers of males and females were tracked. In some cases data were collected from individual birds during several consecutive foraging trips. For the purposes of comparison between taxa, PTT and GPS data were sub-sampled by removing intervening locations such that the mean location interval ranged from 2.37 – 2.75 hrs (Table 4.1). Most birds also carried a British Antarctic Survey Mk IIa-IV logger (5g, 8x18x25 mm or 10g, 12x19x22 mm, Afanasyev & Prince, 1993) or a Francis Scientific Instruments saltwater activity logger (17g, 10x10 x30 mm, Francis Scientific Instruments, Cambridge, UK). These recorded saltwater activity (immersion), either as the total number of wet values in 10 min blocks sampled every 3 s or wet/dry status at intervals of 10 s. Data from both types of device were standardized to the proportion of time wet in 10 min blocks (Phalan et al. 2007). In all cases, birds were captured at the nest, either by hand or using a 1.5m pole fitted with a wire crook, and equipped with loggers in a procedure that took <10 minutes. GPS loggers and PTTs were attached to mantle feathers using Tesa[®] tape, while immersion loggers were attached with cable ties to plastic rings placed around the tarsus. Total instrument mass (including attachment materials) as a percentage of average body mass was 0.6% for wandering albatrosses (range 0.5 – 0.7%); 1.5% for black-browed albatrosses (range 1.2 – 1.9%); 1.6% for grey-headed albatrosses (range 1.3 – 1.9%) and 2.0% for light-mantled sooty albatrosses (range 1.8 – 2.4%). Thus, in all cases instrumentation weight was well within recommended limits of $\leq 3\%$ of body mass (Phillips et al. 2003). Birds were recaptured when they returned to the nest following foraging trips and the loggers recovered. Neither this, nor deployment of loggers caused any observed injury, distress or adverse changes in the birds' behaviour.

Table 4.1 Instrument deployment details for albatrosses tracked from Bird Island, South Georgia during the 2001, 2002, 2003 and 2004 breeding seasons.

Species	Year	Tag	Mean sampling interval (hrs) ± sd	Number of birds tracked (number with saltwater immersion data) ‡						
				Incubation		Brood-guard		Post brood		
				F	M	F	M	F	M	U
Wandering albatross	2004	GPS	2.76 ± 2.20	7 (7)	7 (7)	8 (8)	8 (8)	13 (11)	11 (11)	-
Black- browed albatrosses	2002	PTT	2.52 ± 1.78	9	9	8	14	6 (6)	6 (6)	-
Grey- headed albatrosses	2001 & 2003	PTT	2.75 ± 1.90	9 (8)	14 (11)	6 (6)	10 (10)	4	4	-
Light- mantled sooty albatrosses	2003	PTT	2.37 ± 1.16	-	-	-	-	-	-	4 (3)

† PTT = Platform Terminal Transmitter; GPS = Global Positioning System tag; ‡
Number of male (M), female (F) and unsexed (U) birds tracked at each stage of the
breeding season.

4.2.2 Wind speed and direction

I obtained wind data (6 hourly zonal and meridional wind speed components at a nominal height of 10 m above sea level) from the European Centre for Medium-Range Weather Forecasts on a Gaussian N80 grid (resolution at 54° S, 125 x 75 km). For periods before March 2002, wind data came from the ERA40 reanalysis dataset, while for subsequent periods operational model data were used. To ensure equivalency, operational model data were re-sampled at the same spatial resolution as the ERA40 dataset. I then identified the data subset nearest in time to each tracking location and

calculated wind speed V_{w10} and direction θ_w at that location by interpolation between spatially-adjacent points. Wind speeds were reduced to a reference height h_{ref} of 5 m above sea-level (i.e. the middle of the range of albatross flight heights typically observed in the field, Pennycuick 1982) using a logarithmic model of wind gradient and assuming a scale height h_0 of 0.03 m (Pennycuick 1982, Sachs 2005):

$$V_{w5} = \frac{V_{w10}(\ln 5 - \ln h_0)}{\ln 10 - \ln h_0} \quad (4.1)$$

The flight direction relative to the wind $\Delta\theta$ (i.e. the absolute difference between flight direction θ_f and θ_w , where $0 \leq \theta_f \leq 180^\circ$) was then calculated and the wind speed component in the direction of flight (V_{wf}) was calculated as:

$$V_{wf} = V_{w5} \cos \Delta\theta \quad (4.2)$$

For each section of track analyzed (see below) I calculated the mean wind speed component \bar{V}_{wf} as the average of V_{wf} at all intermediate locations. In addition, I quantified seasonal changes in mean wind speed in the study period/area. For each species, I defined the study area as that bounded by the maximum and minimum latitudes and longitudes reached by tracked birds during the whole breeding season. I then obtained 6 hourly wind speed measurements across this area (reduced to $h_{\text{ref}} = 5$ m) as described above. Finally, I calculated the mean wind speed within the study area during each breeding stage (incubation, brood-guard and post-brood).

4.2.3 Trip stage

I categorized tracking locations as having been recorded during the outward, middle or inward stage of foraging trips. Although central place foraging trips are often regarded as divisible in this way (Orians & Pearson 1979), in albatrosses the distinction between commuting and foraging varies considerably with species and breeding stage (Weimerskirch et al. 1997c, BAS unpublished data). Furthermore, at the individual level it is difficult to objectively identify the transition between such behaviours (BAS unpublished data). Rather than adopting an arbitrary division on a case by case basis, I determined the stage of trips at which these transitions typically occur at the population level. For each location within a foraging trip, I calculated $d_{\text{col}}/d_{\text{max}}$, the distance from the colony as a proportion of the maximum distance from the colony reached during that trip. Similarly, I calculated the time elapsed since the beginning of the trip as a proportion of the total trip time elapsed t/t_{max} . The total variance in $d_{\text{col}}/d_{\text{max}}$ for all locations occurring before t/t_{max} was then plotted against t/t_{max} . At all stages and in all species this curve rose monotonically from zero before leveling off or reaching a point of inflexion. The value of t/t_{max} at this point was determined graphically. I classified tracking locations as having been recorded during outward trips if they occurred before the end of the monotonic phase. The onset of return trips was determined in a similar manner by plotting the total variance in d/d_{max} for all locations occurring after t/t_{max} against t/t_{max} and identifying the value of t/t_{max} at which a monotonic decrease in variance began.

4.2.4 Diel & lunar period

Tracking locations were categorized as day or night, night being defined as the period in which the sun was six degrees or more below the horizon (Phillips et al. 2005a). Sections of track bounded by pairs of locations (hereafter referred to as L_i and L_{i+n}) were then categorized as daytime, if locations L_i to L_{i+n} were all recorded during the day; nighttime if all were recorded in the night or crepuscular otherwise. I also determined the proportion of the moon's disk illuminated m at midnight on the day that L_i to L_{i+n} were recorded using tables supplied by the US Naval Observatory Astrological Applications Department

(<http://aa.usno.navy.mil/data/docs/MoonFraction.php>). Where there were sufficient data (see below), nighttime pairs of locations were further subdivided into nights with $m > 0.5$ and those with $m < 0.5$.

4.2.5 Selection of location data

In order to calculate albatross groundspeeds (V_g) between pairs of tracking locations, I selected a subset of the location data using the following criteria:

Distance travelled (PTT locations only): Because PTT location quality decreases as groundspeed increases (ARGOS, www.cls.fr/html/argos/general/faq_en.html), datasets from fast moving species such as albatrosses tend to include very few high quality locations (Weimerskirch et al. 1992). Errors associated with these locations compromise estimates of speed, unless the distance between locations is sufficiently large. I extended the approach of Hays et al. (2001), who used computer simulations to define minimum distance between PTT locations required to reliably estimate the speed of green turtles *Chelonia mydas*, to select tracking locations from comparatively fast moving albatrosses. Following an initial sensitivity analysis, I defined the minimum distance d_{sep} between two locations as that which would result in 95% of individual speed estimates lying within $\pm 10\%$ of the true groundspeed (c.f. Hays et al. 2001).

I proceeded as follows: Because location errors σ_x and σ_y are independent of the distance (d_n) between locations, the proportion of error in estimates of d_n (and thus the speed) decreases as d_n increases. Hence, uncertainty in estimates of speed is a function of both d_n , and σ_x and σ_y for both locations (Hays et al. 2001). In order to estimate the minimum distance d_{sep} I first specified a maximum distance d_{max} within which to confine my simulations. Twenty distances d_n equally spaced between zero and d_{max} were then specified. A hypothetical pair of locations L_1 at $(0,0)$ and L_2 at $(d_n,0)$ were then considered. Random errors were drawn from a bivariate normal distribution with

$$\boldsymbol{\mu} = \mathbf{0} \text{ and } \boldsymbol{\Sigma}_i = \begin{pmatrix} \sigma_{i,x} & 0 \\ 0 & \sigma_{i,y} \end{pmatrix} \boldsymbol{\Sigma}_{i+1} = \begin{pmatrix} \sigma_{i+1,x} & 0 \\ 0 & \sigma_{i+1,y} \end{pmatrix} \text{ (the variance-covariance}$$

matrices of the error classes of L_1 and L_2 respectively) and applied to these locations. ARGOS (CLS, Toulouse, France) assign PTT locations to one of seven location classes (LC) depending on the number of signals received from the PTT during the satellite pass. In ideal circumstances four signals are received from the PTT during each pass and points are allocated to LC 3, 2, 1 or 0. Of the remaining LCs, A and B indicate locations obtained from three and two signals respectively, whilst LC Z indicates an unclassified location. ARGOS provide accuracy estimates for LCs 3, 2 and 1 (1.5, 0.5 and 0.25 km respectively) and assume that $\sigma_x = \sigma_y$. Brothers et al. (1998) and Hays et al. (2001) obtained empirical estimates of σ_x and σ_y for LC 0, A and B by comparing estimated positions of stationary PTTs to their known positions. Although there was considerable disagreement between their error estimates, both studies showed that σ_x and σ_y were not equal (although there was further disagreement on the direction of the inequality). Hence, in the absence of consistent data on the true errors of ARGOS locations, I adopted a precautionary approach to specifying σ_1 and σ_2 . For each location class, the largest error (either in latitude or longitude) reported by Brothers et al. (1998) or Hays et al. (2001) was selected and σ_x was assumed equal to σ_y . Location errors used for LC 3, 2, 1, 0, A and B were 0.3, 1.0, 2.0, 15.0, 8.6 and 14.9 km respectively. The time taken to fly between the true locations was calculated, assuming flight at an arbitrary but known speed. Using this time, the estimated speed V_{est} between the two erroneous positions was then calculated. This process was repeated 1000 times for each value of d_n and the corresponding 2.5th (V_{lower}) and 97.5th (V_{upper}) percentiles extracted. Next, the value of d_{sep} was determined graphically (Fig. 4.1). The entire simulation was then repeated to calculate d_{sep} for each of the twenty-one possible combinations of ARGOS location classes (Table 4.2). The minimum distance d_{sep} estimated for pairs of PTT locations was independent of the true speed V_{true} and ranged from 9 km for pairs of locations of LC3 to 423 km for pairs of locations of LC0. In this way I estimated d_{sep} between all possible pairs of ARGOS location classes.

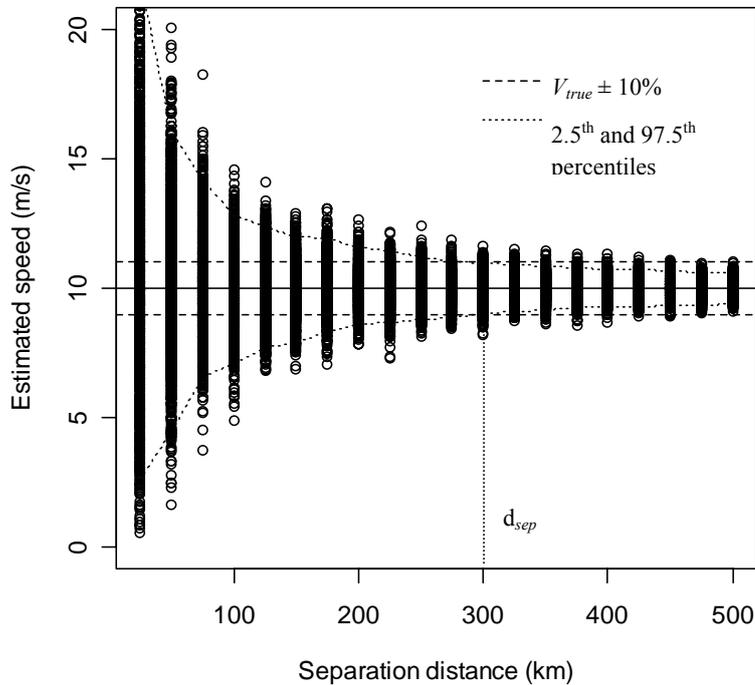
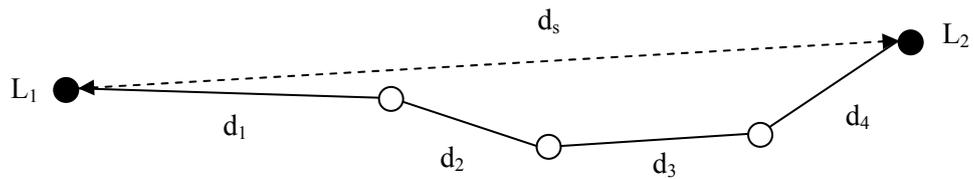


Figure 4.1 Estimated speed of travel as a function of distance between two locations for an animal moving at 10 m/s. Accuracy of the two locations $\sigma_1 = 2.00$ km, $\sigma_2 = 15.02$ km, corresponding to ARGOS location classes 1 and 0 respectively; $d_{sep} = 300$ km.

Track straightness: Changes in flight direction of albatrosses occur at smaller time scales (seconds to minutes) than typical PTT tracking intervals (hrs). Hence, a bird's true track tends to be longer than the sum of straight-line distances between tracking locations. Values of V_g estimated from tracking data are thus lower than instantaneous V_g , with the discrepancy increasing the more the bird's track deviates from a straight line. In order to select only relatively direct sections of track, I calculated the straightness index (s) between L_i and L_{i+n} (Fig. 4.2) by dividing the great-circle distance between these two locations by the sum of the great-circle distances between consecutive locations along the intervening sections of track (Batschelet 1981, Hays et al. 2001).

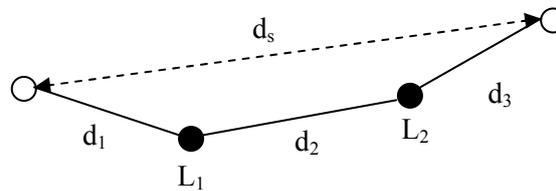
Proportion of time on the water: For those birds equipped with wet/dry loggers, I used immersion data to estimate the proportion of time (p_w) spent on the water between pairs of tracking locations L_i and L_{i+n} .

(i) PTT locations



$$\text{Straightness index} = d_s / (d_1 + d_2 + d_3 + d_4)$$

(ii) GPS locations



$$\text{Straightness index} = d_s / (d_1 + d_2 + d_3)$$

Figure 4.2 Calculation of track straightness index for PTT and GPS tracking data (● locations of interest, ○ other locations considered).

4.2.6 Statistical tests and models

Unless otherwise stated, statistical methods followed Crawley (2007) and all statistical tests and models were implemented using R statistical software (R-Development-Core-Team 2005). I modelled inter and intraspecific variations in groundspeed V_g in response to wind speed component V_{wf} , etc. using Linear Mixed Effects (LMEs) models fitted using Maximum Likelihood (Pinheiro & Bates 2000), implemented with the nlme package (Pinheiro et al. 2005). As multiple pairs of locations were used from some birds, I included individual bird in all models as a random effect. Serial autocorrelation was modelled using a first-order continuous autoregressive structure AR1. I proceeded with backward selection from maximal models (which included all possible interactions and where relevant quadratic terms to investigate the possibility of curvature) using the Akaike Information Criterion to compare models. I tested for differences in wind speeds V_{w5} experienced by albatrosses using the same technique. Similarly, I tested for differences in relative flight direction $\Delta\theta$ using mixed effects Generalized Linear Models (GLMMs) implemented with the lme4 package in R (Bates et al. 2008). Fixed-effects parameters are quoted \pm their estimated 95% CIs, which in a number of cases, where the response variable was square root or double square root transformed to reduce heteroscedascity, are asymmetrical. Unless otherwise stated, means are quoted \pm their standard errors. Details of data selection and modelling for each analysis are given below:

Groundspeed in sustained, direct flight vs. size and wind component in the direction of flight (model I): To test the hypotheses that larger species and sexes of albatrosses fly faster than smaller ones and that groundspeed V_g is proportional to the wind speed component in the direction of flight V_{wf} , I calculated V_g for periods in which birds undertook sustained, direct bouts of flight. I selected pairs of locations using the following criteria: In order to compare only commuting periods of flight, PTT locations were retained if they were separated by distances $> d_{\min}$. As errors associated with GPS locations are small (<10 m Fukuda et al. 2004, Awkerman et al. 2005) all GPS data were retained at this stage. Few pairs of locations with 0, 1 or 2 intervening locations met the PTT selection criterion and so the analysis was restricted to pairs of

locations separated by 3 intervening locations (i.e. L_i and L_{i+4}). From these data I selected locations with contemporaneous immersion data. In each species, the proportion of time (p_w) spent on the water between pairs of L_i and L_{i+4} had a bimodal distribution, with modes at 0.1 and 0.9. Initial analysis indicated that pairs of locations between which the birds spent $>10\%$ of their time on the water resulted in highly variable estimates of groundspeed. Hence, I retained data where p_w was <0.1 . Next, I selected only pairs of locations between which the straightness index s was > 0.8 . Although this ensured that I selected bouts of flight that were relatively direct at the scale of hrs and 100s km, at smaller scales the tortuosity of albatross tracks during foraging varies between species (Pinaud & Weimerskirch 2007). Hence, for greater comparability between taxa I finally retained only pairs of locations drawn from the outward and inward parts of foraging trips, assuming that these were representative in all species of commuting flight.

Following data selection, I estimated the time in flight (t_f) between L_i and L_{i+4} by multiplying Dt , (the time interval between L_i and L_{i+4}) by $1 - p_w$. I then calculated groundspeed by dividing the great circle distance between L_i and L_{i+4} by t_f . No correction was made for track straightness, as it was not consistently clear from the data whether deviations from straightness were real or related to location error. I then compared various models of V_g in response to the fixed-effects of V_{wf} , trip stage (outward vs. return trips) and size group (defined by species and sex), selecting the most parsimonious. The basic fixed-effects model took the form:

$$V_g = \alpha + \beta V_{wf} \quad (4.3)$$

I also considered Dt as a candidate covariate, to correct, if necessary, for potential bias in V_g arising from interspecific differences in the temporal resolution of the tracking data.

