

THEME SECTION

Spatiotemporal dynamics of seabirds in the marine environment

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Introduction and synthesis: spatial ecology of seabirds at sea

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ABSTRACT: The spatial ecology of seabirds has greater precedence today than ever before because of impacts on the marine environment from human exploitation, pollution, and climate change. Specific life history traits make seabirds particularly sensitive to these impacts, currently driving many species to unsustainable population declines. To evaluate the risk posed by human activities, we need integrative studies on seabird abundance, distributions, and movements in relation to the biophysical marine environment. Also interpreting the limits of these relationships is fundamental to understanding historical constraints and behavioural adaptations of seabirds that are shaped by evolutionary processes. In this Theme Section, we assembled 4 review papers and 10 case studies that highlight some of the latest techniques to study seabird spatial ecology. This includes the application of tracking tags, ship-based surveys, and remotely sensed environmental data, to characterize seabird movement patterns, fine scale behaviour, and overall distribution combined with measures of the oceanic habitats to enhance our understanding of the functional role that seabirds play. Overall, this knowledge is crucial for understanding and predicting the impacts that fisheries, climate change and pollution are exerting on marine ecosystems and will provide opportunities for developing marine protected areas, conservation action plans and species management.

KEY WORDS: Ecosystems · Impacts · Marine · Seabirds · Spatiotemporal dynamics · Tracking

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IMPACTS ON MARINE ENVIRONMENT

Human pressure on marine ecosystems has increased enormously over the last several decades (Halpern et al. 2008). This pressure takes many forms, such as massive fishery activities, incidental entanglement in fishing gear by non-target species, episodic and chronic contamination, and ingestion of harmful plastics. Climate change is also beginning to show measurable effects on marine ecosystems, particularly at high latitudes.

As a result, human activities on the marine environment are directly responsible for the deaths of hundreds of thousands of marine predators worldwide each year. Apical species are particularly sensitive to these impacts and may show non-linear responses in the form of sharp unexpected collapses in their populations. Among marine vertebrates, seabirds (comprised of nearly 400 species) are particularly vulnerable because most species are top marine predators that exhibit high adult survival, but low annual fecundity

and slow population growth overall (Ricklefs 1990). Since many impacts increase adult mortality, seabirds, particularly pelagic species, have become threatened at a faster rate globally than all other groups of birds (BirdLife International; www.birdlife.org/worldwide/index.html). Currently about 30% of pelagic species are threatened with unsustainable population declines, e.g. the extinction of the Balearic shearwater is modelled to take place in 40 yr if the impact of long-lining on adult mortality is not minimized (Oro et al. 2004).

Understanding spatiotemporal dynamics in seabirds at sea is critical to identify and manage seabird responses to human-induced or climate-related changes on marine ecosystems. Moreover, it is not just a matter of identifying and describing seabird and biophysical patterns, but also there is an urgent need to understand the specific physical and biological processes that contribute to the dynamic nature of these patterns. This task is particularly difficult to elucidate because seabirds have impressive mobility, unparal-

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leled among marine predators. They can easily move hundreds, thousands, or tens of thousands of kilometres in a matter of hours, days or weeks, respectively. Therefore, integrating a spatial component to the study of interactions between seabirds and the marine ecosystem is particularly relevant and greatly needed.

Technological advances have greatly improved our ability to concurrently examine the movements of free-ranging seabirds and the marine environment at relevant spatial and temporal scales, in ways never dreamed possible even a few years ago. These advances are typified by (1) an incessant miniaturization of electronic tags to monitor seabird movements, distributions, and activity; (2) improvements and standardization of methods to survey seabirds and their prey at sea; and (3) global coverage of remotely-sensed oceanographic features to characterize marine habitat. Integrative approaches are also facilitated by greater computational resources for modelling interactions between seabirds and oceanographic traits, fishing activity, and contamination in a geospatial environment. Consequently, we assembled this Theme Section by bringing together 4 reviews and 10 case studies that clearly integrate these advances to enhance our understanding of the different patterns and processes related to the dynamics in seabirds at sea.

SYNOPSIS OF THEME SECTION

Across broad scales, biological and physical characteristics of the ocean define the potential habitats of seabirds. Since these traits can change over seasons or years, understanding the spatial dynamics in seabirds requires detailed ecologically-based studies on seabird abundances, distributions, and movements in relation to the biophysical marine environment (Catry et al. 2009, Garthe et al. 2009, González-Solís et al. 2009, Kubetzki et al. 2009, Louzao et al. 2009, Phillips et al. 2009, Shaffer et al. 2009, Weimerskirch et al. 2009, all this Theme Section). However, this knowledge is also essential for understanding the effects that climate change is exerting on the spatial ecology of seabirds. Climate is a major driver of biophysical coupling in the ocean and has significant impacts on marine productivity, environmental stochasticity and cyclicity. Physical forcing and bottom-up processes ultimately change prey availability and distribution and can, therefore, induce spatial changes in marine predators. However, rapid modifications may lead to ecosystem instability because not all food-web components respond in the same manner to environmental change, resulting in a spatiotemporal match-mismatch of predators (i.e. seabirds) and their prey (reviewed in Grémillet & Boulinier 2009, this Theme Section).

Beyond the biophysical environment, historical constraints and behavioural adaptations remind us of the evolutionary processes that underlie all aspects of spatial ecology. One major process producing complex spatial patterns is the interaction between seabirds and their prey. Despite its superficial homogeneity, the sea is a heterogeneous environment where prey is patchily distributed in a hierarchical organization. We would expect seabirds to track their prey by closely matching the spatial and temporal dynamics in prey. However, spatial constraints between predators and their prey and behavioural responses of the predatory interactions make these relationships more elusive than expected (reviewed in Fauchald 2009, this Theme Section). Seabirds can be spatially constrained by past and present competition promoting resource partitioning among species. In some circumstances this process can even shape the spatial segregation between males and females at intraspecific levels (Weimerskirch et al. 2009). The fundamental spatial constraint for all seabirds, however, arises from the need to breed on land but also in areas more or less inaccessible to terrestrial predators. This double condition has confined many pelagic seabirds to breed on remote oceanic islands often far from the best feeding grounds, thus promoting the emergence of specific morphological adaptations as well as behavioural strategies that enhance energetic efficiency while breeding. For example, many pelagic seabirds alternate short foraging trips to maximize energy delivery to the chick with long foraging trips to restore their own reserves (Weimerskirch et al. 1994). However, strategies can vary among species and populations, and this needs to be studied in depth before making any generalities about a particular strategy (Phillips et al. 2009).

Currently, the greatest source of competition for seabirds is human fishing activity. Seabirds and fisheries often exploit similar resources at similar spatiotemporal scales, overlapping particularly on most continental shelves worldwide (Karpouzi et al. 2007). Although seabirds are sometimes dismissed as a component of the marine ecosystem, at least 15 species have more than 10 million individuals, which equates to a huge biomass that consumes about 100 Mt of marine prey annually (Brooke 2004). This value represents about 10% of global marine productivity and is close to the overall fishery extraction. However, seabirds exploit marine prey in a sustainable way, whereas fisheries have already overexploited two-thirds of the world's fish stocks (Worm et al. 2009). Overexploitation of marine resources can collapse stocks of seabird prey and drive seabird populations to starvation, exacerbating the effects of climate change, which also purportedly will affect the distribution and abundance of forage fish (reviewed in Grémillet &

Boulinier 2009). Furthermore, some fishery types, such as longlining, are responsible for the direct death of more than a hundred thousand seabirds each year (BirdLife International). Therefore, assessing the spatial overlap between seabirds and fisheries is a critical step for understanding their potential interactions (Pichegru et al. 2009, this Theme Section).

Despite the enormous potential of tracking technology, some limitations and biases make biogeochemically intrinsic markers an excellent complement to study the feeding ecology and spatial dynamics in seabirds (Weimerskirch et al. 2009). Stable isotope or elemental analyses of seabird tissues have emerged as a powerful and sometimes unique alternative, in particular to study species that cannot be tracked because of size limitations or accessibility. It is now possible to use geographic gradients or water mass-specific signatures as tools for determining foraging habitats in the marine environment (Ramos et al. 2009). However, the lack of a detailed spatial knowledge of baseline isotope variations hampers our understanding of the isotopic dynamics. In this context, compound-specific isotopic analyses (CSIA) of trophic versus source amino acids provide a new tool to track isotopic baseline levels, which is also critical for a better understanding of the feeding ecology of seabirds (Lorrain et al. 2009, this Theme Section).

Describing and quantifying the association between seabirds and the marine habitat is also essential to model spatial patterns and predict responses of seabirds to the environment. However, this is not an easy task because new scientific approaches and methodological tools to collect and analyse spatial data are evolving rapidly (reviewed by Tremblay et al. 2009, this Theme Section). For example, oceanic features can now be inferred from the remotely-sensed biophysical traits of the water masses, allowing for more process-based, rather than descriptive, approaches. Moreover, collection of particle-like data (Lagrangian) such as that obtained from tracking devices is increasing compared to the more traditional grid-like data (Eulerian) based on ship surveys. Without question, tracking studies provide opportunities to study individual behaviour from birds of known origin and status. Most importantly, the detection of specific foraging behaviours (e.g. travel speeds, turn angles, etc.) associated with particular environmental traits or feeding events, open new opportunities for understanding seabird spatial ecology as well as identifying key foraging grounds. Although non-independence of tracking data is challenging, new statistical methods are now capable of dealing with these problems (reviewed in Wakefield et al. 2009, this Theme Section). Seabird surveys from vessels, however, provide a more integrative multispecies approach from a large scale perspective.

Clearly, the 2 approaches can yield complementary perspectives on habitat use and suitability, calling for more integrative studies to identify key marine areas for management and conservation purposes (e.g. Louzao et al. 2009). Obviously, a major goal of studying the spatial ecology of seabirds is the contribution made toward identifying important bird areas and to help designate marine protected areas (Garthe et al. 2009, Grémillet & Boulinier 2009, Louzao et al. 2009). However, this process is far more complicated at sea than in terrestrial environments because both risk exposure and key areas are more variable in distribution, time, and extent with changing human activities and biophysical traits of the marine ecosystem.

SUMMARY AND CONCLUSIONS

In summary, the assemblage of contributions provided in this Theme Section demonstrate that it is now possible to integrate spatial and temporal aspects into the study of seabirds at sea more rigorously than ever before. While this integration is not always straightforward, it has substantially enhanced our understanding of complex ecological relationships in general as well as of the risks posed to seabirds at sea. Overall, this knowledge will be crucial for predicting the impacts that fisheries, climate change and pollution are exerting on marine ecosystems, since we now have the first clear signs that spatial dynamics in seabirds at sea are being affected. Therefore, incorporating this knowledge into the management of marine ecosystems will facilitate effective conservation of seabird populations and help preserve their marine habitat and its biodiversity.

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Spatial ecology and conservation of seabirds facing global climate change: a review

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ABSTRACT: In this review we detail the impact of climate change on marine productivity, on marine environmental stochasticity and cyclicity, and on the spatio-temporal match–mismatch of seabirds and their prey. We thereby show that global warming has a profound bottom-up impact upon marine top-predators, but that such effects have to be studied in conjunction with the (top-down) impact of human fisheries upon seabird food resources. Further, we propose seabird ecological features, such as memory effects and social constraints, that make them particularly sensitive to rapid environmental change. We provide examples of how seabirds may nonetheless adapt when facing the consequences of climate change. We conclude that our understanding of the spatial ecology of seabirds facing environmental change is still rudimentary, despite its relevance for the conservation of these vulnerable organisms and for the management of marine ecosystems. We define the following research priorities. (1) Determine the factors affecting seabird distribution and movements at sea using biotelemetry, as well as colony dynamics on land. (2) Link seabird distribution patterns to those of their prey. (3) Determine further the role of historical and metapopulation processes in contributing to the dynamics of the spatial distribution of seabirds. (4) Assess phenotypic plasticity and the potential for microevolution within seabird spatial responses to climate change, since both will greatly affect the quality of modelling studies. (5) Adapt existing models to define and predict the impact of climate change onto seabird spatial dynamics. (6) Synthesize all gathered information to define marine protected areas and further conservation schemes, such as capacity reduction of fisheries. This research effort will require maintaining existing long-term monitoring programmes for seabirds, as well as developing new approaches to permit the integration of processes occurring at various scales, in order to be able to fully track the population responses of these long-lived vertebrates to environmental changes.

KEY WORDS: Fisheries · Marine protected areas · Match–mismatch · Metapopulation dynamics · Phenotypic plasticity · Regime shift · Top-down/bottom-up control

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INTRODUCTION

The oceans have long been considered an unlimited resource and have been used as such for transportation, resource extraction and waste disposal. There are now clear signs that human activities and resulting global changes are exerting considerable stress on marine ecosystems (Halpern et al. 2008). These disturbances affect all components of aquatic food webs, including top-predators such as seabirds. Seabirds are

exposed to a variety of anthropogenic threats (reviews in Schreiber & Burger 2002). (1) Harvest of eggs, juveniles and adults, as well as guano scraping, severely disturbed/depleted seabird populations in historic times, but have ceased more or less completely following efficient protection of breeding sites. Involuntary seabird harvest by fishing vessels (bycatch) nonetheless still occurs and severely threatens numerous populations of petrels and all albatrosses. (2) Substantial efforts have been made to eradicate alien plant and

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animal species from oceanic islands, but such species still have dramatic effects on the breeding performance and survival of some seabirds. (3) Marine pollution via heavy metals, organochlorides, oil products and plastics is a recurrent threat to seabirds on a worldwide scale; the global consequences for this community are difficult to assess. (4) Most seabirds are piscivorous, and two-thirds of the world's fish stocks are overexploited by industrial fisheries, potentially starving numerous seabird populations. (5) Anthropogenic climate change can have direct (review in Schreiber 2002), or indirect impacts on seabirds. In the latter case, climate change affects oceanic processes, and the spatio-temporal availability of seabird prey. This effect is exacerbated by the simplification of upper trophic levels by fisheries (see Österblom et al. 2007, Watermeyer et al. 2008). (6) Finally, global warming and human presence at seabird breeding sites are likely to increase the occurrence and virulence of avian pathogens, as well as their impact on seabird populations (Ricciardi 2008).

All threats listed above cause substantial disturbance to seabird populations, several of which are of major global relevance to the conservation and the management of marine ecosystems. This is particularly the case for ongoing and rapid climatic changes (Ducklow et al. 2007, Hinke et al. 2007). Responses of seabirds to climate changes in historic times, up until the end of the 20th century, have been reviewed by Ainley & Divoky (2001). These authors distinguished between direct and indirect responses to climate change, whereby the former was linked to the thermal preferences of each species and the latter used characteristics of the thermal environment (e.g. sea surface temperature, SST) as a proxy for climate-induced changes in the distribution and abundance of seabird prey. They listed a number of case studies supporting these trends, with a major emphasis on polar and upwelling ecosystems. We take this matter further, with an emphasis on the spatial ecology of seabirds facing climate change. Spatial ecology is concerned with understanding and, ultimately, predicting the processes affecting the spatial distribution of organisms in the environment. It largely relies on the identification of spatial patterns, but it also requires integrating complementary approaches at various spatial scales. Predicting the spatial responses of species facing climate change is one of the great scientific challenges of the 21st century (Clark et al. 2001), above all because it requires an interdisciplinary, metapopulational framework.

In the present review, we first identify the impact of climate change on atmospheric and oceanic circulation and the productivity of marine waters. We then show how climatic changes affect the spatio-temporal distribution of this productivity and its predictability to

seabirds. We also discuss the combined effects of climate change and overfishing on seabird foraging performance, and stress the fact that these disturbances should not be considered in isolation. Further, we show how seabird demographic, social and behavioural traits condition their marked sensitivity to high levels of environmental stochasticity. We then provide examples of seabird species/communities that show behavioural adaptation to the consequences of climate change. We conclude that the study of the impact of climatic changes on seabird spatial ecology and populations has only just begun. We then define key research targets in order to optimise future investigations of the interplay between seabird spatial ecology and climatic changes (see Fig. 4).

GLOBAL WARMING AND MARINE PRODUCTIVITY

Due to human activities, CO₂ levels in the atmosphere have been rapidly rising since the middle of the 19th century, with noted acceleration in the last 50 yr. The related greenhouse effect is strongly suspected to induce increased air temperatures. These changes have profound effects on marine climate. The main known direct impacts of global warming on marine productivity can be summarized as follows. (1) Rising air temperatures tend to warm up surface waters, thereby reducing their density and causing them to expand. Not only does the sea level rise, but such warm surface water does not mix well with deep, cool, oceanic water. This reduces the upward transfer of deep, nutrient-rich water into the euphotic zone, thereby reducing phytoplankton growth and the overall productivity of surface waters, especially in the tropics (Fig. 1; Behrenfeld et al. 2006). (2) Rising air temperatures also induce melt of Arctic and Antarctic coastal and inland ice and Arctic permafrost melt, which, in turn, cause increased freshwater inflow into some regions of the polar oceans and their so-called 'freshening' (Jacobs et al. 2002, Greene & Pershing 2007). Such low-salinity water masses have the same effect as warmer water masses: they build a low-density surface layer, which drastically reduces vertical mixing, nutrient inflow into the euphotic zone and the productivity of surface waters during the summer period. (3) However, rising air/water temperatures also contribute to a reduction of the Arctic and Antarctic sea ice cover and a related increase in spring primary productivity (Greene & Pershing 2007). Warmer water temperatures also directly favour phytoplankton growth at high latitudes (Behrenfeld & Falkowski 1997). However, decreasing ice cover changes the seasonality and extent of the marginal ice zone and its phytoplankton bloom, which, in turn, can have significant effects on

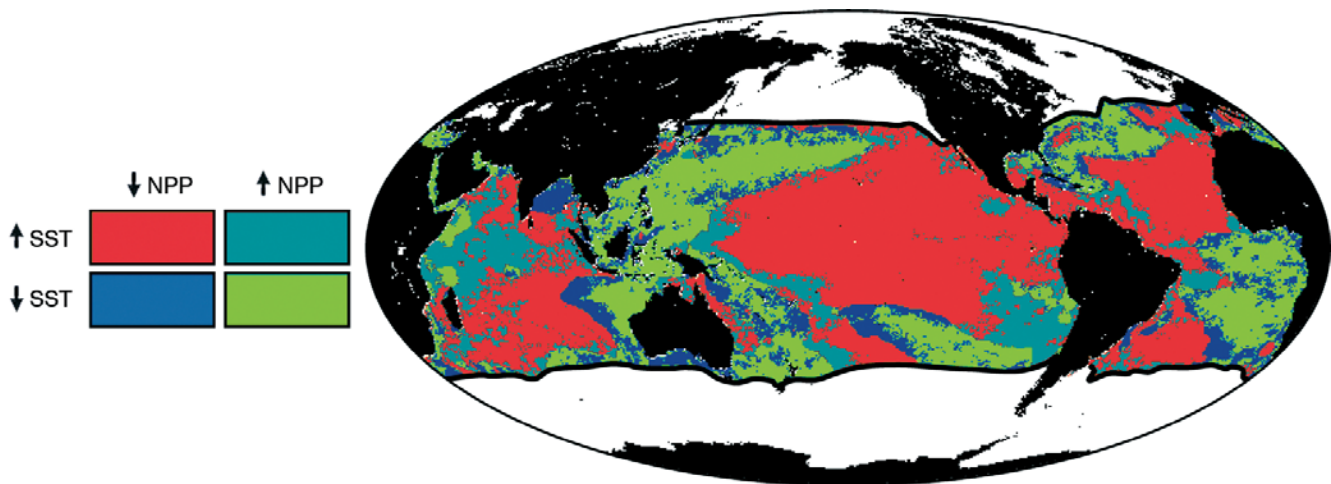


Fig. 1. Over the 1999 to 2004 time period, major changes in sea-surface temperature (SST) and net primary productivity (NPP) occurred worldwide. Overall, SST increased and NPP decreased for 74% of the permanently stratified ocean (red). Green: decrease in SST and increase in NPP. Blue: decrease in SST and NPP. Turquoise: increase in SST and NPP. Adapted from Behrenfeld et al. (2006)

regional productivity/carbon budgets and food web structure (Stabeno et al. 2005, Montes-Hugo et al. 2009). (4) Rising air temperatures generate large atmospheric pressure differentials, which result in stronger winds, frequent storms and hurricanes. Higher wind stress on the surface of the oceans favours the vertical circulation of water masses, the upward transfer of nutrients into the euphotic zone, and enhances primary productivity (Toggweiler & Russell 2008). (5) Most CO_2 released into the atmosphere dissolves in oceanic waters. However, the buffering capacity of the ocean is not endless, and the current massive increase in dissolved CO_2 is resulting in the acidification of marine water. Changes in seawater pH, combined with the temperature increase mentioned above, favour some phyto- and zooplankton species, while putting additional environmental stress upon others (Orr et al. 2005). The actual impact of acidification upon overall marine productivity is still being evaluated, but it is clear that it will lead to major changes in the composition of marine plankton communities (Hays et al. 2005).

The overall impact of these different, antagonistic environmental constraints is difficult to judge and is bound to vary strongly on a regional scale. Nevertheless, global ocean primary productivity, as assessed by remote-sensing, has been shown to have declined significantly since 1999 (Fig. 1; Behrenfeld et al. 2006). This drop in marine primary productivity is highly correlated with large-scale climatic indices, strongly suggesting that global warming has a negative impact on overall marine primary productivity and, hence, on the energy flow in the food web supporting top-predators, such as seabirds (e.g. Le Bohec et al. 2008).

CYCLIC AND EXTREME CLIMATIC EVENTS

Atmospheric and ocean circulation stand in a delicate balance, and so does the earth's climate. Cyclic and extreme climatic events are inherent to these systems, and have taken place long before man-induced global warming. Seabirds evolved in this fluctuating environment, but there is some evidence that environmental stochasticity is increasing rapidly as a consequence of global warming (Alley 2003).

Pressure fields and the resulting atmospheric circulation establish well-defined patterns (e.g. Walker cells, prevailing wind systems), which are nonetheless subject to variability at different spatial (regional and global) and temporal (daily, seasonal, multi-annual, decadal) scales. An array of climate indices has been tailored to characterize atmospheric variability and integrate measurements reflecting several environmental variables. The most famous are the El Niño–Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO) and, in the Southern Hemisphere, the Southern Annular Mode, but every single region of the globe has its own, or several, climate indices that are widely used in studies to decipher the impact of climate patterns on the biosphere (review in Stenseth et al. 2003).

Spectral analyses indicate a certain level of cyclicity within these oscillations. For instance, El Niño events currently have a 5 yr period (Collins 2005). Whether these cycles occur and rotate on a predictable basis is being debated (Park et al. 2004). Their existence is probably linked to the strength of ocean–atmospheric coupling. A strong coupling enables efficient feedback

and predictable cycles, whereas a weak coupling leads to a dilution of these cycles into environmental stochasticity. None of the general circulation models developed so far has been able to entirely grasp the complexity of these phenomena and predict their occurrence (Philander & Fedorov 2003). Maybe this is due to the fact that these events are neither entirely cyclic, nor totally random. In this context Philander & Fedorov (2003) adequately describe the ENSO as 'a damped pendulum subject to modest blows at random times'. Since these cyclic oscillations are weak, environmental stochasticity may trigger phase shifts. For instance, the ENSO tended to swing with a period of 3 yr in the 1960s and 1970s versus a period of 5 yr in the 1980s and 1990s. This phase shift was also linked to different operating modes during past El Niño/La Niña events (Philander & Fedorov 2003).

To summarize, large-scale oceanic-climatic oscillations are subject to substantial spatial and temporal variability, and this variability is extremely difficult to forecast. Recent climate change may have 2 major impacts on these oscillations. (1) It has been suggested that global warming may induce more frequent El Niño events (Timmermann et al. 1999), or may even lead to permanent El Niño conditions. This scenario is still being debated (Collins 2005), but if El Niño conditions become more frequent this will trim the productivity of upwelling ecosystems in the eastern Pacific by reducing nutrient influx to surface waters, or even world-wide (see 'Global warming and marine productivity'), thereby significantly diminishing the availability of pelagic fish to numerous seabird species. (2) Abrupt climatic changes are also more frequent in a warming world (Alley 2003). As seen above, climate oscillations are generally weak and may be prone to disturbance by random events, even of limited magnitude. More frequent and violent winter storms at high latitudes and hurricanes in tropical seas (Alley 2003) are typical examples of extreme events that can disrupt ongoing oscillations and drastically modify the operating modes of these oscillations, with cascading consequences for marine productivity and food availability to avian predators (Frederiksen et al. 2008).

REGIME SHIFTS, BOTTOM-UP AND TOP-DOWN CONTROLS

Marine food webs are unstable constructions and remain prone to sporadic and cyclic reorganisation, as are the oceanic and atmospheric circulations described in the previous section. Such reorganisations are termed 'regime shifts', which are defined as 'a persistent radical shift in typical levels of abundance or productivity of multiple important components of the

marine biological community structure, occurring at multiple trophic levels and on a geographical scale that is at least regional in extent' (Bakun 2004, p. 973). Using multi-disciplinary data sets, regime shifts have been identified in the northeastern Pacific for the years 1925, 1947, 1976 and 1998 (Peterson & Schwing 2003) and in the northern Atlantic in the 1920s and 1930s (Drinkwater 2006), and again in the mid-1980s (Beaugrand 2004). As a trendy concept in biological oceanography, regime shifts and their consequences are now being studied in all regions of the world's oceans (e.g. Oguz & Gilbert 2007). To take just one example of this type of event into consideration, the North Sea regime shift (1982 to 1988) was most probably caused by large-scale changes in wind intensity and direction, and an increase in SSTs. These alterations were coupled with an inflow of warm, nutrient-poor oceanic water into the North Sea and stronger stratification of surface water. These events favoured a northward expansion of warm-water copepod species and a decline in cold-water zooplankton (Beaugrand 2004). During this shift, warm-water conditions were established in the North Sea, thereby modifying primary and secondary productivity and reducing the availability of small pelagic fish to seabirds, which, in turn, influenced the reproductive performance of seabirds (Frederiksen et al. 2006).

This suite of events typifies a bottom-up control of marine food webs: climatic variability influences ocean circulation, which impacts primary productivity (phytoplankton), secondary productivity (zooplankton), fish and, finally, marine top-predators such as seabirds. This line of thought has been promoted by researchers wishing to link some of the climate indices listed in the previous section with population characteristics of marine top-predators. In particular, the ENSO and the NAO have been used extensively (e.g. Jenouvrier et al. 2003, Thompson & Ollason 2001). But 'it cannot all be climate' (Ainley et al. 2007), and a vision of bottom-up controlled marine food webs might be all too simplistic. Equally, there is ample evidence that marine food webs can be controlled via top-down effects (Österblom et al. 2007, Coll et al. 2008). For instance, Ainley and colleagues (2006) showed that enhanced predatory pressure by penguins and whales may have generated a trophic cascade in the western Ross Sea, and Worm & Myers (2003) also demonstrated top-down control by predatory fish (cod, *Gadus morhua*) on North Atlantic food webs.

As so often in ecological science, the actual event has multiple causes, and it seems unwise to focus on single mechanisms. Taking the southeastern Bering Sea as an example, Hunt et al. (2002) proposed the oscillating control hypothesis, which suggests that both top-down and bottom-up forcing may rule marine food webs

alternatively, whereby the latter occurs during 'warm' phases and the former during 'cold' phases. Similarly, Frank et al. (2007) performed a meta-analysis of trophic structure in 9 areas of the western North Atlantic and showed that top-down control tended to rule in northern (colder) areas, whereas bottom-up control occurred more often in southern (warmer) areas, potentially due to lower species diversity at higher latitudes (Fig. 2). Finally, Cury et al. (2000) suggested that upwelling ecosystems have a 'wasp-waist' structure, whereby intermediate trophic levels (small pelagic fish) exert both bottom-up and top-down control, thereby playing a crucial role in the response of these food webs subjected to climate-driven El Niño events.

COMBINED IMPACT OF CLIMATE CHANGE AND FISHERIES

Studies cited in the previous section show that the operating modes of trophic control can vary strongly in space and time within marine food webs (see also Lit-zow & Ciannelli 2007) and that bottom-up control by climate change is not necessarily the overriding force. The visionary statement of Parsons and colleagues (1984, p. 277) 'no form of marine pollution is in any way comparable to the ecological impact which occurs with the removal of ca. 70 million tons per year of predatory fish from the ocean ecosystem' has, sadly, been confirmed by numerous recent studies, and there is now ample evidence that humans are 'fishing down marine food webs' (Pauly et al. 1998). Intense fishery pressure on predatory fish drastically modifies the top-down control of these ecosystems. For instance, the removal of large baleen whales from Antarctic ecosystems by fisheries is strongly suspected to have caused a release of predatory pressure on Antarctic krill, with cascading consequences for regional marine food webs (Ainley et al. 2007). Modelling studies also have shown that harvesting and fisheries, more than climate change, have had a profound impact on the marine ecosystem of the Baltic Sea (Österblom et al. 2007), or the Benguela current (Watermeyer et al. 2008), and it is particularly difficult to envisage what the 'natural' state of North Atlantic ecosystems might have been prior to centuries of exploitation by humans (Pauly & MacLean 2003).

The most recent information indicates that the greatest threat to fish stocks upon which seabirds prey is the combined effect of climate change and overfishing (Brander 2007). Indeed, a number of studies now strongly suggest that rapid climate change and uncontrolled removal of fish resources have drastic consequences for seabird breeding success and survival

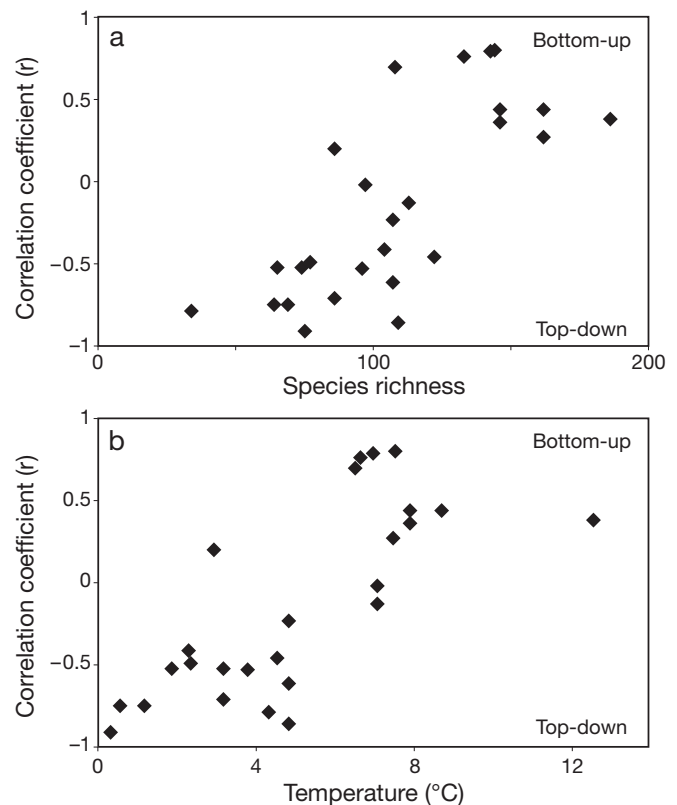


Fig. 2. In the North Atlantic, marine ecosystems are controlled by bottom-up and top-down trophic forces, depending on (a) species richness and (b) temperature, whereby the type of trophic forcing is expressed by the sign of the correlation between predator and prey abundance. The species richness–trophic forcing relationship is significant ($r = 0.75$, $n = 26$, $p < 0.001$), as is the temperature–trophic forcing relationship ($r = 0.74$, $p < 0.001$). Adapted from Frank et al. (2007)

and, ultimately, for population stability (Frederiksen et al. 2004, Ainley & Blight 2009). Therefore, although this review primarily focuses on the impact of climate change on seabird spatial ecology, we wish to stress that such impacts should not be considered in isolation, and we strongly recommend multi-factorial analyses assessing the consequences of the diverse forms of global change (i.e. climate change, overfishing, pollution, infectious disease spread) on seabird spatial ecology.

GLOBAL WARMING AND RANGE SHIFTS IN SEABIRD PREY

The climatic changes alluded to in previous sections have direct and indirect effects on the distribution and abundance of marine fish, the primary resource upon which seabirds forage (Shealer 2002, Cheung et al. 2008). As ectothermic organisms, fish have a well-defined thermal niche of $\pm 2^\circ\text{C}$ (Magnuson & Destasio

1997). Climate-induced warming of surface oceanic waters beyond the boundaries of a fish species' thermal niche can, therefore, have a direct effect on its distribution. Moreover, within this thermal niche, even subtle ($<0.5^{\circ}\text{C}$) temperature changes can have profound effects on growth, survival and reproduction. Such impacts operate via ecological forcing (food availability to fish) and physiological processes (e.g. enzyme kinetics). Examples abound (Perry et al. 2005, Hiddink & Hofstede 2008), but one of the most recent events with consequences for seabirds is the sharp numerical increase of snake pipefish *Entelurus aequoreus* in the northeastern Atlantic (Kirby et al. 2006). This population rise is due to the positive influence of warmer (up to $+0.5^{\circ}\text{C}$) waters on the reproductive performance of snake pipefish, and this numerical increase coincides with a northward range expansion to at least 79°N (Svalbard; Fleischer et al. 2007). Synoptically, lesser sandeels *Ammodytes marinus*, which used to be the food-base of a vast seabird community around the British Isles, have been depleted by the combined effects of overfishing and climate change (Poloczanska et al. 2004), and also show diminished calorific value (Wanless et al. 2005). Seabirds, in particular kittiwakes *Rissa tridactyla*, now feed increasingly on snake pipefish, which have low calorific value (Harris et al. 2007a), and are particularly difficult to swallow for seabird chicks, causing regular suffocation (Harris et al. 2007b). Therefore, there is little chance that numerous snake pipefish will be a valid alternative to the absent/meagre natural prey of many UK seabirds.

MATCH–MISMATCH OF FORAGING SEABIRDS AND FOOD RESOURCES

We have seen that climate change has a profound effect on global primary productivity of the world's oceans. Beyond potentially diminishing the total volume of marine resources upon which seabirds rely, climatic changes also perturb global oceanic circulation and the structure of marine food webs. Regime shifts and associated range shifts of marine species occur naturally, but there is some evidence that recent climate change increases the frequency of abrupt changes, with an overall trend towards chaotic ecosystem dynamics (Alley 2003). Such a trend is most probably facilitated by the combined effects of overfishing and climate change.

Overall, there is therefore a higher probability that food resources will not occur where and when seabirds expect them to be. This would typify a mismatch of predators and resources, and reflects the concept of match–mismatch introduced by Hjort (1914) and

championed by Cushing (1969, 1990). The match–mismatch hypothesis (MMH) was primarily formulated to describe the temporal mismatch of juvenile pelagic fish and of the plankton resources necessary to their growth (Cushing 1969). Nevertheless, it has been demonstrated that this concept can easily be expanded into the spatial dimension, and that it can generally refer to the spatio-temporal match–mismatch of predators and their resources (Fig. 3; Grémillet et al. 2008a). The impact of climate on match–mismatch events has been thoroughly reviewed by Durant et al. (2007, see also Suryan et al. 2006, Cury et al. 2008). In essence, the authors confirm that climate change is very likely to profoundly affect trophic web structure because (1) even (apparently) minor environmental changes can strongly modify the spatio-temporal availability of food resources necessary to predators (via non-linear responses) and (2) different food-web components are unlikely to respond to environmental change in the same manner, causing different degrees of spatio-temporal match–mismatch between these components, with resulting destructuration of the food web in question. This has been demonstrated in the southern Benguela upwelling zone, where primary productivity is still one of the highest of the world's oceans, but where the combined effects of climate change and overfishing have altered the spatial occurrence of pelagic fish (anchovies and sardines) upon which a vast community of seabirds feed. In this situation, seabird foraging ranges still match with areas of high primary productivity, but mismatch with the current distribution zone of pelagic fish (Fig. 3; Grémillet et al. 2008a), thereby greatly diminishing seabird foraging profitability (Pichegru et al. 2007).

SEABIRD LIFE-HISTORY TRAITS, SOCIAL STRUCTURE AND ECOLOGICAL TRAPS

Rapid advances in biotelemetry techniques (Wilson et al. 2002) and systematic observations of seabirds at sea (Tasker et al. 1984) revolutionised our perception of the foraging and migratory behaviour of seabirds. It now appears that the marine environment is reasonably predictable to them (Hunt et al. 1999, Weimerskirch 2007), both at high latitudes and in the tropics (Ballance et al. 1997). Seabirds are long-lived organisms, with delayed sexual maturity. A prolonged bachelor period and extended life-span provide seabirds with ample time to explore marine habitats and to gather crucial information about prey patches and spatio-temporal variability in their availability (Daunt et al. 2007). There is increasing evidence that memory effects help individual seabirds to optimise their foraging strategies, most probably in conjunction with local

enhancement via feeding flocks (Camphuysen & van der Meer 2005), but not necessarily (Irons 1998). It has also been speculated that seabird colonies function as information centres and that individuals within breeding assemblages tend to share specific foraging patterns and foraging distributions, which remain stable through time (foraging site fidelity). In this context Grémillet et al. (2004a) indicated that neighbouring seabird colonies foraging in a similar marine environment may develop different behavioural types due to strong local 'cultural identities' tailored by group and memory effects.