Groundspeed during sustained, direct flight vs. wind component in the direction of flight, sex, breeding stage, trip stage, Dt, diel and lunar period (models IIa-IIId): I next examined each species in more detail, considered potential effects of different covariates and tested the hypotheses 1. that V_g is higher in males and 2. that $V_g \sim V_{wf}$. I calculated groundspeed as described for model I, with the following differences: Firstly, because I did not wish to make interspecific comparisons, I was able to treat the GPS (wandering albatross) data somewhat differently to the PTT data in order to increase sample size and the accuracy of my estimates of V_g . Hence, for wandering albatrosses I used adjacent locations (i.e. L_i and L_{i+1}) to calculate V_g and locations either side of these (L_{i-1} and L_{i+2}) to calculate the straightness index s (s has to be calculated over three or more locations). In addition, for all species I increased sample size further by including locations from throughout foraging trips (outward, middle and inward stages) in this analysis. I then modelled V_g in response to V_{wf} , sex, breeding stage (incubation/brood-guard/post-brood), trip stage, Dt , diel and where possible, lunar period.

Groundspeed during sustained flight vs. sex, breeding stage and trip stage (models IIIa-IIIId): I tested for significant differences in observed groundspeeds between sexes, breeding stages and trip stages as follows: To retain a large sample size, I calculated V_g between adjacent locations L_i and L_{i+1} , selecting pairs of locations if the bird had been in flight for >90% of the time between them. Groundspeeds were corrected, where necessary, for time spent in flight, and both direct and indirect bouts of flight were retained (i.e. no straightness criterion was imposed). I then modelled V_g in response to sex, breeding stage and trip stage. Wind was not considered as a candidate covariate in these models.

Wind speed vs. sex, breeding stage and trip stage (models IVa-IVd): I compared wind speeds experienced by foraging albatrosses by modelling V_{w5} at all tracking locations, in response to sex, breeding stage and trip stage. I also compared wind direction, averaged by individual, between species, sexes, breeding stages and trip stages using circular ANOVA models (Mardia & Jupp 2000), implemented with the ‘circular’

package in R (Lund & Agostinelli 2006). Circular mean wind directions are quoted with ρ , their mean resultant length.

Flight direction relative to wind direction during sustained flight vs. sex, breeding stage and trip stage (models Va-Vd): I calculated $\Delta\theta$ for pairs of adjacent locations L_i and L_{i+1} between which birds were in flight for >90% of the time. For each stage within individual foraging trips, I then calculated median $\Delta\theta$. I modelled the response of this variable to sex, trip stage and breeding stage using mixed effects Generalized Linear Models implemented with the lme4 package in R (Bates et al. 2008). Because median $\Delta\theta$ is bounded above and below I rescaled it from 0-1 and employed a binomial error structure, with the logit link function. Although this approach allows multilevel comparisons to be made while avoiding pseudoreplication, it is rather conservative. Therefore, I also tested the hypothesis that θ_r differed between outward and inward phases of foraging trips by comparing median outward and inward $\Delta\theta$ values using Wilcoxon matched-pairs tests. Similarly, I tested for between species differences in $\Delta\theta$ during the middle stages of trips with a Kruskal Wallance test, making the assumption in both cases that individual foraging trips were independent.

4.2.7 Theoretical groundspeed predictions

A consideration of the morphology of a gliding bird allows its theoretical optimum airspeed in different circumstances to be calculated. The minimum sink speed V_{ms} occurs when height lost per unit time is minimized, whereas height lost per unit distance is minimized at a higher airspeed, the best glide speed V_{bg} (Pennycuick 1989). When V_{wf} is zero, a bird's groundspeed V_g is equal to its airspeed, and can thus be predicted when this condition is met. However, such predictions of V_g relate to instantaneous speeds and are likely to be greater than groundspeeds recorded over larger spatial scales (as in this study). For this reason, I calculated the theoretical differences between group (species and sex) groundspeeds and compared these (rather than absolute values) with differences in V_g given by my empirical models (i.e. differences in the value of the intercepts, α). Theoretical airspeeds (V_{bg} and V_{ms}) of each species and sex were predicted following Pennycuick (1989) using the computer

program Flight Version 1.17 (Pennycuick 2006) at $h_{\text{ref}} = 5$ m. Morphometrics of black-browed, grey-headed and light-mantled sooty albatrosses taken at their breeding colonies on Bird Island (Phillips et al. 2004b, BAS unpublished data) were entered into the program (parameters listed in full in Appendix 3). Insufficient measurements of wandering albatrosses were available from this colony so I used published values for this species at Crozet (Shaffer et al. 2001). The weight of instruments had a negligible effect on predicted parameters and was not considered further in my calculations.

4.3 Results

4.3.1 Empirical and theoretical models of groundspeed

Examination of the variance of $d_{\text{col}}/d_{\text{max}}$ with t/t_{max} showed that in all species, foraging trips were characterized by an initial rapid movement away from the colony, which I classified as the outward stage (Fig. 4.3). Then followed a period of slower and more variable (+ve and -ve) movement with respect to the colony (middle stage), followed by a period of rapid movement back towards the colony (return stage). The division between these stages occurred on average when 20 % and 81 % of the total trip time had elapsed (Table 4.2).

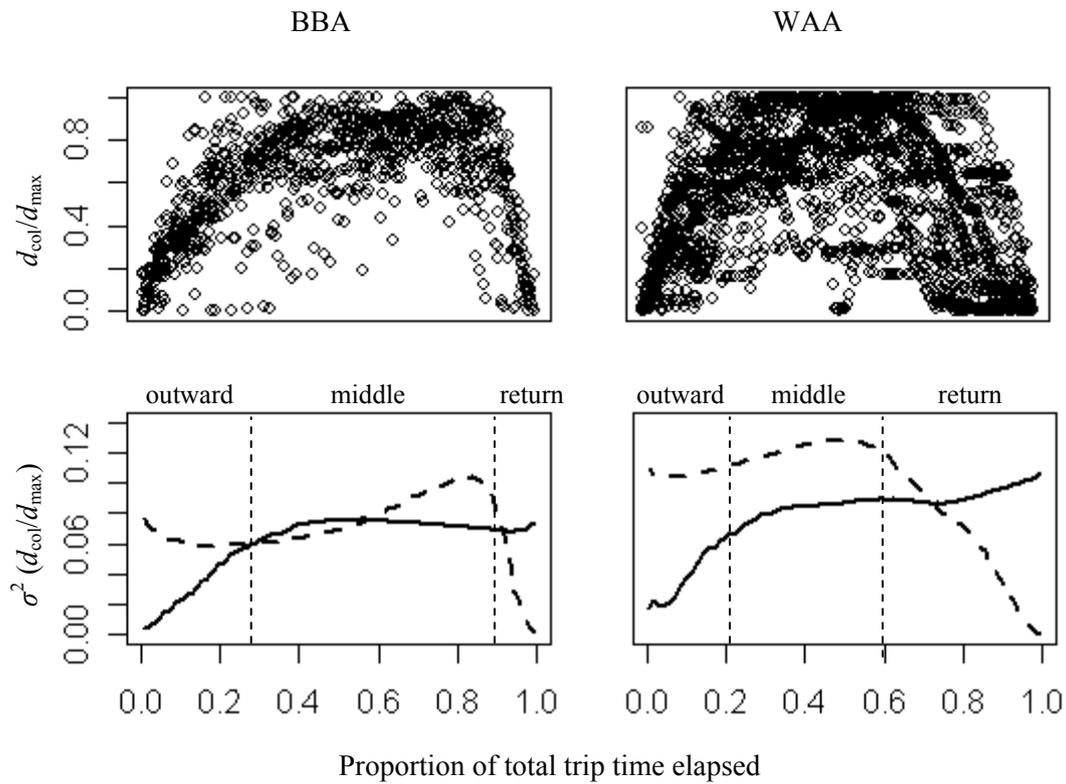


Figure 4.3 Examples of plots used to estimate divisions between outward, middle and inward stages of foraging trips. Upper panels: distance from colony as a proportion of maximum distance from colony reached (d_{col}/d_{max}) during foraging trips vs. proportion of total trip time elapsed (t/t_{max}). BBA - brood-guard stage black-browed albatrosses (21 birds, 21 trips); WAA - brood-guard stage wandering albatrosses (16 birds, 19 trips). Lower panels: Variance in d/d_{max} vs. t/t_{max} for all locations $< t/t_{max}$ (solid line) and all locations $> t/t_{max}$ (broken line). Vertical lines indicate the estimated divisions between outward, middle and return stages of foraging trips.

Table 4.2 Estimated proportion of total trip time (t/t_{\max}) at which outward commuting ceases and inward commuting commences during foraging trips made by breeding albatrosses.

Species	Breeding stage	t/t_{\max}	
		End of outward trips	Onset of return trips
Wandering albatross	Incubation	0.20	0.80
	Brood-guard	0.21	0.60
	Post-brood	0.29	0.82
Black-browed albatross	Incubation	0.18	0.82
	Brood-guard	0.29	0.90
	Post-brood	0.17	0.90
Grey-headed albatross	Incubation	0.10	0.86
	Brood-guard	0.16	0.83
	Post-brood	0.10	0.85
Light-mantled sooty albatross	Post-brood	0.21	0.80

For pairs of PTT locations of the same location class, d_{sep} was directly proportional to the location error σ ($d_{sep} = 28.19\sigma - 0.21$, $R^2 = 1.0$, $p < 0.001$). In total 9% of pairs of PTT locations (L_i to L_{i+4}) were separated by distances $> d_{sep}$ (Table 4.3). This, along with the other selection criteria, meant that 4% of pairs of PTT locations and 8% of pairs of GPS locations, were retained for analysis in model I. Observed groundspeeds V_g between these locations ranged from a minimum of 2.2 m/s for a wandering albatross to a maximum of 26.8 m/s for a black-browed albatross. Mean V_g was very similar across species and ranged from 10.4 ± 0.2 m/s for wandering albatrosses to

13.4 ± 0.3 m/s for black-browed albatrosses (mean V_g of grey-headed and light-mantled sooty albatrosses was 11.6 ± 0.3 and 12.4 ± 0.3 m/s respectively).

Table 4.3 Minimum distance (d_{sep}) required between pairs of PTT locations L_1 and L_2 of known ARGOS Location Class such that 95% of all speed estimates are expected to fall within ±10% of the true value.

Location Class		Standard deviation of maximum reported location error (km)		d_{sep} (km)
L_1	L_2	σ_1	σ_2	
3	3	0.32	0.32	9
2	2	1.00	1.00	28
1	1	2.00	2.00	56
0	0	15.02	15.02	423
A	A	8.60	8.60	242
B	B	14.9	14.9	420
3	2	0.32	1.00	21
2	1	1.00	2.00	46
1	0	2.00	15.02	300
0	A	15.02	8.60	340
A	B	8.60	14.90	350
3	1	0.32	2.00	42
2	0	1.00	15.02	300
1	A	2.00	8.60	170
0	B	15.02	14.90	390
3	0	0.32	15.02	300
2	A	1.00	8.60	160
1	B	2.00	14.90	310
3	A	0.32	8.60	175
2	B	1.00	14.90	300
3	B	0.32	14.90	290

Estimated groundspeed was negatively correlated with Dt in both the PTT and GPS data (Spearman rank correlation – PTT data: $r_s = -0.36$, $N = 231$, $p < 0.001$; GPS data: $r_s = -0.18$, $N = 192$, $p = 0.010$). However, Dt was not retained as an explanatory variable in any of the models describing V_g . In model I both V_{wf} and size-group were retained as explanatory variables (Table 4.4). Trip stage was rejected, however, indicating that there were no significant differences in V_g in response to V_{wf} (measured during direct and uninterrupted bouts of flight) between outward vs. inward stages of foraging trips. As expected, V_g was serially autocorrelated in this and all of the other LME models described below (the autocorrelation parameter ϕ ranging from 0.42 to 0.90). The intercept α (i.e. V_g in zero relative wind, Fig. 4.4) was greatest for male black-browed albatrosses (12.5 m/s) and lowest for male wandering albatrosses (9.8 m/s). In black-browed albatrosses α was significantly greater for males than females (9.6 m/s) but significant intersexual differences were not evident in other species.

Table 4.4 Model I, linear mixed effects model of groundspeed V_g in response to wind speed component in the direction of flight V_{wf} (m/s) of four species of albatross, grouped by species and sex (mean tracking interval 10.27 ± 0.15 hrs).

Species	Sex	Parameter \pm 95% CI (m/s)	df [†]	t-value	p [‡]
Black-browed albatross	F	α 9.59 \pm 1.83	338	10.140	<0.001
	M	12.50 \pm 2.40	71	2.380	0.020
Wandering albatross	F	10.01 \pm 2.09	71	0.402	0.689
	M	9.76 \pm 2.08	71	0.164	0.870
Grey-headed albatross	F	10.63 \pm 2.35	71	0.866	0.389
	M	10.41 \pm 2.20	71	0.737	0.464
Light-mantled sooty albatross	U	10.66 \pm 2.62	71	0.807	0.422
Black-browed albatross	F	β 0.70 \pm 0.22	338	6.109	<0.001
	M	0.58 \pm 0.27	338	-0.908	0.365
Wandering albatross	F	0.45 \pm 0.26	338	-1.856	0.064
	M	0.36 \pm 0.26	338	-2.625	0.009
Grey-headed albatross	F	0.22 \pm 0.33	338	-2.810	0.005
	M	0.45 \pm 0.29	338	-1.738	0.083
Light-mantled sooty albatross	U	0.50 \pm 0.30	338	-1.368	0.172

n birds = 78, n pairs locations = 423; [†] Estimated degrees of freedom.; [‡] For female black-browed albatrosses, p refers to the overall significance of α and β , while for all other species/sexes, p refers to the difference between these and group parameters.

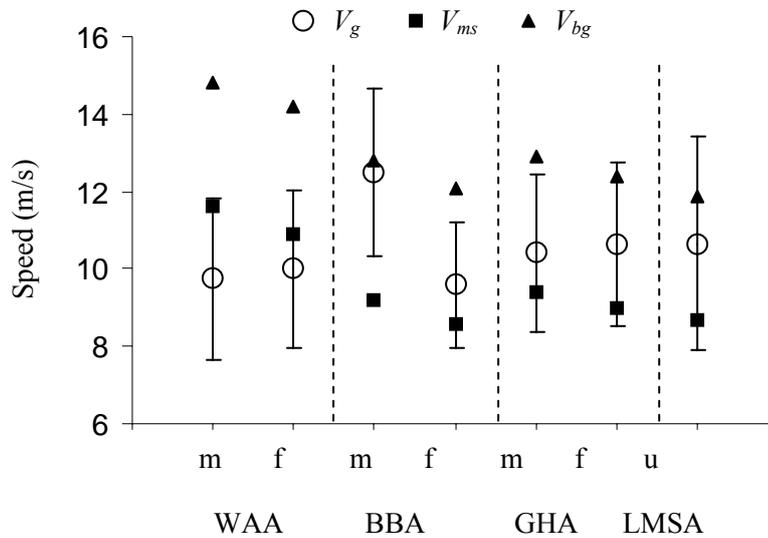


Figure 4.4 Groundspeed (V_g) in zero relative wind of male (m) and female (f) wandering albatrosses (WAA), black-browed albatrosses (BBA), grey-headed albatrosses (GHA), and unsexed light-mantled sooty albatrosses (LMSA) predicted by model I ($\pm 95\%$ CI), and theoretical minimum sink speeds (V_{ms}) and best glide speeds (V_{bg}).

As expected, theoretical values of V_{ms} and V_{bg} (Table 4.5) were proportional to the square root of wing loading ($V_{ms} = 0.91(\text{wing loading})^{0.5}$, $R^2 = 0.9$, $p < 0.001$, $V_{bg} = 4.5 + 0.84(\text{wing loading})^{0.5}$, $R^2 = 0.9$, $p < 0.05$). In the smaller species (*Thalassarche* and *Phoebastria*) absolute values of α lay between V_{ms} and V_{bg} but relative magnitudes differed to those predicted (in male black-browed albatrosses α was ~ 2 m/s greater than expected in comparison to the other species/sexes, in absolute terms being $\approx V_{bg}$). The values of α for wandering albatrosses were ~ 2 m/s lower than expected, their absolute values lying below V_{ms} . In all groups there was a strong linear relationship between V_g and V_{wf} . There was considerable variation in the effect of V_{wf} , however, as indicated by the slope parameter β . This was greatest for female black-browed albatrosses ($\beta = 0.70$) and lowest for female grey-headed albatrosses ($\beta = 0.22$).

Table 4.5 Wing loading, theoretical minimum sink speed (V_{ms}) and best glide speed (V_{bg}) of four species of albatross.

Species	Sex (n).	Wing loading (N/m ²) ± sd [†]	V_{ms} and V_{bg} in m/s [‡]
Wandering albatross	male (20)	148 ± 10	11.6, 14.8
	female (16)	132 ± 11	10.9, 14.2
Black-browed albatross	male (18)	92 ± 5	9.2, 12.8
	female (14)	82 ± 4	8.6, 12.1
Grey-headed albatross	male (19)	97 ± 7	9.4, 12.9
	female (13)	89 ± 6	9.0, 12.4
Light-mantled sooty albatross	unsexed (10)	85 ± 8	8.7, 11.9

† Phillips et al. (2004b), Shaffer et al. (2001) and BAS unpublished data; ‡ Calculated using Flight Version 1.17 (Pennycuick 2006).

The less exclusive criteria used to select data for the species-specific models of groundspeed in response to V_{wf} and other covariates (IIa-IIb) resulted in retention of 7% of PTT and 11% of GPS data. This, together with the larger number of covariates considered, produced better model performance (95% CIs on parameter estimates in models IIa-IId were approximately half those in model I, Table 4.6). Parameter estimates from model IId (light-mantled sooty albatrosses) had relatively large confidence intervals, however, and should be treated with caution. Nevertheless, the groundspeed of light-mantled sooty albatrosses fitted the general trend described for the other species. In all species there was a strong linear relationship between V_g and V_{wf} , and within species this relationship did not differ significantly between sexes. The rate of change of V_g with V_{wf} was greatest in wandering albatrosses ($\beta = 0.59$) and least in grey-headed albatrosses ($\beta = 0.33$). When variability due to V_{wf} is accounted for models IIa-IIc show that male wandering, black-browed and grey-headed albatrosses all flew significantly faster than females (the sex of light-mantled sooty albatrosses was not known). Model IIa (wandering albatrosses) was the best performing model (based

on the width of 95% CIs) and suggests that V_g of males (12.4 m/s) is 1.0 m/s greater than females (Fig. 4.5). This difference is slightly larger than the theoretical sexual difference in V_{ms} and V_{bg} (0.7 and 0.6 m/s) predicted using Flight Version 1.17 (c.f. Tables 4.5 & 4.6). Models IIb and IIc show that in the two *Thalassarche* spp. the V_g of males was 1.4 m/s greater than that of females (male black-browed albatross daytime $V_g = 12.0$ m/s, male grey-headed albatross $V_g = 10.8$ m/s). Again, these were slightly larger than theoretical sexual difference in V_{ms} (0.6 and 0.7 m/s respectively) and V_{bg} (0.4 and 0.5 m/s respectively).

Of the pairs of locations selected for analysis in model IIa (wandering albatrosses), 23% were from the nighttime. The proportion of the moon's disk illuminated (m) when these pairs of locations were recorded was no different than that expected by chance (chi-squared test $\chi^2 = 4.267$, $df = 3$, $p = 0.234$). Of the nighttime pairs of locations, 47 % were recorded when m was <0.5 and 25 % were recorded when m was <0.25 . This, together with the fact that diel/lunar period was rejected as an explanatory variable in model IIa indicates that wandering albatrosses were able to sustain direct, uninterrupted flight during darkness. For the other species, few pairs of nighttime locations met the selection criteria (4%, 1% and 6% for black-browed, grey-headed and light-mantled sooty albatross, respectively). Furthermore, in all species the majority of these pairs of locations (67 %), and significantly more than would be expected by chance alone (chi-squared test $\chi^2 = 15.527$, $df = 3$, $p = 0.001$), were recorded on nights with bright moonlight ($m > 0.75$). As there were insufficient data in the nighttime categories for the purposes of models IIb-IIId, I reclassified pairs of locations as being nighttime if they were recorded wholly or partly in the dark, and the remainder as daytime. Diel period was rejected as an explanatory variable for grey-headed and light-mantled sooty albatrosses but retained for black-browed albatrosses (model IIb). Daytime V_g was 0.9 m/s faster in the last species than nighttime V_g .

Table 4.5 Models IIa-IIId, linear mixed effects models of groundspeed V_g (m/s) in response to wind speed component in the direction of flight V_{wf} (m/s) of four species of albatross during direct, sustained bouts of flight.

Model	Covariate/level	Estimate \pm 95% CI	d.f.†	t-value	p‡
IIa. Wandering albatrosses (n birds = 43, n loc. = 476, μ int. 1.47 ± 0.06 hrs)					
	$V_{wf}(\beta)$	0.59 ± 0.06	430	17.783	<0.001
	Female, outward trip, (group α)	11.40 ± 0.62	430	36.232	<0.001
	Male	$+0.98 \pm 0.65$	41	3.046	0.004
	Middle of trip	-0.69 ± 0.68	430	-1.967	0.050
	Return trip	-0.10 ± 0.79	430	-0.250	0.803
IIb. Black-browed albatrosses (n birds = 12, n loc. = 199, μ int. 10.49 ± 0.12 hrs)					
	$V_{wf}(\beta)$	0.53 ± 0.10	185	9.908	<0.001
	Female, night (group α)	9.69 ± 1.06	185	18.008	<0.001
	Male	$+1.42 \pm 1.29$	10	2.454	0.034
	Day	$+0.86 \pm 0.74$	185	2.282	0.024
IIc. Grey-headed albatrosses (n birds = 30, n loc = 135, μ int. 12.16 ± 0.13 hrs)					
	$V_{wf}(\beta)$	0.33 ± 0.11	104	5.674	<0.001
	Female (group α)	9.43 ± 0.98	104	18.870	<0.001
	Male	$+1.37 \pm 1.21$	28	2.286	0.030
IIId. Light-mantled sooty albatrosses (n birds = 3, n loc. = 127, μ int. 11.62 ± 0.12 hrs)					
	$V_{wf}(\beta)$	0.43 ± 0.14	123	5.913	<0.001
	Unsexed (group α)	9.81 ± 1.81	123	10.669	<0.001

†Estimated degrees of freedom; ‡ p refers to group α and to differences between this and α for the remaining covariates/levels.

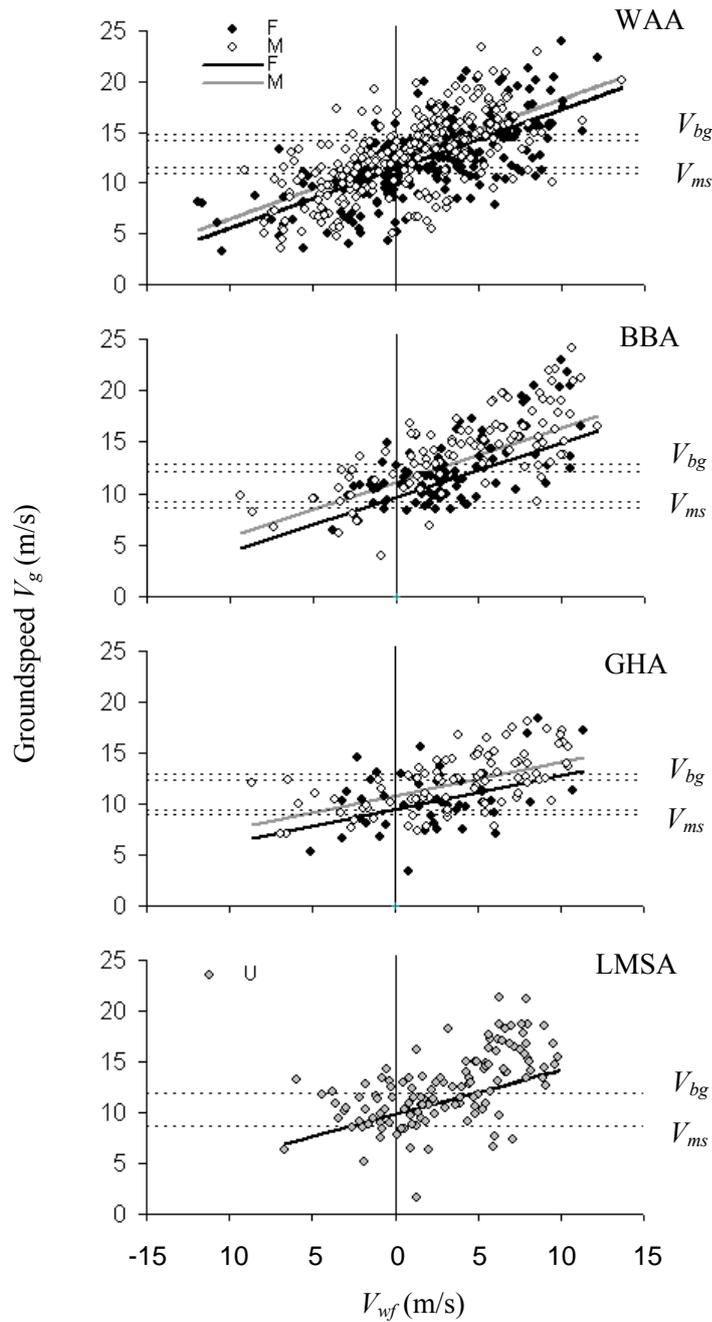


Figure 4.5 Linear mixed effects models of groundspeed (V_g) in response to wind speed component in the direction of flight (V_{wf}) for wandering albatrosses tracked with GPS tags (WAA, model IIa); black-browed albatrosses tracked with PTTs (BBA, model IIb); grey-headed albatrosses tracked with PTTs (GHA, model IIc); unsexed light-mantled sooty albatrosses tracked with PTTs (LMSA, model II d). Also shown are theoretical best glide speeds (V_{bg}) and minimum sink speeds (V_{ms}) of males (upper lines), females (lower lines) or both sexes (light-mantled sooty albatrosses).

Breeding stage was rejected as an explanatory variable in all models. Similarly, trip stage was rejected in all but model IIa, which showed that V_g in wandering albatross was slightly lower (0.69 ± 0.68 m/s) during the middle than the outward stages of foraging trips. This effect, however, was only marginally significant ($p = 0.050$). Models IIIa, IIIb and IIIc (Table 4.7) show that when V_{wf} was not considered, groundspeeds of wandering, black-browed and light-mantled sooty albatrosses (estimated for sustained flight between two consecutive locations) were significantly faster during the return than during the outward stages of trips (1.0, 3.4 and 1.4 m/s faster respectively). In addition the V_g of black-browed albatrosses was *ca.* 1.2 m/s slower during the middle than outward stages of foraging trips. Groundspeeds in the middle stages were also considerably (4.2 m/s) slower in grey-headed albatrosses (model IIIc) but there was no significant difference between outward and inward stages in this species. Sexual differences in V_g could not be detected when the data were treated in this way (sex was not retained as an explanatory variable in any of these models). However, breeding stage was retained for wandering and grey-headed albatrosses. In the former species, birds during the incubation stage flew some 2.6 m/s faster than those during brood-guard. In contrast grey-headed albatrosses during the incubation stage flew 2.2 m/s slower than those during brood-guard.

Table 4.7 Models IIIa-IIIId, linear mixed effects model of groundspeeds V_g (m/s) of four species of albatross, during both direct and indirect flight.

Model	Covariate/level	Estimate (95% CI)	d.f.†	t-value	p‡
IIIa. Wandering albatrosses (n birds = 46, n loc. = 1651, μ int. 1.21 ± 0.04 hrs)					
	Outward trip, brood-guard (group α)	8.7 (7.72, 9.73)	1594	33.858	<0.001
	Middle of trip	-0.23 (-0.83, 0.39)	1594	-0.738	0.460
	Return trip	+1.02 (0.26, 1.81)	1594	2.662	0.008
	Incubation	+2.56 (1.06, 4.16)	43	3.541	0.001
	Post-brood	+0.78 (-0.48, 2.12)	43	1.23	0.225
IIIb. Black-browed albatrosses (n birds = 12, n loc. = 2728, μ int. 2.00 ± 0.06 hrs)					
	Outward trip (group α)	9.09 (8.53, 9.67)	2496	124.696	<0.001
	Middle of trip	-1.2 (-1.61, -0.76)	2496	-5.187	<0.001
	Return trip	+3.39 (2.60, 4.23)	2496	9.143	<0.001
IIIc. Grey-headed albatrosses (n birds = 34, n loc. = 1112, μ int. 2.52 ± 0.06 hrs)					
	Outward trip, brood-guard (group α)	12.27 (11.15, 13.44)	1064	42.1	<0.001
	Middle of trip	-4.19 (-5.00, -3.34)	1064	-8.833	<0.001
	Return trip	-1.10 (-2.22, 0.08)	1064	-1.833	0.067
	Incubation	-2.19 (-3.18, -1.15)	11	-4.503	0.001
IIIId. Light-mantled sooty albatrosses (n birds = 3, n loc. = 641, μ int. 2.33 ± 0.06 hrs)					
	Outward trip (group α)	9.31 (8.23, 10.45)	616	32.707	<0.001
	Middle of trip	-0.43 (-1.40, 0.59)	616	-0.840	0.401
	Return trip	+1.41 (0.13, 2.77)	616	2.158	0.031

†Estimated degrees of freedom; ‡ p refers to group α and to differences between this and α for the remaining covariates/levels.

4.3.2 Wind conditions experienced during foraging flights

Birds of all species and sexes experienced similar wind conditions while foraging. Wind speeds experienced by individuals ranged from 0.1 to 20.6 m/s with an overall mean of 7.7 ± 3.1 m/s. There were no significant differences between mean wind speeds experienced by individual wandering albatrosses (7.7 ± 1.4 m/s), black-browed albatrosses (7.8 ± 0.9 m/s), grey-headed albatrosses (7.6 ± 1.2 m/s) and light-mantled sooty albatrosses (6.6 ± 0.5 m/s, ANOVA $F_{3, 145} = 1.67$, $p = 0.176$). For all species sexed, gender was rejected as an explanatory variable in models IVa – IVc indicating that male and female birds experienced comparable wind speeds throughout the breeding season (Table 4.8). Trip stage was also rejected in models IVa – IVd, demonstrating that wind speed did not differ significantly between the outward, middle and inward stages of foraging trips. In contrast, breeding stage was retained in all models for the species from which multi-stage tracking data were collected (wandering, black-browed and grey-headed albatrosses). In each species, wind speeds did not differ between brood-guard and post-brood stages but were *ca.* 1.2 to 0.6 m/s lower during incubation (although this difference was not significant in grey-headed albatrosses, Fig. 4.6). Mean wind speeds experienced by albatrosses during each breeding stage were generally similar to those calculated across the study area for corresponding periods. This suggests that differences in wind speeds experienced between stages were due to seasonal changes in the intensity of the wind, rather than to habitat preference.

There was little variability in mean wind directions experienced by birds, with all species predominantly experiencing westerly winds (mean wind direction 270° , $\rho = 0.49$, Fig. 4.7). In all but one case there were no significant differences in mean wind directions experienced across species, breeding stages or sex. The exception was wandering albatrosses, which experienced winds from significantly more southerly directions during post-brood (253° , $\rho = 0.81$) than during incubation (277° , $\rho = 0.96$) and brood-guard (273° , $\rho = 0.98$, circular ANOVA $F_{2, 51} = 4.23$, $p = 0.012$). Wind directions did not differ significantly between outward and inward phases of foraging trips.

Table 4.8 Models IVa-IVc, linear mixed effects model of wind speed V_{w5} (m/s) experienced by three species of albatross.

Model	Covariate/level	Estimate (95% CI)	d.f.†	t-value	p‡
IVa. Wandering albatrosses (n birds = 43, n loc. = 2174)					
	Brood-guard (group α)	7.87 (7.21, 8.56)	2125	45.660	<0.001
	Incubation	6.67 (5.92, 7.46)	46	-3.018	0.004
	Post-brood	7.61 (6.80, 8.46)	46	-0.631	0.531
IVb. Black-browed albatrosses (n birds = 50, n loc. = 1750)					
	Brood-guard (group α)	8.16 (7.29, 9.02)	1700	18.593	<0.001
	Incubation	7.12 (6.10, 8.13)	47	-2.062	0.045
	Post-brood	8.18 (7.25, 9.10)	47	0.049	0.961
IVc. Grey-headed albatrosses (n birds = 45, n loc. = 1226)					
	Brood-guard (group α)	8.10 (7.51, 8.68)	1085	27.043	<0.001
	Incubation	7.47 (6.76, 8.18)	95	-1.749	0.084
	Post-brood	8.07 (7.37, 8.78)	43	-0.065	0.949

†Estimated degrees of freedom; ‡ p refers to group α and to differences between this and α for the remaining covariates/levels.

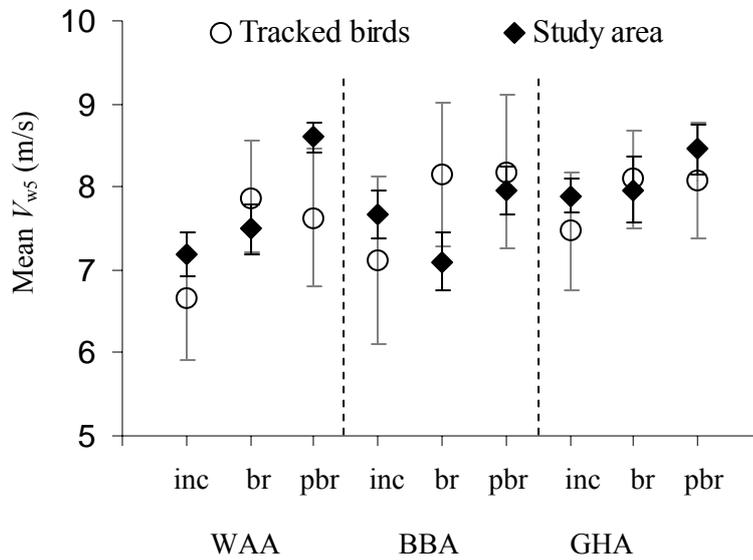


Figure 4.6 Wind speed at 5 m above sea level (\bar{V}_{w5}) experienced by albatrosses tracked from Bird Island, South Georgia and wind speed averaged across the area traversed by each species during the breeding season (\pm 95% CI). WAA = wandering albatrosses; BBA = black-browed albatrosses; GHA = grey-headed albatrosses; LMSA = light-mantled sooty albatrosses; inc = incubation; br = brood-guard; pbr = post-brood.