Cultural identities of seabird colonies are also linked to their social structure and to the paucity of convenient insular breeding sites. It takes a long time (years to decades) to establish a viable seabird colony, and birds born at 1 specific site typically show high levels of philopatry (>80%). Similarly, adult seabirds are reluctant to change breeding sites, and sometimes prefer to forage and breed under unfavourable environmental conditions than to emigrate. In some species, such as the kittiwake, it is now clear that differential recruitment and dispersal at small spatial scales can be driven by adaptive strategies for the selection of breeding habitat, based on the performance of conspecifics (Danchin et al. 1998, Boulinier et al. 2008a). Nevertheless, dispersal at large scales, and factors susceptible to affect this process, are notoriously difficult to study (Cam et al. 2004).

In conclusion, current knowledge of seabird foraging and breeding biology strongly suggest that these top-predators gain detailed knowledge of the marine environment, thereby optimising their use of resources

subject to environmental stochasticity (Grémillet et al. 1999). However, their life-history characteristics and their social structure also result in high behavioural resilience, which makes them particularly vulnerable to the abrupt environmental changes detailed in previous sections. In that sense, they are likely victims of ecological traps, which are defined as habitats 'low in quality for reproduction and survival [that] cannot sustain a population, yet...[are] preferred over other available, high-quality habitats' (Donovan & Thompson 2001, p. 872). Such an ecological trap has recently been identified for Cape gannets *Morus capensis* feeding on fishery wastes in the Benguela upwelling (Grémillet et al. 2008b).

HOW SEABIRDS COPE (OR NOT) WITH CURRENT ENVIRONMENTAL CHANGE

Climatic changes, overfishing and the associated rapid modifications of marine food webs described above might cause single seabird populations/species to: (1) modify their trophic status and their foraging ecology to survive and reproduce within the same distribution zone, (2) modify their distribution zone, or (3) go extinct. These 3 options are not mutually exclusive since a bird population/species can attempt to modify its feeding habits as a response to environmental change, while changing its breeding range (or subsequently), and finally go extinct (Ducklow et al. 2007).

(1) Seabirds are capable of adapting their foraging effort to buffer the consequences of environmental change, in particular lower availability of their preferred prey (Arcos & Oro 1996, Litzow et al. 2002), and of evolving life-history traits that allow them to respond to environmental change (Erikstad et al. 1998). There are nonetheless clear eco-physiological limits to this plasticity, and, below a certain threshold of prey availability, foraging is unprofitable (Enstipp et al. 2007), jeopardising reproduction (Harding et al. 2007) and potentially adult survival. Moreover, seabirds generally have a specialised diet, consisting of a limited number of taxa (fish, squid and crustaceans; Shealer 2002). At the species level, this specialisation is even more pronounced (Barrett 2007), with major exceptions, such as in herring gulls *Larus argentatus* (Pierotti & Annett 1991). Nevertheless, numerous seabirds do seem capable of modifying their diet when confronted with scarcity of their natural prey. Seabird diet shifts following climate and fishery-

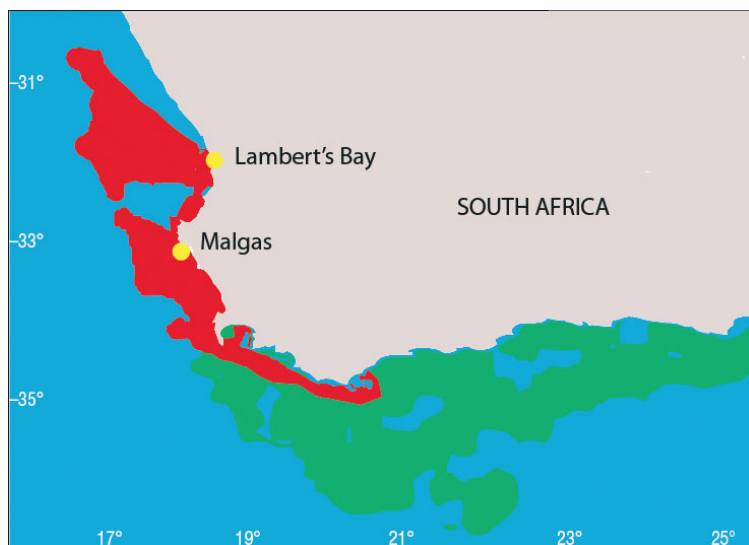


Fig. 3. Combined effects of climate change and overfishing can result in spatial match-mismatch of seabirds and their prey. This is shown here by overlaying Cape gannet *Morus capensis* home ranges (red) from the Malgas and Lambert's Bay breeding colonies with charts of anchovy *Engraulis capensis* distribution (green). Adapted from Grémillet et al. (2008a)

induced environmental change have been demonstrated in many regions of the world's oceans, such as in the Southern Ocean (Hilton et al. 2006, Ainley & Blight 2009), the south-eastern Pacific (Jaksic 2004), the southern California current (Sydeman et al. 2001), the Bering Sea (Springer et al. 2007), the Greenland Sea (Karnovsky et al. 2003), the Norwegian Sea (Durant et al. 2003), the Barents Sea (Barrett & Krasnov 1996), the North Sea (Wanless et al. 2007) and the Benguela upwelling zone (Crawford & Dyer 1995). Whenever assessed, all these shifts had a negative impact on seabird breeding performance, strongly suggesting the importance of dietary specialisation in these marine predators and their difficulties to adapt to rapid environmental change.

(2) Range shifts following climatic changes have been recorded in a variety of seabird species during different phases of their life cycle (breeding and non-breeding). Such patterns are well known within upwelling ecosystems. They were first noticed following El Niño events off the Pacific coast of South America (Ainley & Divoky 2001), and were subsequently extensively studied off California. Veit et al. (1996) showed that non-breeding sooty shearwater *Puffinus griseus* populations that mainly breed in New Zealand, spending the austral winter off the coast of California, declined by 90% in this latter zone between 1987 and 1994, most probably because global warming caused a 90% decrease in zooplankton biomass in the California upwelling system (Roemmich & McGowan 1995, Veit et al. 1997). The distribution of wintering shearwaters then probably shifted towards the central, equatorial Pacific, where climate change had favoured enhanced primary productivity (Ainley & Divoky 2001). A northward distributional shift of further non-breeding species, such as brown pelicans *Pelecanus occidentalis*, Heerman's gulls *Larus heermani* and black *Oceanodroma melania* and least storm petrels *O. microsoma* occurred during the same time period (Ainley et al. 2005), and a warming climate is also the likely cause of a sharp decline of the local Cassins auklet *Ptychoramphus aleuticus* population (Lee et al. 2007). Further examples of seabird range modifications probably caused by climate change (sometimes in interaction with other constraints such as fisheries) were recorded in polar areas (Ainley & Divoky 2001), and in the temperate zone of the North Atlantic (Thompson 2006, Wynn et al. 2007, but see Votier et al. 2008).

(3) Nevertheless, not all seabird species show such geographic plasticity. Some endemics are trapped in restricted areas and face likely extinction due to the impact of climate change. This is most probably the case for the Galápagos penguin *Spheniscus mendiculus* (Vargas et al. 2007) and the marbled murrelet *Brachyramphus marmoratus* (Becker et al. 2007).

MAJOR OBJECTIVES OF SEABIRD SPATIAL ECOLOGY

Determining the factors affecting seabird distribution and movements at sea and on land

Despite the few case studies detailed in the previous sections, it appears that our knowledge of the spatial ecology of seabirds facing the consequences of climate change is rather anecdotal and that such investigations are still at the pioneering stage (Fig. 4). One of the major targets of seabird ecology is, therefore, to make use of the most recent tools to investigate the short- and long-term movements of individual seabirds at sea, as well as distributional shifts in their breeding populations.

Exploration of seabird movements at sea is booming at the moment (Ropert-Coudert & Wilson 2005). This is because the miniaturisation of tracking systems such as Global Location Sensors (GLS, see Wilson et

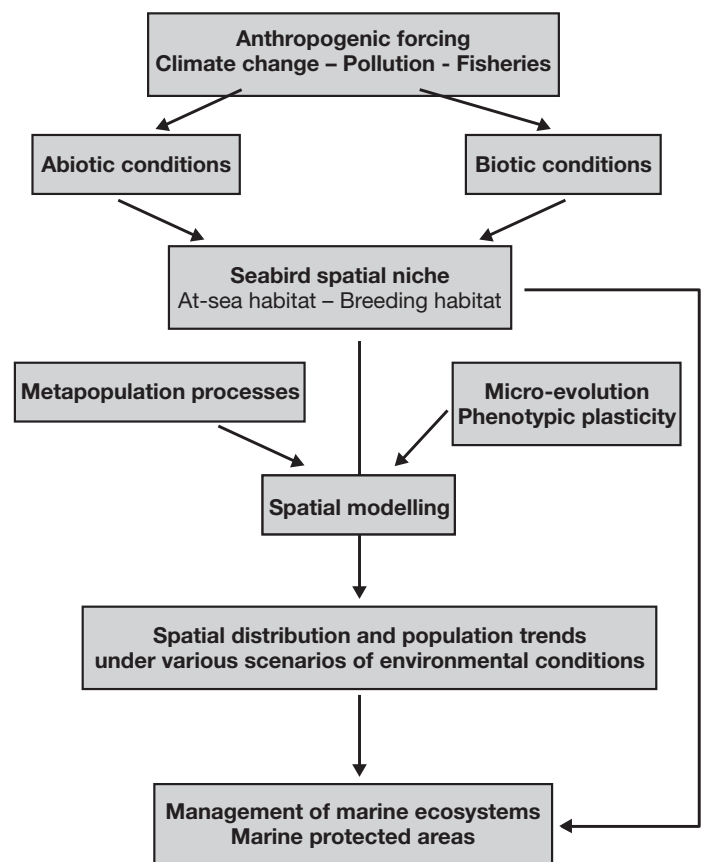


Fig. 4. Factors influencing the spatial niche of seabirds, and key topics for future research. Note that exploration of current spatial niches of seabirds (at sea and on land) and modelling of their future spatial niches both provide major contributions to the design of marine protected areas and management schemes for marine ecosystems

al. 1992) and Global Positioning Systems (GPS) has enabled deployment of <10 g tags on a wide range of seabird species. Information gathered using these techniques, in combination with direct at-sea observations, will fill huge gaps in our knowledge of the home ranges of breeding and non-breeding seabirds, especially for small species that are poorly detected during at-sea surveys (Croxall et al. 2005). Beyond the gathering of crucial spatial information, the range of analytical tools used to define seabird distribution and movements is expanding rapidly. For instance, foraging tracks can be analysed using simple sinuosity indexes, whereby the most tortuous sections are associated with prey consumption and more linear sections with commuting between feeding sites (Grémillet et al. 2004a). First passage time analysis (*sensu* Fauchald et al. 2000) is a refinement of this technique, and enables the identification of oceanic zones within which birds display area-restricted searches, which is also thought to be tightly related to prey consumption (Pinaud 2008). Application of this method to seabird spatial ecology has attracted much attention (Weimerskirch et al. 2007), but has recently been criticised (Barraquand & Benhamou 2008). The adequacy of this technique and of further analytical methods, e.g. the fractal dimension approach (Tremblay et al. 2007), remains a key objective of investigation in the near future. Furthermore, the pertinence of kernel analyses, which have also been routinely used to map the distribution of seabirds at sea, has been criticized (Hemson et al. 2005), and should likewise be reassessed and potentially replaced by more refined mapping techniques.

In parallel to at-sea investigations, further efforts have to be made to understand factors affecting changes in numbers of breeders in the colonies. This is because integrated land-based and at-sea seabird ecology would provide a more complete appraisal of factors affecting seabird distribution. Global warming may, for example, cause breeding habitat loss via sea-level rise and potential shifts in the geographic ranges of predators and parasites, which could, in turn, affect the dynamics of breeding colonies. As seabird populations are subdivided at different spatial scales and are made of breeding groups that can exchange individuals and become extinct, they may function as metapopulations. A key process requiring specific efforts is thus to understand which factors affect the dispersal of individuals and their consequences.

We urge that at-sea and land-based research of seabird spatial ecology be considered in combination. Both areas of research are involved in the same ecological processes, which ultimately determine breeding output and survival and, thereby, shape population dynamics (Fig. 5). Beyond this integrative approach, it is essential that such investigations become part of

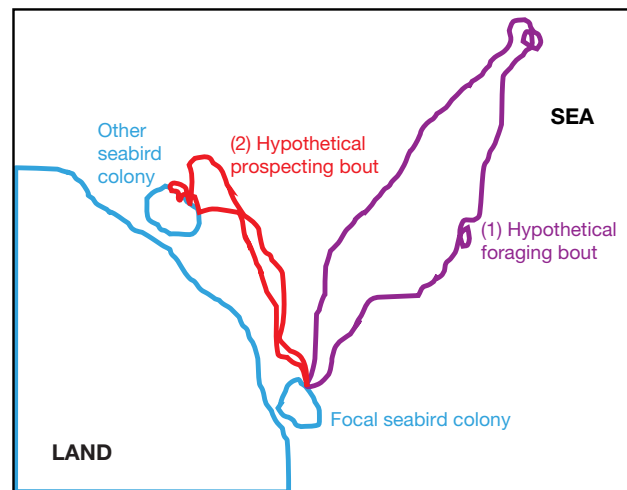


Fig. 5. Hypothetical tracks of the movements of a breeding seabird, illustrating the significance of combining at-sea and land-based studies using modern tools to investigate the responses of seabird populations to environmental changes: (1) foraging bout, showing the spatial scale at which foraging occurs, and (2) 'prospecting bout', showing the spatial scale at which breeding dispersal may occur. Biotelemetry tools have been extensively used for at-sea studies, but they could also be used to explore behavioural processes involved in population dynamics (e.g. prospecting for a potential future breeding site; Boulinier et al. 1996)

long-term monitoring projects (considering seabird longevity, these have to last several decades) developed in a spatial context. In addition to the identification of specific questions that need to be addressed (see the 2 following subsections), the design of such monitoring programmes requires the consideration of spatial variability in the estimated parameters (Yoccoz et al. 2001). Longitudinal data sets collected at multiple study sites should, thus, be very valuable in assessing and modelling the impact of global change in seabird spatial ecology.

Linking seabird distribution patterns to those of their prey

As demonstrated by Aebischer et al. (1990) in a spectacular manner, seabirds cannot be studied in isolation, and spatial information alluded to in the previous section has to be put into a wider ecological context if we are to understand observed trends. Modern seabird ecologists are therefore also oceanographers, capable of analysing seabird distribution, movements, diet and trophic status in combination with biotic and abiotic environmental conditions, in particular prey availability/quality. Indeed, remote-sensed values of chlorophyll *a* concentration, SST and sea-surface

height have been, and are still being, widely used as surrogates for the relative productivity of oceanic waters and their potential profitability to foraging seabirds (Pinaud & Weimerskirch 2007). However, these variables are proxies for primary productivity, while seabirds are top-predators, which usually feed 2 to 3 trophic levels higher up the food chain. Correlations between seabird distribution and indices of primary productivity can consequently be quite misleading (Grémillet et al. 2008a), and we urge investigators to favour spatial analyses linking seabird at-sea ecology with direct assessments of prey availability (the key resource required by seabirds) conducted from research vessels (e.g. pelagic fish population assessments via echo-sounding). The remote-sensing data mentioned earlier may nonetheless feature co-variables useful in complementing statistical models to predict the distribution and movements of seabirds facing climate change.

Impact of historical and metapopulation processes on seabird spatial distribution

Factors affecting dispersal, the dynamics of colonization and the extinction of local populations are keys to understanding the spatial dynamics of seabird (meta-) populations. Constraints on dispersal and historical events may explain some broad patterns of seabird spatial distribution, such as the absence of auks in the southern hemisphere or the absence of albatrosses in the North Atlantic. At the scale of seabird metapopulations (i.e. populations linked by dispersal events), these aspects are particularly important to consider. Estimating dispersal rates and quantifying factors affecting dispersal are difficult tasks, despite strong ecological and evolutionary implications (Clobert et al. 2001), notably in the context of global change (Kokko & López-Sepulcre 2006). This is because the probability of detecting dispersal events is strongly affected by re-sighting probabilities at potential breeding locations, which are difficult to account for (such probabilities are often low, heterogeneous, or not estimated). Comparisons of estimated local population growth rates with those that can be obtained from estimated demographic parameters can provide information on potential source sink dynamics (Pulliam 1988, Oro 2003). Such an approach has, for instance, been used to show that emigration and immigration can be very significant to the dynamics of local breeding populations of gulls (Danchin & Monnat 1992, Danchin et al. 1998, Suryan & Irons 2001). A more formal metapopulation framework and capture–recapture modelling (Spendelov et al. 1995, Cam et al. 2004) allow stronger inference concerning the factors potentially affecting

dispersal rates. Studies inferring dispersal and movements of individuals using indirect methods, such as population genetics and biogeochemical analyses (Riffaut et al. 2005, McCoy et al. 2005, Gómez-Díaz & González-Solís 2007) can provide important information in this context (e.g. on population structure, gene flow and the geographic origin of individuals).

If natal dispersal is now generally considered to be important in many species, relatively little is known about recruitment processes and breeding habitat selection behaviour because of the large temporal scale involved (Boulinier et al. 2008b). Population genetic approaches have nevertheless shown that dispersal can occur at various scales (Riffaut et al. 2005, Shepherd et al. 2005). Further, detailed work on breeding habitat selection (Danchin et al. 1998, Boulinier et al. 2008b) and the role of prospecting individuals in kittiwakes (Boulinier et al. 1996) has stressed that the local breeding success of colonies or sub-colonies could amplify population change via the dispersal of individuals and their differential recruitment as a function of the relative attraction towards successful areas prospected the year before. Such studies have nevertheless been conducted at relatively small spatial scales. Prospecting by individuals not born locally has been recorded to occur over wide spatial scales (Reed et al. 1999). Up until now, most habitat selection studies have nevertheless been conducted at relatively small spatial scales and it is not clear how those processes may translate at broader scales, scales at which effects of climate change may occur. Moreover, competition for sites, density dependence effects on breeding success and the mere attraction conspecifics are other key processes involving individual behaviour that need to be considered and that can complicate observed patterns (Kokko et al. 2004, Oro et al. 2006). One benefit of considering dispersal and breeding habitat selection strategies in an adaptive framework is that it underlines the importance of looking at the spatio-temporal patterns of variation of breeding habitat quality in which a considered species has evolved (Boulinier & Lemel 1996, Doligez et al. 2003), which can be affected by climate change. For instance, if predictable changes in food availability and expected reproductive success become more unpredictable because of global warming and fish depletion, then one could expect some species to be caught in ecological traps. The problem becomes even more complex if we consider that habitat quality will also affect the survival of adult and immature individuals and that variability at various hierarchical scales has to be considered. Breeding habitat selection behaviours, as well as dispersive behaviours at sea, thus have the potential to strongly mediate the effect of climate change on the distribution and abundance of seabirds.

Assessing phenotypic plasticity and the potential for microevolution

Current field investigations and models seldom take into account the capacity of seabirds to display phenotypic plasticity and microevolution of spatial traits (*sensu* Visser 2008). Most models alluded to in the next section are built around sets of empirical/theoretical relationships between seabird spatial variables and further environmental components. Model predictions typically assume that these relationships do not evolve through time, although this is highly unlikely to be the case. Indeed, the shape of existing functional relationships can shift widely due to the phenotypic plasticity of individuals, i.e. their capacity to display behavioural and physiological short-term adaptation to given environmental conditions. In seabirds this becomes most apparent when studying functional relationships between seabird predatory performance and local prey abundance, which are essential to understand and predict seabird spatial patterns. In cormorants for instance, trials under controlled conditions generated significant, positive functional relationships between fish abundance and seabird predatory performance (Enstipp et al. 2007). However, similar investigations in the wild indicated that cormorants are capable of maintaining very high predatory performance, even when exploiting fish resources at low density (Grémillet et al. 2004b). This strongly suggests substantial phenotypic plasticity in the form of behavioural adaptability, which considerably reduces our capacity to predict the spatial response of predators such as cormorants to the consequences of global warming (White et al. 2008).

Beyond phenotypic plasticity, recent investigations in land birds clearly showed the importance of considering the impact of the microevolution of functional traits on the spatial response of individuals and populations to climate change (Visser 2008). True, seabirds are particularly long-lived species and it is unlikely that microevolution will influence their overall spatial response as much as phenotypic plasticity, but it remains a fascinating, and yet largely unexplored, research avenue (Reed et al. 2006).

Exploring phenotypic plasticity and microevolution of functional relationships is not possible via office-based theoretical modelling. This requires detailed, longitudinal field investigations of seabird spatial ecology and population dynamics using the modern tools mentioned earlier, from biotelemetry to quantitative genetics. This, once more, calls for the continuation of the development of long-term monitoring programmes of seabird populations integrating multidisciplinary approaches.

Modelling present and future seabird habitats and populations

A vast panel of algorithms has been computed in recent years to assess future range and abundance of species exposed to global warming. To name just a few, we may use climate envelope models (CEMs), generalized additive models (GAMs), mechanistic models (MMs), discriminant analysis, artificial neural networks, maximum entropy, or hierarchical Bayesian models (see, for instance, Pearman et al. 2008). To take a more general perspective, the evolution of seabird spatial niches might also be considered within the framework of marine ecosystem-based models (Cury et al. 2008). This approach has the major advantage of considering entire predator communities, thereby including interspecific competition, an aspect which may be neglected using other species-centred modelling techniques.

The techniques mentioned here follow different approaches. For instance, widely used CEMs explore and characterise functional relationships between seabird spatial variables (home range size and position, foraging path characteristics) and the abiotic and biotic variables mentioned in the subsection 'Linking seabird distribution patterns to those of their prey'. They then extrapolate these statistical relationships to predict future spatial distributions and abundances of seabirds (Hijmans & Graham 2006). CEMs have 2 major weaknesses: (1) identified functional relationships are correlative and usually cannot be tested and (2) there is no way to test that these relationships will be sustained in the future. Seabird reaction norms may vary due to phenotypic plasticity and microevolution, which, as we have seen in the previous subsection, can be a problem. Beyond CEMs, the use of MMs to evaluate future seabird distribution and abundance is currently being explored. In contrast to CEMs, MMs are not based upon observed statistical correlations, but rebuild the thermal and ecological niche of organisms using first principles of thermodynamics (Hijmans & Graham 2006). In such cases functional relationships between the spatial characteristics of given species and environmental parameters are not fitted, but calculated. MMs provide exciting perspectives, but their pertinence also remains to be tested.

The use of such methods is extremely recent in seabird ecology (e.g. Österblom et al. 2007, Ainley et al. 2008), but is bound to increase dramatically in coming years. Nevertheless, current land-based investigations show that predicting species distribution and abundance in a rapidly changing world is a daunting task, to say the least (Pearman et al. 2008). Knowing that marine ecosystems and marine biodiversity are traditionally much harder to study than their terrestrial

equivalents, it remains unclear whether such modelling approaches will yield significant advances in our understanding of seabird spatial ecology. They will nevertheless be useful to generate broad predictions that can provide useful material to combine with data from population studies. As we have seen in the previous subsection 'Impact of historical and metapopulation processes on seabird spatial distribution', the integration of metapopulation processes is also required in modelling, notably when predictions are to be made at regional spatial scales.

Helping define marine protected areas (MPAs) and refining further conservation schemes

Marine habitats are the last frontier of conservation. Seabird ecologists have the exciting, yet daunting, task to participate in defining marine conservation plans, in particular the design of MPAs and capacity reduction areas for sea fisheries. Seabird breeding colonies have been efficiently protected for about a

century, and have greatly benefited from these measures; for instance, dozens of colonies have been designated Antarctic Specially Protected Areas, which are recognized internationally under the Antarctic Treaty. As another example, around the British Isles, seabird numbers were low at the beginning of the 20th century, due to centuries of hunting. However, as a result of protection of most of their breeding habitats, they increased throughout the second half of the 20th century, and the seabird community of Britain and Ireland on the whole prospered during this latter period (Grandgeorge et al. 2008). In contrast, the early 21st century has witnessed major breeding failures along the North Sea coast of the UK, clearly demonstrating that land-based seabird conservation is not sufficient (Wanless et al. 2007). Indeed, seabird population dynamics are conditioned by food availability at sea just as much as by the availability of suitable breeding habitat on land.

Seabirds are now threatened on a world-wide scale (Butchart et al. 2004), and general agreement exists that they will greatly benefit from MPAs, as will all fur-

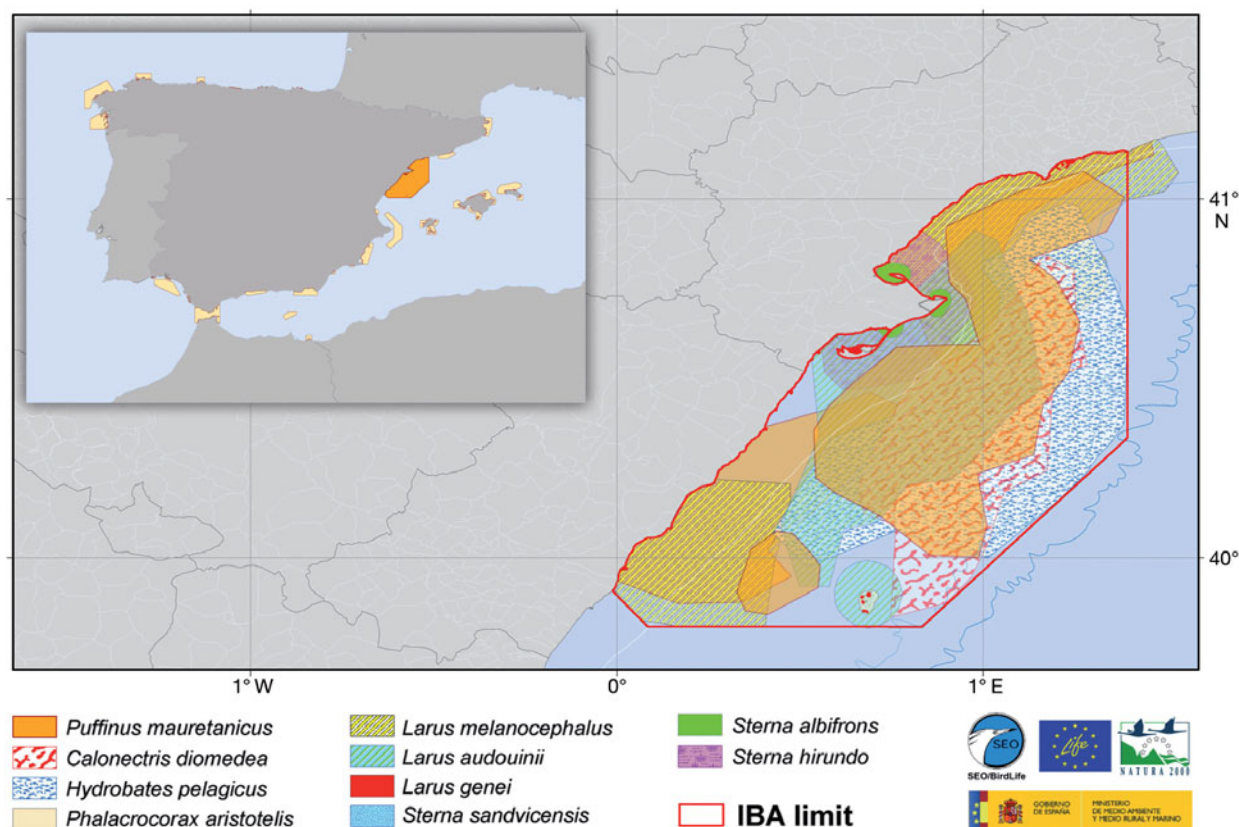


Fig. 6. Seabird spatial studies can help identify marine Important Bird Areas (IBAs). In a study performed by SEO/BirdLife covering the whole of Spanish waters, the assessment of breeding colony distribution, biotelemetry studies (PTT [platform transmitter terminal] and GPS), aerial-surveys, at-sea observations, and land-based observations were used for a series of vulnerable seabird species to identify marine IBAs. The situation map shows proposed marine IBAs around the Spanish section of the Iberian Peninsula, and the detailed map shows the IBA proposed for the Ebro Delta (orange zone on the situation map). Provided by SEO/BirdLife, adapted from Arcos et al. (2009)

ther components of marine ecosystems critically challenged by anthropogenic global change. Australia and the USA have been pioneers in the establishment of MPAs, while European nations have committed themselves to establishing a network of marine IBAs (Important Bird Areas) over their territorial waters by 2012 (Arcos et al. 2009). BirdLife International is in the process of identifying a network of marine IBAs worldwide, with the aim of providing guidance, with respect to seabirds, for the creation of MPAs. Spain and Portugal have led this initiative, with marine IBA inventories published in 2009 that are expected to become Special Protection Areas in the near future (Arcos et al. 2009).

Most unfortunately, as we have seen in previous subsection, marine ecosystem structure is highly labile, both spatially and temporally, and defining marine reserves is immensely more complicated than defining terrestrial reserves (Hyrenbach et al. 2000, Hooker & Gerber 2004). With respect to seabirds, and to marine top-predators in general, one of the major, and most urgent, tasks is to compile algorithms allowing researchers and managers to define the spatial and temporal cover of MPAs, while balancing the contrasting requirements of marine megafauna and human activities (Fig. 6; Harris J et al. 2007, Pichegru et al. 2009, this Theme Section). A range of such statistical methods is already available for the management of terrestrial habitats, and some of these methods are currently being adapted to marine habitats (Fig. 6; Arcos et al. 2009).

Beyond establishing MPAs, and because their efficiency is still being evaluated, it becomes increasingly clear that further conservation measures have to be employed, especially capacity reductions of industrial fisheries (Okes et al. 2009).

Further exploration of the spatial ecology of seabirds using the diverse approaches mentioned in the previous subsections, in particular biotelemetry, will play an essential role in defining these conservation strategies. Present seabird ecologists are living in a challenging, yet highly exciting period.

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Spatial interaction between seabirds and prey: review and synthesis

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ABSTRACT: The Ideal Free Distribution theory predicts a close spatial match between predators and prey. Studies have shown that seabird and prey distribution seldom conforms with this prediction. In this study, I review recent theoretical advances in spatial predator–prey interactions and relate these with studies of seabirds and pelagic schooling fish and crustaceans. Studies on seabirds and prey have generally assumed that prey are nonresponsive. Predator–prey interactions should, however, be viewed as a 2-way spatial game where seabirds track concentrations of prey while prey move away from areas with high risk of predation. The outcome of the game depends on how seabirds and prey are spatially constrained. Constraints include the spatial distribution of resources, interspecific competition, the location of spawning and breeding areas, and limitations on diving depth. Although game theoretic models can explain some general aspects of the spatial interaction, the spatial distribution of seabirds and prey is generally much more aggregated and elusive than can be expected from the game theoretic equilibrium. This is because spatial pattern is formed through self-organizing behavior that includes schooling, local enhancement and area-restricted search (ARS). Schooling and local enhancement are processes with strong positive density dependence that destabilize the predator–prey interaction locally. However, the unstable local dynamics might be stabilized by spatial constraints and the effects of ARS processes at large scales.

KEY WORDS: Game model · Schooling · Local enhancement · Area-restricted search · *Euphausia superba* · *Mallotus villosus* · *Clupea* spp. · *Diomedea* spp. · *Uria* spp. · *Rissa tridactyla*

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INTRODUCTION

The nature of the relationship between the spatial distribution of predators and the spatial distribution of prey affects the foraging success of predators and the mortality rate of prey. To increase their foraging success, predators should seek out areas with high prey density while prey, in order to reduce the risk of mortality, should move away from areas with high density of predators (Sih 1984, 2005). Pelagic seabirds are highly mobile and conspicuous marine predators that forage on small pelagic schooling fish and zooplankton. They can move over long distances at relatively low cost while their prey has a scale-dependent patchy—and often elusive—spatial distribution (reviewed by Weimerskirch 2007). The develop-

ment of acoustic methodology for measuring the abundance of fish and zooplankton has made it possible to investigate the synoptic spatial distribution of seabirds and their prey along ship transects (see reviews in Hunt 1990, Hunt et al. 1999). Seabirds have a high and constant energy demand, and, combined with their high mobility they can be expected to show a strong aggregative response towards concentrations of prey. However, 30 years of spatial studies of seabirds and prey have yielded highly variable results (see Hunt et al. 1999). Many studies find weak positive or even negative spatial relationships between seabirds and prey (e.g. Woodby 1984, Obst 1985, Safina & Burger 1985, Heinemann et al. 1989, Veit et al. 1993, Logerwell & Hargreaves 1996, Swartzman & Hunt 2000). A few studies report strong positive correlations (e.g. Ryan &

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Cooper 1989, Erikstad et al. 1990, Piatt 1990, Mehlum et al. 1996). Finally, many studies find that the relationship becomes stronger at increasing measurement scales (e.g. Heinemann et al. 1989, Erikstad et al. 1990, Hunt et al. 1992, Logerwell & Hargreaves 1996, Fauchald et al. 2000, Skov et al. 2000).

The spatial pattern of seabirds and prey is formed by a number of different environmental, ecological and behavioral factors. Each factor operates within specific spatial and temporal scales. Moreover, the factors are often hierarchically interlinked so that large-scale processes set the condition for processes at smaller scales (Wu & Loucks 1995). For example, large-scale physical properties of the ocean might set limits to the potential habitat of an organism, while within this habitat, the local distribution might be determined by ecological interactions such as competition or predation. Such hierarchically interlinked processes will produce nested patch mosaic hierarchies where small-scale patches are nested within patches at larger scales (Kotliar & Wiens 1990, Fauchald et al. 2000). For example, the Antarctic krill *Euphausia superba* is aggregated within swarms at a scale of 10s of meters. Swarms are aggregated within patches at a scale of kilometers, and patches are aggregated within concentrations at a scale of 100s of kilometers (Murphy et al. 1988).

A major research task is to unravel the processes that produce the complex spatial pattern of organisms in the marine pelagic ecosystem (e.g. Levin 1992). One such process is the spatial interaction between predator and prey. In this paper, I briefly review recent theoretical advances in the understanding of spatial predator–prey interactions. I argue that the interaction between seabirds and prey should be viewed as a 2-way spatial game where the outcome depends on how the participants are spatially constrained. However, in systems where such constraints are lacking or in systems where prey or predators have an aggregative behavior associated with positive density dependence, highly patchy spatial distribution and elusive relationships can be expected. Schooling, local enhancement and area-restricted search (ARS) are behaviors that will produce elusive and aggregated spatial patterns. I relate these theories with empirical findings within a scale-dependent framework.

THE SPATIAL GAME BETWEEN PREDATOR AND PREY

Although the spatial matching of predators and prey is the result of a 2-way interaction (Sih 2005), studies have focused on either the predator or the prey side of the behavioral response race (Lima 2002). On the predator side, studies have generally assumed that

prey are nonresponsive and have typically addressed optimal foraging and patch use (Stephens & Krebs 1986). Central to this perspective is the idea of the Ideal Free Distribution (IFD) (Fretwell & Lucas 1970). This framework assumes that predators act to maximize foraging efficiency, are free to move among habitat patches, have perfect knowledge about the distribution of resources, are equal competitors, and decrease individual resource intake with predator density. The IFD predicts an evolutionary stable strategy where the distribution of predators will match the distribution of resources and all predators will obtain an equal rate of returns (see e.g. Millinski & Parker 1991). This prediction has been termed the 'habitat matching rule' which predicts a positive spatial relationship between predators and prey.

Contrary to the studies from the predator side of the interaction, studies from the prey perspective have assumed a fixed predation risk and have typically addressed questions such as the trade-off between predation risk and foraging (Abrahams & Dill 1989, Lima & Dill 1990). For example, the diurnal vertical migration of zooplankton from the euphotic zone has been viewed as a behavioral response to avoid predation from visual predators, resulting in a trade-off between feeding and predation risk (Iwasa 1982). Recently, it was proposed that alteration of the composition of the predator community may result in fundamental changes in the habitat use of keystone herbivores with subsequent changes in ecosystem properties (e.g. Ripple et al. 2001, Willis 2007).