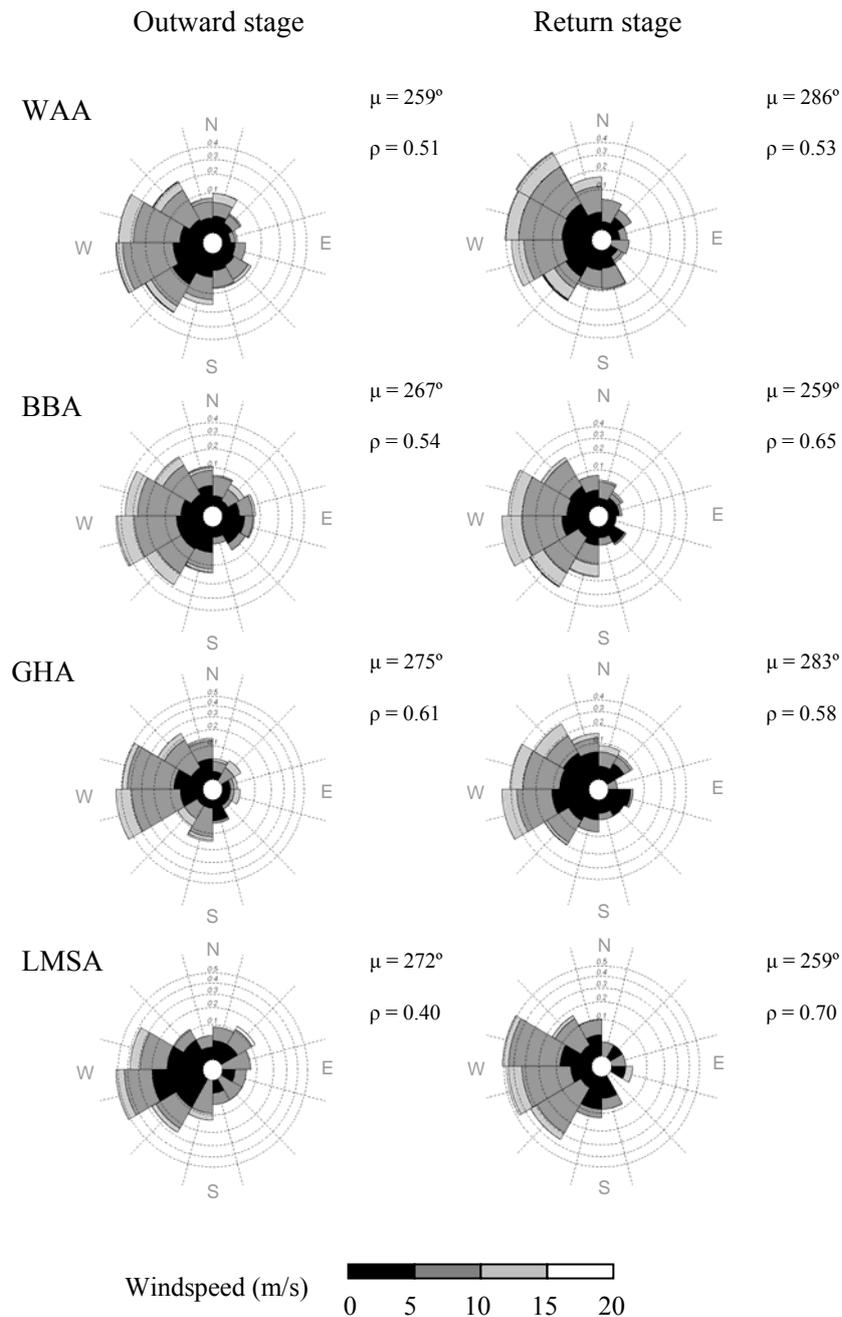


Figure 4.7 Wind speed and direction experienced by albatrosses tracked from Bird Island, South Georgia during outward and return portions of foraging trips. WAA = wandering albatrosses; BBA = black-browed albatrosses; GHA = grey-headed albatrosses; LMSA = light-mantled sooty albatrosses. Circles indicate percentage of winds from a given direction and shading indicates proportion of wind speeds of a given magnitude (μ = mean wind direction, ρ = mean resultant length).

4.3.3 Flight direction with respect to wind

With some exceptions there was a general tendency for albatrosses to avoid headwind flight and there was no evidence of sexual differences in flight direction relative to wind direction $\Delta\theta$. For wandering, grey-headed and light-mantled sooty albatrosses the null model (models Va, Vc and Vd) best described median $\Delta\theta$, indicating that there were no gross differences in relative flight directions between breeding stages and trip stages in these species. Model Vb, however, shows that median $\Delta\theta$ was significantly more downwind during the return stage of foraging trips made by post-brood black-browed albatrosses i.e. birds often encountered headwinds during the outward stages of foraging trips and tailwinds during the return stages (Table 4.9). Furthermore, distributions of $\Delta\theta$ show that this trend was evident in all other species/stages considered, except grey-headed albatrosses during incubation. Indeed, Wilcoxon matched-pairs tests confirm that for individual foraging trips, median $\Delta\theta$ during return stages was significantly more downwind than during outward stages in wandering albatrosses during brood-guard, and black-browed light-mantled sooty albatrosses during post-brood (Fig. 4.8). This difference was most marked in the former two species/stages. Relative flight directions during the middle stage of foraging trips were remarkably similar for all species (Kruskal-Wallis $\chi^2_3 = 5.12$, $p = 0.163$), with birds showing a marked tendency to fly across the wind (Fig. 4.9).

Table 4.9. Model V_b , generalized linear mixed effects model of median flight direction relative to wind direction (θ_r) of black-browed albatross.

Covariate/level	Estimate \pm SE \dagger	z-value	p
Outward trip	0.162 \pm 0.177	0.914	0.361
Middle of trip	-0.102 \pm 0.251	-0.406	0.685
Return trip	-0.915 \pm 0.260	-3.525	<0.001

n birds = 12, n trips = 128; $\dagger \theta_r$, scaled from 0 (downwind) to 1 (upwind) and expressed in logits.

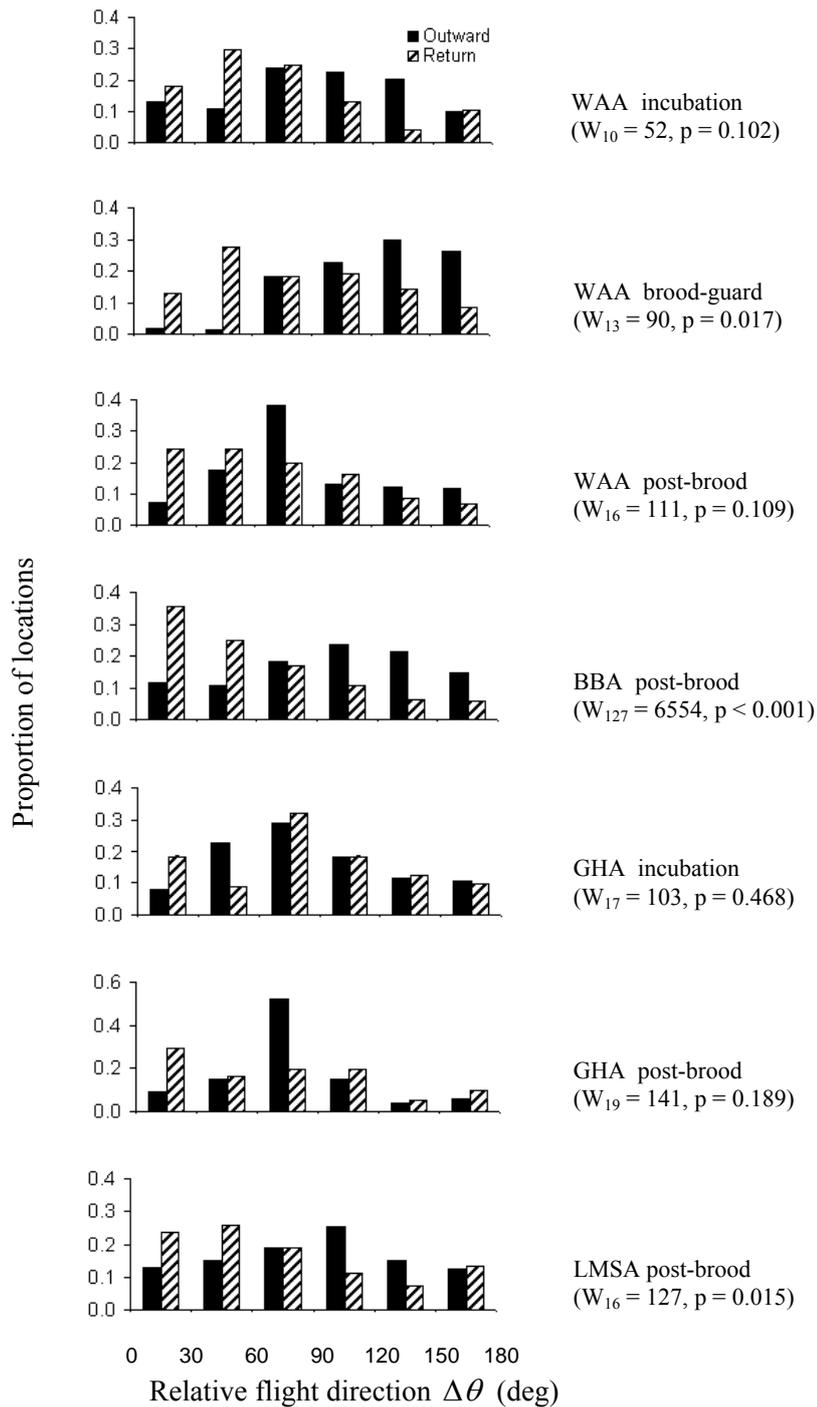


Figure 4.8. Distribution of albatross flight directions relative to the wind ($\Delta\theta$) during the outward and return portions of foraging trips. WAA = wandering albatrosses; BBA = black-browed albatrosses; GHA = grey-headed albatrosses; LMSA = light-mantled sooty albatrosses (also shown Wilcoxon matched-pairs test statistics for outward vs. return $\Delta\theta$).

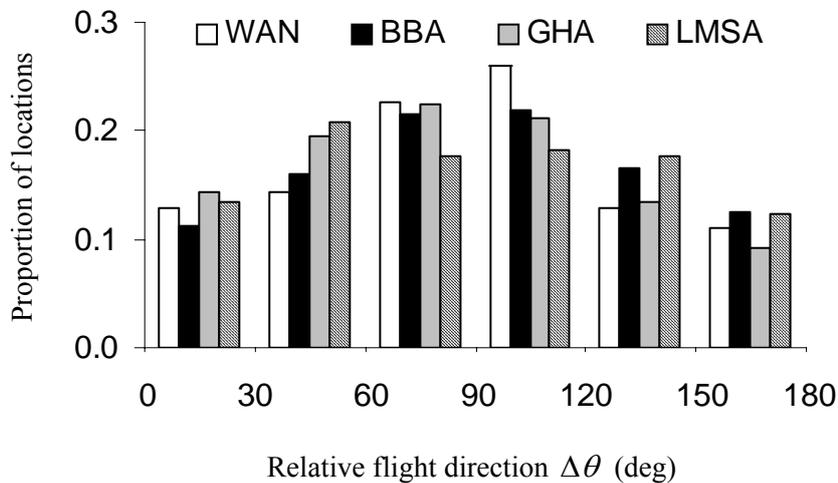


Figure 4.9. Distribution of albatross flight directions relative to the wind ($\Delta\theta$) during the middle portions of foraging trips. WAA = wandering albatrosses; BBA = black-browed albatrosses; GHA = grey-headed albatrosses; LMSA = light-mantled sooty albatrosses.

4.4 Discussion

I modelled the groundspeeds of albatrosses during bouts of direct, sustained flight, over periods of hours. I found that groundspeed is a function of the wind component V_{wf} , species and, where this could be tested, sex. Although female albatrosses had lower groundspeeds than males, they did not experience significantly lower wind speeds. At the scale of hours, albatrosses foraging from South Georgia often encounter headwinds during the outward stages of foraging trips and tailwinds on their return.

4.4.1 Selection of tracking locations

My simulations show that the minimum distances d_{sep} required to obtain accurate estimates of speed using pairs of PTT locations are relatively large. For pairs of locations with equal ARGOS errors my estimates of d_{sep} were approximately three

times those calculated by Hays et al. (2001). This disparity arises for two reasons: firstly, as there is no consensus on the size of ARGOS errors (Brothers et al. 1998, Hays et al. 2001, Vincent et al. 2002), I adopted the precautionary approach of selecting the largest errors reported in the literature to estimate d_{sep} ; secondly, whereas Hays et al. (2001) defined d_{sep} as the minimum distance required between two locations to ensure that the *mean* of speeds estimated from a series of pairs of locations lies within $\pm 10\%$ of the true mean speed on 95% of occasions, I defined d_{sep} more stringently as the minimum distance required to ensure that 95% of *all* speed estimates between locations lie within $\pm 10\%$ of the true speed. Therefore, although fewer pairs of PTT locations are retained using our approach, individual speed estimates are more accurate.

4.4.2 Intrinsic and extrinsic factors affecting groundspeed

With the exception of model IId (light-mantled sooty albatross), my empirical models of groundspeed for each species performed well. In contrast, model I, which considered all species and sexes, performed poorly. Nevertheless, taken together these models give a good indication of the following intrinsic and extrinsic factors affecting groundspeed:

Wind speed component in the direction of flight: I have shown that groundspeeds of albatrosses are proportional to V_{wf} . Pennycuick (1982) reached a similar conclusion after tracking albatrosses optically at a smaller spatial scale. Likewise, other studies have shown V_g to be proportional both to $\cos \Delta\theta$ and to \bar{V}_{w5} , the product of which is V_{wf} (Salamolard & Weimerskirch 1993, Spear & Ainley 1997b, Weimerskirch et al. 2000b). In all species I estimated β to be < 1 (Tables 4.4 & 4.5). Therefore, groundspeed is not simply the product of airspeed and V_{wf} . A possible explanation for this is that the flight height I assumed ($h_{ref} = 5\text{m}$) was inappropriate. Although during dynamic/gust soaring albatrosses periodically perform pull-up manoeuvres to heights of 5 – 10 m (Pennycuick 2002), personal observations suggest that they spend most of their time flying very close to the surface of the sea. As wind speed decays

exponentially with decreasing height above the sea's surface (eq. 1), the apparent wind speeds that birds experience may be lower than that at h_{ref} . More accurate data on flight heights would help to resolve this issue. Airspeed optimization (Pennycuick 1978, 1982) and changes in the degree to which flight paths meander with relative flight direction (Alerstam et al. 1993) may also act to modify β . I found no evidence that β differed between sexes but it did differ between species (Tables 4.4 and 4.6), a possible explanation for which is that the mode of flight (e.g. defined as the change in flight height throughout the dynamic/gust soaring cycle) varied accordingly. The size of β , and thus the effect of wind on V_g , was greatest for wandering albatrosses, followed by black-browed, light-mantled sooty and grey-headed albatrosses.

Species: Interspecific differences in airspeed (i.e. V_g in crosswind flight) differed from theoretical predictions based on morphology. Despite their large size and greater wing loading, wandering albatrosses had comparatively low groundspeeds. This discrepancy may be behavioural in origin rather than due to morphological constraint: By using pairs of locations from the outward and return stages of trips in model I assumed that groundspeed estimates would pertain to commuting only. This may be a better assumption for the smaller species, such as black-browed albatrosses, than for wandering albatrosses. The former tend to undertake rapid commuting flights between the colony and discrete, predictable foraging areas, whereas wandering albatrosses are thought to search for widely spaced prey over larger areas (Weimerskirch et al. 1997c, Weimerskirch & Guionnet 2002, Catry et al. 2004b). When both direct and indirect flight bouts are considered (models IIIa-IIIb) it can be seen that V_g of black-browed and grey-headed albatrosses decrease significantly during the middle stages of trips (Table 4.7). This is probably because at fine scales tracks become more tortuous during prey searching (Veit 1999). That such a difference was seen for wandering albatrosses suggests less of a marked change in behaviour during the middle stages of trips. Optimal foraging theory predicts that gliding birds should fly at airspeeds at or in excess of their best glide speed (V_{bg}) when commuting, and at lower speeds (intermediate between V_{bg} and their minimum sink speed V_{ms}) when searching for prey (Pennycuick 1989, Hedenström & Alerstam 1995). Hence the comparatively low

speeds estimated for wandering albatrosses may be because they were engaged in prey search throughout foraging trips.

Albatross flight paths are convoluted across a range of scales and so estimates of V_g tend to decrease with the scale of measurement (Walker et al. 1995). Hence, my estimates of wandering albatross V_g were ~ 2 m/s higher when calculated between consecutive locations (model IIa) than over five locations (model I). At the scale of minutes and seconds albatross V_g is higher still: Groundspeeds of wandering, black-browed and grey-headed albatrosses measured optically and by radar in zero relative wind were 0.7 to 2.5 m/s faster (Pennycuick 1982, Alerstam et al. 1993) than I estimated with models IIa-IIc, while those of wandering albatrosses tracked with high resolution GPS loggers were 2.9 m/s faster (Weimerskirch et al. 2007). Therefore, my estimates of V_g at the scale of hours are probably ~ 80 – 94 % of instantaneous V_g .

Sex: In accordance with theoretical predications, V_g of males in zero relative winds ($V_{wc} = 0$) were significantly higher than those of females. Though this result is not entirely unprecedented (mean V_g of red-footed boobies *Sula sula*, which exhibit reverse sexual dimorphism but proceed largely by flapping flight, is higher in females (Weimerskirch et al. 2006b)), to my knowledge it is the first time that a sexual disparity in groundspeeds has been identified in gliding birds. However, whether this is entirely due to a size mediated difference in aerodynamic performance remains questionable; firstly, because sexual differences in V_g were in all cases greater than predicted (c.f. Tables 4.5 & 4.6), and secondly I did not take morphometrics from tracked birds, but rather assumed they showed the same degree of sexual size dimorphism as the population as a whole. It is possible, therefore, that these differences arise partly or wholly from sexual variation in behaviour.

Despite confirming the prediction that female albatrosses have lower groundspeeds, and presumably therefore stall speeds, I found no compelling evidence to support the hypothesis that they are better adapted to flight in light winds than males (Shaffer et al.

2001). This hypothesis originally pertained to wandering albatrosses in the Indian Ocean, where colonies are located much closer to the belt of light winds associated with the subtropical high than South Georgia (*ca.* 1000 km vs 2000 km). Black-browed, grey-headed and wandering albatrosses from South Georgia also exhibit some degree of sexual spatial segregation, with females tending to range at times through areas of lighter winds than males (Prince et al. 1998, Phillips et al. 2004b, Xavier et al. 2004). Despite this, in all breeding stages I found no significant differences in the wind speeds experienced by males and females. Indeed, across species and sexes wind speeds during foraging flights were very similar to mean wind speeds throughout the study area (7.6 – 8.2 m/s at $h_{\text{ref}} = 5$ m for the tracking periods). Hence, other explanations for spatial sexual segregation, such as competitive exclusion (Weimerskirch et al. 1993) and breeding role specialization (Weimerskirch et al. 2000a), should be reconsidered.

Diel and lunar phase: To date, V_g of satellite-tracked albatrosses has been reported as faster during daylight than darkness (Salamolard & Weimerskirch 1993, Walker et al. 1995, Phillips et al. 2005a). Data from immersion loggers indicate that this is mainly because birds spend a greater proportion of their time in flight during daylight (70-80 %) than darkness (20-40 %) (Weimerskirch & Guionnet 2002, Phalan et al. 2007). Having corrected for this effect, I found that during direct uninterrupted bouts of flight, wandering, grey-headed and light-mantled sooty albatrosses all attained comparable V_g day and night. Black-browed albatrosses however flew slightly (0.9 m/s) faster during the day. It is not clear why this should be, as the activity patterns of this species are similar to those of the other species (Phalan et al. 2007). I was not able to test whether V_g of black-browed, grey-headed and light-mantled sooty albatrosses varied with lunar phase, as these species engaged in direct, sustained bouts of flight only on moonlit nights, reflecting the fact that they are more sedentary on moonless nights (Phalan et al. 2007). However, wandering albatrosses, which are also less active on moonless nights (Weimerskirch et al. 1997c), engaged in direct, sustained bouts of flight at comparable groundspeeds on both moonlit and dark nights. Hence, low light levels do not inhibit flight in this species to the extent that V_g is reduced.

4.4.3 Flight direction with respect to wind and travel costs

There is still considerable debate about the theory of optimal groundspeeds in central-place foraging birds (Hedenström & Ålerstam 1995, Hedenström et al. 2002, Houston 2006). However, one might hypothesize that albatrosses alter commuting speeds in response to the severity of the central place constraint (Norberg 1981). My results show that the V_g with respect to V_{wf} of albatrosses does not vary with breeding stage (models IIa-IIc). This is presumably because albatrosses rarely use flapping flight, which is the only obvious means by which they could increase their *airspeed* with respect to V_{wf} . As I have shown however, in all species *groundspeed* is proportional to V_{wf} . In wandering albatrosses energetic expenditure (measured by the proxy heart rate) is proportional to the direction of flight with respect to wind θ_r (Weimerskirch et al. 2000b). Hence birds might reduce time and energy costs by choosing to fly only when the winds are relatively strong and/or from a favourable direction. Such behaviour has been observed in both breeding and non-breeding albatrosses (Murray et al. 2003, Catry et al. 2004a). However, I found no differences in wind speeds or directions experienced during different trip stages so it is unlikely that such strategies predominate in the populations I considered. This is perhaps unsurprising, given that South Georgia lies in the middle of the belt of strong, persistent westerly winds that prevail across the Southern Ocean between 35° and 65° S (Kållberg et al. 2005) i.e. there may be insufficient variability in wind strength and/or direction to allow birds to be too selective about when they fly.

An alternative strategy would be to alter V_{wf} by altering flight direction with respect to wind θ_r . This could occur at the level of foraging trips or at smaller scales in response to changes in wind conditions encountered en route. For example, wandering albatrosses breeding in the Crozet Islands (46°25' S, 51°59' E) exploit large-scale semi-persistent wind patterns to make long looping trips, avoiding headwind flight (Jouventin & Weimerskirch 1990, Weimerskirch et al. 2000b). Although the wind regime at South Georgia differs from that at Crozet, showing less variation in direction and strength with latitude (Kållberg et al. 2005), birds from the populations I studied also made long looping flights during incubation and post-brood (Phillips et al. 2004b,

Xavier et al. 2004, Phillips et al. 2005a, BAS unpublished data). However, this strategy is apparently either not always effective or preferable because birds frequently encountered headwinds during outward trips and tailwinds on their return. This trend was most marked in brood-guard stage wandering albatrosses and least so in incubating grey-headed albatrosses. The difference probably reflects the severity of the central place constraint. The dominant response of albatrosses to the increase in this constraint following hatching is to reduce foraging range, with birds making shorter, direct trips to discrete areas (Shaffer et al. 2003). This may leave them with less choice in their flight direction with respect to wind than during the incubation or post-brood stages (Salamolard & Weimerskirch 1993). At South Georgia, where brood-guard stage wandering albatrosses forage to the west colony (Prince et al. 1998), birds therefore encounter headwinds during the outward stages of trips. In the middle stages of foraging trips, when they were less constrained, all species tended to fly most often with side winds. Hence, flight direction with respect to wind is a function of both preference and the relative locations of the colony and foraging areas (Spear & Ainley 1997a).

Clearly this has implications both for the time and energetic costs of foraging trips (Salamolard & Weimerskirch 1993). Within the range of wind speeds typically encountered by birds in my study ($\bar{V}_{w5} \approx 8$ m/s, s.d. ≈ 5 m/s), variability in groundspeed due to relative flight direction was greater than that due to changes in wind speed. For example, a black-browed albatross in downwind flight would only experience a 1.4x (5.3 m/s) increase in groundspeed if the wind speed increased from 3 to 13 m/s, decreasing journey time by 6.3 hrs over 1000 km. In contrast, the same bird flying in winds of \bar{V}_{w5} would experience a 2.1x (8.3 m/s) increase in groundspeed by turning from headwind to tailwind flight. This corresponds to a decrease in journey time 21.6 hrs over 1000 km. However, I did not observe such a large difference in outward and return V_g in those species that foraged upwind of South Georgia (wandering, black-browed and light-mantled sooty albatrosses, Prince et al. 1998, Phillips et al. 2004b, Phillips et al. 2005a). Groundspeeds of these species were on average 1.0, 1.4 and 1.2 m/s faster respectively during return trips. This indicates that

birds are able to use the behavioural strategies outlined above to buffer against the effects of wind.

Given that albatross $V_g \sim V_{wf}$ it is interesting to speculate on the effect of this on habitat accessibility during breeding. Clearly, wind allows birds in some areas, such as the Indian Ocean, to complete long foraging trips, accessing distant resources (Jouventin & Weimerskirch 1990, Weimerskirch et al. 2000b). In contrast, birds foraging from South Georgia are subject to a more uniform wind field. Pennycuik (1989) predicted that the energetic cost of foraging trips made by flapping birds in such an environment would be lower if they foraged upwind rather than downwind of the colony. Similarly, if the energetic cost of flight increases as an albatross gains weight during a chick-provisioning trip (for example by reducing the efficiency of dynamic soaring), it may be more efficient to make such trips upwind of the colony. This type of mechanism could explain why breeding albatrosses from South Georgia rarely forage to the east (downwind) of the islands, whereas non-breeding birds from the same population, which are not subject to central place effects, are distributed both to the east (downwind) and west (upwind) of the islands (Fig. 4.10).

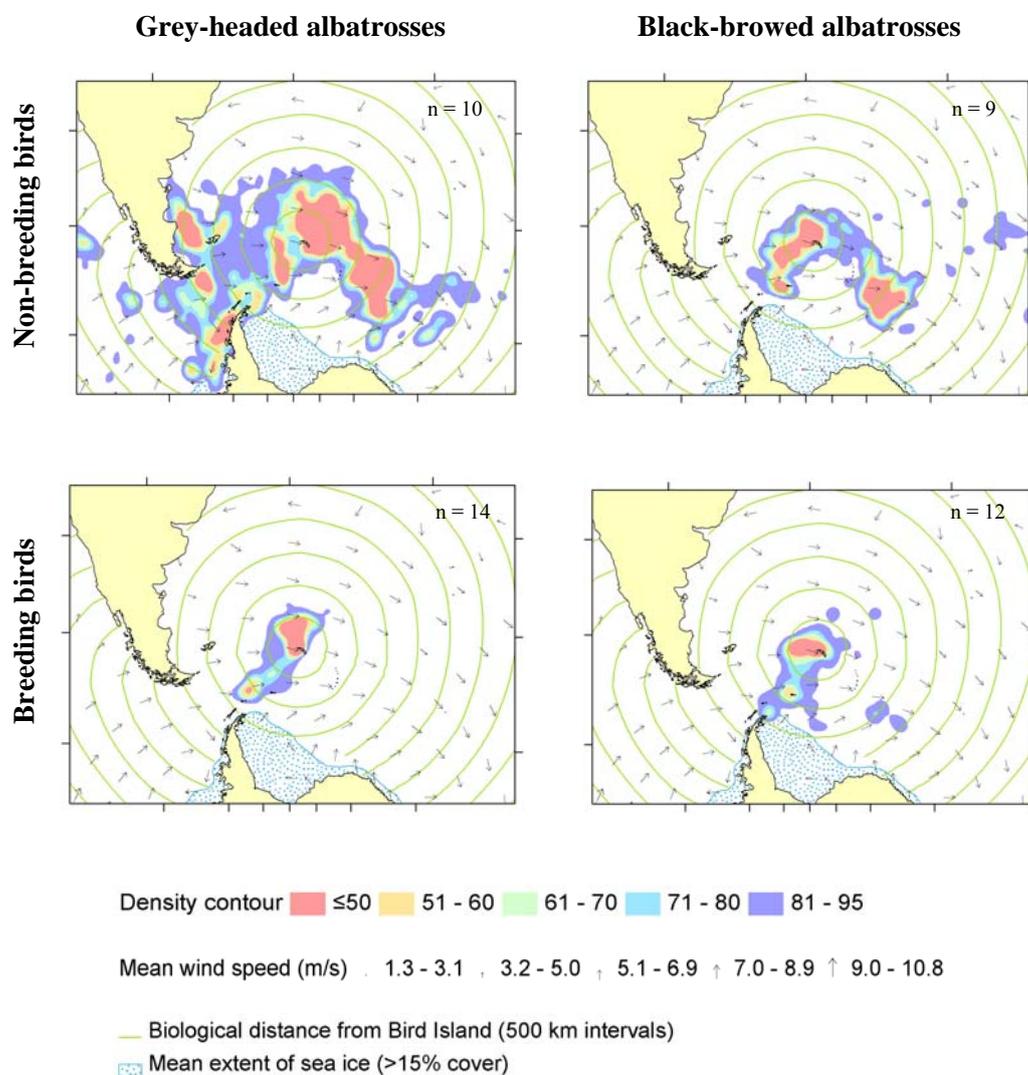


Figure 4.10 The spatial distribution (kernel density) of breeding and non-breeding grey-headed and black-browed albatrosses from Bird Island, South Georgia. All birds were tracked during post-brood (Feb-April), using either PTTs (breeders) or geolocators (non-breeders). Non-breeders were either on their sabbatical year or their breeding attempt had failed early in the season (Phillips et al. 2004b, Phillips et al. 2005b, BAS unpublished data). QuickSCAT satellite scatterometer wind data for the period 1999-2007 obtained from CERSAT, at IFREMER, Plouzané (France).

Despite the complexity of their flight patterns, I have demonstrated that the groundspeeds of albatrosses can be predicted by considering morphology and relative

wind. I suggest that the birds may reduce transport costs by 1. flying only when winds are of a favourable strength and/or direction; 2. routing their foraging trips to exploit large scale wind patterns; or 3. altering flight direction with respect to wind in response to changing wind conditions during trips. Down or crosswind flight is preferred but in some circumstances the additional costs of travelling upwind may be outweighed by rapidly gaining access to resources. Hence, during breeding, when birds are constrained to return regularly to the colony, habitat accessibility should be regarded as a function both of distance from the colony (Matthiopoulos 2003) and wind field. I hope that my findings will stimulate further research into the effects of wind on seabirds such as albatrosses in different wind regimes, especially given the fact that large scale wind patterns are projected to alter across the Southern Ocean over the next century as a result of human induced climate change (Shindell & Schmidt 2004, Bracegirdle et al. 2008).

Chapter 5. General discussion

One of the fundamental motivations of ecologists is to understand how environmental constraints upon individuals affect populations, communities and, ultimately, ecosystems (Levin 1993, Wiens et al. 1993, Lima & Zollner 1996, Begon et al. 2006). This study was concerned primarily with the first three levels in this hierarchy, and aimed to determine how environmental constraints affect the foraging behaviour, spatial usage and population sizes of black-browed albatrosses and related species. Although less concerned with communities, and only indirectly with ecosystems, when placed in these wider contexts, the results of this study are nevertheless informative (Worm et al. 2005, Murphy et al. 2007, Weimerskirch 2007, Jennings et al. 2008). The aims were realized by capitalizing on recent technological advances in the fields of animal telemetry (reviewed by Ropert-Coudert & Wilson 2005, Burger & Shaffer 2008), satellite remote sensing (e.g. Ducet et al. 2000, Reynolds et al. 2002, Behrenfeld et al. 2006), oceanography (Longhurst 1998, Mann & Lazier 2006) and statistical modelling (Pinheiro & Bates 2000, Wood 2006, Aarts et al. 2008).

Albatrosses are inherently appealing to human sensibilities, being at once graceful, imposing and enigmatic - characteristics that have ensured their iconic cultural status (Tickell 2000). However, there are other more prosaic reasons why they are particularly apposite models for investigating the links between the environment, individuals and populations. From a practical point of view, their large size and periodic return to breeding colonies means their movements can be recorded using miniature satellite-transmitters and loggers without appreciably affecting their behaviour (Phillips et al. 2003). What is more, because they are long-lived, strongly philopatric, and easy to individually mark, they have been the subject of a number of long-term studies (e.g. Weimerskirch 2002, Phillips et al. 2007), such that many aspects of their breeding biology, demographics, etc. are well understood (reviewed by Warham 1990, Tickell 2000).

These and other life history traits, such as delayed maturity, small clutch size, and prolonged breeding periods, mean that albatrosses are extreme examples of an already highly specialised group - the pelagic seabirds (Warham 1990, Schreiber & Burger 2002a). Theoretical and empirical attempts to understand the evolutionary causes and consequences of these traits have informed wider ecological theory (e.g. Lack 1954, Wynne-Edwards 1962, Ashmole 1963) so new studies on albatrosses can be placed in this broad context. Studies on albatrosses can also be informative of processes occurring at lower trophic levels and changes across ecosystems as a whole, that otherwise may be difficult to detect (Reid et al. 2005, Boyd et al. 2006). In particular, the ecosystem-level consequences of fisheries (Furness & Tasker 2000, Einoder 2009) and natural and anthropogenically induced climate change (Thompson & Ollason 2001, Croxall et al. 2002) may be more fully understood by studying pelagic seabirds. Finally, there is a great conservation imperative to understand the ecology of albatrosses because they have been subject over the past three decades to highly unsustainable rates of mortality in long-line and trawl fisheries (Brothers 1991, Croxall & Gales 1998, Gales et al. 1998, Tuck et al. 2003, Sullivan et al. 2006).

5.1 Main findings

The principal aims of this study, outlined in section 1.9, can be posed as a series of research questions, the concise answers to which summarise the main findings:

1. *How does the central place constraint affect spatial and habitat use during different breeding stages?*

Use of space by breeding black-browed albatrosses is inversely related to distance from the colony, reflecting the associated increase in time and energy costs. Hence, habitat accessibility can be approximated by the reciprocal of colony distance (Chapters 2 and 3). During incubation, trip duration is ultimately limited by the incubating partner's ability to fast on the nest and, as a result, long trips are made (median maximum colony distance 995 km, range 54-3039 km). During post-brood the energetic demands of the growing chick are limiting and so shorter trips, closer to the colony, are made (median maximum colony distance 304 km, range 24-2949 km).

2. What mesoscale oceanographic foraging habitats do breeding black-browed albatrosses use and which are preferred?

Analysis of individual movement data from 163 black-browed albatrosses satellite-tracked from eight colonies located throughout the species' range (Chapter 2) confirmed that while breeding, this species primarily forages in neritic and upper shelf slope waters. However, birds from some populations also used highly dynamic oceanic waters, characterized by high mesoscale variability. In decreasing order, bathymetric habitat preferences are for neritic (0-500 m), shelf-break to upper shelf-slope (500 – 1000 m), and then oceanic (>1000 m) waters: Preference also increased with sea floor slope, reaching a maximum at 3° (Figures 2.10 and 2.11).

3. Does habitat use and preference differ between breeding stages, populations and closely related species?

Habitat use and preferences differed between incubation and post-brood (Chapter 2). During incubation, black-browed albatrosses spent more time in subtropical waters, indicated by SSTs of 5 - 16°C. This was because, in addition to the bathymetric preferences outlined above, SST preference peaked at 16°C. While black-browed albatrosses from all populations in this study foraged primarily in either local or distant neritic waters during breeding, those from colonies other than in the Falkland Islands also foraged in oceanic waters. This propensity was most marked in birds from South Georgia, which foraged in the Antarctic Polar Frontal Zone and the Brazil-Malvinas Confluence. This was indicated by the Eddy Kinetic Energy preference of birds from this population, which was uniform up to 250 cm²/s² and then increased linearly above this value. During post-brood, the closely-related Campbell albatross also foraged in both neritic and oceanic waters. Although their habitat preference decreased with depth, it differed from black-browed albatrosses' by the absence of a marked preference for neritic waters. Furthermore, Campbell albatrosses also showed a preference for positive sea level anomalies (peaking at ~ 9 cm), indicating a preference for foraging in mesoscale eddies associated with the Subantarctic Front and Antarctic Polar Frontal Zone.

4. Do albatrosses modify their spatial usage in response to intraspecific competition from neighbouring populations?

This was only to a limited extent. During incubation, the foraging ranges of black-browed albatrosses from neighbouring colonies tend to overlap extensively (Chapter 2). However, during post-brood habitat preferences have two minima, the first in the immediate vicinity of neighbouring colonies and the second at ~ 700 km from the next nearest colony. These preferences are reflected by an avoidance, during post-brood, of areas immediately surrounding neighbouring colonies and of foraging zones of neighbouring populations at the meso to macroscale. Despite these effects, there was still some overlap in the foraging areas of birds from adjacent populations.

5. Is it possible to use individual movement and environmental data to estimate the spatial usage of foraging albatrosses from different populations?

Breeding albatrosses are central place foragers and thus habitat accessibility decreases as a function of colony distance. Hence, spatial usage was modelled as a function of habitat accessibility as well as of habitat preference and intraspecific parapatric competition. In this way it was possible to estimate the density of breeding black-browed albatrosses at both regional and global population levels (Chapter 2). The validity of this approach was demonstrated by K-folds cross validation, as well as by the close agreement between estimated spatial usage and satellite-tracking data from a colony excluded from the original analysis. However, the models exhibited some residual spatial autocorrelation. While this can result from conspecific attraction (flocking) it may also indicate that the selected covariates did not capture all of the variability in spatial usage, suggesting that the models could be further refined, perhaps by the inclusion of additional covariates or an improved accessibility function.

6. Does prey availability or intraspecific competition during the breeding season regulate population sizes?

Breeding season prey availability, but not intraspecific competition regulates regional black-browed albatross population size (Chapter 3). When populations are regarded as comprising spatial clusters of colonies, population size was log-linearly related to the extent of preferred neritic waters and the total available Net Primary Production (NPP), which are proxies for prey availability. The strength of the relationship with population size is greater when either preferred habitat or NPP are inversely weighted by colony distance, indicating that habitat accessibility is also limiting. The intensity of competition between adjacent populations does not explain population size well. Therefore, although individual colony sizes may vary in response to parapatric intraspecific competition, regional population size is unaffected. However, at the level of individual colonies this and other factors, including nesting habitat availability, may be limiting.

7. Does the wind field affect the flight performance of albatrosses and therefore limit habitat accessibility?

The groundspeed of albatrosses in direct flight is linearly related to the wind speed component in the direction of flight. Relative flight direction is more important in determining groundspeed than absolute wind speed (Chapter 4). When relatively unconstrained (e.g. in mid-foraging trip), all species (wandering, black-browed, grey-headed and light mantled albatrosses) tend to fly predominantly across the wind. However, commuting birds sometimes encounter headwinds during outward trips and tail winds on their return and consequently groundspeed is 1.0 – 3.4 m/s faster during the return.