Combining both predator and prey perspectives in a modeling framework has been a major task in recent years (van Baalen & Sabelis 1993, Hugie & Dill 1994, Sih 1998, Alonzo 2002, Fiksen et al. 2005, Abrams 2007). These models investigate the behavioral conflict game where predators aggregate in areas of high prey density, while prey are free to move in order to reduce predation risk. The resources are typically distributed in patches of different quality, prey respond to resources and the risk of predation while predators respond to prey availability (Fig. 1). The models evaluate the existence of an IFD in which both prey and predators have reached an evolutionary stable strategy where the system is stable in the sense that individual predators as well as individual prey have equal fitness in different resource patches and cannot do better by moving. According to a number of different models (reviewed in Sih 2005), predators should aggregate in patches with high input of resources. Prey are also predicted to aggregate in the most productive patches; however, as a consequence of increased predation risk, they should have a more uniform distribution among resource patches (Fig. 1). Thus, these models essentially confirm the habitat matching rule, predicting a

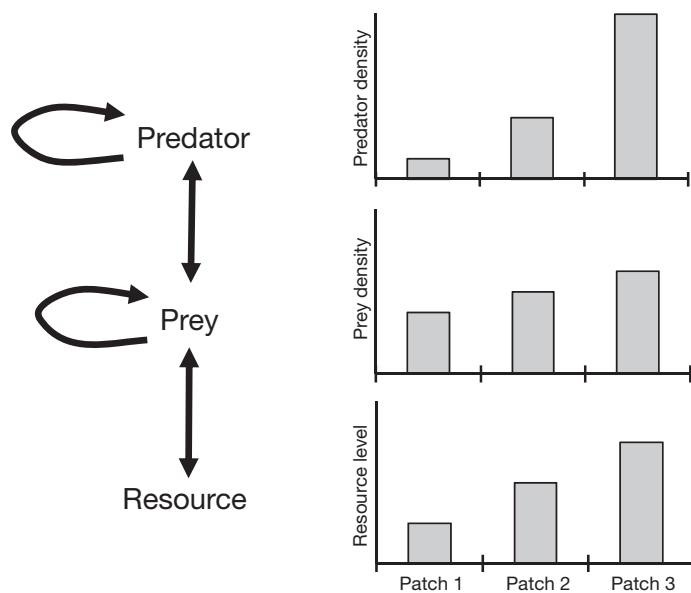


Fig. 1. Behavioral game models of the spatial interaction between predator and prey. Left: general trophic structure of the models (redrawn from Alonzo 2002). Arrows indicate interactions. Predators and prey distribute themselves within patches with different levels of resources. Prey respond to the resource level and the risk of predation, predators respond to prey density. Predators and prey respond to their own density through competition. They are assumed to obey the Ideal Free Distribution assumptions (individuals have perfect knowledge of patch quality and are free to move among patches). The models evaluate the existence of an evolutionary stable strategy where predators and prey are unable to do better by moving to another patch (the gain is equal among patches). Right: generalization of model predictions as suggested by Sih (2005); both predators and prey should aggregate in the most productive patches. However, due to predation risk, prey should have a more uniform distribution across patches than predators

positive relationship between predators and prey. In Sih's (2005) terminology, the predators win the game. He argues that this outcome is due to constraints imposed on prey by the distribution of resources in these models. Because the spatial distribution of resources is fixed, prey is subject to a spatial anchor. If, on the other hand, the predator is subject to a spatial anchor, prey will have a refuge and a negative relationship between predators and prey may be expected. For example, in a model by Alonzo et al. (2003) on the interaction between breeding penguins and krill, penguins were constrained by both the vertical (constraints on diving depth) and horizontal distribution (constraints on travel distance to the breeding colony) of krill. According to this model, krill win the game by distributing themselves offshore and maintaining vertical migration.

In the absence of spatial constraints, conflict games between predators and prey might not have any equilibrium (Schwinning & Rosenzweig 1990, Sih 2005, Abrams 2007). Indeed, changing some of the assumptions of the models might result in a non-equilibrium spatial distribution. For example, Abrams (2007) introduced satiation in the functional responses of predators and prey in a simple resource–prey–predator model and showed that this model was generally spatially unstable. Predator satiation made predator dilution possible and prey accordingly tended to dilute predation risk by aggregating in patches. However, as a consequence of resource consumption and predator aggregation, it would eventually be optimal for prey to move from an aggregation. Consequently, predators chased aggregations of prey from patch to patch in an unstable and cyclic system (Abrams 2007). In these cases where stable and equal fitness between patches is unachievable, the matching between consumer and

resource and between predator and prey should be highly variable.

In summary, theory predicts that spatial constraints will tend to stabilize the spatial distribution of predators and prey (Sih 2005). When prey is constrained by a spatial anchor, the predators will win the race and a positive relationship between predators and prey may be expected. On the other hand, when a spatial constraint is imposed on the predator, prey will win and a negative relationship may be expected. In systems where such constraints are weak and where positive density dependence such as predator dilution is dominant, a highly aggregated and elusive system with no clear pattern of predator and prey matching may be expected (*sensu* Abrams 2007).

Spatial handicaps of prey

The spatial distribution of resources may limit the spatial distribution of prey and thus give the predator an advantage in the spatial 'arms race'. Physical processes in the ocean such as currents, fronts, upwelling, vertical mixing and stratification determine the spatial pattern of primary production and are responsible for the transport and concentration of nutrients and plankton (Haury et al. 1978). The result is a complex and scale-dependent spatial pattern in the resources available to krill and small pelagic schooling fish which in turn are prey for seabirds and other top predators (see review in Hunt & Schneider 1987, Weimerskirch 2007). According to the equilibrium models (see above), seabirds should show a strong affinity to areas characterized by physical properties that enhance or accumulate resources available to their prey.

Several studies have shown that seabirds tend to aggregate in areas with specific oceanographic properties (see Hunt et al. 1999 for review). Elevated abundance of seabirds is found in areas characterized by high production or accumulation of biological matter, such as in frontal areas delineating different water masses (Abrams 1985, Wahl et al. 1989, Pakhomov & McQuaid 1996, Hyrenbach et al. 2007), along the continental edge (Hay 1992, Piatt et al. 2006), or in inshore waters (Harrison et al. 1994). On a smaller scale, local interactions between currents and the sea bottom may structure water masses into zones with different properties. For example, the Pribilof Islands in Alaska are surrounded by a structural tidal front defined as the boundary between well-mixed inshore waters and stratified offshore waters (Fig. 2). This frontal area is characterized by elevated stocks of phytoplankton, zooplankton, fish and seabirds (Kinder et al. 1983, Schneider et al. 1990, Coyle & Cooney 1993, Decker & Hunt 1996, Hunt et al. 1996). Similarly, in the Irish Sea, Durazo et al. (1998) found elevated concentrations of seabirds associated with a tidal front. In the California Current System, small-scale upwelling events

affect prey availability and habitat selection by marbled murrelets *Brachyramphus marmoratus* (Becker & Beissinger 2003). Seabirds that prey on meso zooplankton that are more or less passively transported by ocean currents largely rely on physical processes that concentrate the prey in the upper part of the water column. For example, least auklets *Aethia pusilla* in the northern Bering Sea (Hunt & Harrison 1990, Hunt et al. 1990) and little auks (*Alle alle*) in the North Sea (Skov & Durinck 2000) are found in stratified waters where a shallow pycnocline tends to concentrate copepods close to the surface.

Life history events such as spawning often constrain the spatial distribution of prey to particular areas. For example, the selection of favorable spawning areas by fish might have strong implications for fitness, suggesting strong preference for suitable areas that might be easily predicted and accessed by predators. Studies on auks foraging on small pelagic fish might support this hypothesis. On the eastern shelf of Newfoundland, large breeding colonies of the common murre *Uria aalge* and Atlantic puffin *Fratercula arctica* forage on spawning capelin *Mallotus villosus* (Piatt 1990). Com-

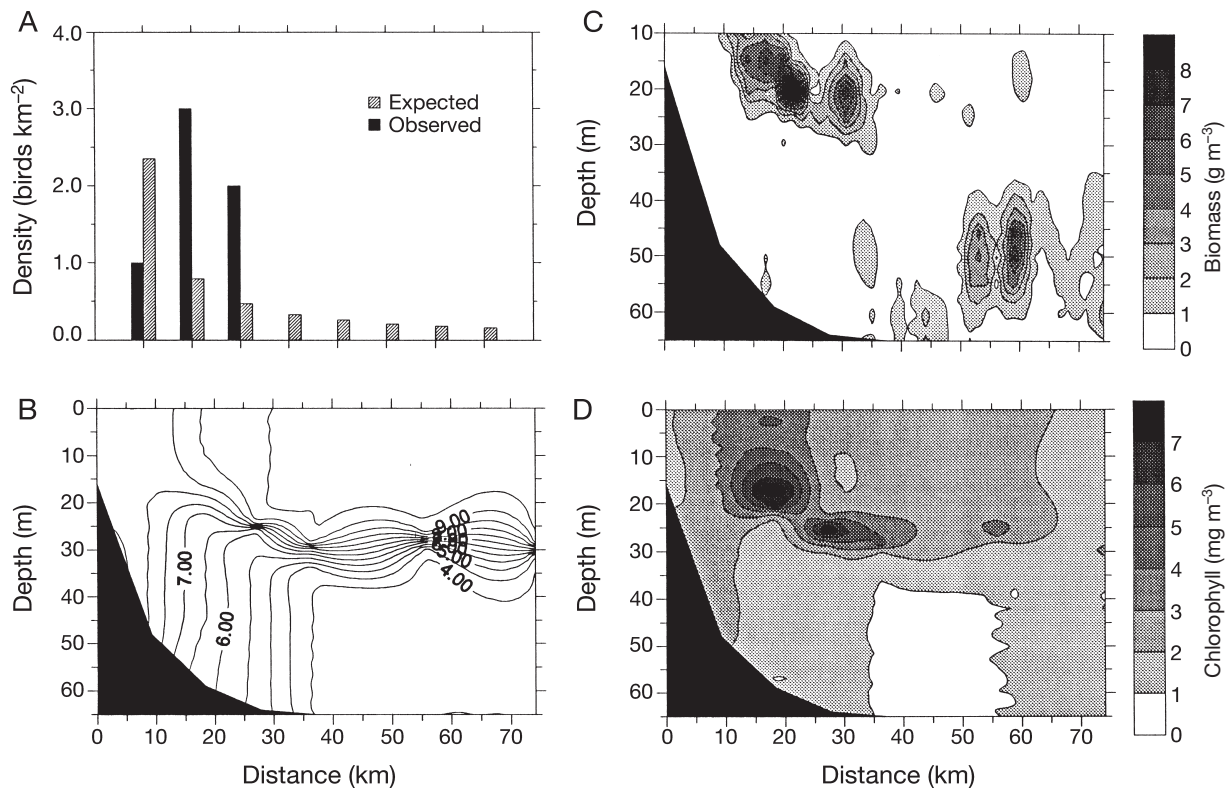


Fig. 2. Aggregation of seabirds, acoustically determined biomass and primary production at a tidal front in the Bering Sea. (A) Expected and observed densities of murrelets (*Uria* spp.). Bars represent densities for each 9.3 km interval along the transect. Expected densities were modeled by a geometric relationship between the distance from the breeding colony and bird density assuming that birds spread out evenly from the colony. (B) Temperature profile (°C), (C) acoustically determined biomass (g m⁻³) and (D) chlorophyll concentration (mg m⁻³). Due to tidal currents, a frontal zone is formed between well-mixed inshore waters and stratified offshore waters. The example is from a 74.1 km long transect radiating out from St. Paul Island (summer 1987).

Figure from Decker & Hunt (1996), with permission

mon murre seem to use a combination of memory and local enhancement to keep in contact with reliable patches of spawning capelin that might last for weeks (Davoren et al. 2003). In the Barents Sea, maturing capelin start a spawning migration from the central parts in late winter towards the coast where they spawn in early spring (Gjøsæter 1998). During migration and spawning, capelin is heavily preyed upon by the cod *Gadus morhua*, seals and seabirds. In a series of studies, Erikstad et al. (1990), Fauchald et al. (2000) and Fauchald & Erikstad (2002) found strong spatial matching between murre (*Uria* spp.) and capelin in this period. However, contrary to the spawning situation, the spatial overlap between capelin and murre during the feeding migration of capelin in late summer is weak (Fauchald unpubl. data). This is in accordance with other studies of murre and nonspawning schooling fish that have shown either weak spatial matching (Woodby 1984, Swartzman & Hunt 2000), matching only on relatively large scales (Skov et al. 2000) or matching that is dependent on oceanographic properties that enhance resource availability to the fish (Cairns & Schneider 1990, Decker & Hunt 1996, Logerwell & Hargreaves 1996).

Spatial handicaps of predators

When predators are spatially constrained, prey may escape into spatial refuges (see e.g. Rose & Leggett 1990). One ecological interaction that can impose a spatial constraint is interspecific competition, which can reduce the realized niche of a predator and therefore potentially constrain its habitat use (Chase & Leibold 2003). Different seabird species have different adaptations and are consequently associated with different parts of the pelagic ecosystem (Abrams 1985, Wahl et al. 1989, Ainley et al. 1992, Harrison et al. 1994, Ballance et al. 1997, Vilchis et al. 2006). For example, in the eastern tropical Pacific, Ballance et al. (1997) identified 3 distinct seabird assemblages associated with areas of different productivity. Small species with low cost of flight, the 'sooty tern flocks', were associated with unproductive waters; intermediate species, the 'Juan-Wedge flocks', were associated with areas of intermediate productivity; and large species with high cost of flight, the 'booby flocks', were associated with areas of high productivity. They suggested that a trade-off between competitive ability (large size) and foraging ability (low cost of flight) was responsible for the niche separation between the different flock types. The spatial constraints imposed by interspecific competition might therefore reduce the possibility of the subdominant species occupying the habitats with the highest availability of prey, con-

sequently reducing the spatial match between these predators and their prey at large scales.

During breeding, seabirds are spatially constrained by their duties at the breeding colony. Because seabirds have to return to a central place (i.e. the nest) between foraging bouts, seabirds act as central place foragers in this period (cf. Orians & Pearson 1979). The feeding area that they exploit is determined by their travel capabilities, the spatial distribution of prey and the frequency by which they return to the nest (see e.g. Weimerskirch et al. 1997). A large majority of seabird species (~96%) are colonial breeders (Coulson 2002) and the competition for food close to the colony might be strong. Accordingly, it has been suggested that the spatial distribution and size of colonies are determined by both the availability of prey and intraspecific competition (Ashmole 1963). Several recent studies support the hypothesis that competition is an important factor in shaping colony size and distribution: foraging range and trip duration have been found to increase with colony size (Lewis et al. 2001, Ainley et al. 2003), the foraging range of birds from neighboring colonies overlap less than could be expected from the distance between the colonies alone (Ainley et al. 2003, 2004, Grémillet et al. 2004), and the availability of prey around the colony decrease with increasing colony size (Forero et al. 2002, Ainley et al. 2003). From the prey's perspective, the risk of predation decreases with increasing distance from the colony, the colonial breeding of seabirds therefore generating a potential refuge. Lewis et al. (2001) suggested that prey could escape into this refuge by a simple mechanism of diffusion. If prey responds to predator attack by lateral movement, then prey will diffuse out from the colony since the attack rate is highest close to the colony. This diffusion would lead to a slowly growing 'halo' (Ashmole 1963) with reduced density of prey close to the colony (Lewis et al. 2001). Alternatively, prey might respond to attacks by swimming downward, thereby becoming inaccessible to surface-feeding seabirds (see below). In this case, prey availability close to the colony would be less. In Prince William Sound, Alaska, Ainley et al. (2003) found that the prevalence of fish schools close to the surface was inversely related to the colony size of black-legged kittiwakes *Rissa tridactyla*. They suggested that predator avoidance might be an important density-dependent factor that regulates the number of foraging kittiwakes in this area.

One important factor that constrains the movement of seabirds is the trade-off between movement under and above the sea surface. Seabirds that are adapted for efficient diving have high energy expenditure for flying, and prey may accordingly escape by moving horizontally. Seabirds that are adapted for efficient flying are able to utilize only the upper meter of the

sea and prey may escape by hiding in the deep. Surface-feeding seabirds are largely dependent on other predators for access to food. Predatory fish, diving seabirds and sea mammals drive schools of prey fish and krill to the surface, making them available to surface-feeding seabirds (Hoffman et al. 1981, Safina & Burger 1985, Harrison et al. 1991, Mills 1998). Multi-species seabird flocks around South Georgia are, for example, generated when seals and penguins drive krill to the surface (Harrison et al. 1991). Black-browed albatrosses *Diomedea melanophrys* initiate and dominate these feeding flocks and act as attractors of other foraging seabirds (Harrison et al. 1991, Grünbaum & Veit 2003). Because surface-feeding seabirds are able to utilize only a very small proportion of the vertical habitat of their prey, prey may easily escape predation with minimum cost. Surface-feeding birds are therefore likely to have a very small impact on the prey population. On the other hand, diving seabirds could cover a larger proportion of the vertical habitat of their prey. Moreover, because these predators operate in the most productive euphotic zone, their prey are likely to face a trade-off between a risky and productive habitat versus a safe and unproductive habitat (Alonzo et al. 2003). Diurnal vertical migration is a strategy that allows prey to escape visual predators during the day while they may feed in the euphotic zone at night (Iwasa 1982). Alonzo et al. (2003) modeled the spatial interaction between penguins and krill and showed that penguins could possibly have a strong effect on the spatial distribution of krill by forcing them to stay offshore and undertake diurnal vertical migration. Willis (2007) suggested that the large baleen whales in Antarctic waters are highly effective predators on krill below the euphotic zone and that krill as a consequence reduce its vertical migration under high predation pressure from whales. He suggested that this behavioral response was responsible for the 'Antarctic paradox', i.e. that krill abundance has failed to increase after the decimation of baleen whales during the 20th century. Under high density of whales, the ecosystem was much more productive simply because krill was forced to stay in the euphotic zone. After the removal of whales, it became optimal for krill to undertake vertical migration to avoid predation from e.g. seabirds, and the ecosystem consequently became less productive.

SPATIAL PATTERN GENERATED BY SELF-ORGANIZATION

Within the framework of the IFD theory, it is expected that predators and prey will distribute them-

selves freely according to costs and benefits until a stable equilibrium has been achieved. According to this theory, both competition and predation are expected to make the distribution of organisms more uniform across resource patches. However, in marine pelagic ecosystems this is not the case. Spatial complexity generally increases with increasing trophic level (Levin 1992). Thus, the spatial distribution of pelagic schooling fish is more aggregated than that of their resources. In fact, while the IFD theory predicts a more even distribution of competitors due to increased competition under high density (Sutherland 1983), the aggregation of capelin actually increases in years of high abundance when intense competition for resources is expected (Fauchald et al. 2006). Moreover, the spatial distribution of predators and prey is highly elusive (e.g. Fauchald et al. 2000, Becker & Beissinger 2003, Fauchald & Tveraa 2006). Predators are not able to stay in contact with patches of prey for long periods of time (Harrison et al. 1991, Grünbaum & Veit 2003) and large portions of prey patches are at some time not subject to predation (Obst 1985, Heinemann et al. 1989, Swartzman & Hunt 2000), suggesting that the distribution of predators and prey is generally far from any IFD equilibrium.

The reason for the discrepancy between the IFD predictions and the observed spatial pattern is that seabirds and prey seldom comply with the IFD assumptions. These assumptions are that predators and prey have perfect information about the environment and that they are free to move to any part of the environment with no associated cost. It has long been known that the process of learning where prey patches are can lead to differences between the actual distribution of a predator and that predicted by the IFD (Bernstein et al. 1988). Constraints on information and movement might accordingly be central for the outcome of the spatial game between predators and prey. Furthermore, relaxation of the assumption of omniscient and unrestricted individuals means that individuals must respond to local stimuli in order to maximize their foraging success or minimize the risk of predation. Such local responses include local interactions between individuals such as those between competitors or between predators and prey. When repeated, local interactions between individuals result in what has been termed 'collective self-organizing behavior' that again produces complex and possibly adaptive spatial patterns at a higher level of organization (see review in Sumpter 2006). For example, in the model of Lewis et al. (2001) (see above), the local response of prey to the attacks from seabirds results in a spatial pattern where the density of prey increases with increasing distance from the seabird colony.

Schooling

Schooling in fish is a classic example of collective self-organizing behavior (self-organization) where simple interactions between individuals produce a complex spatial unit (Parrish & Edelstein-Keshet 1999). More than 50% of all known fish species form schools at some part of their lives (Shaw 1978) and protection from predation has been the main explanation for this behavior (Partridge 1982, Parrish & Edelstein-Keshet 1999). For an individual facing a predator, it is adaptive to seek protection by keeping close to conspecifics, thereby diluting the risk of attacks (Hamilton 1971). However, a school of fish is a highly valuable entity that attracts predators. Joining a school is therefore adaptive only when the increased protection from dilution is greater than the increased risk of predation due to increased conspicuousness to predators. Low visibility reduces the risk of being detected, and Partridge (1982) suggested that low visibility makes schooling a particularly adaptive anti-predator behavior in the marine pelagic environment. However, whenever predators are able to find and aggregate effectively on concentrations of prey, schooling can be a hazardous strategy. Temming et al. (2007) showed for example how an aggregation of >50 million juvenile cod within an area of only 18 km² was entirely wiped out in 5 d by predatory whiting *Merlangius merlangus*. To avoid aggregation of predators, it is therefore essential for the school to move rapidly and unpredictably (see e.g. Mitchell & Lima 2002). Rapid vertical and horizontal movement makes it difficult for predators to stay in contact with the school for long periods of time and will hinder predators from aggregating on the school. Presumably as a consequence, krill and pelagic schooling fish are highly elusive and patchy resources.

In pelagic schooling fish and krill, anti-predator behavior will often conflict with other types of behavior that enhance fitness components such as growth and reproduction. The observed spatial behavior will therefore be the result of a compromise between survival, growth and reproduction (e.g. Nøttestad et al. 1996, Axelsen et al. 2000, Johnsen & Skaret 2008). Such trade-offs change markedly between different life stages resulting in changed anti-predator behavior. For example, one marked shift in behavior happens from pre-spawning to spawning to post-spawning in Atlantic herring *Clupea harengus* (Nøttestad et al. 1996, Axelsen et al. 2000). Prior to spawning, herring should give priority to survival. Accordingly, herring approach the shallow, coastal spawning grounds in dense, nonfeeding, fast and deep swimming schools. In the spawning grounds, spawning takes place on the bottom where the spawners are highly vulnerable to predation. Thus, schools of spawners await in a safe

pelagic position, and then at some point, descend to the bottom for spawning. After spawning, survivors should give priority to recovery and growth. Accordingly, post-spawning herring leave the spawning grounds in smaller, less dense feeding schools with a shallow position in the water column. Shifts in the trade-offs that regulate the spatial anti-predator behavior could be reflected by changes in the spatial predator–prey interaction. For example, a small-scale spatial mismatch between seabirds and prey prior to spawning could be expected to turn into a spatial match during and after spawning. However, I am not aware of any studies that explicitly address this question.

Local enhancement

Seabirds may use a combination of visual and olfactory cues to detect patches of prey (Nevitt et al. 1995, Davoren et al. 2003). However, they may also indirectly locate schools or swarms of prey by observing the foraging behavior of other seabirds (Hoffman et al. 1981, Harrison et al. 1991, Grünbaum & Veit 2003, Silverman et al. 2004). This strategy has been termed 'local enhancement' and simply assumes that it is much easier for a seabird to detect foraging conspecifics than it is to detect prey patches directly. Accordingly, when seabirds search for prey, they can either detect a patch of prey directly or they can join a flock of other seabirds that has already found a patch. Depending on the asymmetry in the detectability of prey versus other foragers, local enhancement will produce a highly aggregated spatial distribution of predators. Accordingly, intense predation will be concentrated to a few resource patches while many patches will be free from predators. This type of spatial distribution of seabirds and prey has typically been found on small spatial scales when prey consists of pelagic schooling fish or krill (e.g. Obst 1985, Heinemann et al. 1989).

Local enhancement is adaptive only when prey is patchy and elusive; thus, this behavior can be viewed as an adaptive response to schooling. Both schooling and local enhancement are examples of self-organization where individual behavior results in a complex and aggregated spatial pattern on larger scales. Moreover, both phenomena are thought to produce positive density dependence. For schooling, there is a minimum number of individuals needed to create an effective school, with the protection from predation through dilution increasing with increasing group size (Courchamp et al. 1999). For local enhancement, more seabirds will be more effective in locating prey patches, and individual foraging success will therefore

increase with increasing seabird density (see Fig. 3, Grünbaum & Veit 2003). Positive density-dependent regulation linked to aggregative behavior will generate highly unstable spatial interactions between predators and prey (Abrams 2007). In light of this destabilizing factor, how is a long-lasting interaction between schooling prey and their predators possible? The answer to this question is probably that schooling and local enhancement are local processes operating on small spatial and temporal scales. Thus, although predation might have devastating effects on local aggregations of prey (e.g. Temming et al. 2007) and elusive prey might have strong negative impact on the foraging success of seabirds locally (e.g. Suryan et al. 2002), the effects may be leveled off on larger spatial scales. Indeed, it can be argued that spatial constraints that tend to stabilize the interaction (e.g. physical oceanography)

generally operate on larger spatial scales (Weimerskirch 2007) while aggregative behavior linked with positive density dependence are mainly prevalent on smaller scales.

Density-dependent migratory waves

Although studies on self-organization have generally focused on phenomena occurring at relatively small spatial scales, simple behavioral mechanisms might also be responsible for spatial patterns generated at much larger scales. One behavioral mechanism that can produce a large-scale spatial pattern in the distribution of organisms is ARS (Wilson & Richards 2000, Fauchald et al. 2006). According to the ARS theory, an individual should increase its turning rate and

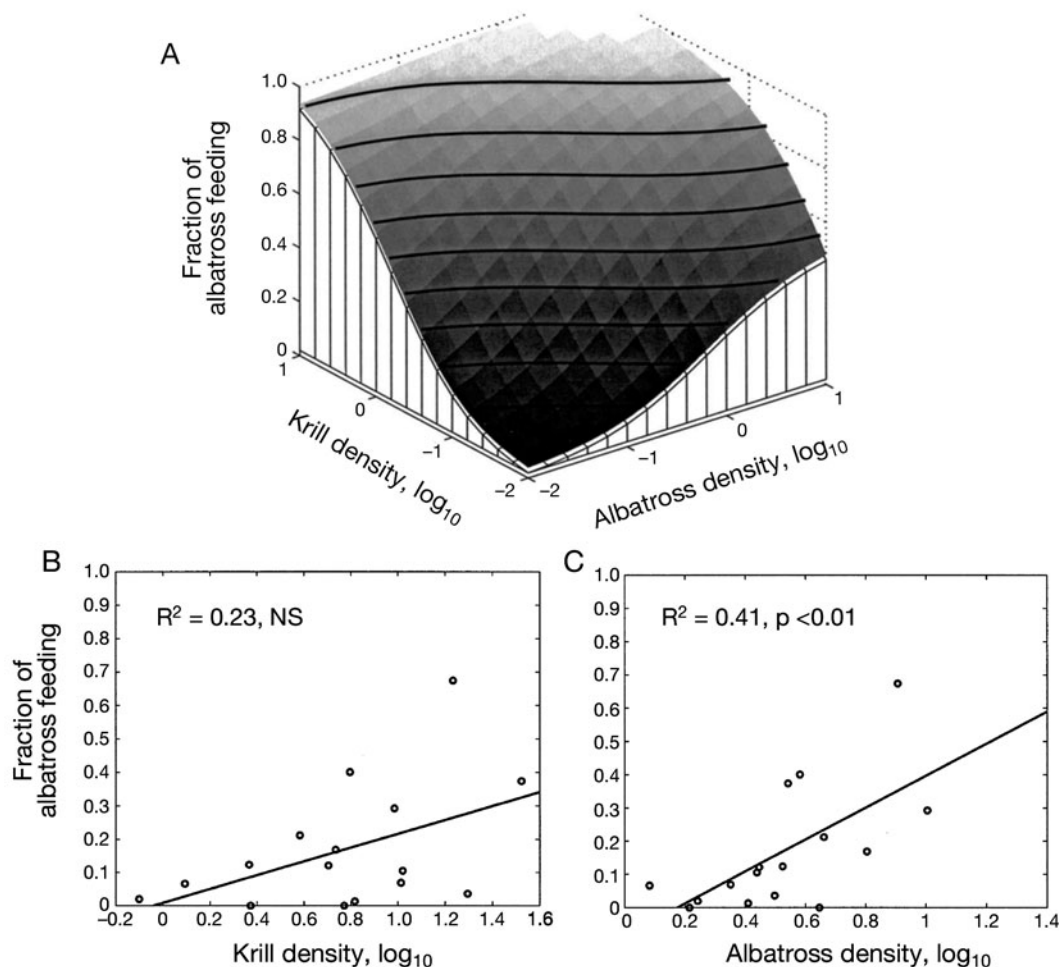


Fig. 3. Positive density dependence through local enhancement in albatross feeding flocks. Foraging success is measured as the fraction of albatrosses feeding. (A) Predictions from a foraging model of local enhancement that assumes that the detectability of foraging albatrosses is 100× the detectability of krill swarms. The model predicts that foraging success should increase with increased density of krill and albatrosses. (B, C) Empirical relationships between krill density, albatross density and albatross foraging success along 16 transects of 50 nautical miles, close to South Georgia (summer 1986). (From Grünbaum & Veit 2003, used with permission)

reduce its speed in response to an elevated reward from a resource. This behavior will concentrate the search activity of a forager to profitable areas with high resource levels (Kareiva & Odell 1987). Wilson & Richards (2000) showed that this simple foraging principle might result in resource-mediated, density-dependent group formations. In their model, dense aggregations of foragers that swept through the habitat were formed under high density. For example, a school of feeding fish might create a spatial gradient in the density of prey, with high density in front and reduced density behind the school. According to the ARS theory, schools lagging behind such resource gradients will speed up while schools ahead of the gradient will slow down. As a result, schools will automatically congregate, and, under high density, will generate a migratory wave that sweeps across the ocean and effectively reduce the density of prey to very low levels. This phenomenon has been termed density-dependent migratory wave (DDMW), and was suggested by Fauchald et al. (2006) to be responsible for the increased aggregation and spatial displacement of capelin during their feeding migration in years of high capelin abundance in the Barents Sea. In a DDMW, simple collective individual behavior is responsible for the formation of a large-scale spatial pattern with potentially strong perturbing effects on the ecosystem.

Nested area-restricted search

It has been suggested that seabirds use ARS to track the scale-dependent and patchy spatial distribution of prey (Fauchald 1999, Veit 1999, Pinaud & Weimerskirch 2005). However, when prey is distributed within nested patch hierarchies, a free-ranging predator should adopt some form of nested ARS (Fig. 4; Fauchald 1999). For example, in a study of murres foraging on capelin during the capelin spawning migration in the Barents Sea, Fauchald et al. (2000) found 3 nested levels of patchiness. They suggested that murres used nested ARS to track the migrating capelin. ARS in its simplest form is a strategy where a predator changes its search pattern according to the encounter rate with prey items. In a nested patch system, it is essential that the scale of the search pattern is tuned to the scale of the level in the hierarchy where the predator is situated (cf. Fig. 4 in Fauchald & Tveraa 2006). Accordingly, the movement pattern of predators will mimic the spatial pattern of the prey. Moreover, depending on their search efficiency, the spatial distribution of predators will resemble the spatial distribution of the prey (Fauchald et al. 2000).

Recently, several telemetry studies have found that the foraging pattern of seabirds conforms with a nested

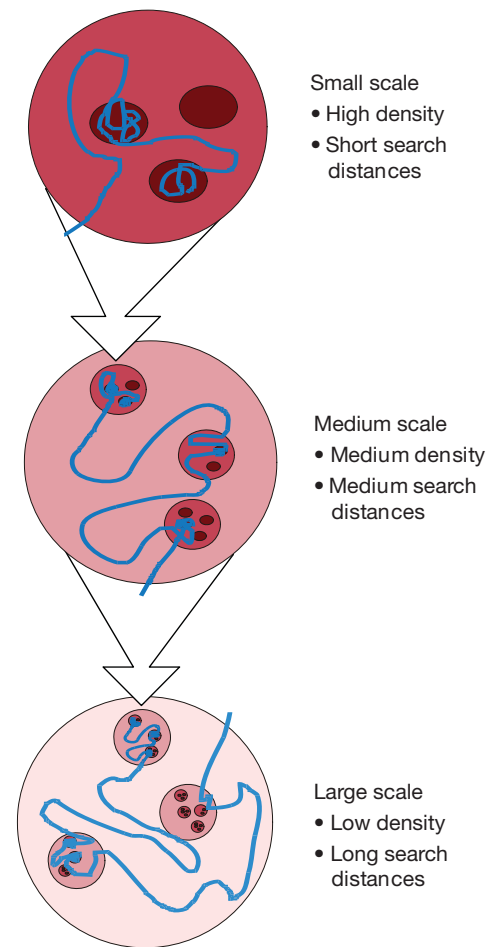


Fig. 4. Hierarchical patch system with high-density small-scale patches (dark red) nested within low-density large-scale patches (light red). Blue line is the search pattern of a forager using a nested area-restricted search

ARS (Fritz et al. 2003, Pinaud & Weimerskirch 2005, 2007, Fauchald & Tveraa 2006). However, few studies have tested whether ARS in seabirds is actually triggered by encounters with prey. Weimerskirch et al. (2007) demonstrated that wandering albatrosses *Diomedea exulans* did not show any strong ARS response to prey capture at large scales. The albatrosses only showed increased sinuosity in their movement pattern after prey encounters at small scales. They suggested that the wandering albatrosses used other cues to modify their movement pattern at large scales. Indeed, when prey density is low, encounter rate might be a very sparse source of information. Other important sources of information can come from e.g. learning and recent spatial experience (Irons 1998, Davoren et al. 2003), olfactory cues (Nevitt et al. 1995, 2008), and the foraging activity of other animals (i.e. local enhancement) (Grünbaum & Veit 2003).

Compared to a random strategy, nested ARS is a highly effective search strategy (Fauchald 1999). The search efficiency depends on how fast information is gathered relative to how fast the system changes. How fast information is gathered depends on 2 factors (Fauchald 1999). First, if the encounter rate between predator and prey is high, then the information flow is also high. Thus, the ability to track the system should increase for increased prey abundance. Second, a big difference in prey density between different levels in the hierarchy increases the predator's ability to discriminate between them, hence increasing the predator's ability to track the system. According to the DDMW mechanism, increased abundance of schooling prey will result in increased aggregation. Presumably within certain limits, both increased prey aggregation and prey abundance should increase the predator's ability to track the system. This was actually observed in the interaction between capelin and murre in the Barents Sea (Fauchald & Erikstad 2002). In years of high capelin abundance, capelin was more aggregated and there was a closer spatial match between capelin and murre compared to years of low capelin abundance. This mechanism would certainly protect the prey population at low density, and would, in contrast to local enhancement and schooling, tend to stabilize the predator–prey interaction.

CONCLUSIONS

Thirty years of studies have shown that the spatial distribution of seabirds and their prey seldom fits the simple habitat matching rule predicted by the Ideal Free Distribution theory. The spatial match between seabirds and prey has often been found to be much lower than expected. One reason for the discrepancy between theory and empirical findings is the assumption of a nonresponsive prey. To understand the spatial interaction between predator and prey, it is essential to realize that this is a 2-way interaction including responses and counter-responses in a behavioral game. Thus, the expectation of a strong spatial correlation has been exaggerated in many cases. How predators and prey are spatially constrained and how such constraints affect the spatial interaction are essential for the outcome of the spatial race. Such constraints include the spatial distribution of resources, interspecific competition, the location of spawning and breeding areas, and limitations with respect to diving depth. The spatial pattern of seabirds and prey is often found to be more aggregated and elusive than could be expected from the equilibria predicted by game theoretic models. The major reason for this is the formation of spatial patterns through collective self-

organizing behavior. Such behavior includes schooling, local enhancement and area-restricted search. Local enhancement and schooling are aggregative behaviors that cause positive density dependence at local scales. This kind of self-organizing behavior will therefore have a strong destabilizing effect on the predator–prey interaction locally. However, spatial constraints on predators and prey will tend to stabilize the interaction at larger scales. Thus, a large spatial extent is of vital importance in stabilizing predator–prey interactions in the pelagic ecosystem.

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Analytical approaches to investigating seabird–environment interactions: a review

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ABSTRACT: A goal of seabird ecology is to relate the physiology, population dynamics, distribution and behaviour of seabirds with their biotic and abiotic environments. One of the most challenging aspects is to understand how seabirds interact with their environment when direct observations are not always possible or practical. In the present paper, we reviewed 218 published studies that examined associations between seabird distribution, behaviour and their environment, in order to assess current trends, weaknesses and the future directions of research. Based on the number of publications, it is evident that the field is growing rapidly and that methods for evaluating seabird distribution are becoming increasingly more sophisticated and are changing from Eulerian (grid-like) to Lagrangian (particle-like) data types. This has been accompanied by a reduction in the spatial and temporal scale of observation, where, in most cases, no behavioural information is inferred from Lagrangian data; instead they are often used as if they were Eulerian data. In parallel, environmental remote sensing is becoming more common; however, we did not record significant changes in the statistical approaches used to describe seabird distributions and used to link them with oceanographic variables. In particular, despite the spatially explicit nature of the data, spatial statistics have rarely been used. The vast majority of studies used environmental variables that described water masses (descriptive approach), whereas a few studies determined oceanographic features that enhance prey availability to seabirds (process-based approach). Future studies could enhance their ecological interpretation of seabird–environment interactions by making greater use of ad hoc statistical approaches that facilitate appropriate pattern detection (e.g. area-restricted searching pattern for birds, mesoscale patterns for environment). Furthermore, appropriate hypothesis testing and modelling that accounts for the spatially explicit, multiscale and multivariate nature of the interaction between seabirds and their habitats is recommended. Although quantitative methods currently exist (but are rarely used), further application could greatly improve our understanding of the processes linking seabird distribution to their environment.

KEY WORDS: Habitat · Top-predators · Seabirds · Interactions · Surveys · Tracking · Methods · At-sea ecology

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INTRODUCTION

Marine ecosystems are often difficult to study; as so aptly stated by Monod (1991): nothing is more difficult to study than something you cannot see. Furthermore, studies of seabird foraging ecology are complicated by the great distances covered by foraging marine birds

coupled with the associated difficulty of observing prey distributions far-out at-sea. As a result, the functional relationships between seabird behaviour and their biotic and abiotic environments remain elusive. The first investigations into seabird ecology (e.g. Ashmole 1971) relied on land-based observation of seabird behaviour and diet studies (Ainley et al. 1981, Ainley

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1990). Observations of seabirds at-sea were later undertaken from opportunistic or dedicated vessel surveys (Haney 1985a, 1987a, Hunt 1991, Hunt et al. 1992, Veit et al. 1993). More recently, traditional land- and ship-based observations have been complemented by modern observation technologies, the implementation of which now provides powerful 'eyes' to observe the ecosystem: satellite remote sensing, acoustic surveying, or miniaturized electronic tagging (Haney 1985b, 1986c, Ainley et al. 1995, Wilson et al. 2002, Cooke et al. 2004, Burger & Shaffer 2008). Undoubtedly, the field of seabird ecology has been burgeoned by this rich set of scientific approaches; to our knowledge, no critical evaluation of the tools commonly employed to link seabird locations and their environment exists.

The goal of the present paper was to review and summarize how scientific approaches and methodological tools in seabird ecology have evolved. In this review, we also highlight state-of-the-art techniques for evaluating seabird distribution and habitat associations, as well as speculate on promising future directions for research. It is important to note that, contrary to classical reviews, our goals were not to be instructive about methods per se, but rather to highlight utilization trends by authors in the field and to speculate on how these trends might relate to changes in conceptual approaches.

MATERIALS AND METHODS

This work is based on the analysis of contents from published research articles. Research articles were selected with the 'ISI Web of Knowledge' (Thomson Reuters) search engine, using the following search criteria:

Topic=((seabird* AND (distribution OR abundance OR track* OR at-sea observation)) AND (ocean* OR front* OR edd* OR prey))

Timespan=All Years

Refined by: Subject Areas=(Environmental Sciences & Ecology OR Zoology OR Marine & Freshwater Biology OR Oceanography OR Biodiversity & Conservation OR Fisheries OR Behavioral Sciences OR Evolutionary Biology)

These search criteria returned 1286 papers from which we removed all papers that focused exclusively on toxicology, parasites, pollution, population trend or breeding performance, predation and interaction with terrestrial mammals, diet and chick growth, or prey biology. The remaining 461 papers were collected and further evaluated for relevance to the topic.

Papers were considered relevant and included in subsequent analyses if they reported both positional data of seabirds and at least one associated environ-

mental variable. The presence of fishing vessels or fisheries effort data were considered environmental variables. This yielded a total of 218 publications on which our review was based. We recognize that some relevant publications may have been missed (particularly book chapters, books and unpublished reports); however, our review should be representative of research in the field.

The following questions were used to characterize the analyses presented in the reviewed manuscripts:

- How was the distribution of seabirds obtained?
- How was the distribution of seabirds modeled/summarized/analyzed?
- How were the environmental variables obtained?
- Which environmental variables were used?
- How was the association between seabird distribution and environmental variables characterized?

Responses to these questions were then summarized in order to quantify the methodological techniques used in the reviewed papers. In order to analyze temporal trends in publication and methodological techniques, we separated publications into 5 yr bins, as a compromise between the time resolution and the number of publications in each bin (as shown in Fig. 1).

We have created a bibliographic library of the relevant papers, and interested parties can contact the corresponding author for copies.

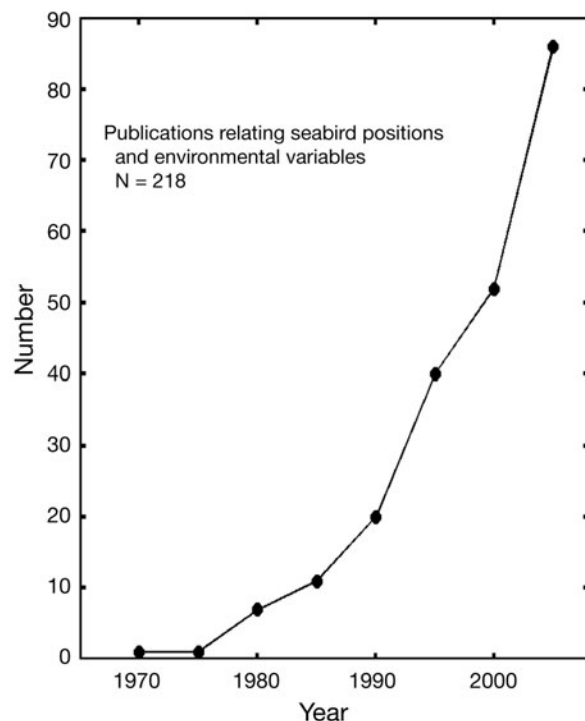


Fig. 1. Temporal distribution of the 218 research articles analyzed in the present study (see 'Materials and methods' for selection criteria)

RESULTS

Research on free-ranging seabirds and ecology at-sea has increased from a few papers a year in the 1970s, to over 15 yr⁻¹ today (Fig. 1). This trend coincides with the increased availability of personal computers, a change that impacted not only the way data were collected, but also the level of analytical sophistication employed.

Seabird locations

At-sea, ship-based observation of seabirds has been the traditional method of determining seabird distribution. Across all years surveyed, at-sea surveys and observations of birds at sea have been the dominant form of study (Fig. 2). Ship-based observations can be further divided into 2 methodological groups: the classical transect method and the punctual observation method. This latter method typically represented seabird observations performed by observers on board vessels during fishing operations (Abrams 1983, Abello et al. 2003). Punctual observations represented <10% of the number of studies using ship-based observations in all 5 yr bins since 1985, except in the 2005 bin, in which it rapidly increased to 23.5% of the number of papers using ship-based observations.

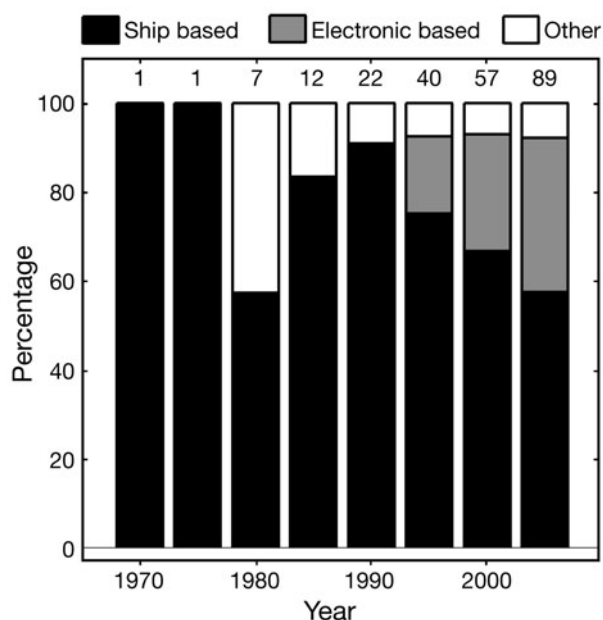


Fig. 2. Temporal distribution of methodological approaches used to obtain positional observations of seabirds at-sea in 218 relevant research articles. Bins span 5 yr, and numbers indicate the total number of occurrences of the methodological techniques, not the number of papers. The category 'other' includes land-based counts, plane transects and bycatch

In contrast to traditional ship-based methodologies, seabird distributional data have also been obtained using microprocessor-based transmitting or data logging tags. This methodology consists of calculating animal locations using electronic tags directly attached to the animal. This includes satellite tracking (Argos transmitters [Berrow et al. 2000], GPS receivers [Awkerman et al. 2005]), global location sensing (GLS) based on light (archival light-level tags; Phillips et al. 2006), radio telemetry (VHF transmitter; Furness et al. 2000) and dead-reckoning (speed/bearing recorders; Benvenuti et al. 1998). The use of electronic-based methodologies, which appeared in the literature in the early 1990s, has continued to increase ever since, due to rapid advances in related technologies (Fig. 2) (Wilson et al. 2002). The Argos tracking system was the only electronic methodology used in papers published in the mid-1990s, and remains the most common method used (>67% of papers using electronic-based methods). However, its relative application has decreased recently as GPS-based and GLS-based tagging studies increased, both of which equally contributed 26% of all papers using electronic methodology in the 2005 bin. VHF and dead-reckoning methods appeared marginal, and therefore we do not detail their contribution here. With the advent of daily diary tags (Wilson et al. 1991, 2006, 2007, 2008), it is conceivable that dead-reckoning tags will be used more often in the future.

Other methods to determine seabird distribution have also been reported in the literature (e.g. plane transects, land-based observations and bycatch during fisheries operations), but these methods contributed minimally to the number of published research papers (Fig. 2). The apparent importance of the 'other' group in the 1980 bin results from small sample size bias (only 7 papers in this category).

Seabird distribution data have been reported in the literature as simple locations or density grids, as well as using more quantitative indices such as computing kernel densities (van Franeker et al. 2002, Awkerman et al. 2005, Clarke et al. 2006). The simple display of distribution data has been much more commonly used than quantitative indices, with proportions ranging from 80 to 100% of the number of papers for any given 5 yr period.

Environmental variables

Environmental data collected *in situ* are found in the majority of studies in all 5 yr bins (Fig. 3). The use of aerial surveys, data from the literature, animal-borne sensors, or general geographic knowledge to extract environmental information does not show a

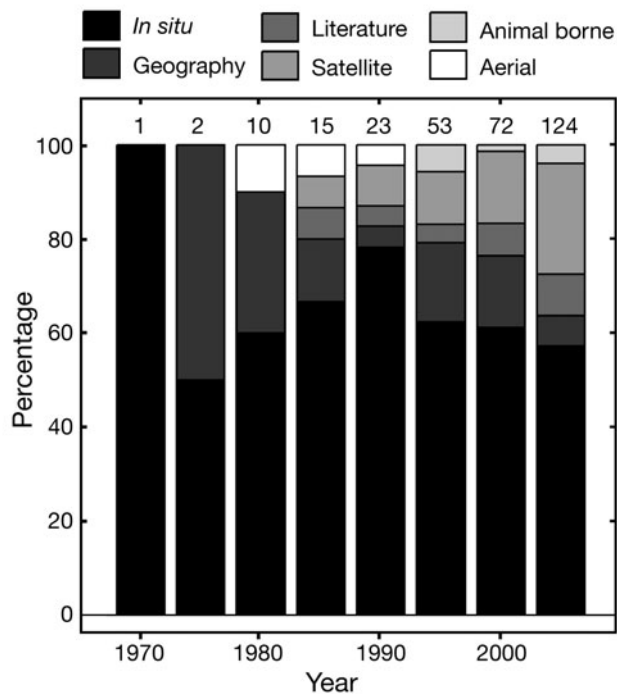


Fig. 3. Temporal distribution of the methodological approaches used to collect environmental data in the 218 relevant research articles used in the present study. Numbers indicate the total number of occurrences of the methodological techniques, not the number of papers

clear trend in time (Fig. 3). The relative contribution of satellite remote-sensing data increased at a relatively slow rate (2.3 more papers per 5 yr) between the mid-1980s and the mid-1990s, but has now become much more common in the last decade (6.0 more papers per bin). The trend has increased exponentially (data not shown) and does not show signs of slowing down (23.4% of occurrence in the 2005 bin, the largest so far).

We identified a total of 101 different environmental variables in all of the 218 research articles. These variables were regrouped into 22 'variable types' based on the type of environmental parameters involved (Table 1). The relative utilization of these variable types is extremely unbalanced, with 4 types (temperature, salinity, prey and zone) representing >50% of all variables (Table 1). The remaining 18 types contributed 45% of all variables, and included extremely diverse variables, from dissolved oxygen to bathymetry (Table 1). The contribution of variables describing an oceanographic structure (grouped as 'mesoscale features'; Ribic et al. 1997, Ainley et al. 1998, Nel et al. 2001) and thought to have a positive effect on the availability of prey to seabirds, such as a front or an eddy (as opposed to variables physically describing a water mass), is relatively minor (4.8% of all variables; Table 1).

Table 1. Description and relative contributions of environmental variables used in 218 research articles linking seabird positional information with environment characteristics. Variables are ranked by relative contribution

Variable	Short description	Relative contribution (%)	Cumulative (%)
Temperature	Sea surface temperature (SST), SST gradient, anomaly	23.53	100.00
Salinity	Salinity, salinity at depth, halocline	14.62	76.47
Prey	Prey distribution, density, depth	9.77	61.86
Zone	Sanctuary, oceanic domain, exclusive economic zone	6.80	52.08
Bathymetry	Bathymetry, bathymetry gradient, substrate	6.40	45.28
Meteorological features	Storm, rain, weather, cloud, air pressure	5.56	38.88
Mesoscale features	Eddy, any type of front, Langmuir circulation	4.81	33.32
Distance	Distance to colony, distance to shore	4.12	28.51
Chlorophyll	Chlorophyll, chl gradient, depth of chl max.	3.90	24.39
Ice	Ice, iceberg, ice edge, ice movement	3.53	20.49
Wind	Wind speed, wind direction, wind stress curl	2.62	16.96
Boats	Boat following, fisheries effort, fisheries type, fishing area	2.59	14.34
Plankton	Plankton distribution and/or abundance	2.47	11.75
Swell / Wave	Swell height, swell direction, sea state	2.32	9.27
Prim. prod.	Primary productivity / production	1.78	6.95
Other	Oil, human recreational use, aquaculture, <i>Sargassum</i> , internal wave	1.71	5.17
O ₂ / CO ₂	Dissolved oxygen and/or carbon dioxide	1.71	3.46
Upwelling	Upwelling, upwelling intensity	0.46	1.75
Tide	Tide, tide speed	0.43	1.29
SSH	Sea surface height (SSH), SSH gradient, anomaly	0.42	0.86
Density	Water density	0.29	0.43
Current	Current, current profile	0.15	0.15

Association between seabird distribution and environmental variables

We categorized a total of 43 different statistical techniques in all selected papers that we grouped into 6 broad categories (Fig. 4, Table 2): (1) qualitative approaches (e.g. mapping, geographic information systems [GIS]) aimed at displaying the data and supporting pertinent hypotheses for further testing (Harrison 1982, Joiris 1991, Hull et al. 1997, Ollason et al. 1997), (2) classic hypothesis-testing approaches examining patterns between areas, species, time periods, etc. (Abrams 1985, Garthe 1997, Skov & Durinck 2000, Roycroft et al. 2007), (3) classic statistical modelling approaches (e.g. linear regression, correlation, generalized linear or additive models [GLM-GAM]) examining functional relationships between distribution and environmental variables (Ribic & Ainley 1997, Spear et al. 2003, Olivier & Wotherspoon 2006), (4) spatially explicit approaches (e.g. point process methods, geostatistics) quantifying spatial co-occurrence and coherence between different ecosystem processes (Russell et al. 1992, O'Driscoll 1998, Navarro & Gonzalez-Solis 2007, Villablanca et al. 2007), (5) multivariate approaches (e.g. principal components analysis [PCA], classification trees, etc.) examining complex, non-linear relationships in seabird distribution patterns (Ballance et al.

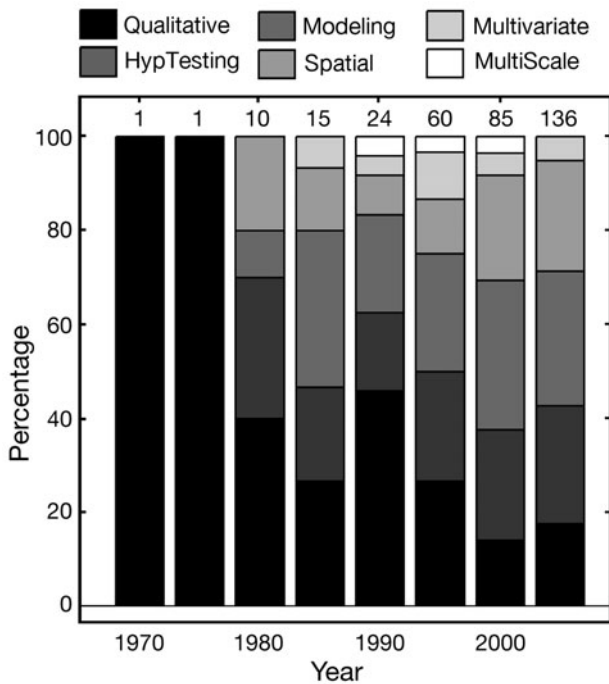


Fig. 4. Temporal distribution of the statistical approaches used in 218 relevant research articles associating seabird locations and environmental variables. Numbers represent the number of occurrences of statistical approaches in each bin, not the number of papers. See Table 2 for further details

Table 2. Contents of the categories that group statistical techniques used to relate seabird distributions and environmental variables

Qualitative approach	Hypothesis testing	Modelling		Spatial statistics	Multivariate analysis	Multiscale analysis
		Parametric	Non-parametric			
Maps, SIG	ANOVA (parametric and Kruskal-Wallis), MANOVA, ANCOVA	Correlation: (Pearson) and cross correlation	Correlation: Spearman and Kendall	Mono- and bivariate Ripley's K	Correspondence analysis PCA	Fractal dimension Spectral analysis Wavelets
Co-occurrence with specific oceanographic features	Chi-squared, G, F, Z, t, U, Wilcoxon signed-rank, Tukey-Kramer, etc., tests Discriminant function analysis, etc.	Regressions: linear, multiple, curvilinear, quadratic, polynomial, etc. GLM Linear mixed effects models, etc.	Logistic and quantile regressions GAM	Kernel Spatial overlap Variogram	Cluster analysis and CART Non-parametric, multi-dimensional scaling Boolean factor analysis	

1997, Karnovsky et al. 2003, Weichler et al. 2004, Hyrenbach et al. 2007) and (6) multi-scale approaches (e.g. wavelets, fractal geometry) investigating ecological functional relationships (Russell et al. 1992b, Logerwell et al. 1998, Mehlum et al. 1999, Swartzman & Hunt 2000) that are known to change with scale (Levin 1992).

The analytical methods used are often predicated by the data available. However, long-term, high-resolution data for seabirds along with environmental data (sea surface temperature [SST], El Niño Southern Oscillation [ENSO] index, chlorophyll, etc.) of marine ecosystems are increasingly available. Therefore, it is surprising that we did not observe increased use of more powerful, spatially explicit, multivariate and multiscale approaches. In fact, the use of the 6 approach categories did not show any clear trend with time.

All approaches have been used in a fairly constant way since the 1980s (Fig. 4). Multivariate and multi-scale analyses combined represented <10% of all analyses in any given 5 yr bin. Spatial approaches have tended to be used more frequently since the mid-1990s, but only 1 out of 5 spatial analyses actually used spatial statistics. The remaining studies used classical statistics in a spatial context, such as group comparison of distinct zones in a hypothesis-testing framework.

DISCUSSION

The at-sea ecology of seabirds is a rapidly growing field of research. We showed that both the number of research articles published and the methods of data collection are rapidly changing. However, improvements in methodological approaches can provide greater enhancement to maximize the richness of the available data.

Change in the methods, scales and units of observation

Ship-based observations of seabird distributions still contribute to the majority of these studies, but the use of electronic-based methods is rapidly increasing. Unfortunately these 2 approaches are often used in isolation, but, if used together, they could be complementary. For example, *in situ* environmental data can be collected using animal-borne electronic tags to supplement ship-based data outside of the range of detection of the observation platform. Tagging data can provide a long-term time series of position data, as well as providing behavioural information that can be used to identify behavioural modes, such as diving or area-restricted searching, and their relationship to marine habitats. Such behavioural data are important to

identify differences in the movement patterns and habitat utilization of different species. For example, some species may travel over considerable distances, while others may remain within a smaller home range. Such differences in behaviour may not always be apparent with traditional survey methods. However, tagging data have some significant limitations as well. Foremost among these is that data can only be collected from animals that can be tagged and that there is, as yet, no way to derive estimates of animal abundance.

The move from survey data to tracking data has also led to a fundamental change in the nature of the data collected—from an Eulerian to a Lagrangian form. In the Eulerian view, seabird observations are plotted on a grid and each cell gets a value representing a measured or estimated metric of the seabirds' presence. This is the typical grid survey type of data. In the Lagrangian view, the presence of seabirds is assimilated to moving particles in time and space. This is the typical tracking type of data. This distinction is fundamental in both the way we interpret our data and the way we deal statistically with the data (Aarts et al. 2008). Indeed, the Lagrangian approach appears particularly well suited for individual-based studies and fine-scale behaviour, whereas the Eulerian approach is more suited for population-based studies. As such, the observed trend in the way seabird distribution data are collected is associated with a reduction in temporal and spatial scales (through more precise and continuous recording of behaviour), as well as in the units of observation of the system studied (from the population to the individual). The trend towards a reduction in the scales of observation will likely continue as high-resolution GPS technology becomes more commonly used.

The diminution of the scales of observation might be seen as a consequence of the desire to pinpoint mechanistic relationships between seabirds and their environment. These mechanisms are typically expressed at the level of individual behaviour, and, therefore, they are unlikely to be captured in a 'large-scale' Eulerian study design. However, it was surprising to note that only 20.7% of the publications using electronic-based tracking of seabirds actually inferred behavioural indexes, such as area-restricted search patterns, turning rate, or feeding events (Charrassin & Bost 2001, Catry et al. 2004, Pinaud & Weimerskirch 2005).

The constant miniaturization of electronic devices will probably allow us to work on a wider range of seabird species, and, therefore, the trend towards a growing contribution of electronic-based studies will likely continue, especially as we learn more about previously unstudied species. However, it is highly unlikely and certainly not desirable that electronic-based methods supplant ship-based observations of seabirds, as these 2

approaches are highly complementary. For example, ship-based observations provide opportunities to observe the context in which seabirds are foraging, including interactions with conspecifics, prey, or associations with marine mammals or flock formations, and could be complemented by electronic tagging methods that provide detailed behavioural information.

We also noted that ship-based observations have evolved towards more punctual observations rather than dedicated transects. This shift is probably a direct consequence of the increasing concerns posed by seabird bycatch in fisheries operations, which has produced a need for greater at-sea monitoring of fishing activity. Seabird ecology is therefore increasingly contributing to applied ecology, including fisheries management (Einoder 2009).

Finally, seabird observations at-sea are increasingly being regrouped (or about to be) into publicly available databases, such as (non-exhaustively) the North Pacific Pelagic Seabird database (www.absc.usgs.gov/research/NPPSD/), the OBIS seamap project (<http://seamap.env.duke.edu/>) and Movebank (www.movebank.org/). By making data accessible to a wide community of persons, it is to be anticipated that new approaches and new types of research will appear through data mining, allowing us to study seabird–environment interactions at larger geographical and temporal scales. In a mature field like seabird ecology, it seems unfortunate that seabird observation data are used for a few studies and then virtually disappear. We believe that public sharing of ancient data should be considered by data producers, following a number of standardized data formats and exchange protocols (see for example the Global Biodiversity Information Facility [GBIF]; <http://data.gbif.org/welcome.htm>).

Environmental data

Although *in situ* measurements of environmental variables are and have always been used in the majority of studies, we observed an increasing use of satellite remote-sensing technology. Surprisingly, remote-sensing data have been used since the mid-1980s, but their use has increased only slowly until recently. This may be due to recent increases in the accessibility of these data sets to seabird ecologists, together with the increase in computing power. We also observed a surprising diversity in the environmental parameters that have been used (101 variables!). Among these, the most frequently used variable types typically described water masses (temperature, salinity, oceanic domain) or prey distributions. Occasionally, some environmental variables were used that described oceanographic structures likely to concentrate prey for forag-

ing seabirds, such as thermal fronts. However, in general, these mesoscale features were a less-frequently used group of variables, including fronts, Langmuir circulation and eddies; they represented only about 5% of all variables examined. This observation is fundamental in the sense that it splits the studies into 2 philosophies: those that focus on the descriptions of habitats where seabirds are present (usually on a relatively large scale), and those that focus on processes that are expected to influence the availability of prey (presence + concentration + accessibility), and, therefore, the habitat-use strategies of seabirds (usually on a smaller scale). The choice of dependent variables is inevitably conditioned by these 2 approaches. In some cases, these approaches are closely linked and may seem similar. For example, using SST gradients (description of water mass) is related but fundamentally different from using thermal fronts or distance to a thermal front (oceanographic structure). The definition of fronts according to SST gradients is not straightforward, and implies defining thresholds and assumptions supposed or showed to be relevant to specific oceanographic processes (Miller 2004, Valavanis et al. 2005). Consequently, choosing a SST front instead of a SST gradient implies a difference in the initial assumptions about processes driving seabird distributions.

It is not surprising that relatively few studies focus on oceanographic processes, because these are complex in nature, dynamic, scale-dependent and vary over time. To overcome these issues, many researchers have used a ‘shotgun’ approach, incorporating a host of variables into a multivariate analysis with the hope of identifying appropriate parameters that correlate with seabird abundance. While it is assumed that these parameters are associated with prey availability and associated oceanographic processes, the actual mechanisms responsible are rarely identified. Indeed, only during the last decade, has mesoscale dynamics in the oceans emerged as an influential factor on the distribution of seabirds (Haney 1985b, 1986a,b, 1987a,b, 1988, Ribic et al. 1997, Nel et al. 2001, Weimerskirch et al. 2004, Ballance et al. 2006, Hyrenbach et al. 2006, O’Hara et al. 2006), marine turtles (Polovina et al. 2001, 2006, Lambardi et al. 2008), marine mammals (Ream et al. 2005, Campagna et al. 2006, Biuw et al. 2007), fish (Brandt 1981, Bakun 2006, Zainuddin et al. 2008), squids (Rodhouse et al. 1996, Waluda et al. 2001), zooplankton (Huntley et al. 2000, Labat et al. 2002, Strzelecki et al. 2007), phytoplankton and marine production (McGillicuddy et al. 1998, Martin 2003, Mitchell et al. 2008).

Certainly, a promising avenue of future research would be to identify the oceanographic processes and the specific mechanisms responsible for seabird distribution at various scales, a route that is distinct from the

physical description of water masses and that is clearly an underutilized approach. These notions are, however, linked together, since it is arguable that an oceanographic structure that concentrates food at a mesoscale can be seen as a physical characteristic of a wider habitat or ecological niche. An illustration of such an approach can be seen in Fig. 2 of the paper by Tew-Kai et al. (2009).

Among all these variables, it is difficult to decide which are more important than others. Intuitively we might think of prey distribution as the major factor. However, this might depend on many factors, including (non-exhaustively) the seabird considered, the region, the breeding status, the sex and also the scale considered. For example, a procellariiform seabird might look for an oceanographic feature at large scales using its demethyl/sulfide (DMS)-sensing capabilities (a large frontal system for example), and then it might actually look for the edge of a mesoscale eddy, and only after that it would look for its prey at smaller scales. In this view, the prey factor is not necessarily the first variable used by the animal to select its habitat. Furthermore, in the case of seabirds using associations with marine mammals and schools of tunas to feed, the presence of prey might not be related to their catchability. In spite of this, obtaining real distribution maps of seabirds' prey at appropriate spatial and temporal scales is probably the holy grail of the discipline, yet obtaining these data usually remains out of reach.

Finally, the use of hydrodynamic model data and variables derived from 3-dimensional flow dynamics was virtually absent from our selection of papers. The output from these models (although they are not strictly considered data) could be used to gain environmental information on the third dimension (depth), which is virtually absent from most studies. Such contribution could help in understanding the relationships of diving seabirds with subsurface fronts or other underwater oceanographic features.

Statistical analyses

Similar to the diversity of approaches and data types found in the literature, the statistical techniques used to link seabird locations with environment variables were also highly diverse. Qualitative approaches were heavily used (~20% of approaches), and explicit spatial statistics (statistics dependent on the position of an observation in space) were seldom utilized. The trend observed towards using Lagrangian data types was not associated with a temporal change in the statistical modelling used. This suggests that Lagrangian data (i.e. time series of spatial locations) are often used as if they were Eulerian data, in that data are treated as

independent positions in space and their inherent temporal autocorrelation is often ignored. Occasionally, the temporal autocorrelation between observations is acknowledged formally, but it is most often treated as a nuisance for statistical inference. Methods do exist to overcome this problem, but these were often absent in the papers we reviewed (Legendre 1993, De Solla et al. 1999, Keitt et al. 2002, Dormann et al. 2007).

Spatial data can be described using a variety of techniques (Dale et al. 2002, Perry et al. 2002) and effort should be made to extract more information from data sets that are lacking at this stage. This would allow further standardization in the way seabird distributional data are treated, facilitating the comparison of results between studies. For example, the centre of gravity, inertia, indexes of lacunarity and variograms could be used more regularly as common descriptors of spatial distributions.

Another interesting point is that, although many individual tracks of seabirds have been gathered, very few reports have analyzed seabird behaviour with respect to the environment. Indeed, authors consider the animal's position as a consequence of the behaviour, but rarely do they use behavioural data, such as change in turning rate, speed, bearing, or any derivative thereof, in relation to the environment. Such analyses are becoming possible with the increased availability of high-resolution, multi-sensor recording devices.

CONCLUSIONS

Given the trends in approaches and methodologies used in studies of the at-sea ecology of seabirds, we identified a few important topics that merit future attention. First, given the spatial nature of the data, it is important to fully utilize the appropriate statistical tools available to both describe the data and quantify the link between seabirds' locations and environmental variables. Second, seabird locations and seabird behaviour are distinct, and the latter is an important component that can be extracted from Lagrangian data types. Associating locations of particular behavioural events (e.g. area-restricted searches) with environmental parameters is a promising route that could improve our understanding of the mechanisms underlying seabird behaviour. Third, in addition to describing water masses, the choices of the environmental variables could gain by being driven by the need to identify the underlying oceanographic processes and mechanisms. Their identification implies more complex processing of the data for describing the marine environment, but there are a number of recent examples of how this might be done (Boehme et al. 2008, Chaigneau et al. 2008).

Seabird ecology is a dynamic field of research, and its development is still growing, promising years of exciting discoveries to come.

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Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review

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ABSTRACT: Colonial seabirds are relatively easy to observe, count, measure and manipulate, and consequently have long been used as models for testing ecological hypotheses. A combination of animal tracking and satellite imagery has the potential to greatly inform such efforts, by allowing seabird–environment interactions to be observed remotely. We review how this can be achieved by applying innovative statistical techniques to quantify habitat use and preferences. Seabird movements are now observable at scales of meters using GPS loggers, and up to several years using light-based geolocation, while satellite remote sensing systems, at resolutions of km, are capable of characterizing the millions of km² of habitat that are accessible to seabirds. Physical forcing and biological processes result in a hierarchical, patchy distribution of prey. Hence, analyses of seabird movements should be conducted at appropriate scales. Variation in habitat accessibility should also be considered: this declines with distance from the colony during the breeding season, when seabirds are central place foragers, and may be limited in the nonbreeding period by migration corridors that are defined by wind patterns. Intraspecific competition can further modify spatial usage, leading to spatial segregation of birds foraging from different colonies. We recommend that spatial usage be modeled as a function of habitat preference, accessibility and, potentially, competition. At the population level, this is currently best achieved using an empirical approach (e.g. using mixed-effects generalized additive models). At the individual level, more mechanistic models (e.g. state–space models) are more appropriate and have the advantage of modeling location errors explicitly.

KEY WORDS: Satellite tracking · GPS · Platform transmitter terminal · Geolocator · Spatial models · Generalized additive model · State space models · Albatross

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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 behavior (Orans & 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 behavior 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 address 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 lifestyles of seabirds could be investigated in detail. At the same time, in the field of oceanography, data provided by remote sensing

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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 has enabled the observation of an ever-increasing range of behaviors (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), we argue that a lack of access to appropriate statistical techniques has hampered further progress. Fortunately, in recent years, significant innovations have been made in the analysis of individual movements and spatial modeling (e.g. Aebischer et al. 1993, Jonsen et al. 2003, Aarts et al. 2008), which is 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, we focus on quantifying and modeling habitat use and preferences of pelagic seabirds, using approaches analogous to those frequently used in the discipline of landscape ecology (Wiens et al. 1993, Lima & Zollner 1996, Scott et al. 2002).

In this review, we use the term 'habitat' to refer to a set of environmental conditions rather than to geographical locations (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). We define pelagic seabirds as those that 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, and some terns, (cf. Ashmole 1971) tends to comprise 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; hence,

analytical techniques discussed will be applicable to all pelagic seabirds. Before describing these approaches in detail, we discuss the context of their application by considering issues of scale, measurement, behavior, habitat availability, accessibility and competition.

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, thus 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 behavior (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, Table 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).