8. Could differences in flight performance between species and sexes mediate spatial segregation?

There are significant differences in the effects of wind on the groundspeeds of different species and sexes (Chapter 4). Wandering albatrosses are more affected by wind than black-browed, light-mantled and grey-headed albatrosses. Furthermore, the groundspeeds of females are lower than those of males. The latter is thought to be

related to sexual size dimorphism, as males are larger and have higher wing loadings than females. However, no evidence was found that this led to sexual segregation, as males and females experienced comparable wind speeds during foraging trips.

5.2 Limitations of the study

Before discussing the wider implications of this work, it is important to consider how the scope and findings of such studies can be limited by the available data and analytical techniques. As discussed in Chapter 1, the observable spatiotemporal window on the environment is limited by instrument performance (Fig. 1.1). In this study, the locations of individual albatrosses were recorded with PTTs approximately every two hours, accurate to $\sim 0.1 - 30$ km, and in the case of wandering albatrosses, with GPS loggers at intervals of 0.5 to 2 hours, accurate to ~ 10 m (Fukuda et al. 2004, Soutullo et al. 2007). For all species, activity data were recorded at a temporal resolution of 10 minutes (Afanasyev 2004). Only breeding adults were tracked - generally for periods of days to weeks and sometimes over multiple foraging trips. Black-browed albatrosses were tracked from multiple colonies, located throughout their range, but other species were tracked only from South Georgia. Environmental data were collected by remote-sensing at spatial resolutions ranging from ~ 10 km (depth) to ~ 100 km (ERA40 wind data). Dynamic variables, such as OISST were averaged by month (e.g. Reynolds et al. 2002), except wind, which had a temporal resolution of 6 hours. Black-browed albatross population data were obtained from censuses generally carried out during only one or two breeding seasons, with errors of the order of 10% (Robertson et al. 2008, Appendix 1).

Despite these limitations, the analysis of black-browed albatross spatial usage presented in Chapter 2 was able to detect spatial responses of birds at mesoscales and above (> 50 km), over periods of weeks to months (Fig. 1.1). At these scales, the habitat preferences were representative of breeding birds during incubation and post-brood from populations throughout the species' range. However, without further tracking data the habitat preferences of other life history stages, including immature and non-breeding birds, as well as those expressed by all classes at finer spatial and

temporal scales, could not be quantified. Furthermore, the potential spatial response of birds to fishing vessels was not considered because of the four species tracked from South Georgia, only the wandering albatross shows a high level of fisheries interaction during the breeding season and furthermore, information on individual vessel movements was not available.

The analysis of population regulation (Chapter 3) was limited in that it regarded population size as static. Had population trend data been available from adjacent colonies, a dynamic treatment of the effects of habitat availability and accessibility, as well as intraspecific competition, would have proven informative (Olea 2009). The estimates of Net Primary Production used in this analysis were based on AVHRR SST and SeaWiFS Chl-a SST data, both of which are prone to inaccuracies due to cloud interference at mid to high latitudes and in coastal waters (Woodward & Gregg 1998, Martin 2004). Finally, the analysis of flight performance (Chapter 4) pertained to variation in the flight speeds of breeding adults in response to the wind at temporal scales of hours and spatial scales of 100s of km. At scales of seconds to minutes, and metres to 100s of metres, dynamic or gust soaring enables the birds to reach faster and more variable speeds (Pennycuick 1982, Alerstam et al. 1993, Pennycuick 2002) but high resolution tracking data at this level was not available.

The spatial modelling of individual movement is an active area of research and no completely satisfactory ‘off the shelf’ methodology exists (Schick et al. 2008, Matthiopoulos & Aarts 2009). However, Aarts et al. (2008) recently developed an analytical framework which addresses many of the problems inherent in modelling the spatial usage of animals foraging from a central place. This was used to model the spatial usage of black-browed albatrosses as a function of habitat preference, accessibility and availability (Chapter 2). It uses mixed-effects Generalised Additive Models (GAMs, Wood 2006), which I implemented using the *mgcv* package in R (R-Development-Core-Team 2007). Although GAMs are very useful, in that they allow a flexible, non-linear response and binomial errors, their mixed-effects implementation requires high processing power. With the large volumes of tracking data available in

this study, this limited the number of explanatory covariates that could be considered, and precluded inclusion of spatial or temporal autoregressive terms. Furthermore, parameter estimation was achieved by maximising the Penalised Quasi-Likelihood. This precludes model selection on the basis of information criteria, such as AIC, so models had to be selected by cross validation, which incurs a risk that those selected were under-specified (i.e. important covariates were falsely rejected (Burnham & Anderson 1998)). Similarly, although dynamic variables were included in the analysis, in order to limit the potential number of models, it was not feasible to include time-lagged effects of covariates such as SST on spatial usage (Ainley et al. 1993, Hunt et al. 1999, Gremillet et al. 2008). Future advances in the implementation of mixed-effects GAMs will doubtless meet these shortcomings. Meanwhile, selection of candidate covariates and models in an ecologically informed manner (Austin 2007), should have ensured that the result presented here are realistic.

5.3 Ecological implications

The analyses presented in this thesis have demonstrated how a number of environmental constraints, such as the distribution of prey relative to colonies and the strength and direction of the wind, affect the foraging behaviour, spatial usage and population sizes of albatrosses. In order to draw these results together it is useful to consider the wider context. The two most obvious constraints faced by seabirds are the need to return to land periodically to breed, and to return to or remain above the surface of the sea in order to breathe. Both of these constraints are common to pinnipeds and marine turtles, whereas cetaceans share only the second. Unlike seabirds, marine turtles do not incubate their eggs, or provision or care for their offspring. Hence, in terms of basic life history traits, pelagic seabirds have most affinity with pinnipeds. However, pinnipeds differ from flying seabirds in their mode of locomotion, being functionally closer to penguins, which have evolved similar diving capabilities at the cost of the ability to fly. The flying seabirds can be further divided into those that use flight to travel but forage only during long dives (e.g. the auks and diving petrels) and tend to forage relatively close to their colonies, and those that do not (Pennycuik 1987). The latter group encompasses the pelagic seabirds, as defined in Chapter 1, including the albatrosses. Hence, albatrosses are wide-ranging,

higher marine predators that travel by flying, have only limited diving capabilities and are constrained to return to land to breed. I suggest that the last of these characteristics is key to understanding their ecology.

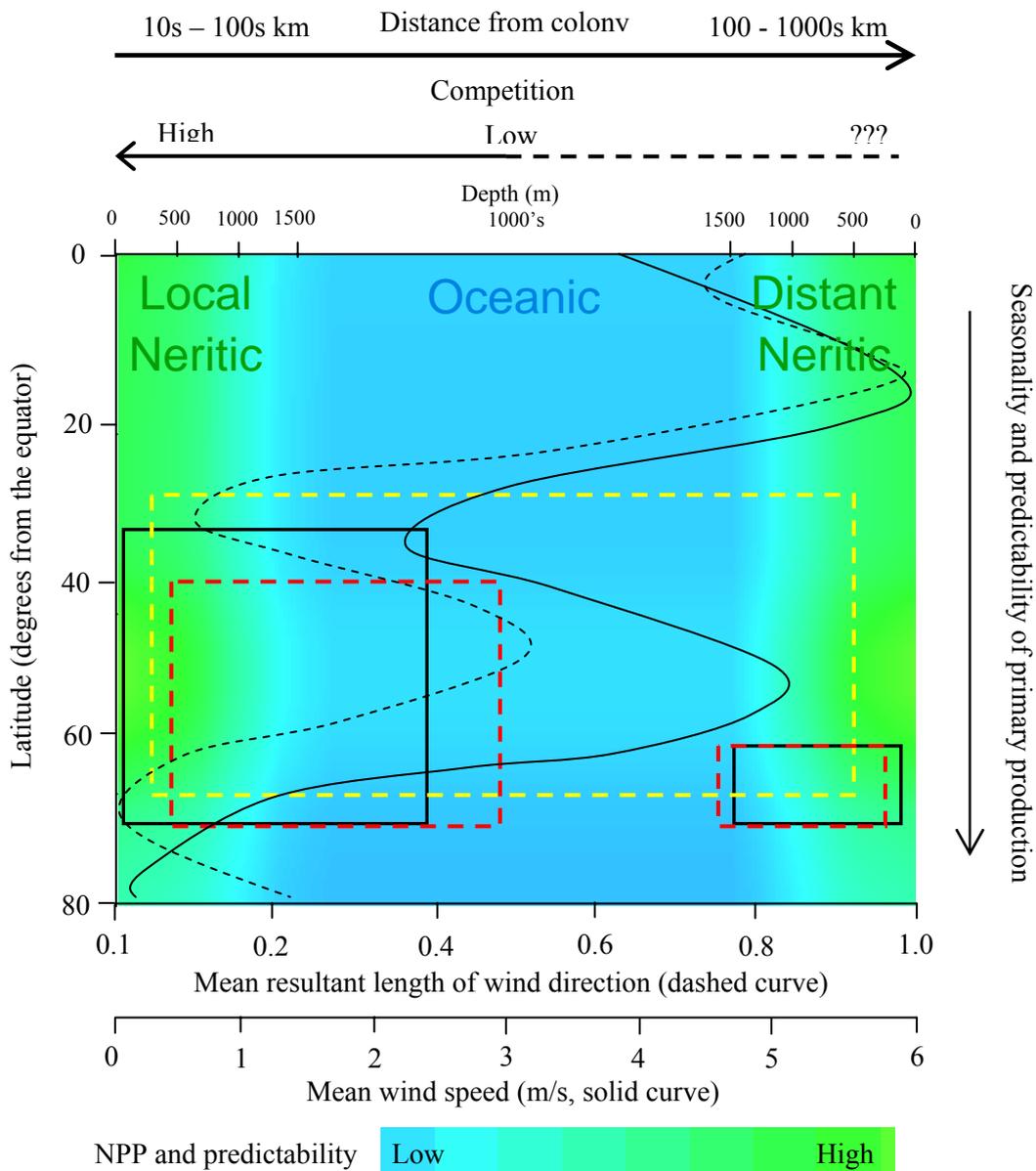
Depending on the species, albatrosses breed every 1 - 2 years, for periods of 7 - 12 months (Warham 1990). During this time they forage at sea but return to their colonies at regular intervals, either to relieve their partner from incubation, brooding or chick guarding duties or to provision their offspring. They therefore act as central place foragers for almost half of their adult lives. Although factors operating during non-breeding periods, such as seasonal (Lack 1954, 1968) or episodic food shortages, (e.g. caused by El Niño events, Schreiber & Schreiber 1984, Anderson 1989, Jaksic 2004) may play a role in regulating seabird populations, the strong correlation between population sizes and the availability and accessibility of preferred habitat and NPP shown in Chapter 3 supports Ashmole's (1963) hypothesis that populations are ultimately regulated by food availability during breeding. Albatrosses are highly philopatric and have very low adult mortality (Prince et al. 1994b, Pinaud & Weimerskirch 2002), so this is most likely to regulate populations by influencing productivity. Immature albatrosses suffer high mortality in the days immediately after fledging (Reid et al. 2000, BAS unpublished data), so productivity in this context means not only the proportion of breeding attempts resulting in fledged offspring but also the likelihood that these will survive into adulthood. Immature survival has been shown to correlate with body condition at fledging in several species (Magrath 1991, Sagar & Horning 1998, Van der Jeugd & Larsson 1998, Keedwell 2003) and the same may well be true of albatrosses. Selective pressures brought to bear on albatrosses during breeding are likely to be at least as important as those experienced during other life history stages. Furthermore, the large amount of variability in black-browed albatross population sizes accounted for by food availability and accessibility (88 % for populations consisting of colony clusters ≤ 200 km wide, Table 3.1) indicates that the effects of central place constraint outweigh those of other breeding pressures, such as nesting habitat availability (Forbes et al. 2000) and parasite infestation (Boulinier & Danchin 1996).

Some ecologists tend to treat central place foraging as a special case of optimal foraging (Pyke 1984), making and testing predictions about patch choice, giving up times, competition, etc. (Orians & Pearson 1979, Schoener 1979, Giraldeau et al. 1994). Central place theory has also long been applied in sociological disciplines, such as geography, economics and criminology (Berry & Garrison 1958, Brantingham & Brantingham 1981, Eaton & Lipsey 1982). The fundamental tenet is that the time or energetic costs of travelling to a location increase as a function of distance from the central place (Dukas & Edelman-Keshet 1998). Hence, as shown in Chapter 2, habitat accessibility and therefore albatross spatial usage declines inversely with distance from colonies. All other things being equal, it should be most economical for breeding albatrosses to capture prey as close as possible to the nest (Olsson et al. 2008), yet tracking data show that they routinely forage 100s – 1000s km away (Weimerskirch et al. 1993, Prince et al. 1998, Phillips et al. 2004b, Chapter 2). In order to understand this paradox, and explain why the very wide-ranging foraging strategies of albatrosses are effective, it is first necessary to consider the spatial distribution of food resources.

Because of the necessity of leaving their chicks unattended for long periods, albatrosses do not breed successfully in areas with land predators such as rodents (Wanless et al. 2007). Hence, they breed almost exclusively on offshore islands. At all latitudes, the neritic waters that surround such islands tend to support levels of Net Primary Production (NPP) one to two orders of magnitude higher than in oceanic waters (Field et al. 1998, Longhurst 1998), with concomitantly high production at mid and upper trophic levels. This is due to the effects of biogeochemical cycling and physical forcing. Specifically, the supply of nutrients from terrigenous sources to coastal waters is relatively high, and tidal and wind induced turbulence and fronts cause re-suspension and mixing of nutrients in shallow areas (Mann & Lazier 2006). Furthermore, wake turbulence and in some areas, iron supply, means that NPP in the vicinity of oceanic islands may be higher than further afield (Sokolov & Rintoul 2007, Pollard et al. 2009). Depending on local bathymetry, zones of enhanced productivity adjacent to breeding colonies tend to be 10s – 100s of km wide (Fig 5.1).

As shown in Chapter 2, black-browed albatrosses breeding at colonies throughout their range prefer to forage in neritic habitats, and population sizes are regulated by the availability and accessibility of such habitat relative to colonies (Chapter 3). However, other species, such as the grey-headed albatross, which is morphologically very similar to the black-browed albatross, forage more frequently in oceanic areas (Nel et al. 2001, Catry et al. 2004b, Phillips et al. 2004b, Terauds et al. 2006a), and the larger *Diomedea* spp. tend to range widely over oceanic and shelf-break waters (Weimerskirch et al. 1993, Nicholls et al. 2002, Waugh et al. 2002, Waugh et al. 2005, Pinaud & Weimerskirch 2007). Of course, other features such as oceanic fronts, convergences and neritic areas at distance from colonies, may under some circumstances be considerably more productive than local waters (Lutjeharms et al. 1985). For example, the seasonal retreat of sea ice causes a seasonal peak in NPP in the marginal ice zone, which can be an order of magnitude higher than that in sub-polar neritic waters (Arrigo et al. 1998). In addition, at the mesoscale, the habitats described above may be more profitable not only in terms of their mean prey abundance, but also show less variability, i.e. prey occurrence is more predictable (Real & Caraco 1986). Considering the temporal, as well as spatial dimension, it is notable that seasonal variation in NPP becomes increasingly marked and therefore predictable with latitude (Fig. 5.1). This, together with the clear peak in NPP between $\sim 40^\circ$ and 60° (Field et al. 1998), may explain why higher latitudes support greater abundances of seabirds (de L. Brooke 2002, Weimerskirch 2007). However, even at tropical latitudes, high NPP may occur with very little temporal variability, such as in the quasi steady-state upwelling zones of the eastern tropical Pacific (Ballance et al. 2006). In short, although the spatiotemporal distribution and variability of food may influence the latitude of breeding colonies, the general tendency for prey resources to diminish with distance from offshore islands should, like habitat accessibility, make foraging close to colonies the most profitable strategy. It will only be preferable to forage further afield if the resulting energetic gain outweighs increased transport costs, or if the net rate of prey capture and delivery is faster (Dukas & Edelman-Keshet 1998, Weimerskirch et al. 2005a, Olsson et al. 2008).

Before exploring these points further, it is first necessary to consider the effects of competition. Although breeding albatrosses have catholic diets, taking both live prey and carrion, they feed predominantly on mesopelagic fish, squid and swarming zooplankton, such as Antarctic krill (Cherel & Klages 1998). Sympatric species such as penguins, pinnipeds and other pelagic seabirds also forage on these prey but the potential for competition is reduced by specialisation in different prey size classes, the vertical segregation of foraging zones, and differences in foraging technique (Croxall & Prince 1980, Cherel et al. 2008). For example, albatrosses feed at the surface by dipping and pecking, or during shallow (< ~ 15 m) dives. As such, they forage exclusively in epipelagic waters and so do not usually compete directly with deep divers (Croxall & Prince 1994, Prince et al. 1994a, Huin & Prince 1997, Martin 1998). Nevertheless, because sympatric competitors are subject to the same central place constraint, any indirect interspecific competition that they do suffer will be most intense in the vicinity of colonies (Ashmole & Ashmole 1976). At the community level, this may result in a partial annular segregation of foraging zones (Ashmole & Ashmole 1976, Ichii et al. 2007). For example, sympatrically breeding seabirds often segregate into inshore and offshore zones (Ashmole 1971, Croxall & Prince 1980, Bocher et al. 2000). Hence, albatrosses could range far from their colonies in order to avoid interspecific competition.



Approximate foraging niche of breeding black-browed (———), grey-headed (- - - -) and wandering albatrosses (- - - -).

Figure 5.1 The macroscale foraging niches occupied by breeding albatrosses. Relative summer NPP based on Field et al. (1998) and Mann & Lazier (2006), wind speed and direction climatology calculated from QuickSCAT satellite scatterometer data for the period 1999-2007, obtained from CERSAT, at IFREMER, Plouzané (France).