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, we use the terms for spatial scale proposed by Haury et al. 1977; Fig. 2). Although the behavior of pelagic seabirds varies over timescales of seconds (Weimerskirch et al. 2005) to years (Phillips et al. 2005), and over distances of meters (Pennycuik 1982) to 10 000s of km (Shaffer et al. 2006), clear asso-

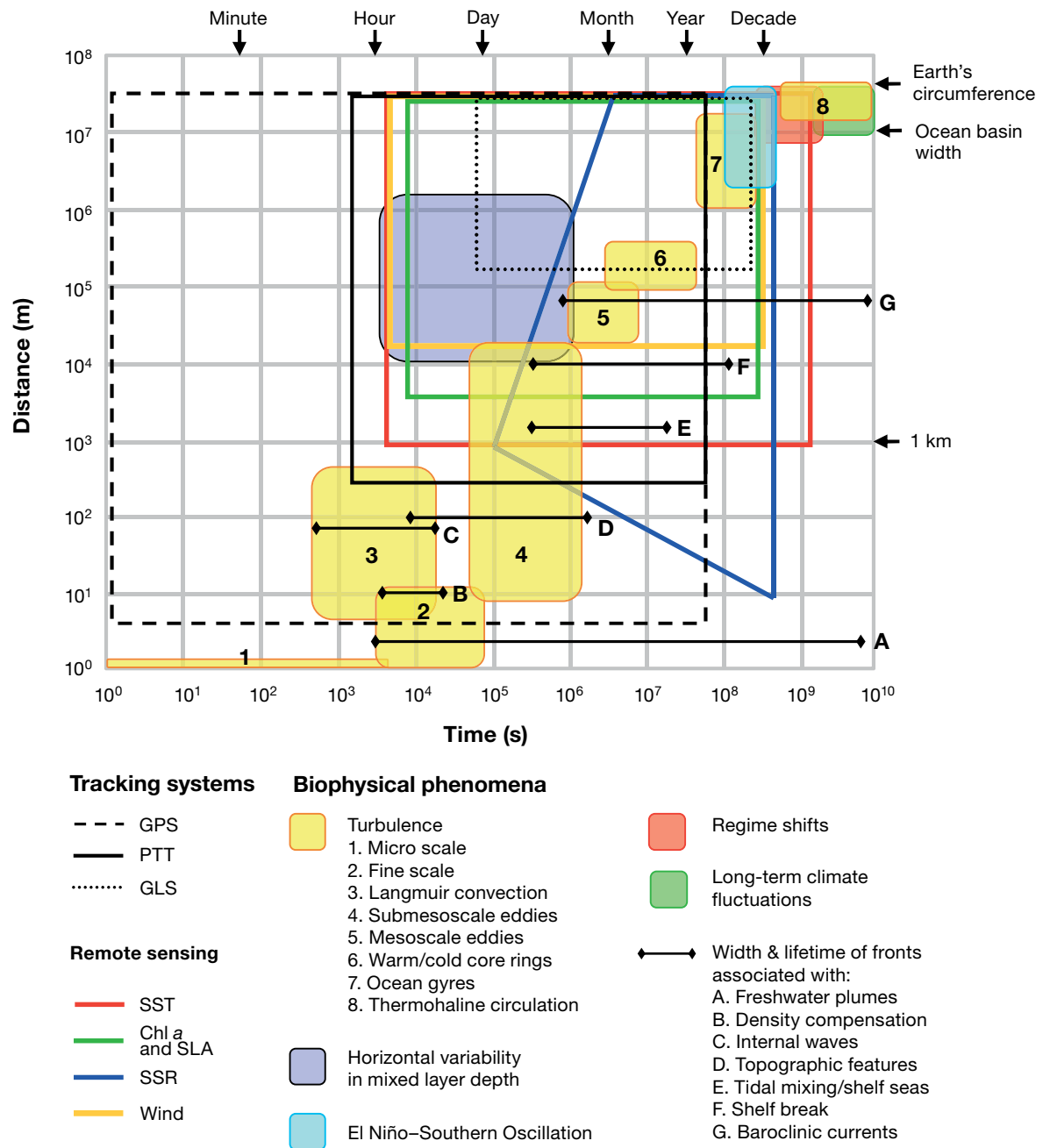


Fig. 1. Spatiotemporal scales of climatic and oceanographic processes compared to the resolution and coverage of human observation in pelagic seabird habitat studies. Tracking systems shown are PTTs (platform terminal transmitters), GPS tags and GLS (global location sensing, geolocator) tags. Remotely 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)

ciations 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 (Hoefer 2000, Pinaud &

Weimerskirch 2002). A diverse range of pelagic seabirds associate with the edges of mesoscale eddies (Nel et al. 2001, Weimerskirch et al. 2004), and many pelagic seabirds show affinities for eutrophic, mesotrophic or oligotrophic waters at coarse, meso- and macroscales (Hyrenbach et al. 2002, Awkerman et al. 2005, Pinaud & Weimerskirch 2005). In the equatorial

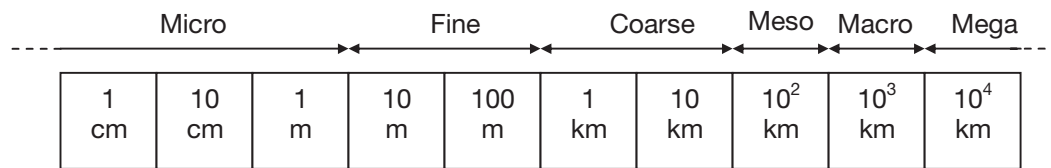


Fig. 2. Definition of terms used to describe spatial scale in habitat studies of pelagic seabirds (after Haury et al. 1977)

Table 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. 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 marginal ice zone (MIZ) and horizontal extent of other processes. Process tends to increase (↑), decrease (↓) or have both effects (↕) on production; (?) effect on production unknown; (✓) under the column AG indicates that the process tends to cause physical aggregation of biomass. Data based on Lutjeharms et al. (1985), Moore et al. (1999), Eldevik & Dysthe (2002), Rudnick & Martin (2002), Kaiser et al. (2005), Mann & Lazier (2006). ACC: Antarctic Circumpolar Current, dec: decades

Process phenomenon	Scale		Effects			Areas/examples
	Horizontal (km)	Temporal	PP	SP	AG	
Turbulence						
Small scale turbulence caused by wind, currents, tides, etc.	0.00001 – 0.001	s – min	†	†		All
Large scale turbulence caused by wind, currents, tides, etc.	0.001 – 0.01	1 – 10 h	†	†		All
Sub-mesoscale eddies/spiral eddies	0.01 – 20	d – wk	?	?	✓	All
Meanders, barotropic mesoscale eddies	20 – 100	wk – mo	†	†	✓	Margins of ocean currents
Meanders, warm and cold core baroclinic rings	100 – 300	1 mo – 1 yr	†	†	✓	Margins of major ocean currents, Gulf Stream rings, ACC rings
Langmuir convection cells	0.005 – 0.5	min – h	?	?	✓	All
Changes in mixed layer depth caused by wind, insolation, fresh water, currents, tides, upwelling, internal waves, fronts, etc.	10 – 1000	h – wk	†	†	✓	All. Spring and autumn blooms in temperate latitudes (only really marked in N Atlantic)
Fronts						
Freshwater plumes and plume fronts	0.005 – 100	h – mo	†	†	✓	Coastal waters
Compensating fronts	0.01 – 5	h – d	†	?	?	All areas with deep mixed layer and significant thermohaline variability
Surface rips/slicks caused by internal waves/bores	0.1 – 1	min – h	†	?	✓	Neritic waters
Fronts associated with geomorphic features	0.1 – 100	h – wk	†	†	✓	All areas except central ocean basins
Shelf sea fronts caused by tidally induced mixing	2 – 10 – 100	d – mo	†	†	✓	Neritic waters, Patagonian shelf
Coastal upwelling due to Ekman transport and upwelling fronts	10 – 100 – 1000	5 d – yr	†	†	✓	Eastern margins of ocean basins at sub-tropical latitudes, Humboldt and Benguela upwellings
Shelf-break fronts	10 – 500	wk – mo	†	†	✓	All shelf breaks but more intense on western sides of ocean basins, Patagonian shelf
Fronts in baroclinic currents, shear fronts	50 – 21 000	wk – yr	†	†		Open ocean, Antarctic polar front
Circulation						
Water masses	100 – 15 000	mo – dec	–	–		Antarctic surface water, Subantarctic surface water, subtropical surface water
Sea ice						
MIZ and polynyas	0.01 – 200	d – mo	†	†	✓	Polar waters
Biogeochemical processes						
Trace nutrient limitation	1000 – 10 000	wk–yr	↓	↓		Eastern equatorial Pacific, Southern Ocean, possibly south Pacific
Climatic fluctuations						
El Niño – Southern Oscillation	15 000 – 40 000	4 – 7 yr	†	†		Eastern Pacific and worldwide
Other climatic oscillations and regime shifts	15 000 – 40 000	10 – 100 yr	†	†		Antarctic oscillation; Pacific decadal oscillation
Medium/long-term climate fluctuations	40 000	>100 yr	†	†		All

Pacific, piscivorous seabirds prefer well-stratified waters that are 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 timescales, 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 changes in the size and distribution of seabird colonies occur in response to regime shifts and climate fluctuations over still longer timescales (Olson & Hearty 2003, Jenouvrier et al. 2005, Lewis et al. 2009).

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, 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 ‘Behavior’), or by adopting a multi-scale approach (e.g. Garcia & Ortiz-Pulido 2004, Suryan et al. 2006).

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) (e.g. Pakhomov & McQuaid 1996). Similarly, environmental data can be collected e.g. by some animal tracking devices (e.g. Shaffer et al. 2006), auxiliary loggers (reviewed by Wilson et al. 2002), autonomous buoys, and moorings. However, these approaches do not provide a 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 that tends to prioritize global or near-global data collection at the expense of resolution, such that sub-km phenomena remain poorly resolved (Table 2). Nevertheless, innovative instruments such as synthetic aperture radars (SAR) can now detect e.g. submesoscale eddies, freshwater plumes, sea ice, with a 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 3-dimensional structure of water masses using remotely sensed sea level and

Table 2. Measurements made using satellite-borne instruments and the oceanographic processes and phenomena that they can identify (see ‘Measuring the marine environment’ for references)

Variable	Resolution (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, shelfbreak fronts, coastal upwelling)
Sea surface color	4	1	Primary production (suspended sediment and ‘gelbstoffe’ concentration, coastal processes)
Sea level	4	1	Mesoscale eddies (meanders, shelf sea fronts, shelfbreak 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)

sea surface temperature (SST), especially by using these data to drive numerical oceanographic models (Thorpe et al. 2005); these models can provide estimates of e.g. current velocity, temperature, salinity, at horizontal resolutions as low as 1/8° (~13 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 (e.g. from ships, ARGO floats) to provide daily cloud-free images at 1/20° (~6 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) 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 the movement capabilities of prey species themselves (e.g. Murphy et al. 2004). Although there may be enough information in some studies 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).

Despite their limitations, remotely sensed environmental data can describe habitats in a biologically meaningful way (Table 2), especially when multiple variables are used synergistically to derive other descriptors of habitat, such as the rate of primary production (Behrenfeld & Falkowski 1997), 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).

TRACKING TECHNIQUES AND DATA PREPARATION

The measurement of individual movement using tracking devices has been reviewed by Tremblay et al. (2009, this Theme Section), Burger & Shaffer (2008) and Phillips et al. (2008). Briefly, platform terminal transmit-

ters (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 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, Magalhães 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. 2005) 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 >~3% of body mass can result in behavioral changes (Kenward 2001, Phillips et al. 2003). Recently, however, species as small as the Cook's petrel *Pterodroma cookii* (~200 g) have been tracked using archival geolocators (Rayner et al. 2008), which can weigh as little as 1 g (Mk. 10, British Antarctic Survey, Cambridge, UK).

PTTs, geolocators and GPS tags have very different performance characteristics (Fig. 1), there being a general trade-off between temporal resolution, deployment duration and device mass. PTTs use the ARGOS (CLS: Collecte Localisation Satellites) 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 d⁻¹. However, the accuracy and precision of these locations are 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 of low quality, predominantly with ARGOS location classes of 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 behaviors such as resting, commuting, searching, and diving, 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 are 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, Grémillet et al. 2004, Awkerman et al. 2005). They also have the advantage of obtaining locations at high temporal resolutions (up to 1 Hz, for periods of hours), allowing fine-scale behavioral information to be inferred from movement (Weimerskirch et al. 2007, Guilford et al. 2008). Initially, GPS units were archival and thus 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 yr (e.g. Urios et al. 2007).

Geolocators record ambient light levels, which, following tag retrieval, are used to derive 2 positions d^{-1} , with comparatively low mean accuracy of ~190 km (± 110 km SD) (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. 2005).

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 assuming 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^{-1} 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 modeling approach (SSM) (Patterson et al. 2008).

BEHAVIOR

Birds may engage in many different behaviors, including foraging, commuting, migrating, preening, and resting. These may be initiated by exogenous (e.g. a change in wind direction or movement into a prey

patch) or endogenous (e.g. physiological state) cues. Hence, habitat use and preference is dependent on time-activity budgets, which in turn change with life history stage, environmental conditions, and other factors (Phalan et al. 2007, Guilford et al. 2009). As such, behavioral 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) behavior (Lima & Zollner 1996). Hence, many individual-based studies aim to infer behavioral state from measures of path geometry, such as speed and direction (Johnson et al. 2002, Jonsen et al. 2007). At all but the microscale, tracks tend to deviate from straight lines; 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 birds are not in flight, and are thus variously interpreted as foraging (Weimerskirch et al. 1997b, Weimerskirch & Guionnet 2002), resting (Nel et al. 2001), waiting for favorable winds (Murray et al. 2002), or rafting prior to entering a colony (Awkerman et al. 2005, Guilford et al. 2008). However, these behaviors have not yet been distinguished using path geometry alone.

It is assumed that birds that are traveling 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 behavior termed as 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 (FPT; 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: 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 behavioral data (reviewed by Ropert-Coudert & Wilson 2005). Frequent landings and takeoffs recorded by activity loggers are regarded as indicative of foraging (Weimerskirch et al. 1997b), 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 behavior (Ropert-Coudert & Wilson 2005, Weimerskirch et al. 2005). However, regardless of whether behavioral state is measured directly or inferred from path geometry, it should be cautioned that although some behavioral 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 should be treated as such during analyses.

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 meaningful 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 costs of moving to different habitats may differ. Hence, during breeding, when birds act as central place foragers, habitat 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 breeding 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 generally not 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 would be 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 then becomes 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 incurred by seabirds during flight (Weimerskirch et al. 2000, Suryan et al. 2008, Wakefield et al. in press). Flight performance is partly dependent 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 Procelariiformes route their journeys and make behavioral decisions so as to exploit favorable 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 nonbreeding periods to use discrete migration corridors (Gonzalez-Solis et al. 2007, Guilford et al. 2009), and to windier areas in general, limiting habitat accessibility during such periods. 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 nonbreeding stages. However, the pelagic wind field is highly dynamic and modeling its effect on transport costs and accessibility is challenging.

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 the 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 1998, Adler & Gordon 2003). An analogous situation arises in seabirds foraging from adjacent colonies (e.g. Huin 2002, Ainley et al. 2003, Grémillet et al. 2004). As seabirds are not territorial at

sea, indirect competition is thought to be a 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, Grémillet et al. 2004). This is probably because intraspecific competition intensity varies with conspecific density, and thus decreases as a continuous function of distance from neighboring 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 behavior 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, e.g. 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 (Grémillet et al. 2004, Ford et al. 2007). However, this is now a realistic proposition since conspecifics from neighboring colonies and sympatric species from the same foraging guild can be tracked simultaneously.

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 the locations of 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 are 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 dom-

inated 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-square 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. 2009, this Theme Section).

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 behavior, such as the time spent searching or traveling, track straightness, FPT and flight speed with habitat have also been tested to identify which habitats are used more frequently for foraging (Weimerskirch et al. 1997b, Hyrenbach et al. 2002, Weimerskirch et al. 2002, Suryan et al. 2006, Pinaud & Weimerskirch 2007). Discriminant function analysis has been used to test which environmental covariates best predict behavioral state (Awkerman et al. 2005, Pinaud & Weimerskirch 2007).

Most early studies treated individual 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 the 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 et

al. (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 modeling 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 the individual (reviewed by Patterson et al. 2008, Schick et al. 2008), or the population (reviewed by Moorcroft & Barnett 2008). The key problems facing population-level modelers were discussed by Aarts et al. (2008) and Matthiopoulos & Aarts (2009). In addition to issues already mentioned, they include nonlinearity in animal 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. We have recently extended this approach to model the spatial usage of breeding black-browed albatrosses *Thalassarche melanophrys* as a function of habitat accessibility, preference and conspecific competition (Fig. 3; Wakefield et al. unpubl.). 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 behavioral responses of animals to their environment are being modeled 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 modeling geolocator data (Royer et al. 2005). Recently, Schick et al. (2008) proposed incorporating RSFs and SSMs in a hierarchical Bayesian framework, effectively modeling a moving animal's behavioral response to a habitat map centered on the present location (see also Christ et al.

2008). Although such techniques are complex and computationally demanding, they are becoming more practicable and seem 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 animal movement models and theory were historically developed for taxa that are very different from pelagic seabirds. For example, much effort has gone into modeling 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 modeling 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.

FUTURE DIRECTIONS

Over the past 25 yr, tracking technology has greatly advanced our understanding of the interactions between pelagic seabirds and their environment (Wilson et al. 2002, Burger & Shaffer 2008, Phillips et al. 2008). Although the habitat use of many species has been described and quantified, only one tracking study has to date formally compared habitat usage to availability, and thus quantified habitat preference (Pinaud et al. 2005). This has partly been due to a lack of theoretically grounded statistical methods for treating individual movement data that nonspecialists are able to

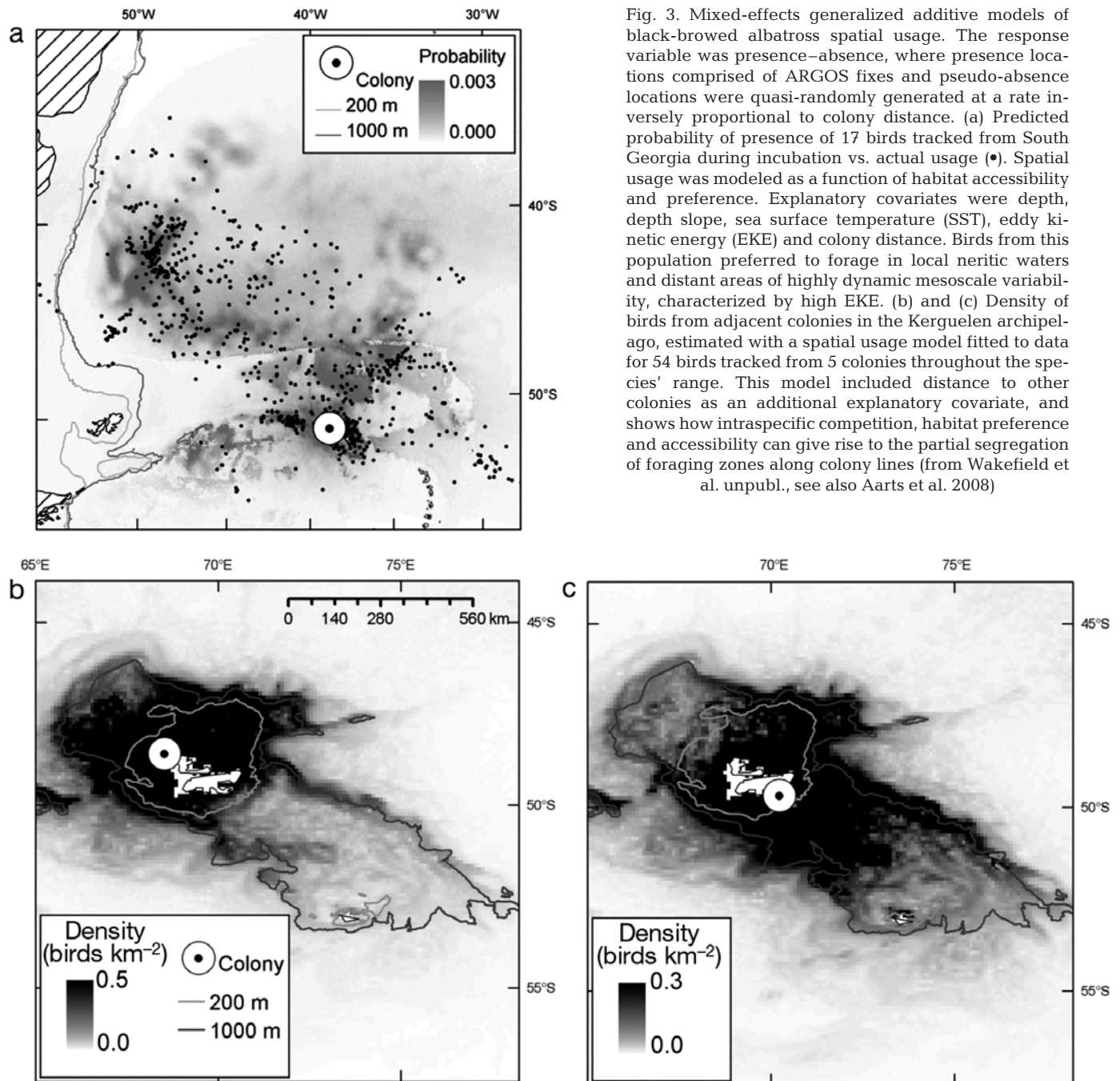


Fig. 3. Mixed-effects generalized additive models of black-browed albatross spatial usage. The response variable was presence-absence, where presence locations comprised of ARGOS fixes and pseudo-absence locations were quasi-randomly generated at a rate inversely proportional to colony distance. (a) Predicted probability of presence of 17 birds tracked from South Georgia during incubation vs. actual usage (•). Spatial usage was modeled as a function of habitat accessibility and preference. Explanatory covariates were depth, depth slope, sea surface temperature (SST), eddy kinetic energy (EKE) and colony distance. Birds from this population preferred to forage in local neritic waters and distant areas of highly dynamic mesoscale variability, characterized by high EKE. (b) and (c) Density of birds from adjacent colonies in the Kerguelen archipelago, estimated with a spatial usage model fitted to data for 54 birds tracked from 5 colonies throughout the species' range. This model included distance to other colonies as an additional explanatory covariate, and shows how intraspecific competition, habitat preference and accessibility can give rise to the partial segregation of foraging zones along colony lines (from Wakefield et al. unpubl., see also Aarts et al. 2008)

implement. We suggest that this is no longer an impediment, and that tracking data for pelagic seabirds can be used to address a wider range of ecological questions. For example, by quantifying the effects of habitat preference and accessibility on spatial usage (Fig. 3), the effects of central place constraint and competition on populations can be better understood. Ultimately, this approach may allow the prediction of carrying capacities for pelagic seabird populations (Beck et al. 2006, Jennings et al. 2008). At present, it is feasi-

ble 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 behavioral information inherent in individual movement data more fully. Inferences of behavioral states, such as ARS, which are based on theoretical predictions of animal movement, should also be validated more directly, e.g. by using auxiliary loggers to indicate when an animal actually ingests prey (Catry 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 of 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 nonbreeding 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), breeding stages (Weimerskirch et al. 1993, Phillips et al. 2004b), 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 inter-annually (Xavier et al. 2003, Pinaud et al. 2005), and between populations (González-Solis et al. 2000a, Grémillet et al. 2004, Rayner et al. 2008), potential plasticity in habitat preferences should be considered, and if possible incorporated into analyses before drawing far-reaching conclusions.

Although the response of pelagic seabirds to certain phenomena (e.g. 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). Responses to shorter-term climate fluctuations (e.g. ENSO events and even regime shifts) may soon be measurable by tracking birds from the same populations repeatedly over consecutive years and decades. Most studies on pelagic seabirds to date have combined satellite tracking with medium resolution environmental data (e.g. SST, chl *a*, sea surface height anomalies or SSHa) to examine habitat prefer-

ences at scales of days to weeks and 100s to 10 000s of km. At macro- to megascales, pelagic areas of higher than average productivity are recognized as hotspots for seabird abundance (Worm et al. 2005), and there is increasing evidence for definable habitat preferences at the mesoscale (e.g. for eddies, upwelling and shelf-break fronts). At finer scales, it has been contended that the distribution of mobile vertebrates 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). Why such associations have not been apparent in tracking studies may simply be because the resolution of tracking and remotely sensed environmental data was hitherto insufficient to detect them. However, at coarse scales, SAR imagery now reveals processes that are 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).

Our increasing ability to understand, and therefore predict, individual- and population-level spatial usage is timely, since a large proportion of pelagic seabirds (especially albatrosses and large petrels) is threatened by incidental mortality in longline and trawl fisheries (Tuck et al. 2003, Butchart et al. 2004, Phillips et al. 2006). Hence, knowledge of their habitat use and preferences will be critical for the monitoring and mitigation of these and other anthropogenic impacts on the marine environment, as well as for addressing wider ecological questions.

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Combining vessel-based surveys and tracking data to identify key marine areas for seabirds

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ABSTRACT: An understanding of the distribution and habitat associations of far-ranging marine predators is being increasingly applied to protect these species from anthropogenic threats at sea (e.g. oil spills and fisheries bycatch). Within this framework, this research on Cory's shearwater *Calonectris diomedea* integrates vessel-based survey and tracking data to provide 2 distinct, yet complementary, perspectives of the habitats of this species in the western Mediterranean during incubation in June and chick rearing in August of 2007. We used a hierarchical modelling approach to (1) delineate the foraging habitat of the species using vessel-based surveys and (2) identify its feeding habitat based on tracking data within the Information-Theoretic framework. Our habitat modelling analyses suggest that shearwaters respond to complex bio-physical coupling, illustrated by their association with frontal features and elevated ocean productivity. Our models yielded moderate predictions of Cory's shearwater habitats within 2 distinct spatial scales. At the mesoscale, the foraging range of the species comprised the continental and insular shelf-slope waters of the Iberian Peninsula and the Balearic Islands, between the Gulf of Lions to the north and Cape Palos to the south. At the coarse scale, the tracking data highlighted important feeding areas within this larger foraging range: 3 continental shelf-slope 'hotspots' — (1) Gulf of Lions, (2) Cape Creus–Barcelona–Ebro Delta and (3) Cape La Nao–Cape Palos; from north to south — as well as the insular shelf-slope areas around the Balearic Islands. These results match previous observations of the foraging range and feeding patterns of the species, and are consistent with the interpretation of the regional oceanography. This study highlights how the integration of tracking and vessel-based survey data can provide a wider understanding of the predictability of aggregation (i.e. hotspots) and the key oceanographic habitats of far-ranging seabirds at multiple spatial scales. Thus, complementary data integration is a step forward in conservation studies of far-ranging marine top predators.

KEY WORDS: *Calonectris diomedea* · Cory's shearwater · Feeding hotspot · Foraging range · Habitat modelling · Important Bird Area (IBA) · Information-Theoretic approach · Ocean remote sensing · Conservation · Western Mediterranean

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INTRODUCTION

The distribution of marine top predators and their prey is influenced by dynamic and complex physical and biological processes (e.g. Hunt et al. 1999). Seabirds forage within heterogeneous and dynamic

environments, where the vertical and horizontal distributions of prey resources are governed by diverse oceanographic processes operating at a range of spatial scales, from macro–mega (1000s of kilometres) to coarse–meso (10s to 100s of kilometres) (Hunt & Schneider 1987). Dense prey patches of drifting and

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weakly swimming prey become concentrated at specific features with enhanced vertical (upwelling/downwelling) and horizontal (convergence/divergence) water flow (e.g. Hammer & Schneider 1986, Franks 1992, Haury et al. 1978). In turn, mobile predators concentrate and forage at these same features in response to elevated localized productivity and dense prey patches (e.g. Rodhouse et al. 1996, Johnston et al. 2005).

The increasing awareness of the serious threats that marine top predators face at sea, such as fisheries bycatch and oil spills, has triggered the development of conservation measures to ensure the protection of important key marine areas (e.g. foraging areas and migration corridors; see BirdLife International 2004, Hooker & Gerber 2004). Understanding the distribution patterns and habitat associations of these highly mobile organisms is critical to effectively monitor and protect them. In particular, the large ranges of most marine top predators make spatially explicit conservation approaches targeting high-use areas (hereafter termed 'hot spots') especially attractive (e.g. Hyrenbach et al. 2000, Alpine & Hobday 2007). Following this principle, BirdLife International is expanding the Important Bird Areas (IBAs) programme to the marine environment with the aim of creating a network of marine protected areas (MPAs) that will provide effective protection for seabirds and their underlying habitats (BirdLife International 2004). This initiative has lagged behind similar initiatives in terrestrial ecosystems due to the difficulty of obtaining systematic seabird distribution and movement data at sea. However, this situation has dramatically changed in the last 2 decades, with the advent of systematic seabird surveys and the development of miniaturised tracking technologies (Boyd et al. 2006). Taking advantage of these advances and benefiting from EC-LIFE Natura funding, 2 BirdLife partners, SEO/BirdLife in Spain and SPEA in Portugal, have recently provided comprehensive inventories of marine IBAs for their whole territorial waters (Ramírez et al. 2008, Arcos et al. 2009).

Within the context of the Spanish marine IBA project, the present study showcases our research to identify key marine areas for Cory's shearwater *Calonectris diomedea* in the western Mediterranean, where the local subspecies (*C. diomedea diomedea*) is listed as Threatened in Spain (Carboneras 2004, Red List of Spanish birds at: www.seo.org/media/docs/LR%20completo%20para%20web.pdf), and therefore requires rapid conservation action. This study focuses on vessel-based surveys and GPS-tracking data to assess the predictability of aggregation hot-spots and the key supporting oceanographic habitats. These approaches are complementary, since vessel-based surveys pro-

vide a broad scale (10s to 100s of kilometres) perspective of population-level distribution and habitat associations, whereas the tracking data provide detailed information on the fine-scale (0.1s to 10s of kilometres) use of the marine environment by individual foragers. While both methodologies have been proved to be useful for mapping and prioritizing the critical migration routes and foraging grounds of protected seabirds (e.g. Hyrenbach et al. 2002, Louzao et al. 2006, González-Solís et al. 2007, Harris et al. 2007), few studies have integrated these 2 disparate methodologies (but see Rodhouse et al. 1996, Hyrenbach & Dotson 2003, Hyrenbach et al. 2006).

Herein, we develop habitat suitability models for Cory's shearwater in the western Mediterranean during incubation in June and chick rearing in August, 2007, on the basis of concurrent tracking of individual birds and vessel-based surveys. Habitat suitability techniques use information on species records (time/space) and concurrent environmental factors to generate statistical predictions of potentially suitable species habitats (see review by Guisan & Zimmermann 2000), critical for conservation planning (Gray et al. 2007). In a first step, we used a hierarchical modelling approach to identify those environmental variables that most accurately reflected the oceanographic habitat of Cory's shearwater by (1) delineating the foraging habitat of the birds using vessel-based surveys (i.e. where the birds search for food) and (2) identifying the feeding habitat of the species using tracking data (i.e. where the species feed). After developing the habitat suitability models accounting for the peculiarities of the 2 disparate methodologies, the second step entailed predicting the suitable foraging and feeding habitats of Cory's shearwater within the Information-Theoretic approach. The third step involved evaluating the predictive performance of the models using resampling techniques.

This paper reports the results of this modelling exercise and discusses the limitations and opportunities of both contrasting datasets for the development of improved habitat suitability models. We also examine the conservation implications of this integrated habitat modelling approach and its findings for identifying key areas for marine birds.

MATERIALS AND METHODS

Study site. In spring–summer of 2007, we conducted vessel-based surveys along the Iberian coast and around the Balearic Islands, whereas Cory's shearwaters breeding at the Balearic archipelago were tracked with global positioning system (GPS) loggers (western Mediterranean; Fig. 1). The Balearic Sea, a sub-basin

of the western Mediterranean located between the Iberian Peninsula and the Balearic Islands, is considered a key transition zone between the Gulf of Lions and the Algerian basin (see Supplement 1 available in MEPS Supplementary Material at: www.int-res.com/articles/suppl/m391p183_app.pdf).

Vessel-based data. At-sea seabird surveys were conducted onboard the R/V 'Cornide de Saavedra', taking advantage of the annual Mediterranean International Trawl Survey (MEDITS; Bertrand et al. 2002); this survey coincided with the incubation period of Cory's shearwater (May 30 to June 29, 2007). Seabird counts followed the methodology proposed by

Tasker et al. (1984), adapted to the study area (Louzao et al. 2006): birds were counted within a 300 m strip-transect band, on 1 or both sides ahead of the vessel according to census conditions; snap-shot counts were used to census flying birds. Shearwater observations were summed into 10 min survey bins.

Tracking data. We deployed GPS loggers on 29 Mediterranean Cory's shearwaters breeding at 3 Balearic Island colonies between early August and mid September 2007, coinciding with the chick-rearing period: 13 birds from Cala Morell and 6 from Illa de l'Aire, both locations in Menorca, and 10 from Pantaleu in Mallorca (see details in Table S1 in Supplement 2 — available in MEPS Supplementary Material at: www.int-res.com/articles/suppl/m391p183_app.pdf — and Fig. 1b for colony locations). Cala Morell is the main breeding colony of Cory's shearwater in the Balearic archipelago, with ca. 1000 to 6000 breeding pairs; Pantaleu holds ca. 200 pairs, and Illa de l'Aire ca. 35 to 40 pairs (Carboneras 2004).

The loggers weighed 25g with dimensions of $46.5 \times 32 \times 18.5$ mm (Earth & Ocean Technologies); they were fixed to the back feathers of the birds with TESA tape, thus increasing total weight to almost 30 g. This represented slightly more than 3 % of body mass of the species, which is the recommended threshold for instruments deployed on tubenose birds (Phillips et al. 2003). However, we made efforts to minimise the impact of loggers by deploying them for very short periods (4 to 17 d) (see Table S1 in Supplement 2). Whenever an instrument was not retrieved, the attachment system would guarantee the release of the logger after a few

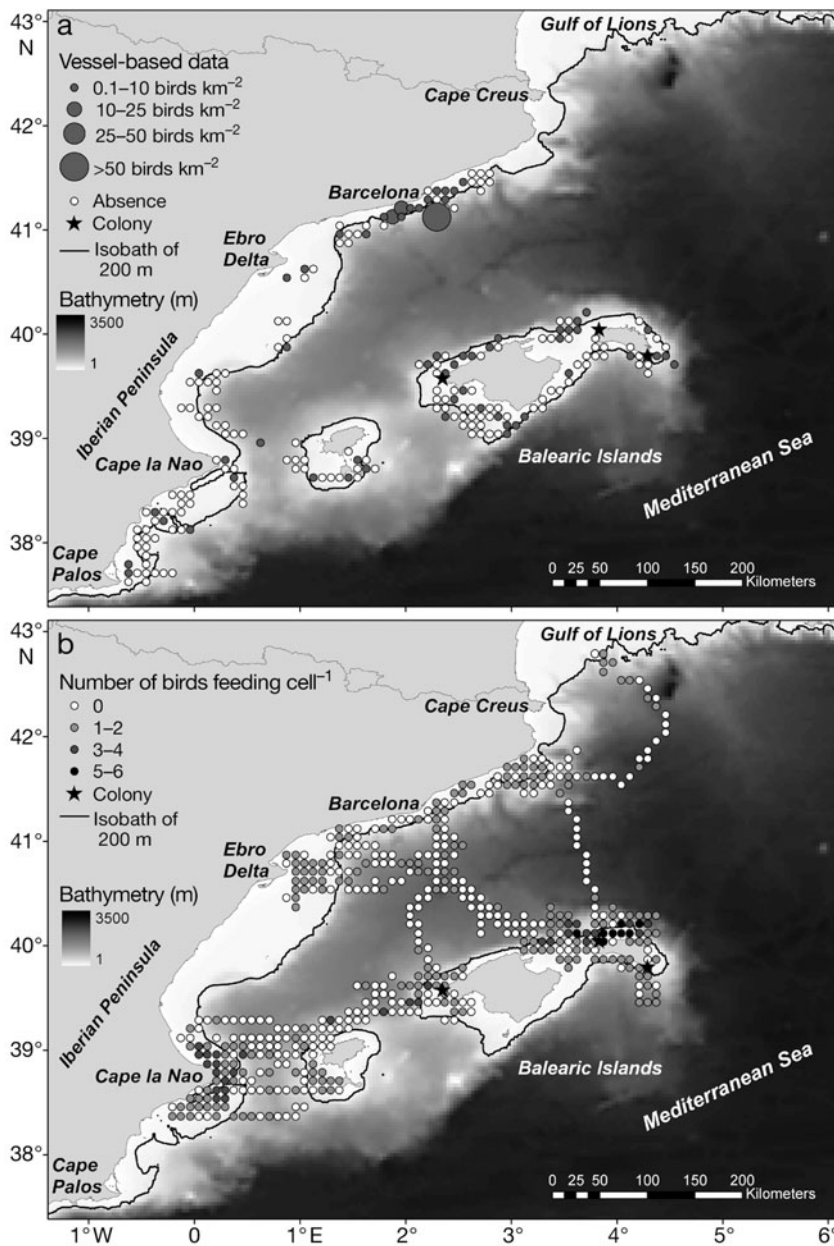


Fig. 1. *Calonectris diomedea*. (a) Foraging and (b) feeding patterns of Cory's shearwaters inferred from vessel-based surveys and tracking data after processing based on 5 n mile cell size, respectively. Vessel-based data corresponds to the presence (represented by density, with filled circles proportional in size to their values) and absence (open circles) of the species, whereas tracking data corresponds to the number of feeding birds by 5 n mile cell. Breeding colonies within the study area are also indicated, as well as the bathymetry (dark grey) and the 200 m isobath (i.e. the limit of the continental shelf). Note that some observations are over the coastline due to an artefact of binning the data in a standard grid

weeks of deployment. Moreover, the species does not seem to be particularly sensitive to carrying devices, as no detrimental effects were detected with smaller loggers (12 g GLS) attached for far longer periods (1 yr) (Igual et al. 2005).

The programmable GPS recording interval was set at 5 min initially (first 12 deployments) and extended to 10 min thereafter (remaining 17 deployments) to increase battery performance (see Table S1 in Supplement 2). Average battery life-span was 3.7 d (range 2.0 to 4.4) and 8.3 d (range 6.0 to 10.5) for the 5 and 10 min sampling rates, respectively. At these 2 sampling intervals, we registered an average of 245 and 132 positions per trip.

Although 29 birds were equipped, we obtained tracking data for 19 of them. Due to the small positional error of the GPS loggers (< 20 m for 90 % of locations), we were able to precisely assess fine-scale habitat use patterns by following the birds' trajectories in detail. Moreover, we inferred bird behaviour on the basis of the apparent flying speeds of the tracked birds: traveling, searching, feeding, and resting (sitting on the water or nesting). We classified the bird behaviour into 4 categories, on the basis of the movement rates calculated between successive positions (km h^{-1}) and visual inspection of trips: resting on the water (< 2), feeding (2 to 10), searching (10 to 15), and travelling (> 15) (see example in Fig. S1 in Supplement 2). Then, we grouped these behaviours in 2 classes: 'feeding' or 'not feeding' (the latter corresponding to resting on the water, searching, and travelling) and assigned this categorical variable to each location.

Data processing. To compare the habitat modelling results from the vessel-based surveys and the tracking data, we first standardised these 2 disparate datasets using a common spatial scale of 5 n miles (~9.3 km) and a temporal resolution of 1 mo. This resolution, selected on the basis of the coarser of the inherent scales of the datasets, was previously used to characterize the oceanographic habitat of the Balearic shearwater *Puffinus mauretanicus* within the same area (Louzao et al. 2006). Thus, all subsequent analyses were performed using a grid of 5 × 5 n mile cells, with an extent delineated by the spatial distribution of the tracking and survey data.

For vessel-based surveys, 10 min Cory's shearwater observations within each cell were summed and then re-coded into a binary presence/absence variable, indicative of whether at least 1 bird was recorded within a given cell. Thus, a total of 660 bins (10 min bins) were aggregated into 212 grid cells corresponding to 30 survey d. Due to cloud cover, we discarded 0.94 % of the surveyed grid cells with incomplete remote sensing information and we used the remaining grid cells (n = 210) as the training dataset for the

analysis of shearwater occurrence, containing 60 'presences' and 150 'absences'.

Regarding tracking data, we derived a binomial response variable for assessing the feeding habitat coding those cells containing at least 1 feeding event (GPS location characterized by 2 to 10 km h^{-1}) as 'feeding'. Conversely, those cells where no feeding events were observed were coded as 'not feeding'. To avoid pseudoreplication, we randomly selected a complete foraging trip per bird (tracking dataset: independent trips of 19 individuals). Thus, the initial training dataset of 7324 locations from 19 foraging trips was aggregated into 715 diurnal cells, containing 300 'feeding' and 415 'not feeding' events.

Concurrent environmental variables. We selected environmental variables on the basis of possible biological relevance and the availability of data (see Table 1 for a complete list). Bathymetry (BAT), sea surface temperature (SST) and chlorophyll *a* concentration (CHL, as a proxy of biological production) were extracted for the study area containing all locations (Table 1). Bathymetric data were obtained from NOAA's ETOPO 2-minute dataset (www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html?dbase=GRDET2). We derived monthly composites of SST (night-time) and CHL from MODIS/Aqua (available at ca. 0.04° spatial resolution in <http://poet.jpl.nasa.gov/> and at ca. 0.05° in <http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW180.jsp>, respectively). For dynamic variables such as SST and CHL, it is unlikely that marine top predators distribution responds instantaneously to changes in oceanographic variables (Redfern et al. 2006). Thus, we used the integrated value of those variables for the period from February to April preceding the surveys as a proxy of oceanographic patterns (see Fig. S2 in Supplement 3, available in MEPS Supplementary Material at: www.int-res.com/articles/suppl/m391p183_app.pdf, for details of the analysis). Since these 3 habitat variables (SST, CHL, and BAT) were not normally distributed, we used the median as a central tendency statistic instead of the mean within each 5 n mile cell grid. The median is less strongly influenced by outliers, thus minimizing potential biases in the dataset (Whitmire et al. 2007). Additionally, we estimated their spatial gradients by estimating their proportional change (PC) within a surrounding 3 × 3 cell (15 × 15 n mile) grid using a moving window as follows: $\text{PC} = [(\text{maximum value} - \text{minimum value}) \times 100] / \text{maximum value}$. This dimensionless metric expresses the magnitude of change in each habitat variable, scaled to the maximum value (e.g. Louzao et al. 2006). Dynamic variables such as SST and CHL corresponding to vessel-based surveys and tracking data are shown in Fig. S3a–d, as well as static variables such as BAT and its gradient

(Fig. S3g,h, available in MEPS Supplementary Material at: www.int-res.com/articles/suppl/m391p183_app.pdf).

Distance to oceanographic fronts (FRONT) was estimated in a monthly basis using the analysis of satellite-derived SST fields (monthly MODIS/Aqua from <http://oceancolor.gsfc.nasa.gov>) under a geographic information system (GIS). Our approach was based on the Cayula-Cornillon algorithm (Cayula & Cornillon 1992), which identifies fronts by detecting the edge of adjacent water masses of different surface water temperature. We used the algorithm implemented in the Marine Geospatial Ecology Tools (available at <http://code.env.duke.edu/projects/mget>) for front detection and estimated the distance to the closest oceanographic front for each analysis grid cell (Fig. S3e,f).

To account for the influence of central-place foraging shearwaters (Orians & Pearson 1979), we included the distance between each grid cell and the nearest breeding colony in the case of vessel-based surveys (unknown origin of shearwaters) and to the colony of origin in the case of tracking data (COLONY, hereafter). The distance from each grid cell to the nearest shoreline (COAST) was also included in the model to take into account onshore-offshore distribution patterns. Finally, we also estimated the distance to the limit of the continental shelf (SHELF, delimited by the 200 m isobath) since the shelf-break is a productive bathymetric feature exploited by Cory's shearwater (Abelló et al. 2003). All distances were calculated using the Nearest Features extension of ArcView 3.2 (Jenness 2004).

Statistical analysis. We applied a quantitative habitat modelling procedure in order to identify key areas for Cory's shearwater, which involved 3 steps: analysis of spatial correlation patterns, development of habitat suitability models within the Information-Theoretic framework, and model evaluation using resampling techniques.

Spatial autocorrelation: Species distributional data are characterised by spatial autocorrelation, which occurs when adjacent observations are more similar than would be expected in randomly distributed data (Sokal et al. 1998). When aggregations are present, such as seabird flocks, significant positive autocorrelation can cause the false rejection of the null hypothesis (Type I error), increasing the probability of finding spurious significant habitat relationships (Hurlbert 1984).

Therefore, prior to habitat modelling, we checked the independence of the foraging and feeding patterns of shearwaters by means of the Moran's I coefficient, which measures the similarity of the response variables by relating the values for all pair-wise combina-

tions of cells as a function of their spatial distance. Moran's I values range from -1 (negative autocorrelation) to $+1$ (positive autocorrelation), and the resulting correlograms typically show a decrease of spatial autocorrelation to a value of 0, indicating no spatial autocorrelation at increasing distance between locations (Sokal et al. 1998). We considered up to 15 lags at 1 grid cell (9.3 km) intervals in all directions (i.e. isotropic spatial autocorrelation structure). Then, significance of the Moran's I values was assessed by performing 1000 permutations at each lag distance and contrasting the observed Moran's I values with those predicted by Monte Carlo randomization tests, after applying the Bonferroni correction for multiple testing (modified $\alpha = 0.05 / 15$; 15 lags for each dataset). All spatial autocorrelation analyses were performed using the excel add-in Rook Case (Sawada 1999).

Habitat modelling: We used a hierarchical modelling approach to identify those environmental variables that most accurately reflected the oceanographic habitat of Cory's shearwater by (1) delineating its foraging habitat using vessel-based surveys and (2) identifying its feeding habitat using tracking data of individual birds. Habitat suitability models were developed, accounting for the peculiarities of these 2 disparate methodologies.

Prior to modelling, all variables were tested for normality and, where necessary, were log-transformed (natural logarithms; in order to avoid the influence of outliers) and standardized to have a mean of 0 and an SD of 1 due to differing ranges of variables (Table 1) (Zuur et al. 2007). A preliminary screening of explanatory variables was undertaken to check for collinearity (cross-correlation analysis) by calculating all pairwise Spearman rank correlation coefficients. When pairs of predictor variables were strongly correlated ($|r_s| > 0.5$), we discarded one of the redundant variables (e.g. Gray et al. 2007, McAlpine et al. 2008). We selected the 'non-correlated' predictors using the lowest Akaike Information Criteria (AIC) from univariate models of the 2 predictors (Burnham & Anderson 2002). This approach led to the removal of 6 predictors in the case of tracking data (SST, CHLG, BATG, COAST, COLONY, SHELF) and 2 predictors in the case of the vessel-based surveys (CHL, BAT) (see Table 2).

Habitat suitability models were developed by means of logistic regressions in order to generate a statistical function that would facilitate the prediction of the potential suitable habitat for the species (review in Guisan & Zimmermann 2000). We used generalized linear models (GLMs) for delineating the foraging habitat of species based on the 'glm' function, whereas generalized linear mixed models (GLMMs) were applied for identifying the feeding habitat using the 'lmer' function implemented in the 'lme4' package

(R Development Core Team 2008). Both logistic regressions were fitted with a binomial error distribution ('presence/absence' and 'feeding/not feeding') and a logit link function. In the case of GLMMs, we included the individual as random intercept term in order to account for individual effects. Models were built for all possible linear combination of 'non-correlated' explanatory variables ($|r_s| < 0.5$) and no interaction terms were included.

Model selection strategy: Models were ranked based on their AIC value corrected for small sample sizes (AIC_c) and we calculated the Akaike weight (w_i) for each model, which represents the relative likelihood of candidate models (Burnham & Anderson 2002). If the model with the lowest AIC_c is not undoubtedly the 'best' (e.g. $w_i > 0.90$), a model averaging procedure might be more appropriate to account for parameter uncertainty (Burnham & Anderson 2002). Therefore, we constructed a 95 % confidence set of models where the sum of Akaike weights was > 95 , starting with the model with the highest Akaike weight (Burnham & Anderson 2002). Accordingly, averaged coefficients were estimated from the 95 % confidence set of models containing that variable, as well as the variance estimator in order to assess the precision of the estimates (Burnham & Anderson 2002, Johnson & Omland 2004).

Then, we calculated the probability of shearwater foraging and feeding for each grid cell using the averaged logistic model developed with 'presence/absence' and 'feeding/not feeding' data. We calculated the linear predictor (LP) using the intercept and the variable coefficients from the averaged models, and calculated the probability of models (Pr) as follows: $Pr = e^{LP} \times (1 - e^{LP})^{-1}$.

Finally, we could have ranked predictor importance summing the Akaike weights for all models containing an explanatory variable (e.g. Burnham & Anderson 2002, McAlpine et al. 2008), but Murray & Conner (2009) found that this approach was not sufficiently sensitive to correctly rank variable importance, suggesting alternative methods such as hierarchical partitioning. As an alternative, Burnham & Anderson (2002) recommended a randomization procedure to estimate the baseline value for w_i , denoted as w_{i0} , and then measure variable importance by computing the difference between w_i and w_{i0} . For those predictors with negligible predictive value, these differences should be close to zero. We used this approach for ranking predictor importance (see Supplement 5, available in MEPS Supplementary Material at: www.int-res.com/articles/suppl/m391p183_app.pdf).

Table 1. *Calonectris diomedea*. Median (range) of the explanatory variables for Cory's shearwater vessel-based survey data (presence, $n = 60$, and absence, $n = 150$) and tracking data (feeding, $n = 300$, and not feeding events, $n = 415$) corresponding to 19 trips. An oceanography interpretation is also provided

Habitat variables	Vessel-based surveys		Tracking data		Indicative of the following processes
	Presence	Absence	Feeding	Not feeding	
Sea surface temperature (SST, °C)	13.97 (13.19–14.74)	14.2 (13.25–14.88)	14.31 (13.5–14.9)	14.3 (13.42–14.87)	Water mass distribution
SST gradient (SSTG)	1.65 (0.45–4.87)	1.66 (0–3.97)	0.86 (0–11.16)	1.02 (0–10.07)	Small-scale SST variability
Chlorophyll <i>a</i> (CHL, $mg\ m^{-3}$)	0.37 (0.26–1.22)	0.38 (0.25–1.21)	0.38 (0.26–1.52)	0.37 (0.25–2.43)	Ocean productivity domains
CHL gradient (CHLG)	11.19 (1.49–75.84)	9.47 (0.83–66.25)	15.22 (1.12–62.26)	9.95 (0.22–75.44)	Small-scale CHL variability
Bathymetry (BAT, m)	154.12 (32.5–971.25)	149 (20.33–973.5)	153.5 (30–2511)	767 (35.5–2518.5)	Coastal vs. pelagic domains
BAT gradient (BATG)	90.39 (39.93–99.61)	84.08 (16.45–99.42)	81.12 (4.21–97.84)	70.77 (4.05–99.64)	Presence of topographic features (shelf-break, seamounts)
Distance to colony ^a (COLONY, km)	36.76 (1.67–196.25)	47.04 (0.94–198.41)	139.36 (0.94–313.65)	122.37 (0.94–310.41)	Colony influence on central place foragers
Distance to shoreline (COAST, km)	10.58 (0.03–40.59)	16.12 (0.45–43.30)	15.19 (0–86.02)	27.29 (0–101.91)	Onshore–offshore distribution patterns
Distance to oceanographic fronts (FRONT, km)	50.71 (0–84.21)	69.14 (0–197.54)	97.24 (0.78–184.36)	93.38 (0–186.62)	Mesoscale frontal systems
Distance to continental shelf (SHELF, km)	5.27 (0.12–39.05)	6 (0.06–25.04)	9.45 (0.003–74.05)	13.37 (0.03–79.76)	Proximity with shelf-break (slope currents, vertical mixing and prey concentration)
^a Distance between the centroid of each grid cell and the nearest breeding colony for vessel-based surveys, and distance to the colony of origin for tracking data					

Model fit: To assess the fit of the model with the lowest AIC_c , we used a Pearson χ^2 goodness-of-fit test (Crawley 1993); we checked for spatial autocorrelation in model residuals constructing Moran's I correlogram (see Supplement 5).

Model evaluation: Assessing the predictive ability of a model is a crucial step for allowing its proper use in ecological applications, especially when conservation issues are the main objective. The area under the curve (AUC) of a receiver operating characteristic (ROC) plot is widely utilised to assess habitat models developed through logistic regression (e.g. Brotons et al. 2004, Elith et al. 2006, Louzao et al. 2006, McAlpine et al. 2008), and was used here to validate our model predictions (Fielding & Bell 1997). This approach can also be applied to any model that produces estimates of probability for a binomially distributed response variable (e.g. feeding/not feeding). ROC curves are simply plots of sensitivity (the fraction of correctly predicted presences) against 1 – specificity (the fraction of correctly predicted absences) with changing critical values of threshold probability. AUC is a threshold-independent summary statistic that ranges from 0 to 1 (from negligible to perfect discriminatory power, respectively). AUC values represent the discriminatory ability of a model as follows: higher than 0.9, excellent; from 0.9 to 0.8, good; from 0.8 to 0.7, moderate; from 0.7 to 0.6, poor; and from 0.6 to 0.50, unsuccessful (Swets 1988).

We applied a cross-validation procedure to assess the predictive performance of the averaged model resulting from the Information-Theoretic approach using 2 different approaches: (1) use of an independent dataset for each of the 2 types of data and (2) resampling techniques (e.g. bootstrap) which provide an alternative approach for evaluating the model with the original data (Guisan & Zimmermann 2000, McAlpine et al. 2008). Concerning vessel-based survey data, we used the MEDITS surveys corresponding to 2006, which also covered the same geographic area comprising 216 cells (5 n mile cells; 51 presences and 165 absences). For tracking data, the independent dataset was built by randomly selecting a second foraging trip for each individual, which includes 15 foraging trips (15 individuals at least performed 2 foraging trips) with a total of 664 cells (5 n mile cells; 266 'feeding' and 398 'not feeding'). Both datasets should be preferably mentioned as quasi-independent data sets since they covered the same geographic extent of the original dataset (Guisan & Zimmermann 2000).

The cross-validation procedure was repeated 1000 times, and during each simulation we randomly assigning the 70 % of the original data to the training dataset and 30 % to the test dataset (e.g. Brotons et al. 2004). The best subset of models resulting from the Information-Theoretic approach (Table S2 in Supplement 5) was fit-

ted to the training dataset, the averaged coefficients extracted and the averaged model was fitted to the test dataset. AUC values were estimated in each simulation for both training and test datasets. After the 1000 simulations, the mean and upper and lower 95 % CI of the AUC of both training and test dataset were used as a cross-validation measure of the predictive performance of the averaged model (McAlpine et al. 2008). If the lower 95 % CI limit does not include the 0.5 value, then there is evidence that the model has an ability to discriminate between the 2 groups (Hanley & McNeil 1982). We also conducted the same cross-validation procedure to the quasi-independent dataset following the same random procedure as previously described.

Mapping habitat probability. We represented probabilities of suitable habitat for the vessel-based survey dataset (June 2007) and the tracking dataset (August 2007) with GIS. A regular lattice of 5 n mile cells was placed over the study area, and environmental variables considered in the averaged model were extracted. Model-averaged predictions of the foraging and feeding habitat of Cory's shearwater were estimated. We could have transformed probabilistic predictions into a binomial response variable based on threshold values in order to identify the suitable potential habitat; however, providing a continuous probability surface may be the most flexible and powerful method, thus allowing managers to select different thresholds depending on the model objective (Freeman & Moisen 2008). Additionally, the formal combination of both datasets was disregarded due to the different timing of the datasets, which corresponded to the Cory's shearwater incubation period for vessel-based surveys and chick-rearing for tracking data, respectively. Therefore, although multiplying both probabilities might be statistically correct, the most biologically correct approach might be multiplying probabilities of the 2 disparate datasets only when available for exactly the same period.

RESULTS

The seascape of Cory's shearwater

The seascape occupied by Cory's shearwater is characterised by the oceanographic patterns typical of the western Mediterranean Sea, including strong habitat gradients evidenced by the significant cross-correlations between several habitat variables ($|r_s| > 0.5$, Table 2). The west and north of the study area (the Ebro Delta and the Gulf of Lions, respectively) were characterised by a higher oceanographic variability at the small scale, reflected in both CHL and SST, and represent the most productive (8 mg m^{-3} , maximum

integrated CHL values between February and April) and coldest waters of the study area (see Supplement 4, available in MEPS Supplementary Material at: www.int-res.com/articles/suppl/m391p183_app.pdf for oceanographic characterisation). Additionally, important mesoscale frontal systems were also identified within the study area, mainly at the north of the Balearic Islands (Fig. S3e,f).

Spatial autocorrelation

We found no evidence of significant spatial autocorrelation in Cory's shearwater distributions for either the vessel-based survey data or the GPS tracking data at the selected scales of analysis (9.3 km cells, with lags from 9.3 to 139.5 km) (Fig. 2). Both datasets yielded small magnitude Moran's I values (from +0.2 to -0.1), suggestive of weak aggregated spatial patterns (Fig. 2). Thus, the correlograms revealed that the selected spatial scale of analysis yielded independent observations, suitable for performing the habitat modelling.

Modelling foraging probability

For vessel-based data, the model with the lowest AIC_c (AIC_c = 241.581) contained SST, BATG and

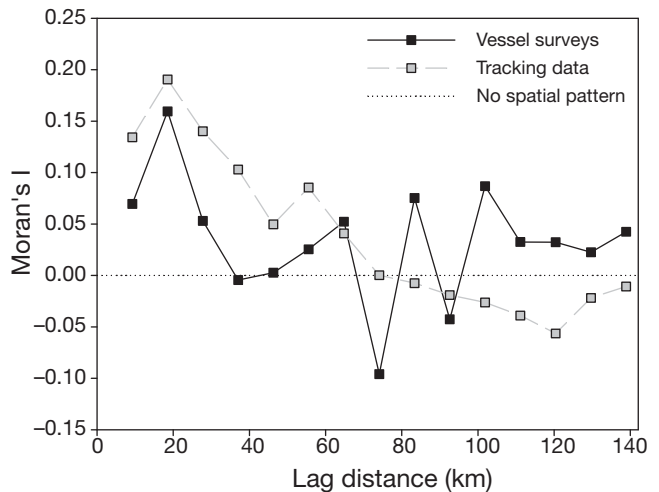


Fig. 2. *Calonectris diomedea*. Results of the spatial autocorrelation of vessel-based survey and tracking data within 15 distance lags (each lag increment corresponds to 5 n miles [9.3 km]). No evidence of significant spatial autocorrelation was found for any values of either dataset

COAST (see Table S2 in Supplement 5). Based on the correlogram analysis, we did not find any significant spatial autocorrelation in the residuals (see Fig. S4 in Supplement 5). Also, the Pearson χ^2 goodness-of-fit test revealed no evidence of significant lack of fit ($\chi^2 = 212.29$, $p = 0.366$, $df = 206$). Finally, the area under

Table 2. *Calonectris diomedea*. Results of the cross-correlation analysis of environmental variables for tracking data and vessel-based survey based on the Spearman-rank correlation coefficient r_s (in bold $|r_s| > 0.5$) and corresponding significant levels (lower and upper diagonal, respectively). Significant level set at <0.05, <0.01 and <0.001; NS: not significant. See Table 1 for abbreviations

	SSTG	SST	CHLG	CHL	BATG	BAT	COLONY	COAST	FRONT	SHELF
Vessel-based survey data										
SSTG	–	NS	NS	NS	NS	NS	NS	0.01	NS	0.05
SST	–0.080	–	NS	0.001	NS	NS	0.001	NS	0.05	NS
CHLG	–0.056	–0.068	–	0.001	NS	0.001	0.001	NS	NS	NS
CHL	0.065	–0.261	0.385	–	0.001	0.001	0.001	NS	NS	0.05
BATG	–0.095	0.005	–0.071	–0.318	–	NS	0.01	0.001	0.001	0.001
BAT	0.097	–0.069	–0.392	–0.288	–0.058	–	NS	0.001	NS	NS
COLONY	0.093	–0.494	0.356	0.586	–0.204	–0.022	–	0.001	0.001	NS
COAST	0.198	–0.135	–0.132	0.082	–0.480	0.580	0.303	–	0.05	NS
FRONT	–0.041	0.161	–0.001	0.099	–0.290	0.030	–0.308	0.167	–	NS
SHELF	0.153	–0.105	0.050	0.150	–0.493	–0.118	0.079	0.083	0.072	–
Tracking data										
SSTG	–	0.001	0.000	0.001	0.001	0.001	0.001	0.001	0.001	0.001
SST	–0.377	–	0.001	0.001	0.010	0.010	0.001	0.001	0.001	0.001
CHLG	0.048	–0.310	–	0.001	0.001	0.001	0.001	0.001	0.010	0.001
CHL	0.348	–0.436	0.319	–	0.001	0.001	0.001	0.010	0.001	0.001
BATG	–0.305	0.121	0.287	–0.290	–	0.001	0.001	0.001	0.001	0.001
BAT	0.227	–0.116	–0.534	–0.150	–0.564	–	0.001	0.001	0.001	0.001
COLONY	0.379	–0.492	0.281	0.769	–0.308	0.133	–	0.001	0.001	0.001
COAST	0.400	–0.242	–0.392	0.114	–0.744	0.830	0.193	–	0.001	0.001
FRONT	–0.326	0.713	–0.097	–0.248	0.258	–0.251	–0.353	–0.332	–	0.001
SHELF	0.241	–0.156	–0.262	0.181	–0.788	0.582	0.143	0.667	–0.207	–

the ROC curve was 0.714 ± 0.038 , indicating moderate discriminating ability. However, this model had an Akaike weight of 0.133, indicating substantial model uncertainty (66 models in the 95 % confidence set) and that a model averaging approach was appropriate.

All ‘non-correlated’ explanatory variables were included within the 95 % model set, and the relationship between the response variable and predictors is based on the sign of the averaged coefficients (between brackets). The SST (–) showed the strongest negative effect on shearwaters occurrence, whereas the rest of predictors ranked from BATG (+) > COLONY (–) > COAST (–) > CHLG (+) > FRONT (–) > SHELF (–) > SSTG (+) (Fig. 3 and Table S2 in Supplement 5). At the wider scale, foraging might occur in cool waters characterised by high bathymetric variability close to the colonies and the coast. If within these areas, high chlorophyll variability and the presence of frontal systems are expected to increase the foraging probability of shearwaters both along the Iberian Peninsula (from the Gulf of Lions to Cape Palos) and around the Balearic Islands (Figs. 1 & 4, Supplement 4).

The AUC value (\pm SD) of the vessel-based surveys averaged model showed a moderate model performance (0.745 ± 0.038). The cross-validation of the original vessel-based survey data yielded moderate values of AUC: 0.747 for the training dataset (CI 95 %: 0.700 to 0.806) and 0.676 for the test dataset (CI 95 %: 0.570 to

0.780). Similarly, cross-validation of the quasi-independent dataset showed that our averaged model failed to provide reasonable foraging predictions: AUC of 0.684 for the training dataset (CI 95 %: 0.627 to 0.746) and 0.600 for the test dataset (CI 95 %: 0.510 to 0.710).

Modelling feeding probability

For the tracking data, the model with the lowest AIC_c ($AIC_c = 903.94$) contained BAT and FRONT (see Table S2 in Supplement 5). Based on the correlogram analysis, we did not find any significant spatial autocorrelation in the residuals (Fig. S4 in Supplement 5). Also, the Pearson χ^2 goodness-of-fit test revealed no evidence of significant lack of fit ($\chi^2 = 712.86$, $p = 0.473$, $df = 711$). Finally, the area under the ROC curve was 0.724 ± 0.019 , indicating moderate discriminating ability. However, this model has an Akaike weight of 0.44, indicating substantial model uncertainty, with 6 models in the 95 % confidence set. This indicates that a model-averaging approach was appropriate.

All ‘non-correlated’ explanatory variables were included within the 95 % model set with BAT (–) having the strongest negative effect on shearwaters feeding probability and occurring in all models in the 95 % set (see Table S2 in Supplement 5). The relative importance of individual variables ranked additional variables as FRONT (–) > SSTG (–) > CHL (+). At the finer scale, feeding might occur in relatively shallow waters, close to frontal systems in areas of low fine-scale SST variability and highly productive areas along the Iberian Peninsula and around the Balearic Islands (Fig. 1, Supplement 4). Within this oceanographic context, tracking observations allowed us to identify 3 important feeding hotspots along the continental shelf-slope area of the Iberian Peninsula (Gulf of Lions, Cape Creus–Barcelona–Ebro Delta, and Cape La Nao–Cape Palos; from north to south), as well as the shelf-slope areas around the Balearic Islands (Figs. 1 & 4).

The AUC value (\pm SD) of the tracking averaged model showed a moderate model performance (0.700 ± 0.019). The cross-validation of the original tracking data demonstrated that our averaged model showed a moderate predictive performance: AUC of 0.701 for training dataset (CI 95 %: 0.674 to 0.730) and 0.700 for test dataset (CI 95 %: 0.640 to 0.748). However, the cross-validation of the quasi-independent dataset showed that our averaged model failed to provide reasonable feeding predictions: AUC of 0.583 for the training dataset (CI 95 %: 0.548 to 0.615) and 0.561 for the test dataset (CI 95 %: 0.51 to 0.623), but still discriminate between ‘feeding’ and ‘not feeding’

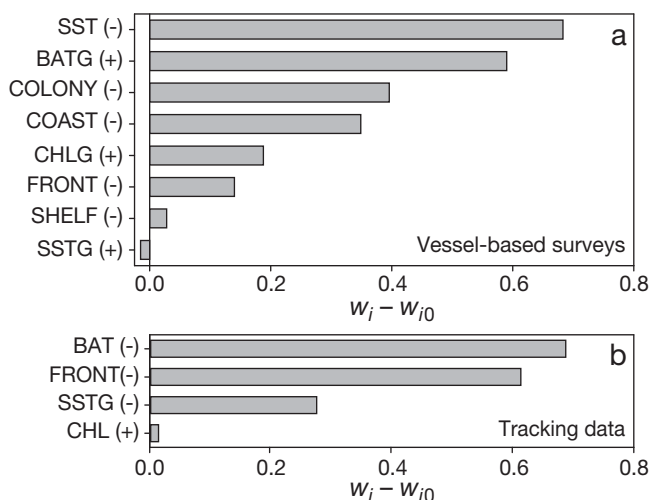


Fig. 3. *Calonectris diomedea*. Ranking of seascape variables based on a randomization procedure to estimate the baseline value for Akaike weight (w_i), denoted as w_0 , for (a) vessel-based survey and (b) tracking data. If the difference between w_i and w_0 is close to zero, the predictor may not have any predictive value (Burnham & Anderson 2002). The sign within parentheses indicates the sign of the effect of the variable on the probability of Cory’s shearwaters foraging and feeding (see Table S2). See Table 1 for definition of variable abbreviation

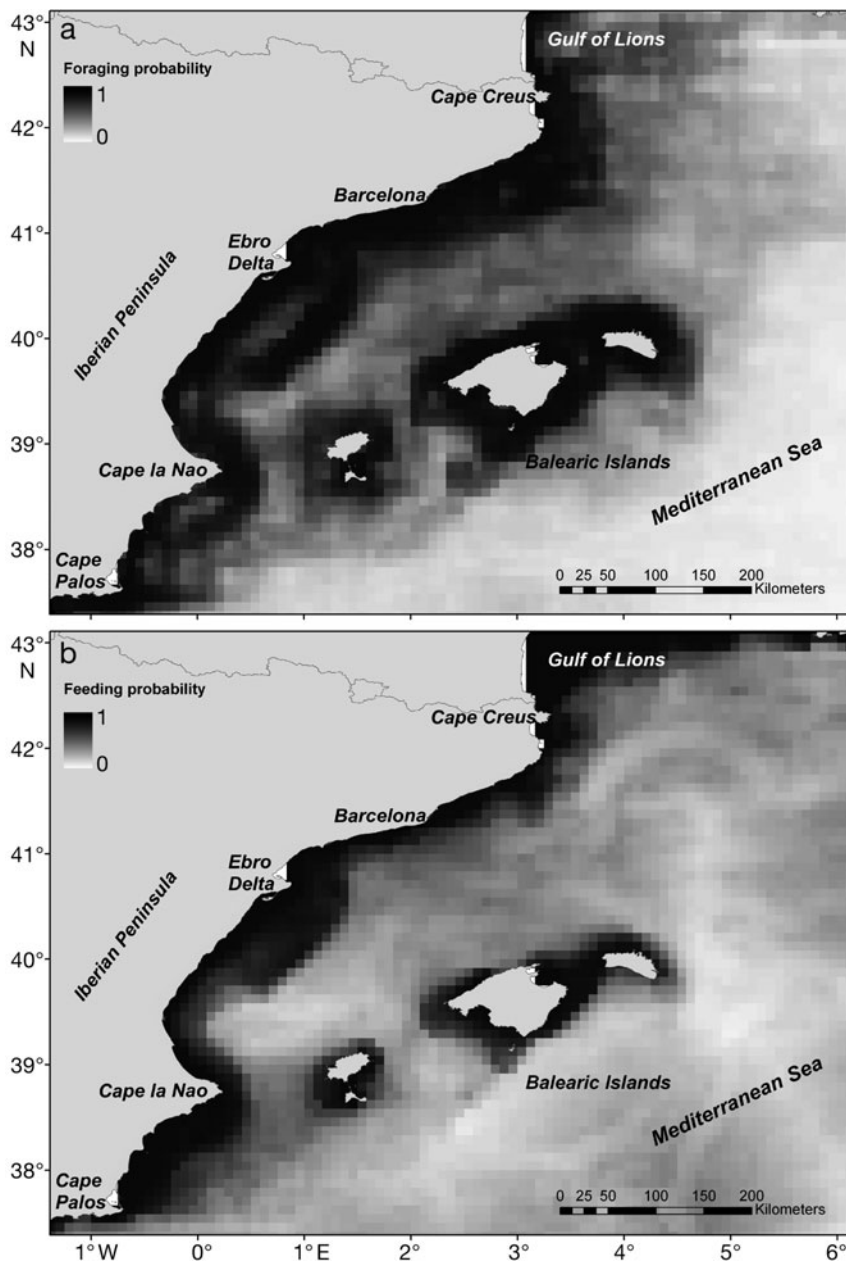


Fig. 4. *Calonectris diomedea*. Averaged models predicted (a) foraging probability (vessel-based survey data) and (b) feeding probability (tracking data) of Cory's shearwater

DISCUSSION

We undertook a hierarchical analysis of the oceanographic features influencing the feeding and foraging habitat of a vulnerable marine top predator, Cory's shearwater, in the complex and dynamic seascape of the western Mediterranean by combining 2 disparate and complementary data sets. Our results provided new relevant insights for defining the oceanographic

habitat and for predicting the distribution of shearwaters during the breeding season. In the following sections, we discuss the conservation implications of this integrated habitat modelling approach and its findings for identifying key areas for marine birds.

The seascape of Cory's shearwater: identifying key areas

The integration of tracking and vessel data provided a unique opportunity for identifying key marine areas for Cory's shearwaters by providing 2 distinct, yet complementary habitat perspectives that reinforced each other. Our habitat modelling analyses suggested that shearwaters respond to complex bio-physical coupling illustrated by their association with frontal features and elevated ocean productivity. Within a mesoscale perspective, the foraging range of the species comprised the continental and insular shelf-slope areas between the Gulf of Lions to the north and Cape Palos to the south. Within a coarser perspective, the tracking data highlighted 3 important feeding hotspots along this continental shelf-slope area of the Iberian Peninsula (Gulf of Lions, Cape Creus to Ebro Delta, and Cape La Nao to Cape Palos). Despite the more restricted spatial coverage of the vessel-based surveys, these data identified a further important feeding hotspot (showing feeding densities >76 birds km^{-2}) off Barcelona (Fig. 1a). All 4 feeding hotspots might be influenced by the Northern Current, which interacts with different physical (e.g. submarine canyons in the Cape Creus) and chemical features (e.g. river run-off such as the Ebro) along its path, creating diverse meso- and coarse-scale oceanographic processes along the shelf-slope region and transporting rich nutrient waters from the Gulf of Lions southwards to the Cape Palos (Millot 1999). Our results agree with previous studies, which have underscored the shelf-slope distribution of Cory's shearwater and its tendency to occur along the Iberian continental shelf,

mainly between the Ebro Delta and Cape La Nao (Abelló et al. 2003). However, to our knowledge, this is the first study to quantitatively assess Cory's shearwaters marine habitat use on the basis of both static and dynamic habitat variables. Dynamic variables such as coastal water masses and frontal systems within productive continental shelves often delineate key feeding habitats for breeding seabirds (Skov et al. 2008). Contrary to the productive temperate and subpolar continental shelf habitats, the Mediterranean is considered an oligotrophic Sea, although remotely-sensed chlorophyll *a* values documented in the study area were generally characteristic of a mesotrophic regime (Louzao et al. 2006, present study).

Our tracking data also provided a larger ecological context for the interpretation of these feeding hotspots, by revealing that central-place foraging Cory's shearwaters repeatedly commuted between the less productive waters around the breeding colonies (Balearic Islands) and the highly productive waters of the shelf-slope areas of the Iberian Peninsula, thus exploiting 2 distinct shelf-slope foraging areas during the breeding period: continental (Iberian Peninsula) and insular (Balearic Islands). Commuting seems to be a common behaviour of pelagic birds within temperate and polar regions, and might suggest that breeding seabirds 'know' where to find food, probably from previous experience (Weimerskirch 2007). In fact, the predictability of marine resource dispersion is time-scale dependent, and likely varies across marine habitats (Weimerskirch 2007). For instance, the location of resources at large and intermediate scales appears reasonably predictable for seabirds over long time periods (e.g. seasons). The association of Mediterranean pelagic seabirds with the same mesoscale features along the Iberian continental shelf year after year exemplifies this long-term predictability (Arcos & Oro 2002, Louzao et al. 2006). Within the coarse spatial scale, prey patches are likely to be scattered within mesoscale features (Weimerskirch 2007), which might vary both spatially and temporally depending on the influence of physical and biological drivers, including riverine discharge, the timing and location of spawning stocks of small pelagic fish, and spatio-temporal dynamics of fisheries in the western Mediterranean (Lloret et al. 2004).

Habitat modelling approach and limitations

While the Information-Theoretic approach has been widely applied to terrestrial ecosystems (Gray et al. 2007, McAlpine et al. 2008), it has not been used in the more dynamic marine ecosystem as a robust model selection strategy (but see Ribic et al. 2008). Within this framework, competing models are evaluated by assessing their relative support in relation to observed

data, rather than using the best single model approach (Buckland et al. 1997, Burnham & Anderson 2002, Johnson & Omland 2004). Furthermore, when models have similar levels of support, model averaging can be used to make robust predictions. Nevertheless, Richards (2005) raised some concerns related to model averaging with Akaike weights and stressed the need for continued research on the effectiveness of model averaging, as did Burnham & Anderson (2004). When comparing different methods for ranking variable importance, Murray & Conner (2009) found that summing the Akaike weights for all models containing x_i explanatory variables was not sufficiently sensitive to correctly rank variable importance. Burnham & Anderson (2002) also acknowledged some limitations of the summing of Akaike weights, since it cannot yield zero, even if some of the explanatory variables x_i have no contextual predictive value at all. They suggest (among others) a randomization method that we developed in the present study which might deserve further research (see Supplement 5).

We used logistic regressions (GLMs and GLMMs) to develop habitat suitability models using binary response variables. GLMs and GLMMs are robust tools for modelling species distributions and they allow the generation of statistical functions that allow predictions of potentially suitable habitat distribution for species within a GIS framework (Guisan & Zimmermann 2000, Brotons et al. 2004, McAlpine et al. 2008). However, presence/absence data rely on the need to obtain standardized absence data and the reliance on arbitrary criteria of the minimum amount of survey effort required to ascertain the absence of the species of interest in the sampling unit being considered (Redfern et al. 2006). Other methods, including envelope models and presence-only models, have been widely used in the literature to generate habitat suitability maps without requiring standardized effort and presence data (Brotons et al. 2004). These novel modelling approaches may be particularly suitable for tracking data, due to the lack of standardized effort and absence data (Skov et al. 2008).