Similarly, direct and indirect competition among conspecifics is likely to be highest in the vicinity of colonies (Ashmole 1963, Lewis et al. 2001), and because conspecifics

occupy essentially the same niche (although there may be sexual and age related niche differentiation), this is likely to be more intense than interspecific competition (Simberloff & Dayan 1991). It has been predicted that as colonies grow and the density of foraging conspecifics increases, prey in the vicinity will become depleted or disturbed (Ashmole 1963, Furness & Birkhead 1984), and therefore that birds from larger colonies range over wider areas in order to locate sufficient prey (Cairns 1989). Although this response could lead to greater foraging ranges in albatrosses, there was no correlation between colony size and the size of foraging zones used by black-browed albatrosses (Chapter 2). However, partial spatial segregation of foraging zones of birds from neighbouring populations was observed. This phenomenon is also seen in a diverse range of central place foragers, including pelagic seabirds, pinnipeds, rodents and colonial insects (Giraldeau et al. 1994, Adler & Gordon 2003, Gremillet et al. 2004, Lea et al. 2008), supporting the view that intraspecific competition can dramatically modify spatial usage.

From the preceding discussion, it is apparent that breeding albatrosses face two competing needs: firstly to minimise transport costs, which increase with distance from the colony, and secondly to minimise inter and intraspecific competition, which is most intense in the vicinity of colonies. The foraging strategies that balance these needs form a continuum (Weimerskirch 2007): At one extreme, there is a preference for predictably productive areas, such as neritic waters, which are reached by direct commuting flight (Fig. 5.2 and Chapter 4). All albatross species so far tracked adopt this strategy during the brood-guard stage, when they are most time limited, tending to forage within 10s to 100s of km from their colonies (Weimerskirch et al. 1994, Hyrenbach et al. 2002, Shaffer et al. 2003, Phillips et al. 2004b, Awkerman et al. 2005). At this stage they doubtless experience high levels of intra and interspecific competition. Some species, such as the black-browed and waved albatross *Phoebastria irrorata* also use this strategy during incubation and post brood (Fernandez et al. 2001, Phillips et al. 2004b). However, during these stages they are less time constrained and so may make longer commuting trips to distant areas, which presumably have predictably high productivity and lower densities of conspecifics (Fig. 5.1). At the other extreme, in a strategy exemplified by wandering albatrosses during incubation

and post-brood, long looping trips are made, generally in oceanic waters, with birds searching wide areas for prey that are scarce and poorly predictable at the submesoscale (Weimerskirch et al. 1994). Species such as the grey-headed albatross, which forages in association with dynamic oceanic features such as the Antarctic Polar Frontal Zone, as well as in neritic waters, may adopt strategies that lie somewhere between these two extremes (Nel et al. 2001, Catry et al. 2004b, Phillips et al. 2004b).

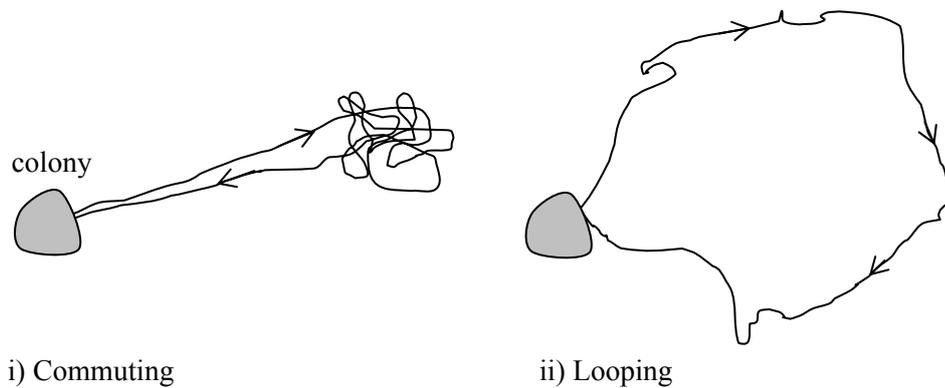


Figure 5.2 Typical foraging strategies of breeding albatrosses (after Weimerskirch 2007).

Although the long range commuting and looping strategies differ in many respects, the success of both relies on foraging trips being completed within a finite time. During incubation, the limitation is the partner's ability to fast on the nest, whereas after hatching it is the chick's endurance (Shaffer et al. 2003, Humphreys et al. 2006). Furthermore, foraging trips can only be successful if energetic demands are met. During all stages, adults must maintain or restore their body condition and in addition, during chick rearing, they must meet the energetic demands of their offspring. It has been widely noted that seabird breeding seasons are long in comparison to those of terrestrial birds (Lack 1968, Schreiber & Burger 2002b), and those of albatrosses particularly so, extending to 12 months in biennially breeding *Diomedea* spp. Black-browed albatrosses are annual breeders and take approximately 7 months to fledge their young. In contrast, sympatrically breeding grey-headed albatrosses, which are

morphologically very similar, take approximately one month longer and breed biennially (Prince et al. 1994b). This may be because grey-headed albatrosses forage in more oceanic habitats, where prey are at lower density and are less predictable than in the neritic habitats preferred by their congeners. This supports Lack's (1968) hypothesis that extended breeding seasons in seabirds are an adaptive response to food scarcity and unpredictability in the marine environment (but see Schreiber & Burger 2002b for a critique of this hypothesis). Regardless of the origin, the existence of long breeding periods in albatrosses means that adults are less time-constrained during foraging trips than most sympatric species, allowing them to make longer foraging trips (Croxall & Prince 1980). This may give them a competitive advantage, in that they can commute to more distant prey patches.

The ability in albatrosses to make very long foraging trips is shared by some penguins, which also have extended breeding periods (Jouventin et al. 1994, Hull et al. 1997). However, albatrosses and large petrels exhibit two other very considerable advantages: their ability to reduce prey to highly energy rich stomach oil in their proventriculus (Warham 1990) and to travel rapidly and with very little energetic expenditure (Bevan et al. 1995, Arnould et al. 1996). They achieve the latter by extracting energy from the wind and waves to sustain soaring flight, only resorting to more energetically-demanding flapping flight in light winds or during takeoff and landing (Pennycuik 2002). As shown in chapter 4, albatrosses are able to sustain mean groundspeeds of 10 – 14 m/s for long periods. This is partly because of their large size: smaller procellariiformes, which have lower wing loadings, generally use flap-gliding or flapping flight, and average groundspeeds of only ~ 7 – 9 m/s (Pennycuik 1987). Swimming speeds of penguins and pinnipeds are an order of magnitude lower still and are unrelated to body size (Sato et al. 2007). Hence, in commuting trips, albatrosses can travel an order of magnitude further in a given time period than sympatrically breeding competitors, allowing them to access more distant resources. Similarly, in looping trips they are able to search a concomitantly larger area, making them better able to exploit the widely dispersed prey characteristic of low productivity oceanic waters. Equally, by allowing them to search a given area more quickly, they may be better able to locate ephemeral prey patches, such as zooplankton swarms.

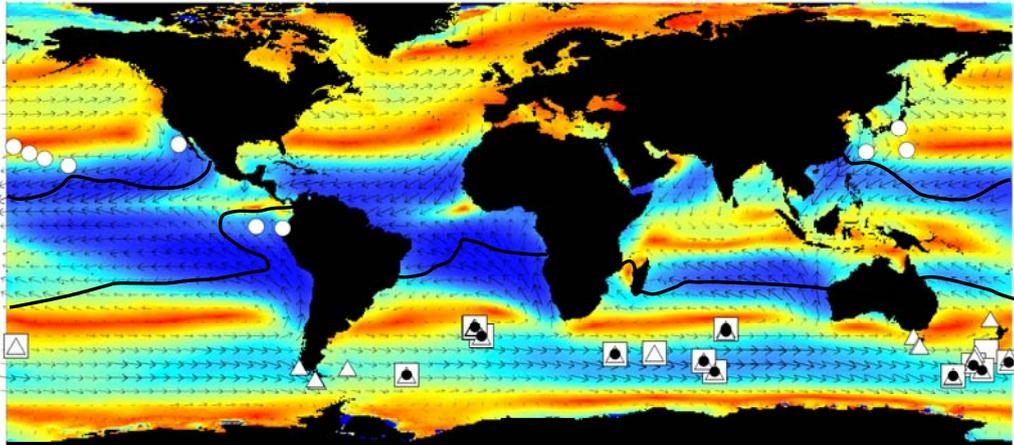
Furthermore, although penguins and pinnipeds may be able to increase their travel speed somewhat by exploiting favourable currents (Campagna et al. 2006, Cotte et al. 2007), wind speeds are an order of magnitude greater than those of ocean currents, allowing albatrosses greater scope for flight speed regulation. For example, a grey-headed albatross has been tracked not only travelling but successfully locating prey at mean speeds in excess of 30 m/s (110 km/h) in downwind flight (Catry et al. 2004a). As shown in Chapter 4, albatross flight speeds are linearly related to the wind speed in the direction of flight. The energetic cost of flight is also related to the relative wind direction and hence can be reduced by flying downwind (Weimerskirch et al. 2000b). For these reasons, at macro to megascales, albatrosses take advantage of prevailing winds to conduct long looping cross or downwind foraging flights (Jouventin & Weimerskirch 1990, Weimerskirch et al. 2000b). This strategy is most characteristic of wandering albatrosses, whose ground speeds are more affected by the wind than in smaller species (Chapter 4).

Although soaring flight is advantageous in terms of time and energy cost minimisation, reliance by albatrosses on this mode of travel may also place them under a number of constraints. Firstly, aerodynamic theory predicts that wind speeds in excess of 5 m/s are required to sustain dynamic or gust soaring flight (Pennycuick 2002, Sachs 2005), and empirical data show that below 4 m/s, albatrosses fly predominantly by flap-gliding (Pennycuick 1982), which is energetically more costly. It is also thought that albatrosses find it very energetically demanding to take off in light winds (Weimerskirch et al. 2000b, Sato et al. 2008). As such, it may be impracticable for them to forage in areas with light winds, especially if there is a risk of becoming becalmed (Spruzen & Woehler 2002), with implications for the capacity to complete foraging trips within acceptable time limits. It is likely that this explains why breeding albatrosses forage infrequently in subtropical latitudes (Fig. 5.3), which are subject to persistent high pressure and are thus dominated by light (2 - 3 m/s) winds (Fig. 5.2). Indeed, it has frequently been suggested that their reliance on the wind means that albatrosses are unable to cross the doldrums (Tickell 2000), and it is notable in this respect that of the procellariiformes, only smaller flap-gliding species undertake trans-equatorial migrations (Shaffer et al. 2006, Felicísimo et al. 2008, Guilford et al. 2009).

The second potential constraint arises as a consequence of stronger winds: If there were no variability in wind direction, the relationship between wind speed and groundspeed shown in Chapter 4 implies that albatrosses foraging from a colony could maximise overall trip speed by visiting locations in a direction perpendicular to the prevailing wind. However, if, as seems likely, their flight performance declines during foraging trips as they gain weight, it would be more energetically efficient to forage upwind of the colony (i.e. the additional speed increment would be lent by the wind on the return leg of the journey (Chapter 4 and Pennycuick (2002))).

Although these factors may account in part for the foraging distributions of breeding albatrosses, which tend on the whole to lie either upwind or across the wind from colonies (Fig. 5.3), wind direction in areas surrounding colonies are in fact relatively variable (Figs. 5.1 and 5.3). This in itself may reflect a further constraint. Variability in wind direction may be necessary to allow sufficient flexibility to commute to different areas in response to spatiotemporal variability in prey occurrence, or to conduct looping trips over wider areas. In the extreme, albatrosses may be precluded from breeding in areas with strong and very directionally invariant winds, both because of the high energetic cost of foraging upwind of the colony or, conversely, the high cost of return if they stray downwind. This is somewhat at odds with the commonly held view that the areas inhabited by albatrosses, such as the Southern Ocean, are characterised by strong and persistent winds. However, in global terms, the winds of the Southern Ocean, as well as those of other areas in which albatross colonies are located, are quite variable (mean resultant length of wind direction 0.2 – 0.6, Figs. 5.1 and 5.3). Furthermore, with one exception (waved albatrosses), no albatross colonies are located in the subtropical trade wind zones, in which strong (~ 6 m/s) and directionally very invariant (Mean Resultant Length ~ 0.8 – 1.0) winds are incident for much of the time. As such, it may be the adaptation of albatrosses to strong but variable wind regimes that has precluded them from breeding in the North Atlantic in modern times. This hypothesis could be tested by examining changes in the wind regime between the late Tertiary, when albatrosses bred in the North Atlantic (Olson & Hearty 2003, Dyke et al. 2007), and the present day.

(a)



(b)

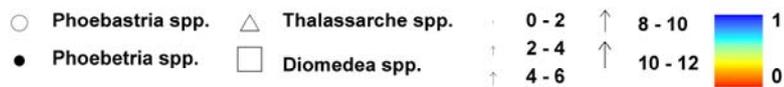
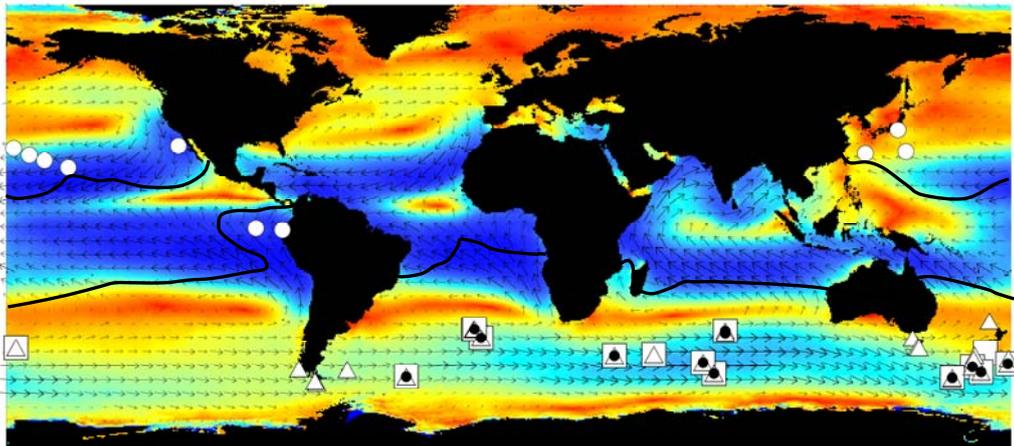


Figure 5.3. Global wind climate during the (a) austral summer, and (b) austral winter, showing all breeding locations of the four albatross genera. Arrows show 9 yr average wind speed (m/s), and colours the *mean resultant length* of wind direction (0 = high variability, 1 = low variability). Black lines indicate approximate range limits of birds from the southern and northern hemisphere during breeding (BirdLife-International 2004). Albatrosses are largely absent from the equatorial Pacific, N Atlantic and N Indian Ocean. Wind climatology based on monthly QuickSCAT satellite scatterometer data for the period 1999-2007, obtained from CERSAT, at IFREMER, Plouzané (France).

5.4 Conservation implications

The global expansion of longline and trawl fishing over the past thirty years has resulted in large and unsustainable rates of albatross bycatch (Brothers 1991, Croxall & Gales 1998, Gales et al. 1998, Tuck et al. 2003, Sullivan et al. 2006), such that eighteen of the twenty-two species of albatross are classified as threatened (IUCN 2009, Appendix 4). From a conservation perspective, the ability to estimate their distribution at sea and thus to identify areas of potential conflict with fisheries is therefore at a premium. The spatial modelling techniques applied in Chapter 2, which allow this to be achieved using tracking and remotely sensed environmental data, could therefore be usefully applied more widely by seabird conservationists. For example, despite some uncertainties, the estimates of spatial usage indicate that the vast majority of the world's black-browed albatrosses are concentrated during the breeding season on the Patagonian Shelf, Southern Chilean continental shelf and in the Humboldt Current Upwelling (Fig. 2.7), whereas tracking data alone give a view of spatial usage that is biased by variable tagging effort. These highly productive areas support large trawl and longline fisheries, which are responsible for unsustainable levels of black-browed albatross bycatch (Croxall & Gales 1998, Sullivan et al. 2006). To date, although considerable efforts have been made to put bycatch mitigation measures in place on the Patagonian Shelf, less attention has been paid to Chilean waters, which hold large numbers of BBA throughout the year (Moreno et al. 2006). Efforts to reduce the bycatch of this endangered species should therefore include both areas as a priority.

The findings presented in Chapter 3, that black-browed albatross populations are regulated by food availability during the breeding season suggest that the carrying capacity of this and, by inference, other threatened species may be predictable. This would necessitate modelling population size as a function of available prey biomass, which may be predictable using ecosystem models (Jennings et al. 2008), as well as accessibility and other limiting factors such as nesting habitat availability. From a conservation perspective, knowledge of the theoretical carrying capacity of threatened species is very useful in that it allows anthropogenic impacts to be detected and assessed objectively (Pastor et al. 1997). This may be particularly useful in determining whether population changes are due to bycatch or climatic fluctuations,

mediated through changes in the availability of lower trophic level prey (Croxall et al. 2002, Pinaud & Weimerskirch 2002, Nevoux et al. 2007, Rolland et al. 2008).

Similarly, an understanding of the constraints placed on albatrosses by their reliance on gliding flight may be crucial in assessing how populations will respond to changes in the global wind regime. These are predicted to be substantial in the coming decades because of human-induced climate change, particularly in the subantarctic, where the expectation is that winds will become stronger and less variable (Shindell & Schmidt 2004, IPCC 2007, Bracegirdle et al. 2008, Suryan et al. 2008).

5.5 Future directions

During the course of this project a number of interesting questions have arisen that I have been unable to address, either because of a lack of time, data or appropriate analytical techniques. This thesis ends therefore with a brief overview of the ways in which spatial modelling may be used in coming years to develop some of the themes covered during this project.

Over the past 25 years, tracking technology has greatly advanced our understanding of the interactions between pelagic seabirds and their environment (Wilson et al. 2002, Burger and Shaffer 2008, Phillips et al. 2008). Although the habitat use of many species has been described and quantified, to date this and only one other tracking study (Pinaud et al. 2005) have formally compared habitat usage to availability and thus quantified habitat preference. In part, this has been due to a lack of statistical methods for treating individual movement data that non-specialists are able to implement. I suggest that this is no longer an impediment and that tracking data from pelagic seabirds can be used to address a wider range of ecological questions. For example, as I have shown, by quantifying the effects of habitat preference and accessibility on spatial usage, the effects on populations of central place constraint and competition can be better understood. Ultimately, this kind of approach may allow the prediction of carrying capacities for pelagic seabird populations (Beck et al. 2006, Jennings et al. 2008). At present, it is feasible to implement models at the population level using empirical, Eulerian approaches such as GLMs and GAMs (Moorcroft &

Barnett 2008). Although it is possible to account for individual variation and serial autocorrelation using a mixed-effects framework with an autoregressive structure (Pinheiro & Bates 2000, Wood 2006), analyses of fewer data from many animals are more powerful than those of many data from a few animals, even if this makes data collection logistically more demanding.