Comparisons of these novel approaches with the more established presence/absence models underscore the disparity between models requiring high quality presence/absence data (e.g. GLMs) and models where absences are inadequate or unavailable (e.g. Ecological Niche Factor Analysis, ENFA; Brotons et al. 2004). Comparing the predictions of both methods revealed that the presence/absence predictions were more accurate than presence-only predictions, particularly when species were using available habitats proportionally to their suitability, thus making the absence data reliable and useful to enhance model calibration (Brotons et al. 2004). Because presence-only models

are continuously being developed, newly available approaches (e.g. boosted regression trees or maximum entropy methods) have been shown to out-perform more established methods, such as GLMs and generalised additive models (GAMs) (Elith et al. 2006, S. J. Phillips et al. 2006). Ultimately, the type and quality of the data (e.g. presence/ absence or presence-only, availability of standardized effort data), and the inherent characteristics of the focal species (e.g. habitat specificity, degree of aggregation) influences the selection and performance of habitat modelling approaches.

Also, species with less restricted ecological requirements and/or distribution ranges are modelled less accurately than species with more restricted requirements/ranges (Segurado & Araújo 2004, but see Elith et al. 2006), irrespective of the modelling methods employed (Brotons et al. 2004). Our work revealed a similar result in the western Mediterranean, where our habitat suitability model developed for the critically endangered Balearic shearwater performed better ($AUC \pm SE: 0.8 \pm 0.006$) than for the more widespread Cory's shearwater (Louzao et al. 2006). The Balearic shearwater is currently listed as Critically Endangered on the IUCN Red List due to its restricted breeding range (constrained to the Balearic Islands) and small (ca. 2000 breeding pairs) and declining population (7.4 % decrease per year; BirdLife International 2008). Despite the moderate predictive performance of our models, their predictions matched the observed foraging and feeding patterns. Moreover, the interpretation of the modelling output was consistent with the regional oceanography. The moderate discrimination ability of the models might reflect the potential exclusion of an important explanatory variable or the non-linear relationship with a critical habitat variable (McAlpine et al. 2008). Including different seasons and years (when long-term data are available) will help to overcome some of the habitat modelling limitations by validating and refining current habitat suitability models. Future research should also focus on obtaining a mechanistic understanding of the small-scale interactions between local oceanographic conditions, prey distribution, and the aggregation patterns and behaviour of Cory's shearwaters within the high-use feeding hotspots identified in the present study.

Combining vessel-based surveys and tracking data: conservation implications

This study demonstrates how the combination of vessel-based surveys and tracking data provides a wider understanding of the predictability of aggregation (i.e. hotspots) and the key oceanographic habitats of far-

ranging seabirds at different spatial scales (Rodhouse et al. 1996, BirdLife International 2004). While seabird conservation initiatives have independently addressed seascape patterns from either vessel-based surveys (e.g. Louzao et al. 2006) or tracked individuals (e.g. R. A. Phillips et al. 2006, González-Solís et al. 2007, Skov et al. 2008), few studies have integrated these distinct seascape and individual perspectives due to both logistical limitations (e.g. lack of concurrent tracking and survey data; but see Hyrenbach & Dotson 2003, Hyrenbach et al. 2006) and specific characteristics of both disparate datasets. It is critical to acknowledge the advantages and disadvantages of both approaches in order to reinforce the lessons learnt from these 2 perspectives and to reconcile potential discrepancies.

Overall, vessel-based surveys provide a large-scale (100s to 1000s of kilometres) perspective of the population level distribution and habitat associations, although constrained, to a varying degree, by the ship-following behaviour of certain species and the inability to determine the origin, sex, and reproductive status of observed individuals, as well as by the small survey area covered by vessel-based surveys. On the other hand, tracking data provide fine-scale (0.1s to 10s of kilometres) and detailed information at the individual level, due to the advent of GPS-loggers with small positional errors (0.01s of kilometers) and a higher rate of data acquisition (sampling intervals of seconds to minutes), compared to satellite-linked platform transmitter terminals (PTTs) (errors in the order of 100s of metres to 10s of kilometres and a sampling interval of hours) (Weimerskirch 2007). Nevertheless, the tracking perspective is often limited to small sample sizes (few tagged individuals tracked over short time periods) due to the cost of both devices and fieldwork for deployment/retrieval of tags. Therefore, these distribution data may not be representative of the population as a whole, owing to variation in ranging behaviour according to specific characteristics such as colony of origin, age, sex, breeding status, and season (e.g. BirdLife International 2004).

The commonly used variables for key marine area identification include the overall number of birds in a given area (i.e. density) and their behaviour (i.e. proportion of foraging versus flying birds). While these metrics are easier to infer from landscape-level vessel-based surveys than from tracking studies of individual foragers, when loggers of low positional error and high rate of data acquisition are used, researchers can use animal behaviour to infer finer-scale habitat use patterns, such as migration corridors and feeding grounds (Weimerskirch 2007). Other available methodologies, such as land-based counts, are also key approaches for monitoring migration flows, mostly through narrow cor-

ridors defined by topographical features (e.g. the Strait of Gibraltar), which concentrate large numbers of migrating seabirds (del Hoyo et al. 1992). Yet, while these methods provide information on the timing and magnitude of the flow through, they cannot provide seascape level data on the distribution of these marine top predators (e.g. habitat associations, background densities).

Once the location and extent of key seabird habitat areas are identified, the next step is to ensure their legal protection. In the European Union, the Natura 2000 network provides the opportunity of effectively protecting the identified marine IBAs through their designation as Special Protection Areas (SPAs) within the EC Bird Council Directive 79/409/EEC for the protection of wild birds. Beyond the identification and designation process, further effort must be directed towards the establishment of long-term monitoring programmes for assessing significant threats affecting seabirds and to develop the appropriate management plans in the protected areas. Because some threats faced by seabirds are to some extent diffuse and widespread (e.g. oil spills), any spatially explicit conservation action (e.g. designation of SPAs) needs to be framed within a larger conservation approach, addressing the status and the threats to the species through its range and life cycle. For instance, Cory's shearwaters are highly susceptible to longline fisheries in the western Mediterranean (Belda & Sánchez 2001), where the implementation of both an observer programme and mitigation measures on the fishing vessels are critical for the conservation of the species. Both measures should be implemented within the whole range of the species, controlling longlining to a greater degree and intensifying the monitoring efforts within the key marine areas for the species. Ultimately, we believe that spatially explicit protective measures will help to catalyze a comprehensive ecosystem-based management approach to protect marine far-ranging species of conservation concern.

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Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: implications for marine protected areas

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ABSTRACT: Industrial-scale fisheries are often thought to reduce food availability for top predators. It is essential to estimate the spatial and temporal overlap over a fine scale between fisheries and predators during their breeding season, when their energy demand is greatest and when they are most spatially constrained, in order to understand and manage this potential impact on their populations. In the Benguela upwelling region, 2 endemic vulnerable seabirds, Cape gannets *Morus capensis* and African penguins *Spheniscus demersus*, mainly eat anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*, both of which are exploited by the purse-seine fishery. A recent eastward displacement of small pelagic fish off the South African coast has reduced fish availability for both birds and fisheries along the west coast. Using GPS-recorders, we studied the foraging dispersal of birds from 8 colonies containing 95 % of the global Cape gannet and 60 % of the global African penguin populations to assess their overlap with fish catches. Despite the fact that bird data were gathered at very fine spatial and temporal scales (meters and hours), and fisheries data were recorded at much coarser spatial and temporal scales (20 km and months), there was clear overlap in areas used. The main foraging areas of both species were located where purse-seine fisheries caught most fish, with most catches occurring during the birds' breeding season. As birds and fisheries also overlap in the size of the targeted prey and the depth of exploitation, our study suggests the potential for intense competition between purse-seine fisheries and decreasing seabird populations in the southern Benguela. Long-term protection of these seabird species requires the inclusion of a suitable ecological buffer when setting fishery quotas, and implementing marine protected areas closed to fishing around key breeding sites and foraging hotspots may improve their breeding success.

KEY WORDS: African penguins · Biotelemetry · Cape gannets · Conservation · Industrial fisheries · Offshore reserves · Foraging hotspots

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INTRODUCTION

The oceans are one of humanity's most important resources, and human welfare, economics, and survival are tightly linked with the health of marine eco-

systems (Costanza 1999). However, marine ecosystems are deeply altered by humans, to an extent that has long been underestimated (Jackson et al. 2001). The most profound effect is due to exploitative use of marine resources, mainly through fishing (Pauly et al. 1998).

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Industrial-scale fisheries have altered and degraded marine ecosystems (Botsford et al. 1997, Williams 1998, Worm et al. 2006), probably reducing the biomass of fish top predators by an estimated 90 % compared to pre-industrial levels (Myers & Worm 2003). Many marine top predators (such as pinnipeds, cetaceans, seabirds and sharks) that play an important role in the maintenance of ecosystem function (Myers et al. 2007) are threatened by fishing both through mortality caused by fishing gear (e.g. González-Zevallos & Yorio 2006) as well as direct competition with fisheries (e.g. Furness & Tasker 2000). Upwelling systems, such as the Humboldt and the Benguela regions, are wasp-waist ecosystems (Cury et al. 2000), largely rely on a species-poor intermediate trophic level dominated by 2 genera of small pelagic fish (sardines *Sardinops* spp. and anchovies *Engraulis* spp.) that regulate the transfer of energy from lower to upper trophic levels. In these ecosystems, the breeding success and/or abundance of top predator populations are related to the availability of these small pelagic fish (see Crawford & Jahnke 1999). Because the populations of such fish fluctuate at large temporal and spatial scales, these top predators have developed life-history traits to buffer against these fluctuations, and thus can show behavioural flexibility. However, fisheries exploitation increases the pace and scale of these fluctuations to a scale of magnitude beyond the range of natural variation, reducing the possibility for predators to accommodate them (Duffy 1983, Crawford 1999).

For instance, in the Benguela upwelling system, over-exploitation of sardines *Sardinops sagax* off South Africa in the 1960s and off Namibia in the 1970s lead to their populations collapsing (Griffiths et al. 2004). Anchovies *Engraulis encrasicolus* largely replaced sardines in the fisheries landing off South Africa (Cochrane et al. 1998), but small pelagic fish populations off Namibia have still not yet recovered (Griffiths et al. 2004). Consequently, the global population of the endemic Cape gannets *Morus capensis* and African penguins *Spheniscus demersus*, which depend upon small pelagic fish (Crawford 1999), decreased by 50 %, rendering them vulnerable to extinction (Crawford 1999, IUCN 2006). Off the west coast of South Africa, bird numbers have further decreased since the mid-1990s due to a lack of food (Crawford et al. 2006, Pichegru et al. 2007) associated with recent shifts in the distribution and availability of their prey (van der Lingen et al. 2005, Roy et al. 2007, Grémillet et al. 2008a). It is essential to estimate the spatial and temporal overlap between purse-seine fisheries that target small pelagic fish, and the location and extent of feeding grounds of these birds during the breeding season, in order to understand and manage potential fishery impacts on seabird populations. Food availability during reproduction plays a key role in the population dynamics of

highly mobile species (e.g. Lewis et al. 2006), especially during young-rearing when (1) the energetic constraints are strongest upon breeding adults (Stearns 1992) as they need to feed both themselves and their growing offspring, and when (2) they are most spatially constrained.

Because scale is a critical factor in determining resource-use overlap between top predators and fisheries (e.g. Reid et al. 2004), results from studies that attempted to estimate the impact of competition between seabirds and fisheries have often been contradictory (see Tasker et al. 2000 and references therein). Often some overlap can be found at a coarse scale (> 300 km), but not at a fine scale (< 3 km) (e.g. Fauchald et al. 2000). In this analysis, we estimate the overlap between vulnerable seabirds and South African purse-seine fishery activities at a spatial scale of < 20 km and a monthly temporal scale. We used GPS tracking of birds from 8 colonies—containing 95 % of the global Cape gannet (Crawford 2005) and 60 % of the global African penguin populations (Crawford & Whittington 2005)—to determine their foraging distribution and overlap with spatially explicit data on catches of sardines and anchovies made by the pelagic fishery during the chick-rearing period. Despite the disparate scales of the 2 datasets, with the bird data gathered at very fine spatial and temporal scales (meters and hours), and the fisheries data recorded at coarser spatial and temporal scales (20 km and months), we contend that a significant overlap over such a fine spatial and temporal scale would provide strong evidence for competition. This method would also reveal areas of important conservation value and can help in the design of marine protected areas (MPAs).

MATERIALS AND METHODS

Bird foraging behaviour: data collection. The foraging behaviour of breeding Cape gannets and African penguins was studied between 2002 and 2007 under permits issued by Cape Nature Conservation and South African National Parks. Cape gannets were studied at all 3 South African colonies: Bird Island (Lambert's Bay, 32° 5' S, 18° 18' E), Malgas Island (33° 03' S, 17° 55' E), and Bird Island (Nelson Mandela Bay, 33° 50' S, 26° 17' E). African penguins were studied at the 5 largest of the 17 South African sites: Dassen Island (33° 25' S, 18° 04' E), Robben Island (33° 47' S, 18° 22' E), Boulders Beach (34° 12' S, 18° 27' E), Dyer Island (34° 40' S, 19° 25' E) and Bird Island (Nelson Mandela Bay) (Fig. 1).

The tracking loggers deployed on the birds have been used on several occasions and are only briefly described here (see details in Grémillet et al. 2004, Ryan et al. 2004). Two types of data loggers were used: (1) GPS

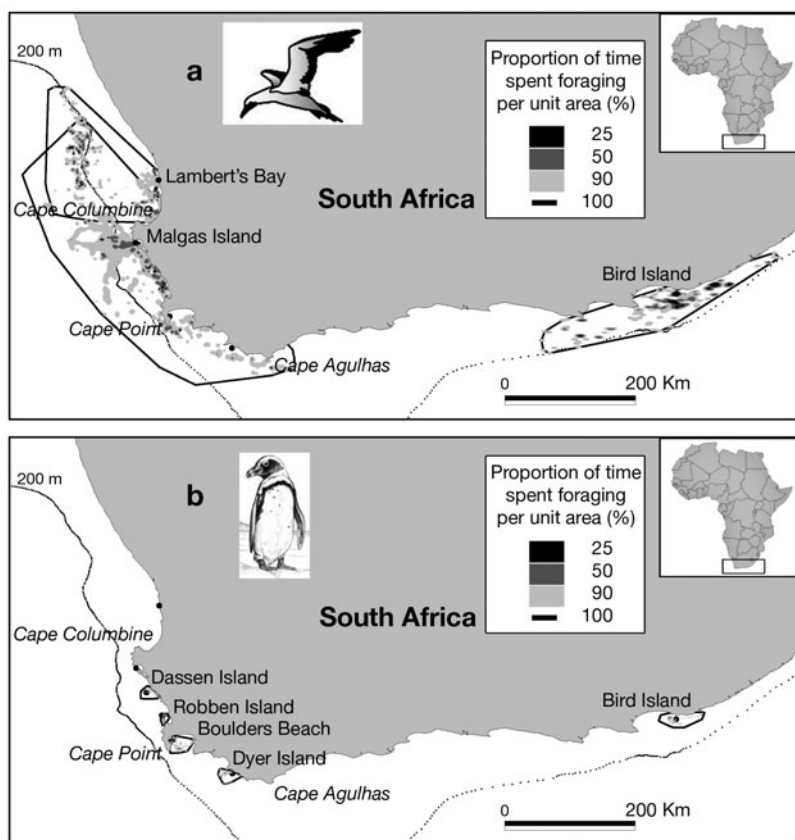


Fig. 1. Foraging grounds (kernels 25, 50, 90 % and minimum convex polygon [MCP] 100 %) of (a) breeding Cape gannets from 3 colonies and (b) African penguins from 5 colonies during 2002 to 2007

data-loggers (95 × 48 × 24 mm; Technosmart), that record latitude and longitude at 10 s intervals to an accuracy better than 10 m. (2) GPS-TD loggers (a GPS combined with a time-depth recorder; 96 × 39 × 26.5 mm; Earth and Ocean Technologies), that record latitude and longitude at 1 min intervals to an accuracy better than 10 m, and temperature and depth at 1 s intervals to the nearest 0.1 m. All devices were housed in streamlined fibre-composite containers and weighed <2.5 % of both species' adult body mass, which is below the 3 % limit recommended for flying birds (Phillips et al. 2003).

Cape gannets breed a single chick between September and February, whereas African penguins raise a brood of one or 2 chicks between March and August. In both species the parents share the care of their young, with typically one adult attending the nest or burrow when the partner is at sea (Crawford 2005, Crawford & Whittington 2005). Adult birds rearing small chicks of similar age (average of 3 and 2 wk old for gannets and penguins, respectively) were caught on their nest site. The devices were attached to feathers on their lower back with waterproof tape, allowing minimal damage to the plumage (Wilson et al. 1997).

Handling lasted 4 to 8 min from capture to release and care was taken to minimize the bird's stress (the birds' heads were covered, and those equipped during the day were shaded). After deployment, nest sites with instrumented birds were monitored until the adult returned, allowing it to be recaptured and the logger removed. Previous studies showed no significant difference in the foraging behaviour of experimental and control birds (Petersen et al. 2006, Pichegru et al. 2007), and no apparent impacts have been detected on the welfare of the animals.

Bird foraging behaviour: data analysis. Because African penguins have relatively small foraging ranges (Wilson 1985), their foraging habitat was inferred from their complete GPS tracks. By comparison, Cape gannet often commute over long distances to reach their foraging areas. Therefore, their foraging locations were inferred from their GPS tracks based on the path sinuosity, after Grémillet et al. (2004). For each colony, we defined different core foraging areas, covering their home range (Minimum Convex Polygon [MCP] – 100 %) and a range of proportional use ranges, based on 3 to 99 % (in 3 % intervals) of the time spent foraging per

unit area (kernel analysis, smoothing factor chosen according to the Least Square Cross Validation method, Girard et al. 2002), using Arcview GIS 3.2 (ESRI). When data from more than 1 breeding season were available for a colony, they were pooled. This method takes into account inter-annual variability and birds' maximum foraging range, and it reveals feeding hotspots, giving more statistical weight to areas that are used consistently over several years, which is part of BirdLife criteria to define marine Important Bird Areas (www.birdlife.org).

Fisheries' activities: temporal and spatial distribution. The weight (t) of anchovies and sardines caught per 10 × 10 nautical mile (18.6 × 18.6 km) grid cell by the South African purse-seine fishery between 2002 and 2007 was obtained from catch data recorded monthly by Marine and Coastal Management (South African Ministry of Environment and Tourism). The purse-seine fishery is active throughout the year (Fairweather et al. 2006). The temporal heterogeneity in fishery catches was tested with a General Linear Model, with the fisheries' catches as an independent factor, and months and years as explanatory variables.

The analyses were performed on anchovy and sardine catches separately. Spatial heterogeneity in the presence/absence of fish catches over the 6 yr period for the 341 cells overlapping Cape Gannet locations was calculated as follows: for each grid cell we scored the heterogeneity as the count of presences or absences, whichever was lower, so that e.g. 0,0,1,1,0,0 and 1,1,0,0,1,1 both score 2. The overall heterogeneity was expressed as the sum over all the cell scores, this gives values ranging from 0 (perfect similarity) to 1364 (maximum heterogeneity). To test the significance of this statistic, we performed a randomization test by taking 999 random samples with replacement across years. We used the R software for calculations.

Spatial overlap between birds and fisheries. The spatial overlap between fishing activities and birds' foraging behaviour was determined using the 10×10 nautical mile (18.6×18.6 km) grid. Each grid cell was associated with an amount of fish catch (if any) and the lowest kernel contour of the birds' foraging range (if the cell was also used by the birds). Thus, we calculated the proportion of the annual average catches of small pelagic fish by the purse-seine fisheries that occurred within the total foraging range of penguins for each colony, and within areas where gannets spent 50, 75 and 90 % of their time spent foraging, following BirdLife's criteria for the selection of Important Bird Areas. Although we analyzed the amount of fishing activities in the foraging range of birds from each colony separately, we had to analyze together the

areas used by gannets breeding on the colonies from the west coast (Bird Island, Lambert's Bay, and Malgas Island), as their foraging ranges overlapped (Fig. 1). Testing the overlap of fisheries and birds from these 2 colonies separately would lead to an overestimation of the competition between boats and gannets on the west coast.

RESULTS

Between 2002 and 2007, 166 gannet and 91 penguin foraging tracks were gathered from the 8 breeding colonies (Table 1). Gannet foraging trips lasted almost twice as long as those of penguins and had a mean foraging range (112 km) an order of magnitude greater than those of penguins (12.5 km, Table 1). The total foraging area (MCP 100%) of gannets covered $40\,176\text{ km}^2$, an area >10-fold greater than the total foraging area of the 5 penguin colonies studied (5022 km^2 , Table 2). The gannets' foraging range also included the locations of all other South African penguin colonies (Crawford & Whittington 2005). Although both species can show substantial inter-annual variability in some foraging parameters (trip durations during the same period of the breeding cycle can almost double between colonies and years, see Table 1), core foraging areas of gannets and penguins were located mainly in shallow shelf waters (< 200 m), where most of the annual catch of purse-seine fisheries

Table 1. *Morus capensis* and *Spheniscus demersus*. Average trip duration, foraging path length and foraging range of Cape gannets and African penguins from 8 colonies and 6 years in South Africa (values are mean \pm SD). Track numbers in parentheses are incomplete tracks from which no foraging parameters could be extracted but which were included in the spatial analyses

Colony	Year	N (tracks)	Trip duration (h)	Path length (km)	Foraging range (km)
Cape gannets					
Bird Island, Lambert's Bay	2002	41	13.1 ± 8.8	244.6 ± 126.1	68.2 ± 39.0
	2003	30	20.0 ± 9.3	434.1 ± 166.2	132.2 ± 45.3
Malgas	2002	26	23.1 ± 9.7	368.6 ± 200.2	105.8 ± 59.0
	2003	20	18.3 ± 13.1	412.7 ± 323.1	114.5 ± 82.7
	2004	14	31.3 ± 14.1	476.9 ± 199.5	122.8 ± 55.9
	2005	36	29.1 ± 12.7	514.4 ± 234.8	132.6 ± 62.7
	2006	43	22.8 ± 11.1	397.6 ± 199.6	104.0 ± 55.7
Bird Island, Nelson Mandela Bay	2005	27	13.8 ± 7.2	367.0 ± 232.0	112 ± 89
Total		166	21.4 ± 6.5	402.0 ± 81.5	111.5 ± 20.6
African penguins					
Dassen Island	2003	3 (4)	9.2 ± 1.3	33.6 ± 2.7	10.1 ± 0.9
	2004	28	11.3 ± 4.7	33.5 ± 2.5	5.6 ± 1.2
Robben Island	2003	7 (11)	11.1 ± 2.0	34.4 ± 7.7	9.5 ± 3.7
Boulders Beach	2003	10 (12)	14.4 ± 4.0	46.5 ± 13.3	19.3 ± 6.2
	2007	9	10.2 ± 1.8	25.1 ± 2.6	9.7 ± 2.4
Dyer Island	2007	12	14.0 ± 7.6	46.8 ± 18	15.76 ± 4.0
Bird Island, Nelson Mandela Bay	2007	15	21.8 ± 5.2	57.8 ± 17	17.1 ± 11.2
Total		91	13.1 ± 4.2	39.7 ± 11.1	12.5 ± 5.0

is also taken (Fig. 2). An annual average of 222 000 tons of anchovies and 255 000 tons of sardines were caught by the pelagic fishery over the period 2002 to 2007 all along the South African coast. Almost all anchovy catches occurred on the west coast (Fig. 2), where most of the seabird colonies are also located.

Temporal overlap

Small pelagic catches by purse-seine fisheries fluctuated over time between 2002 and 2007. Sardine catches varied significantly between months ($F = 4.95$, $df = 11$, $p < 0.01$) and years ($F = 5.92$, $df = 5$, $p < 0.001$), with a sharp decrease from 2004 onward, from 374 000 t in 2004 down to 140 000 t in 2007. The peak of sardine catches on the west coast occurred between September and March (although the catches in December were low, Fig. 3), which coincides with the timing of the Cape gannet breeding season (Crawford 2005). Anchovy catches remained constant over the years ($F = 1.68$, $df = 5$, $p = 0.155$), but varied significantly between months ($F = 11.61$, $df = 11$, $p < 0.001$), peaking in the austral autumn (Fig. 3), which is also peak breeding season for African penguins (Crawford & Whittington 2005). Although there are no anchovy catches on the east coast (Fig. 3), anchovies are caught as by-catch in sardine fisheries (Fairweather et al. 2006), and sardine fishing peaks on the east coast also during the austral autumn.

Spatial overlap

The overall heterogeneity score obtained for the purse-seine fishing overlapping Cape gannet locations was 224; this lies within the 95 % confidence interval (125 to 278) calculated by the randomization test, indicating that spatial differences between years in presence/absence of fishing do not differ from a random process. Purse-seine fishing boats thus exploited consistently the same zones over the years of our study.

Although penguins show a restricted foraging range (Tables 1 & 2, Fig. 1), their colonies are located in areas of important concentrations of fishery catches (Figs. 1 & 2, Table 2). The entire foraging range of the 5 colonies covered only 3.7 % of the entire marine area exploited by purse-seine fisheries. Yet, fisheries caught 14.2 % of their average annual catches in this small area (Table 2). Also, different colonies endured different intensities of competition. For instance, fishing boats took 6 % of their annual catches in the foraging range of penguins from Dassen and Robben Islands on the west coast, the surface of which represents less than 1 % of the total industrial fishing area (Table 2). Similarly, fisheries were catching the same amount of pelagic fish in the foraging area of the single colony of Dyer Island (Table 2), the eastern most colony of the west coast (Fig. 1).

Although the area where gannets spent 90 % of their foraging time was almost 10-fold larger than the penguins' entire foraging range, fisheries caught only

Table 2. *Morus capensis* and *Spheniscus demersus*. Foraging area of Cape gannets and African penguins (50, 75, 90 % kernel contours for gannets, minimum convex polygon [MCP] 100 % for penguins) for each studied colony, proportion of these respective areas of the total area exploited by purse-seine fisheries, and proportion of average annual catches of small pelagic fish by purse-seine fisheries taken from these different areas. Proportion of global population supported by each studied colony is also given

Colony	Proportion of global population (%)	Kernel or MCP (%)	Foraging area (km ²)	Proportion of size of foraging area vs. total fisheries area (%)	Proportion of fisheries' catch within foraging range (%)
Cape gannets					
West coast (Bird Island [Lamberts Bay], Malgas Island)	27.4	50	10 602	7.8	11.3
		75	19 716	14.4	17.2
		90	28 644	21.0	27.5
Bird Island (Nelson Mandela Bay)	65.6	50	5022	3.7	0.7
		75	9672	7.1	1.4
		90	11 532	8.4	1.5
Total	93		40 176	29.4	29.0
African penguins					
Dassen Island	36.7	100	558	0.4	3.3
Robben Island	10.2	100	744	0.5	2.8
Boulders Beach	3.0	100	1116	0.8	1.9
Dyer Island	5.7	100	1116	0.8	6.1
Bird Island (Nelson Mandela Bay)	7.8	100	1488	1.1	0.1
Total	63.4		5022	3.6	14.2

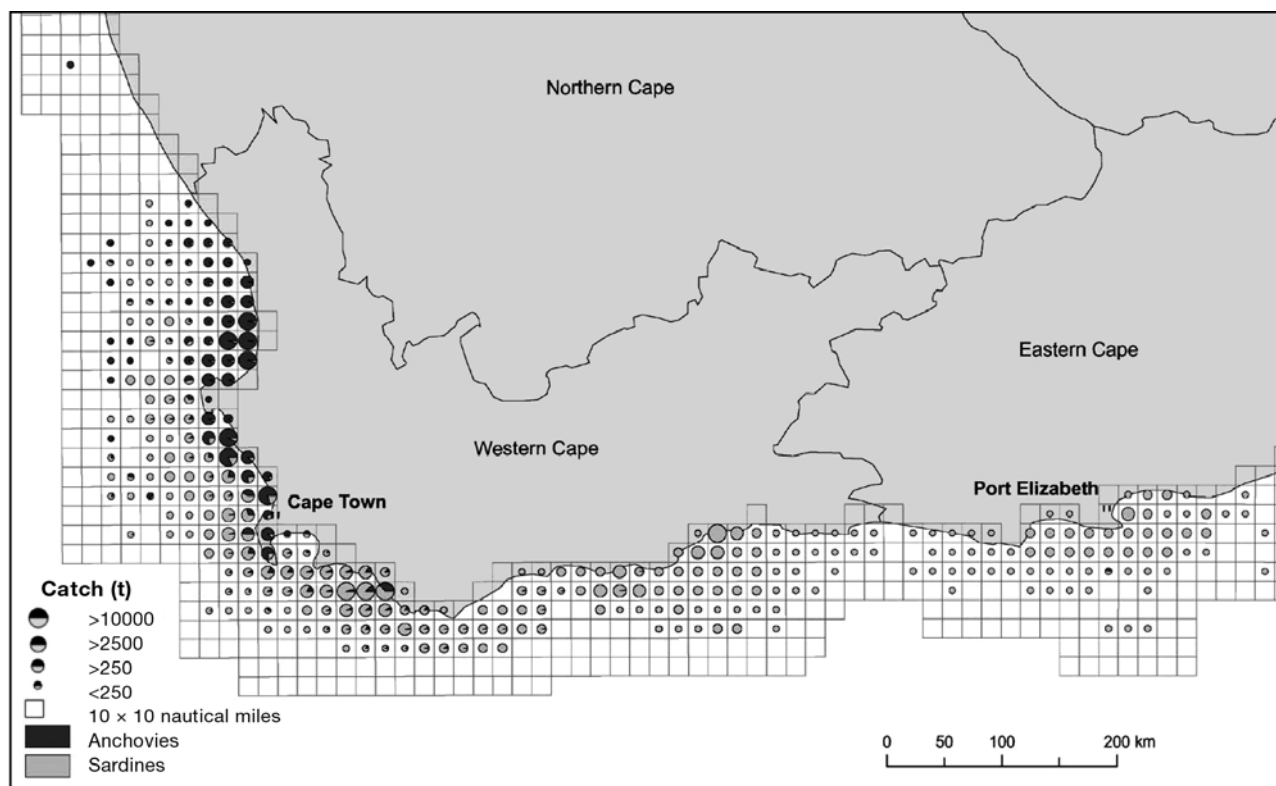
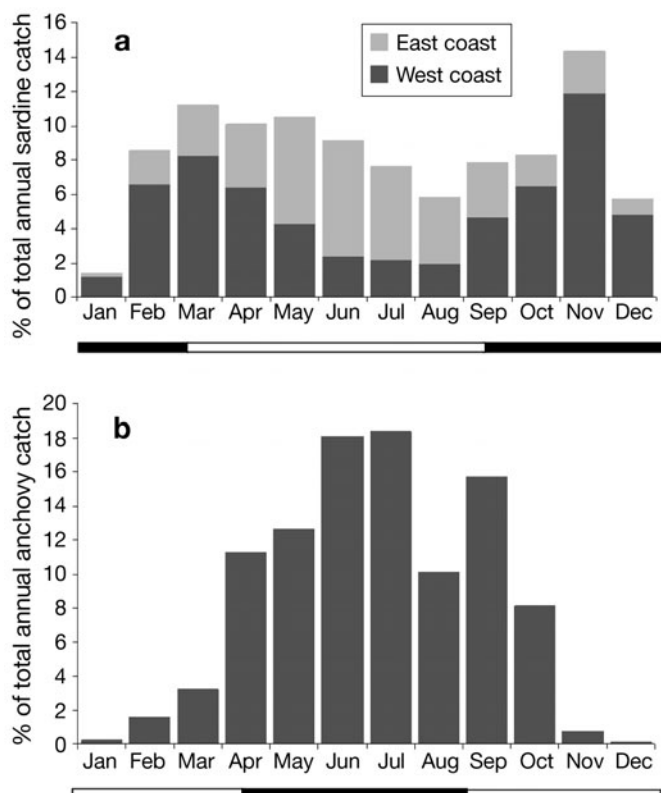


Fig. 2. *Engraulis encrasicolus* and *Sardinops sagax*. Average annual catch (in tons) of anchovies and sardines per 10×10 nautical mile (18.6×18.6 km) block off South Africa by the purse-seine fishing industry averaged for the period 2002 to 2007 (courtesy of H. Bohbot, CEFE-CNRS Montpellier)



twice as many fish as they caught in the penguin foraging area (Table 2). However, the competition between gannets and fisheries was much stronger on the west coast. Gannets breeding on Bird (Lambert's Bay) and Malgas Islands, showed a foraging range twice as large as that of birds breeding on Bird Island (Nelson Mandela Bay) (Fig. 1, Tables & 2), within which fishing pressure was almost 20 times greater than it was in the foraging area of the birds from the south coast, in Nelson Mandela Bay (Table 2). Gannets breeding on Bird (Lambert's Bay) and Malgas Islands also exhibited a greater foraging effort, with longer foraging trip durations and foraging path lengths, despite the fact that their population was half the size of that from Bird Island (Nelson Mandela Bay) (Tables 1 & 2 this study, Pichegru et al. 2007).

Fig. 3. *Sardinops sagax* and *Engraulis encrasicolus*. Monthly proportions of the average annual catch of (a) sardine and (b) anchovy west of Cape Agulhas (west coast) and east of Cape Agulhas (east coast) during (a) gannet and (b) penguin breeding (horizontal black bars) and non-breeding (horizontal white bars) seasons for the period of 2002 to 2007

DISCUSSION

Our study shows a strong spatio-temporal overlap between seabirds and fisheries targeting small pelagic fish. Purse-seine fisheries caught most of their catches from the core foraging areas of both species of birds (Figs. 1 & 2, Table 2). The peak of their catches also occurred during the birds' breeding period (Fig. 3), when the food demands of these marine predators are highest (Stearns 1992). Although interpretation of the data is complicated by the different scales of analysis used between birds and fisheries, there was a clear disproportionate overlap in the areas used.

Both birds and fisheries target prey of the same size. Gannets and penguins target fish of an average length of $\sim 15 \pm 6$ cm (Batchelor & Ross 1984, Klages et al. 1992, Crawford & Dyer 1995), whereas the size of the fish caught by fisheries is between 5 and 20 cm for sardines and 6 and 12 cm for anchovies (Fairweather et al. 2006). African penguins may reduce competition by targeting smaller, diffuse schools of fish, whereas the fishery targets large aggregations (Wilson 1985). However, both dense and diffuse schools probably form part of the same stock (Duffy & Wissel 1988). Finally, both birds and fisheries overlap in the depth at which they exploit their prey, as gannets do not dive deeper than 30 m (Ropert-Coudert et al. 2004), and most penguin dives occur between 10 and 70 m (Wilson 1985, Petersen et al. 2006). Purse-seine fisheries seldom operate at a depth > 50 m (Armstrong & Thomas 1989).

Our results illustrate the interactions between birds and fisheries during the whole life cycle of the birds. Indeed, competition between the 2 during the non-breeding period has been implicated in the decline in African penguins off South Africa (Burger & Cooper 1984) at that time. Overlap with fisheries activities during post-natal dispersion can also be crucial in juvenile survival (Weimerskirch et al. 2006) and immature African penguins showed a very low survival in areas open to fishing, compared to those in areas closed to fisheries (Duffy et al. 1984), probably due to the combined threats of by-catch and competition over the same prey. Although some fisheries can provide food for some seabirds through their wastes (e.g. Tasker et al. 2000), African penguins do not feed on fishery offal, as no fishery waste has ever been found in their diet samples (Marine and Coastal Management unpubl. data). Cape gannets from the west coast colonies can make extensive use of wastes from a demersal fishery (Berruti et al. 1993, Pichegru et al. 2007); however, their chick survival on such a diet is extremely low (Grémillet et al. 2008b). Therefore, gannets do not benefit from these fisheries in terms of reproductive output. Finally, purse-seine fisheries do not process their catches on board, so their waste production is minimal (N. Okes, WWF, pers. comm.).

The recent eastward shift in the distribution of both anchovy and sardine off the South African coast has further reduced fish availability along the west coast and the sardine population has also decreased substantially in recent years (van der Lingen et al. 2006), which is reflected in this study by the sharp decrease in sardine catches between 2004 and 2007. The direct competition between birds and fisheries demonstrated by our data, particularly on the west coast (Figs. 1 & 2, Table 2), is probably increased during prey scarcity to the detriment of the birds, thus weighing heavily on already vulnerable species. African penguin and Cape gannet populations may soon be re-classified as Endangered (Kemper et al. 2007), probably due to lack of food (Crawford et al. 2006, Pichegru et al. 2007), and conservation measures are urgently required.