Individual-level SSMs are advancing rapidly (Patterson & Fraser 2000, Schick et al. 2008). SSMs are particularly useful for analyzing geolocator data, which are prone to large errors, and may exploit the behavioural information inherent in individual movement data more fully. The inference of behavioural states, such as ARS, based on theoretical predictions of animal movement should also be validated more directly, e.g. by using auxiliary loggers to indicate when albatrosses actually ingest prey (Cтры et al. 2004b, Austin et al. 2006, Weimerskirch et al. 2007). Such studies would greatly enhance the utility of high temporal resolution data collected using GPS loggers, which are increasingly replacing PTTs as the tracking instrument of choice.

To date, the majority of tracking studies of pelagic seabirds have concentrated on large species during breeding. The continued miniaturization of tracking devices, and particularly geolocators, means that very small, and hitherto little-known species such as the storm petrels (*Hydrobatidae*), may soon be targeted. Annual and multi-year deployments of geolocators and even GPS units are already garnering data on non-breeding and immature birds, which may represent up to half of the total number of some species (Shaffer et al. 2006, Weimerskirch et al. 2006a, Bugoni et al. 2009). Differences in habitat use have been detected between species (González-Solis et al. 2000a, Phillips et al. 2004b, Pinaud & Weimerskirch 2007, Chapter 2), breeding stages (Weimerskirch et al. 1993, Phillips et al. 2004b, Chapter 2), sexes (González-Solis et al. 2000b, Phillips et al. 2004b, Weimerskirch et al. 2006b) and age groups (Weimerskirch et al. 2006a). Hence, it would be informative to include individual characteristics in habitat preference models (Aarts et al. 2008). Similarly, as habitat use may vary interannually (Xavier et al. 2003, Pinaud et al. 2005), and between

populations (Chapter 2), potential plasticity in habitat preferences should be considered and if possible incorporated into analyses before drawing far-reaching conclusions.

Although the response of albatrosses to certain phenomena, such as small-scale turbulence and long-term climate fluctuations, are not presently detectable, improvements in tracking and remote-sensing technologies are widening the observable window on pelagic habitats (Fig. 1.1). Responses to shorter-term climate fluctuations may soon be measurable, e.g. ENSO events, and even regime shifts, limited mainly by the number of years of repeated tracking of birds from the same population. Most studies on albatrosses to date have combined satellite tracking with medium resolution environmental data (e.g. SST, chl-a, SSHa) to examine habitat preferences at scales of days to weeks, and 100s to 10000s of km. At macro to mega scales, pelagic areas of higher than average productivity are recognized as hotspots for higher predator abundance (Worm et al. 2005), and there is increasing evidence for definable habitat preferences at the mesoscale (e.g. for eddies, upwelling and shelfbreak fronts). At finer scales, it has been contended that the distribution of albatrosses is uncoupled from the underlying physical structure of their environment (Pinaud & Weimerskirch 2005). However, ship-based studies often find that seabirds aggregate at fine to coarse-scale features, including fronts (e.g. Hunt 1991, Skov & Prins 2001). Such associations may not have been apparent in tracking studies simply because the resolution of tracking and remotely-sensed environmental data were hitherto insufficient. However, at coarse scales, Synthetic Aperture Radar imagery now reveals processes not observable using conventional remote sensing techniques. Furthermore, the mixed layer depth can now be predicted with remotely sensed data (Zawada et al. 2005), and further investigations of its influence on habitat use would be profitable (Spear et al. 2001, Vilchis et al. 2006). Finally, although the influence of wind on the distribution and behaviour of albatrosses is widely acknowledged (Airy 1883, Pennycuick 1987, Weimerskirch et al. 2000b, Suryan et al. 2008), the mechanisms of soaring flight, and the implications for foraging of a reliance on wind during trips from a central place remain poorly understood (Pennycuick 2002).

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Appendix 1. Black-browed albatross colony size estimates

No	Region† & colony	Pairs	Lat	Lon	Year	Method‡
1	CH, Is. Diego de Almagro	15,594	51° 25.08' S	75° 12.23' W	2001	A (Lawton et al. 2003)
2	CH, Is. Evangelistas	4,669	52° 22.80' S	75° 04.80' W	2002	A (Arata et al. 2003)
3	CH, Is. Leonard	594	53° 22.80' S	74° 04.20' W	2004	A, B (Martin & Oehler 2006)
4	CH, Is. Ildefonso	47,000	55° 44.18' S	69° 25.63' W	2002	A, B (Robertson et al. 2008)
5	CH, Is. Albatros	50	54° 27.00' S	69° 01.00' W	2002	A, B (Aguayo et al. 2003)
6	CH, Is. Diego Ramirez	55,000	56° 31.00' S	68° 43.00' W	2001	A, B (Robertson et al. 2007)
7	FK, New Is.	10,191	51° 42.92' S	61° 18.49' W	2000	A, B (Huin & Reid 2006)
8	FK, North Is.	17,737	51° 39.38' S	61° 13.80' W	2000	C (Huin & Reid 2006)
9	FK, Steeple Jason Is.	189,427	51° 01.97' S	61° 13.19' W	2000	C, D (Huin & Reid 2006)
10	FK, Grand Jason Is.	52,279	51° 03.42' S	61° 05.70' W	2000	C, D (Huin & Reid 2006)
11	FK, Bird Is.	10,189	52° 10.22' S	60° 55.45' W	2000	C (Huin & Reid 2006)
12	FK, South Jason Is.	1,745	51° 12.40' S	60° 53.26' W	2000	C (Huin & Reid 2006)
13	FK, Elephant Jason Is.	1,699	51° 09.88' S	60° 50.85' W	2000	A, B (Huin & Reid 2006)
14	FK, West Point Is.	14,561	51° 21.02' S	60° 43.56' W	2000	A, B (Huin & Reid 2006)
15	FK, Grave Cove	226	51° 23.57' S	60° 38.71' W	2000	A, B (Huin & Reid 2006)
16	FK, Saunders Is.	11,004	51° 19.02' S	60° 13.46' W	2000	C (Huin & Reid 2006)
17	FK, Keppel Is.	1869	51° 19.33' S	59° 57.94' W	2000	C (Huin & Reid 2006)
18	FK, Beauchêne Is.	103,341	52° 53.18' S	59° 12.22' W	2000	C, D (Huin & Reid 2006)

						2006)
19	SG, Main Is., Willis Is.	14,559	54° 00.63' S	38° 12.50' W	2003	A, E (Poncet et al. 2006)
20	SG, Trinity Is., Willis Is.	13,960	54° 00.08' S	38° 10.10' W	2003	A, E (Poncet et al. 2006)
21	SG, Bird Is.	8,264	54° 00.33' S	38° 02.66' W	2003	C (Poncet et al. 2006)
22	SG, Paryadin Pen. N.	3,789	54° 04.33' S	38° 00.58' W	2003	A, E (Poncet et al. 2006)
23	SG, Paryadin Pen. S.	1,428	54° 00.65' S	37° 59.98' W	2003	A, E (Poncet et al. 2006)
24	SG, Sorn & Bernt Coasts	74	53° 59.95' S	37° 54.20' W	2003	A, E (Poncet et al. 2006)
25	SG, Cape North	1,546	53° 58.80' S	37° 43.36' W	2003	A, E (Poncet et al. 2006)
26	SG, Kluschak Pt.	784	54° 10.52' S	37° 40.84' W	2003	A, E (Poncet et al. 2006)
27	SG, Welcome Is.	188	53° 58.18' S	37° 29.02' W	2003	A, E (Poncet et al. 2006)
28	SG, Cape Nunez	981	54° 16.00' S	37° 25.28' W	2003	A, E (Poncet et al. 2006)
29	SG, Sheathbill Bay	481	53° 59.42' S	37° 24.58' W	2003	A, E (Poncet et al. 2006)
30	SG, Sitka Bay	816	53° 59.42' S	37° 23.07' W	2003	A, E (Poncet et al. 2006)
31	SG, Cape Buller	177	53° 59.78' S	37° 22.31' W	2003	A, E (Poncet et al. 2006)
32	SG, Cape Wilson	205	54° 02.70' S	37° 10.17' W	2003	A, E (Poncet et al. 2006)
33	SG, Cape Crewe	42	54° 02.83' S	37° 08.00' W	2003	A, E(Poncet et al. 2006)
34	SG, Annekov Is.	9,398	54° 29.57' S	37° 04.43' W	2003	A, E (Poncet et al. 2006)
35	SG, Green Is.	3,404	54° 53.73' S	36° 05.99' W	2003	A, E (Poncet et al. 2006)
36	SG, Rumbolds Pt.	2,340	54° 52.92' S	35° 58.72' W	2003	A, E (Poncet et al. 2006)
37	SG, Cooper Is.	10,606	54° 48.83' S	35° 47.32' W	2003	A, E (Poncet et al. 2006)

38	SG, Clerke Rocks	1,254	55° 01.00' S	34° 41.00' W	2003	A, E (Poncet et al. 2006)
39	IO, Île des Pingouins	300	46° 24.80' S	50° 24.93' E	2006	F*
40	IO, Îlots des Apôtres	330	45° 56.97' S	50° 26.01' E	2006	F*
41	IO, Île de l'Est	350	46° 25.25' S	52° 13.92' E	2006	F*
42	IO, Îles Nuageuses	1,350	48° 38.05' S	68° 39.12' E	2006	F*
43	IO, Jeanne d'Arc Pen.	2,000	49° 40.52' S	70° 09.33' E	2006	C*
44	IO, Heard Is.**	600	53° 03.68' S	73° 29.50' E	2000	A (Woehler et al. 2002)
45	AU, Bishop & Clerk Is.	141	55° 06.00' S	158° 41.00' E	1993	C (Gales 1998)
46	AU, Macquarie Is.	46	54° 45.60' S	158° 46.80' E	1995	C (Gales 1998)
47	AU, Snares Is.	1	48° 12.00' S	163° 30.00' E	1986	C(Miskelly et al. 2001)
48	AU, Bollons Is.	115	49° 38.65' S	178° 49.20' E	1994	A, B (Tennyson et al. 1998)
49	AU, Campbell Is.***	>30	52° 33.00' S	169° 09.00' E	1995	B (Gales 1998)

† CH, Chile; FK, Falkland Is.; SG, South Georgia; IO, Indian Ocean; AU, Australasian region.

‡ Census methods (for further details, see references): A, photographic; B partial direct count; C, direct count; D, density estimation; E, model based correction; F, estimate. All colonies were censused during incubation, except #5 which was visited during brood-guard.

* H. Weimerskirch, pers. com.

** MacDonald Is. held ~ 90 pairs in 1981 but is subject to severe volcanic activity and so current population size is unknown.

*** *D. melanophrys* breeds sympatrically with *D. impavida* on Campbell Is. Given the morphological similarity and some level of hybridisation between the two species, the number of *D. melanohphrys* at that site is unknown.

Appendix 2. Grouping of black-browed albatross colonies into super-colonies

Col. no.	Region [†] & colony	Super-colony, colonies grouped such that max. $d_{\text{sep}} \leq$				
		50 km	100 km	200 km	400 km	800 km
1	CH, Is. Diego de Almagro	1	1	1	1	1
2	CH, Is. Evangelistas	2	2	1	1	1
3	CH, Is. Leonard	3	3	2	1	1
4	CH, Is. Ildefonso	4	4	3	2	1
5	CH, Is. Albatros	5	5	4	3	1
6	CH, Is. Diego Ramirez	6	4	3	2	1
7	FK, New Is.	7	6	5	4	2
8	FK, North Is.	7	6	5	4	2
9	FK, Steeple Jason Is.	8	7	5	4	2
10	FK, Grand Jason Is.	8	7	5	4	2
11	FK, Bird Is.	9	6	5	4	2
12	FK, South Jason Is.	10	7	5	4	2
13	FK, Elephant Jason Is.	10	7	5	4	2
14	FK, West Point Is.	10	7	5	4	2
15	FK, Grave Cove	10	7	5	4	2
16	FK, Saunders Is.	11	7	5	4	2
17	FK, Keppel Is.	11	7	5	4	2
18	FK, Beauchêne Is.	12	8	6	4	2
19	SG, Main Is., Willis Is.	13	9	7	5	3
20	SG, Trinity Is., Willis Is.	13	9	7	5	3
21	SG, Bird Is.	13	9	7	5	3
22	SG, Paryadin Pen. N.	13	9	7	5	3
23	SG, Paryadin Pen. S.	13	9	7	5	3
24	SG, Sorn & Bernt Coasts	13	9	7	5	3
25	SG, Cape North	13	9	7	5	3

26	SG, Kluschak Pt.	14	10	7	5	3
27	SG, Welcome Is.	15	9	7	5	3
28	SG, Cape Nunez	14	10	7	5	3
29	SG, Sheathbill Bay	15	9	7	5	3
30	SG, Sitka Bay	15	9	7	5	3
31	SG, Cape Buller	15	9	7	5	3
32	SG, Cape Wilson	15	9	7	5	3
33	SG, Cape Crewe	15	9	7	5	3
34	SG, Annekov Is.	16	10	7	5	3
35	SG, Green Is.	17	11	8	5	3
36	SG, Rumbolds Pt.	17	11	8	5	3
37	SG, Cooper Is.	17	11	8	5	3
38	SG, Clerke Rocks	18	11	8	5	3
39	IO, Île des Pingouins	19	12	9	6	4
40	IO, Îlots des Apôtres	20	12	9	6	4
41	IO, Île de l'Est	21	13	9	6	4
42	IO, Îles Nuageuses	22	14	10	7	5
43	IO, Jeanne d'Arc Pen.	23	15	10	7	5
44	IO, Heard Is.	24	16	11	8	5
45	AU, Bishop & Clerk Is.	25	17	12	9	6
46	AU, Macquarie Is.	25	17	12	9	6
47	AU, Snares Is.	26	18	13	10	7
48	AU, Bollons Is.	27	19	14	11	8
49‡	AU, Campbell Is.	na	na	na	na	na

† CH, Chile; FK, Falkland Is.; SG, South Georgia; IO, Indian Ocean; AU, Australasian region

‡ Campbell Is. was not included in the analysis (see footnote to Appendix 1).

**Appendix 3. Morphometric and aerodynamic parameters
used to estimate theoretical flight performance with
Flight Version 1.17 software.**

Parameter	<i>D. exulans</i>		<i>T. melanophrys</i>		<i>T. chrysostoma</i>		<i>P. palpebrata</i>
mean (sd)	m	f	m	f	m	f	u
n	20	16	18	14	19	13	10
Body mass (kg)	9.440 (0.59)	7.840 (0.62)	3.665 (0.30)	3.048 (0.17)	3.516 (0.25)	3.065 (0.18)	2.555 (0.30)
Wing span (m)	3.11 (0.04)	2.99 (0.05)	2.28 (0.05)	2.21 (0.03)	2.21 (0.04)	2.16 (0.06)	2.06 (0.040)
Wing area (m ²)	0.63 (0.03)	0.59 (0.02)	0.39 (0.15)	0.37 (0.09)	0.36 (0.01)	0.34 (0.01)	0.30 (0.00)
Body frontal area (m ²)	0.062 (0.000)	0.054 (0.000)	0.026 (0.001)	0.023 (0.001)	0.025 (0.001)	0.023 (0.001)	0.022 (0.001)
Location measured	Crozet				Bird Island		
Reference	(Shaffer et al. 2001)		(Phillips et al. 2004)			BAS unpub. data	
Crop mass (kg)	0	0	0	0	0	0	0
Air density (kg m ⁻³)	1.22	1.22	1.22	1.22	1.22	1.22	1.22
Altitude asl (m)	43	43	43	43	43	43	43
Gravity ms ⁻²)	9.81	9.81	9.81	9.81	9.81	9.81	9.81

Appendix 4. Conservation status of the world's albatrosses.

Species	Population (individuals)	Population trend	Status†
Waved albatross <i>Phoebastria irrorata</i>	35,000	Decreasing	Critically Endangered
Short-tailed albatross <i>Phoebastria albatrus</i>	2,200 - 2,500	Increasing	Vulnerable
Black-footed albatross <i>Phoebastria nigripes</i>	120,000	Decreasing	Endangered
Laysan albatross <i>Phoebastria immutabilis</i>	1,200,000	Decreasing	Vulnerable
Wandering albatross <i>Diomedea exulans</i>	26,000	Decreasing	Vulnerable
Antipodean albatross <i>Diomedea antipodensis</i>	25,000	Decreasing	Vulnerable
Amsterdam albatross <i>Diomedea amsterdamensis</i>	80	Decreasing	Critically Endangered
Tristan albatross <i>Diomedea dabbenena</i>	9,000 - 15,000	Decreasing	Critically Endangered
Northern royal albatross <i>Diomedea sanfordi</i>	17,000	Decreasing	Endangered
Southern royal albatross <i>Diomedea epomophora</i>	28,000 - 29,500	Stable	Vulnerable
Sooty albatross <i>Phoebastria fusca</i>	42,000	Decreasing	Endangered
Light-mantled albatross <i>Phoebastria palpebrata</i>	58,000	Decreasing	Near Threatened
Black-browed albatross <i>Thalassarche melanophrys</i>	1,200,000	Decreasing	Endangered
Campbell albatross <i>Thalassarche impavida</i>	49,000	Increasing	Vulnerable
Shy albatross	26,000	Unknown	Near

<i>Thalassarche cauta</i>			Threatened
White-capped albatross <i>Thalassarche steadi</i>	100,000- 499,999	Unknown	Near Threatened
Chatham albatross <i>Thalassarche eremita</i>	11,000	Stable	Critically Endangered
Salvin's albatross <i>Thalassarche salvini</i>	62,000	Unknown	Vulnerable
Grey-headed albatross <i>Thalassarche chrysostoma</i>	250,000	Decreasing	Vulnerable
Atlantic yellow-nosed albatross <i>Thalassarche chlororhynchos</i>	55,000 - 83,200	Decreasing	Endangered
Indian yellow-nosed albatross <i>Thalassarche carteri</i>	65,000	Decreasing	Endangered
Buller's albatross <i>Thalassarche bulleri</i>	64,000	Stable	Near Threatened

† from IUCN (2009)

Appendix 5. Reprints of papers in press.

1. Wakefield E.D., Phillips R.A. and Matthiopoulos J. (2009) Quantifying the habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series*. 391: 165-182.
2. Wakefield E.D., Phillips R.A., Matthiopoulos J., Fukuda A., Higuchi H., Marshall G.J. and Trathan P. (in press) Wind field and sex constrain the flight speeds of central place foraging albatrosses. *Ecological Monographs*.