A first step is to integrate the birds' needs into an Ecosystem Approach to Fisheries (EAF; Shannon et al. 2006). An EAF for the pelagic fishery is being developed by the Marine and Coastal Management, the regulatory authority for South Africa's marine fisheries. One aspect of this EAF is a consideration of the amount of small pelagic fish needed by penguin populations in order to survive and breed successfully, and incorporation of this consideration into the Operational Management Procedure (OMP) used to set the annual Total Allowable Catch (TAC) for the pelagic fisheries. However, further measures may be necessary, and although progress has been achieved establishing a number of MPAs in South Africa¹, the marine area that is currently protected (1.6% of the Exclusive Economic Zone of South Africa) is still far from the 10% goal set by the United Nations Convention on Biodiversity. Studies such as the present one provide crucial information in revealing biological hotspots under environmental pressure, and suggesting zones that should be protected as a priority. Cape gannets and African penguins forage in offshore environments (deeper than 30 m) while breeding, and these environments are poorly protected (Game et al. 2009), even though they play a central role in the stability and resilience of ecosystems as top predators (e.g. Myers et al. 2007). Moreover, top predators benefit from an ecologically justified charisma (Sergio et al. 2006), which can help in raising funds and finding support in the public and stakeholders. As such, the African penguin is a 'flag-ship' and an economically valuable species (Crawford 2005). Offshore MPAs for pelagic predators are needed to preserve ecosystem resilience and stability (Hyrenbach et al. 2000, Worm et al. 2006, Game et al. 2009), but a crucial issue regarding their establishment is to determine their boundaries in a dynamic environment.

¹Lemm & Attwood (2003) State of marine protected area management in South Africa. Unpublished report, WWF

In many instances, indices of marine primary productivity and abiotic features such as bathymetry are used to define seabird MPAs (Louzao et al. 2006). However, the most important guide for defining the boundaries of such MPAs is the prey field utilised by the birds (Hooker & Gerber 2004). Our study is one of the first to bypass proxies of marine productivity, and to link seabird foraging hotspots directly with the spatio-temporal abundance of their prey, as well as fishing activities sharing this resource (Grémillet et al. 2008a).

From our results, we recommend protecting areas that include the foraging range of penguins breeding on Dassen, Robben and Dyer Island colonies. Indeed, such areas fulfil criteria for marine Important Bird Areas as defined by BirdLife International (www.birdlife.org). African penguin numbers have decreased dramatically in recent years (by 50% between 2004 and 2006, Crawford et al. 2008), threatening this species with rapid extinction. The areas delimited by our study birds were used consistently over several breeding seasons, thus representing important pelagic feeding grounds for African penguins. These areas were also exploited by other species, such as Cape gannets (as shown in this study) and Cape cormorants *Phalacrocorax capensis* (M. Hamann et al. unpubl. data). These 3 seabird species have a restricted distribution, and are all endemic to Southern Africa. Therefore, African penguins, even though showing a small foraging range compared to other seabird species, act as an umbrella species (Roberge & Angelstam 2004), and protecting their foraging habitats will benefit large sections of the southern Benguela upwelling ecosystem.

The concept of area closures certainly warrants further exploration (Hooker 2006), particularly for spatially constrained predators such as African penguins that depend on a reliable prey base within a short commuting distance of their breeding islands while feeding chicks. Closure to purse-seine fishing of an area of 20 km radius around Dassen Island (see Fig. 1) has been implemented for 2008 and 2009 by Marine and Coastal Management, as part of an experiment to test whether such closure improves penguin reproductive success compared to an adjacent colony on Robben Island, which will not be closed to fishing². This assumes that limited closures will enhance fish availability locally, despite large-scale movements by pelagic

fish (Roy et al. 2007). Ideally, MPAs for highly mobile seabirds should have flexible boundaries (Hyrenbach et al. 2000), with limited catches in these areas. By monitoring the foraging behaviour and reproductive output of predators before and after the formation of an MPA, it is possible to test its efficacy as a conservation tool. Foraging behaviour is at the interface between population dynamics and the environment within which populations evolve, since any changes in the environment will affect the foraging behaviour of predators before they affect their life history traits (Hamer et al. 2006). Coupled with energetic modelling, GPS monitoring thus provides a rapid and powerful index of population health and trends (Grémillet et al. 2006, Pichegru et al. 2007) and can be used as a relevant tool in conservation management.

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Spatiotemporal habitat use by breeding sooty shearwaters *Puffinus griseus*

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ABSTRACT: Breeding sooty shearwaters *Puffinus griseus* cycle between long (11 to 14 d) and short (1 to 2 d) foraging bouts at sea, but no information exists on bird behavior during these trips. We tested the hypothesis that shearwaters use these long trips to travel to distant Antarctic waters compared to remaining in local waters. Patterns of habitat use of 28 breeding sooty shearwaters were studied using 6 g archival data loggers that recorded location, environmental temperature, and diving behavior. Dive activity was compared to remotely-sensed environmental data to characterize the habitats visited by shearwaters on long and short trips. Sooty shearwaters traveled predominantly (70 % of all long trips) to cold oceanic waters along the Polar Front (mean \pm SD, 1970 \pm 930 km from colony) on long trips or remained within warmer neritic waters of the New Zealand shelf (515 \pm 248 km from colony) on short trips. Diving depths (mean depth 15.9 \pm 10.8 m, max depth 69.9 m, n = 2007 dives) were not significantly different between excursion types. Activity patterns suggest that shearwaters commuted between distant foraging grounds (e.g. Polar Front) and the breeding colony and that more than 95 % of diving activity occurred during daylight hours. Although shearwaters traveled primarily to Antarctic waters on long trips, occasional trips around New Zealand waters were observed; all but 2 birds were from the northern-most study colony. Oceanic habitats in Antarctic waters were substantially different from neritic habitats around New Zealand, indicating that shearwaters experience dramatically different environmental conditions associated with each excursion type. The ability of sooty shearwaters to use 2 vastly different habitats provides greater flexibility for maximizing resource acquisition during breeding and reduces competition near the colony.

KEY WORDS: Activity · Archival data logger · Diving · Geolocation · *Puffinus griseus* · Tracking · Sea surface temperature · Sooty shearwater

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INTRODUCTION

Oceanic processes can create a highly dynamic and heterogeneous environment with considerable influence on biological productivity at varying spatial and temporal scales (Schneider 1994). Top marine preda-

tors that rely on prey aggregated at or by these physical features are themselves ultimately connected to the dynamic nature of these processes, affecting the predators' distribution in time and space (Hunt & Schneider 1987, Schneider 1993, Hunt et al. 1999). Thus, studies that focus on where and when top marine

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predators occur, combined with associated correlates of the physical environment, can improve our understanding of their spatio-temporal relationships of habitat use, particularly when breeding.

For top predators like seabirds that breed on land and forage at sea, parents are fundamentally constrained by the distance separating them from where and when food is acquired and the location of their nesting colony (cf. Pennycuik et al. 1984, Weimerskirch et al. 1997). Oceanic processes therefore play a pivotal role in shaping the evolution of seabird breeding strategies, because it is generally regarded that most seabird species hatch young when biological productivity in the oceans peaks (Ashmole 1971, Ricklefs 1990). Numerous studies have also shown that some seabird species (mainly albatrosses and petrels) alternate between long and short duration bouts to balance energy flow between parents and offspring (e.g. Chaurand & Weimerskirch 1994, Weimerskirch et al. 1997, Weimerskirch 1998, Weimerskirch & Cherel 1998). Despite the observed alternation of long and short duration bouts, there is a lack of complementary behavioral data, especially for small species (<1 kg), to evaluate whether birds use different marine habitats or have different activity patterns while conducting long and short trips.

By virtue of their abundance (ca. several million individuals; Brooke 2004), sooty shearwaters *Puffinus griseus* Gmelin, 1789 are major Southern Ocean predators. They are consummate flyers and capable divers, with the capacity to reach diving depths exceeding 60 m (Weimerskirch & Sagar 1996, Shaffer et al. 2006). However, the movement patterns, at-sea activity, and habitat use of breeding birds are poorly defined. Colony-based studies of sooty shearwaters (cf. Richdale 1963) indicate that parents alternate nest attendance patterns in a cyclical manner whereby adults mix short (1 to 2 d) and long (5 to 18 d) duration bouts at sea (Weimerskirch 1998). Based on the number of sooty shearwaters observed at the Polar Front (Warham 1996), Weimerskirch (1998) suggested that breeding birds probably foraged in productive Antarctic waters approximately 1500 to 2000 km from the colony. However, without studying the movement patterns of individual birds, it is difficult to determine the plausibility of this prediction. Therefore, we used tracking tags to test the hypothesis that sooty shearwaters exploit Antarctic waters on long trips as opposed to remaining in neritic waters around New Zealand. The tracking tags were data logging devices that also recorded diving behavior and environmental temperatures (cf. Shaffer et al. 2005, 2006), so we were able to characterize at-sea activity and habitat use (based on tag-derived and remotely sensed data) on long and short duration bouts. This additional informa-

tion allowed us to test another prediction: habitat use (i.e. time spent and activity) varies with trip type based on the habitats visited.

MATERIALS AND METHODS

The distribution, movements at sea, diving behavior, and activity patterns of 28 sooty shearwaters were studied during the chick-rearing phase of breeding at 3 colonies in New Zealand. Two birds were studied from February to March 2003 on North East Island, the Snares Islands (48° 02' S, 166° 36' E), 20 birds were studied from January to February 2005 on Codfish Island (46° 46' S, 167° 39' E), and 6 birds were studied from March to April 2005 on Mana Island (41° 06' S, 174° 50' E; see Fig. 2a inset for map of colonies). All shearwaters were known breeders with 30- to 75-d-old chicks.

Sooty shearwaters return to their nesting burrows during nighttime hours only, but peak colony attendance occurs within the first hour after sunset (Weimerskirch 1998). Burrows were checked hourly between 21:00 and 02:00 h and again at 05:00 h local time. When adults were found to be tending a chick, both adult and chick were removed from the burrow and weighed with a spring balance (± 10 g). If it was determined that a chick had been fed (based on prior weighing done hours earlier), the chick was returned to the burrow and the adult was equipped with a data logger and placed back into its burrow. Upon return to the nest from a foraging excursion, both adult and chick were reweighed, the logger removed, and both birds were placed back into the burrow.

Archival tag deployments. Each shearwater was equipped with a 6 g Lotek LTD 2400 archival data logger (hereafter called an archival tag or tag; Lotek Wireless) following methods described by Shaffer et al. (2006). In brief, tags were mounted to a plastic leg band using UV-resistant cable ties, Tesa tape®, or a rubber strap. In total, the tag and attachments weighed <1.5% of total bird body mass.

The tags recorded ambient light intensity every 60 s to determine a single fix of latitude and longitude per day (i.e. Global Location Sensing [GLS] or geolocation; Wilson et al. 1992). Given the known errors in this methodology (Wilson et al. 1992, Phillips et al. 2004), especially for latitude estimates, we incorporated measurements of sea surface temperatures (SST) recorded by the tag and compared these to remotely sensed SST to refine location estimates following methods and validation described elsewhere (Teo et al. 2004, Shaffer et al. 2005). Overall great circle error estimates of our tags averaged 202 ± 171 km (Shaffer et al. 2005).

Archival tag deployments were based on 2 schedules. The first involved deployments where 11 adults

were equipped for a single trip to sea. During these deployments, tags were programmed to sample light intensity, temperature ($\pm 0.1^\circ\text{C}$, resolution 0.05°C), and pressure (± 0.1 m, max depth 200 m) every 24 (9 of 11 tags) or 32 s (the 2 rates are hereafter referred to as 'fast' sampling rate tags). These sampling rates were frequent enough to provide behavior over a 2 to 3 wk deployment before tag memory filled to capacity. Trip durations were determined by monitoring colony visitations on a nightly basis. The second deployment schedule was designed to record behavior throughout the remainder of breeding and the 6 mo migration that followed (Shaffer et al. 2006). Therefore, tags were programmed to sample light, temperature, and pressure every 432 s (hereafter referred to as 'slow' sampling rate tags), which provided a coarser temporal resolution of behavior, but lasted over 300 d before tag memory filled. Regardless of sampling interval, all tags recorded the same number of bird locations (i.e. 1 d^{-1}). During the latter phase of breeding (ca. March through May), colony visitations were not monitored directly; rather, trip durations were determined by evaluating track data and temperature/light records (i.e. dark burrows were generally several degrees warmer than ocean temperatures). Given the error in GLS, we used a buffer of 300 km around each colony. If a bird location was within this buffer and the temperatures were above 25°C , we assumed that the bird had visited its burrow.

Analysis of geolocations, diving behavior, and activity. Location estimates were filtered for unrealistic travel rates using a speed filter (McConnell et al. 1992) with a threshold speed of 50 km h^{-1} (Spear & Ainley 1997). In total, 93 % of locations were kept after filtering. Track lines for each bird were created from the remaining locations using a curvilinear interpolation scheme (hermite spline; Tremblay et al. 2006) at 10 min intervals. The track interpolation allowed us to estimate dive locations based on synchronizing dive dates/times with the nearest location along the interpolated track. Total distance traveled and maximum distance from the colony (or range), were estimated from each interpolated track.

Given the temporal sampling rates of the loggers (24, 32, or 432 s), we do not report exact dive durations, surface intervals, or descent and ascent rates because it is likely that birds surfaced and dove again in between sampling intervals, which would bias our estimates of these behaviors (Wilson et al. 1995a). Furthermore, we only report specific diving behaviors for tags that sampled every 24 or 32 s. This included diving depths at sampling times, temperatures at the surface or at depth, and the frequency of diving activity, which may have been underestimated by missed dives that occurred between sampling intervals.

Diving behavior was evaluated using the Iknos Dive Analysis program (Y. Tremblay unpubl.) developed in MatLab (The MathWorks). This program performs a 0 offset correction to account for sensor drift by re-evaluating the sea surface pressure level between dives. A single dive was counted and characterized if the depth was below 25 times the resolution of the pressure sensor (i.e. deeper than 2.5 m) and if the duration lasted at least 2 times the sampling interval (i.e. 48 or 64 s). Given our low sampling rates, these thresholds were chosen to reduce as much as possible the likelihood of concatenating consecutive dives or splitting long dives. Although not optimal, we were confident that these parameters allowed a good estimate of diving activity, even if they could not resolve fine-scale diving behavior. Based on these criteria, we estimated that 95 % of all surface intervals were less than 20 min apart. Therefore, surface intervals greater than 20 min were used to distinguish the breaks between diving bouts.

Utilization Distribution (UD) kernels were calculated from all dive locations (2005 only) to characterize the spatio-temporal patterns of habitat use by breeding shearwaters. UD kernels were calculated using the Iknos Kernel program (Y. Tremblay unpubl.) developed in MatLab, with a grid size of 80 km; a minimum of 2 individual birds within a grid cell were required to be counted, and each cell was normalized for bird effort by dividing each cell by the number of birds contributing to all dive locations within a grid cell (BirdLife International 2004). Spatial area was calculated for kernels after subtracting the area of each major land mass that overlapped with a UD kernel.

At-sea activity was quantified by determining when sooty shearwaters were on or off the sea surface by evaluating temperature changes measured by the loggers (Wilson et al. 1995b, Shaffer et al. 2005). Temperature data were analyzed using a purpose-built routine developed in MatLab. This routine determined when birds landed or took off from the sea surface by evaluating the rate of temperature change and the stability of the temperature once a bird was on the water (Wilson et al. 1995b). For this analysis, we only quantified activity of birds with tags that sampled at 24 or 32 s, and we report the number of landings per day or per trip, mean durations on the water or in flight, and the proportions of each.

Habitat analyses. To examine the habitat characteristics where sooty shearwaters traveled to and conducted dives, we used tag-derived temperatures and complementary remotely sensed data. Remotely sensed data were obtained from time series of environmental data at <http://coastwatch.pfel.noaa.gov/> (see website for metadata on satellite sensors and parameters). These data sets included science quality products

for primary productivity (PP) estimated using methods described by Behrenfeld & Falkowski (1997) with a resolution of 0.1° , SST that was a multiple-satellite blended product with a resolution of 0.1° (see Powell et al. 2008 for details on specific SST datasets), and 3 d average surface wind vectors (0.25° resolution) measured from the Seawinds sensor on the QuickSCAT spacecraft (e.g. Frielich 2000). Bathymetry was extracted using data from ETOPO2 (Smith & Sandwell 1997).

Data for each environmental parameter were extracted from the global time series within a 1° longitude by 2° latitude grid (the approximate error of the geolocation method) centered on the location and date of each dive. The mean \pm SD of the data at a given dive location were used in subsequent analyses.

Statistical analyses. All statistical analyses were performed using MatLab or SAS® (SAS Institute) with a significance level of $p \leq 0.05$ for statistical tests (e.g.

t -tests, general linear models [GLMs]). In some instances, mixed-effects analyses of variance (ANOVAs; Pinheiro & Bates 2000) were used to test for differences between habitats (i.e. sectors) for a given environmental parameter (e.g. SST) using individual birds as a random factor in the ANOVA. Restricted Maximum Likelihood (REML) estimations were used, and because the number of observations of habitat parameters varied by individual bird, Type 3 Sums of Squares were compared to account for the unbalanced design. All data are presented as mean \pm 1 SD.

RESULTS

Shearwaters conducted a combined total of 88 excursions across 862 bird-days at sea. Trip durations were variable between birds, but the frequency distribution

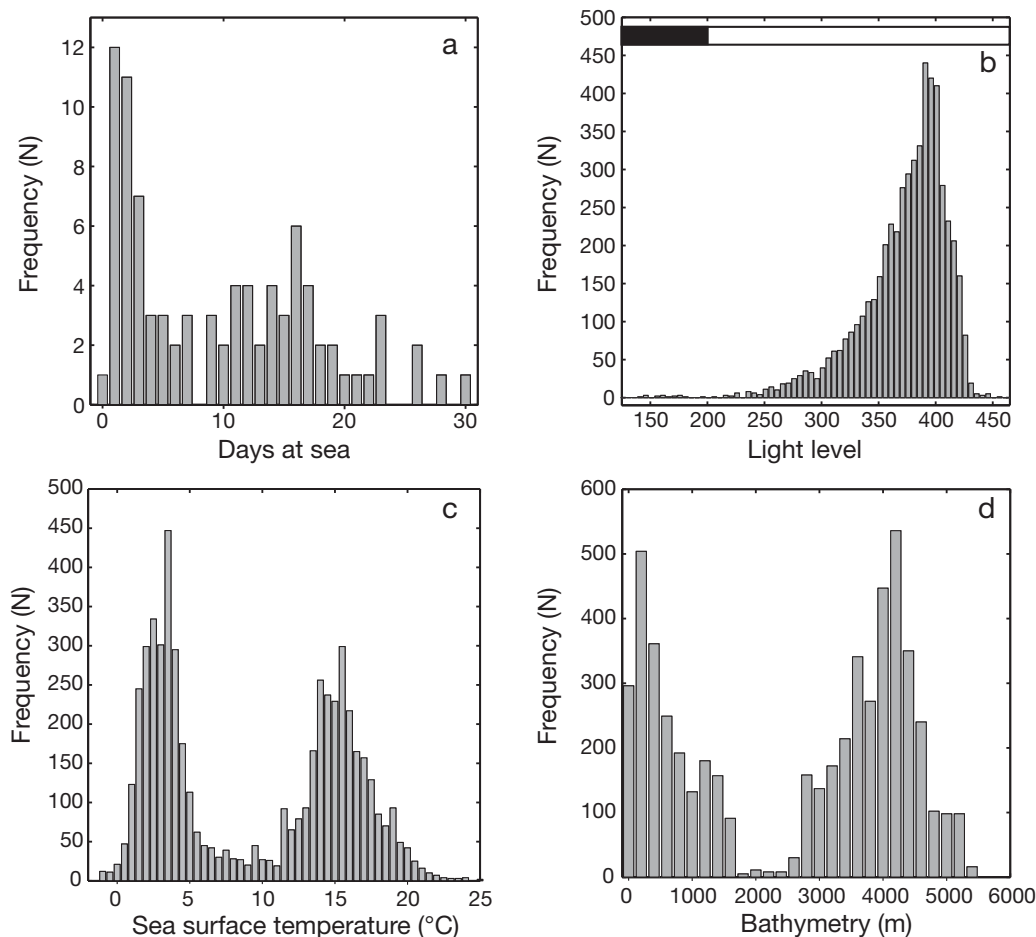


Fig. 1. *Puffinus griseus*. Frequency distribution of (a) foraging trip duration, (b) light level, (c) sea surface temperature, and (d) ocean bathymetry. All data were obtained by studying breeding sooty shearwaters equipped with data logging tags. In total, 88 foraging trips are shown in (a). Light levels and sea surface temperatures were recorded by the data loggers ($n = 5433$ observations) prior to or just after diving. Ocean bathymetry at each dive location (see Fig. 2b for dive locations) was obtained from remotely sensed data. The horizontal bar in (b) represents values for night (black) and day (white)

of trip duration was roughly bimodal (Fig. 1a). Using 4 d as a cutoff between short and long trips (Weimerskirch 1998), the average duration of short trips was 1.93 ± 0.92 d, whereas long trips were 14.51 ± 6.25 d in duration. For those individuals monitored over multiple excursions to sea ($n = 17$ birds), the mean number of trips conducted by each bird was 5.1 ± 2.2 .

Distribution at sea

Both shearwaters from the Snares Island colony traveled to oceanic waters southwest of the colony, whereas shearwaters from the Codfish Island colony traveled to coastal waters around New Zealand or to oceanic waters southwest and southeast of the colony. Shearwaters from the Mana Island colony remained in coastal waters around New Zealand or traveled to oceanic waters southeast of the colony (1 bird only).

Two main patterns of distribution were exhibited by the shearwaters. The first was the concentration of short ($n = 33$) and long ($n = 17$) duration trips within neritic waters of the New Zealand shelf (maximum range from colony was 515 ± 248 km; Fig. 2a). The second pattern involved long duration trips ($n = 38$) to oceanic waters southwest or southeast of each breeding colony (maximum range from colony 1970 ± 930 km). The distribution of these long trips differed in that shearwaters conducted 24 trips to oceanic waters southeast of the colony compared to only 14 trips conducted to the southwest region. Like trip duration, maximum distance from the breeding colony was also variable between and within individuals and overall varied as a function of trip duration ($F_{1,86} = 164$, $p < 0.001$, $r^2 = 0.653$). Estimates of total distance flown by shearwaters conducting short trips along the New Zealand shelf ranged between 800 and 1500 km compared to estimates for trips to oceanic waters along the Polar Frontal Zone that ranged between 4500 and 12 700 km. Estimates of total distance traveled per trip also varied as a function of duration at sea ($F_{1,86} = 435$, $p < 0.001$, $r^2 = 0.833$).

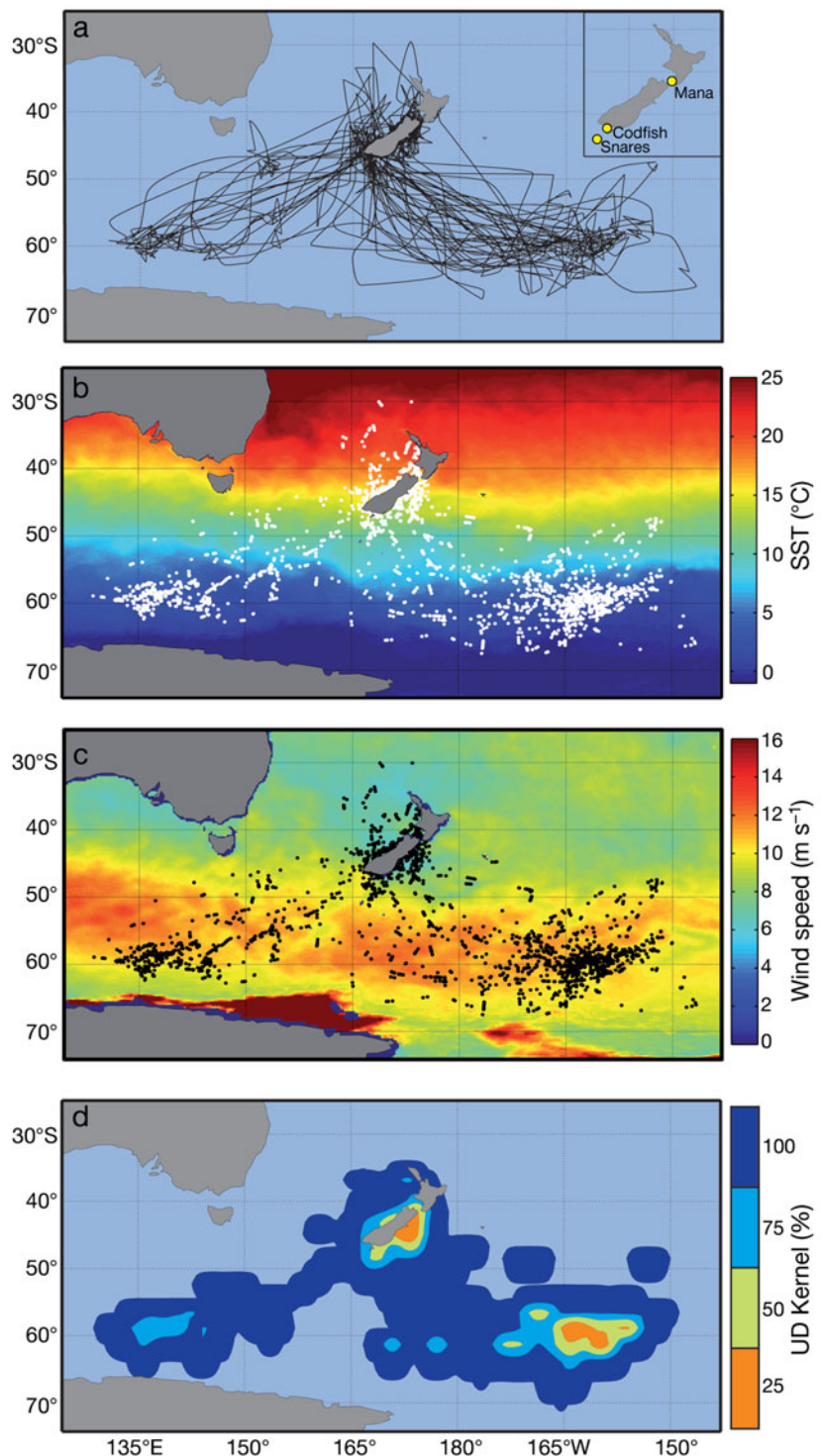


Fig. 2. *Puffinus griseus*. (a) Track lines of individual foraging trips made by breeding sooty shearwaters. (b) Estimates of diving location (white dots; $n = 5433$ dives) overlaid onto remotely sensed sea surface temperature (SST) in °C. (c) Estimates of dive location (black dots) overlaid on average wind speeds in m s⁻¹. (d) 25%, 50%, 75%, and 100% utilization distribution (UD) kernels of the diving activity in (b). The environmental data (SST and wind speed) shown are averages across the same periods starting on 28 January 2005 and ending on 01 May 2005. Note the relative concentration of diving activity in 3 main regions

Diving behavior

Sooty shearwaters made a combined total of 5981 dives (for 2003 and 2005), clustered in 3 discrete regions (Figs. 2b, c; only 2005 is shown). These regions exhibited the highest density of diving activity as shown by the 25, 50, 75, and 100% kernel UD based on diving activity (Fig. 2d). A total of 2955 dives occurred within the 50% UD contours, comprising a total area of approximately 510 600 km².

Closer inspection of diving activity for tags with higher sampling frequencies (24 to 32 s intervals) revealed that sooty shearwaters were capable of diving to depths as deep as 69.9 m (Table 1). On average, however, diving depths were 15.9 ± 10.8 m ($n = 2007$ dives) with 90% of all dives occurring to depths less than 30 m. Although it was not possible to determine dive durations accurately, given the coarse sampling intervals, we estimated that 90% of all dives were less than 100 s in duration.

The number of dives that individual birds made varied with trip duration, but it was also evident that birds dove in discrete bouts of activity (e.g. Fig. 3). Bouts of diving activity were interspersed between periods lasting several hours during which no diving activity was recorded (Table 1). Another pattern generally consistent for all birds was the lack of diving activity during nighttime hours (Fig. 3). Ambient light levels measured by the data loggers just before or just after a dive also confirm that >95% of all diving activity occurred during daylight hours (Fig. 1b).

The data loggers also revealed information about the environmental conditions that shearwaters experienced while diving. For example, it was clear from water temperatures recorded by the tags that shearwaters dove in cool Antarctic waters (-1.7 to 5.0°C) or

warmer temperate waters around the New Zealand shelf (12 to 22°C ; Figs. 1c & 2b). The frequency distribution of SSTs was distinctly bimodal with few measured SSTs in the range of 6 to 12°C . Like SST, ocean bathymetry associated with the approximate locations of diving activity was bimodal with few dives occurring within waters that were 1500 to 3000 m deep (Fig. 1d).

At-sea activity patterns

Sooty shearwaters spent an average of 76.1% ($\pm 9.9\%$) of their total time at sea in flight, but they landed on the sea surface an average of 26.3 ± 10.5 times d⁻¹ (Table 2). Daily activity did not vary between short and long duration trips. The mean duration of each landing was 14.08 ± 30.10 min per event. In contrast, the average time spent in continuous flight without landing was longer and more variable (50.78 ± 90.24 min).

Habitat analyses

Dive activity was not uniform among neritic or oceanic habitats (Fig. 4a). The total number of dives was greatest within waters surrounding New Zealand followed by the oceanic sector southeast of New Zealand (Fig. 4b). When normalized for numbers of individuals, however, diving effort was greatest in the southeast sector and lowest in the center sector.

Multiple trips to oceanic sectors were made by 11 (39%) shearwaters. The remaining birds either did not visit oceanic sectors during the time that they were tracked or they visited an oceanic sector only once before the logger was recovered (i.e. short-term

Table 1. *Puffinus griseus*. At-sea diving behavior of breeding sooty shearwaters equipped with fast sampling tags (see 'Materials and methods' for details). The hours at sea were based on the duration between the first and last landing on the sea surface. Surface ocean temperatures were recorded by the tag just prior to diving or just after surfacing, and temperature at depth was recorded at the deepest part of the dive. Sampling interval (SI): data logger sampling frequency in seconds, IBI: inter-bout interval. Two additional birds were equipped with fast sampling tags, but no viable behavioral data were obtained due to sensor/memory failures. All data are means ± 1 SD

Bird	Hours at sea	SI (s)	Diving behavior						Ocean temperature ($^\circ\text{C}$)	
			Dives per trip	Dives per hour	# of bouts	IBI (h)	Depth (m)		Surface	At depth
							Mean	Max		
10357	270.2	32	548	2.0	34	2.93 ± 3.92	19.4 ± 12.1	61.6	5.4 ± 1.5	5.3 ± 1.1
12901	372.4	24	427	1.1	52	5.36 ± 10.76	16.6 ± 9.8	69.9	4.1 ± 4.0	4.0 ± 3.9
12915	353.6	24	520	1.5	58	4.89 ± 7.06	15.0 ± 11.1	66.7	7.2 ± 5.0	7.1 ± 5.0
12932	38.6	24	51	1.3	3	0.96 ± 0.64	11.4 ± 4.0	17.5	17.8 ± 0.9	17.4 ± 0.8
13001	94.8	24	31	0.3	4	17.56 ± 21.74	15.8 ± 8.2	36.2	14.2 ± 0.7	14.0 ± 0.7
13005	220.5	24	128	0.6	16	9.16 ± 7.81	12.6 ± 7.5	34.0	14.9 ± 1.2	14.6 ± 1.0
13116	371.8	24	211	0.6	52	4.22 ± 5.75	13.4 ± 9.2	49.5	18.1 ± 1.5	17.8 ± 1.3
13122	261.2	24	79	0.3	18	7.66 ± 8.99	9.7 ± 8.8	66.1	15.9 ± 3.0	15.7 ± 3.0
13142	23.3	24	12	0.5	4	3.67 ± 5.58	13.2 ± 9.0	31.4	20.3 ± 4.0	19.9 ± 3.7

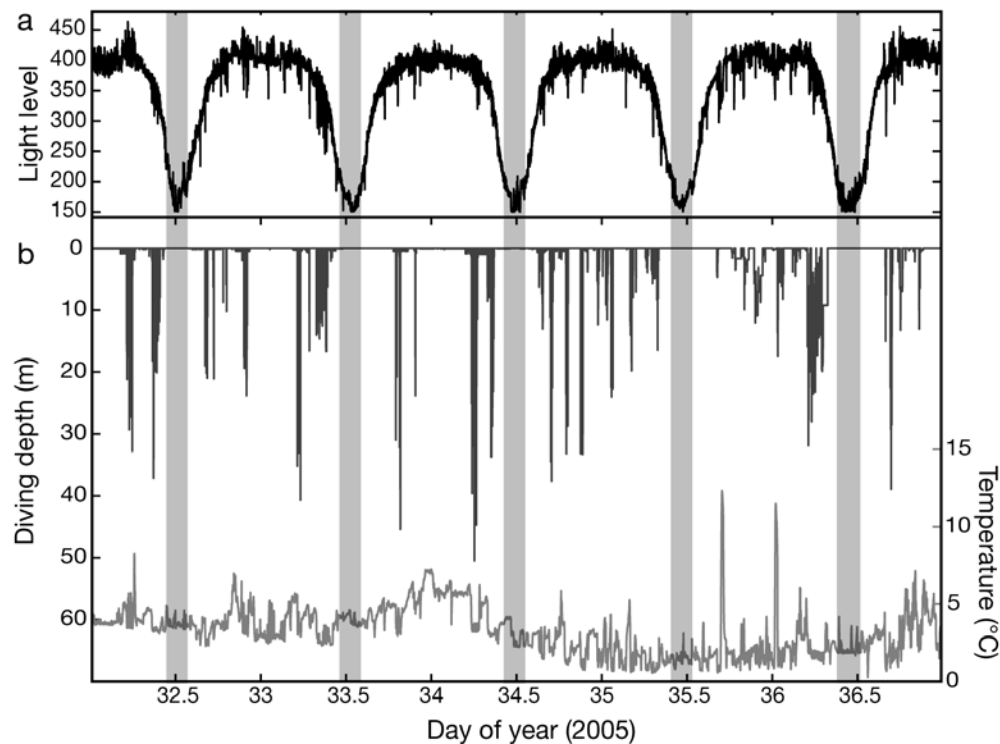


Fig. 3. *Puffinus griseus*. A 5 d portion of a 17 d trip to sea by a sooty shearwater (12901) equipped with a Lotek LTD 2400 archival data logger. This bird made 427 dives and landed on the sea surface 728 times during this trip (see Tables 1 & 2 for more details). (a) Changes in light level measured by the logger illustrating 5 day/night cycles. (b) Diving activity (dark gray line, scale on left y-axis) and environmental temperature (light gray line, scale on right y-axis) measured by the logger every 24 s throughout the trip. Note the short nights (relative light around 150), long days, and cool environmental temperatures during this portion of the record, indicative of diving activity in Antarctic waters. Also note the lack of diving activity during nighttime hours (denoted by shaded regions and see also Fig. 1b) and the prominence of diving in discrete bouts. These patterns were generally consistent across all tagged birds

deployments). Of the birds that conducted multiple trips, only 2 (7%) made all trips to the same sector. Otherwise, all remaining birds visited a different sector from the previous trip at least once during the time that they were tracked. No birds visited multiple sectors in a single foraging trip.

Environmental characteristics of the core habitats were strikingly and significantly different (mixed-effects ANOVA, $p < 0.001$ for all comparisons) between neritic and oceanic sectors. Bathymetry was 2000 to 3000 m shallower, SST was 8 to 10°C warmer, PP was an order of magnitude greater, and wind speeds were

Table 2. *Puffinus griseus*. At-sea activity and behavior of breeding sooty shearwaters equipped with fast sampling tags (see 'Materials and methods' for details). Prop: proportion of time in flight or on the water. Two additional birds were equipped with fast sampling tags, but no viable behavioral data were obtained due to sensor/memory failures. All data are means \pm SD

Bird	Landings		Time on water per trip			Time in flight per trip		
	Per trip	Per day	Prop (%)	Mean \pm SD (min)	Max (h)	Prop (%)	Mean \pm SD (min)	Max (h)
10357	365	32.4	32.6	14.50 \pm 43.05	8.83	67.4	29.86 \pm 45.07	5.87
12901	728	43.0	23.8	7.96 \pm 23.38	5.39	76.2	25.50 \pm 105.26	23.64
12915	507	33.4	18.4	7.93 \pm 7.30	1.22	81.6	35.12 \pm 58.78	7.63
12932	55	28.7	21.9	11.16 \pm 14.35	1.31	78.1	39.19 \pm 71.95	6.92
13001	93	22.0	17.8	11.65 \pm 31.68	3.48	82.2	53.32 \pm 135.22	12.00
13005	302	32.8	30.5	13.38 \pm 23.10	4.13	69.5	30.50 \pm 44.42	5.13
13116	479	30.4	19.0	9.01 \pm 27.58	7.78	81.0	38.32 \pm 64.77	10.77
13122	203	18.6	36.0	27.88 \pm 78.93	11.27	64.0	49.32 \pm 56.68	6.28
13142	35	32.9	38.3	16.75 \pm 27.23	1.72	61.7	26.23 \pm 28.62	2.18

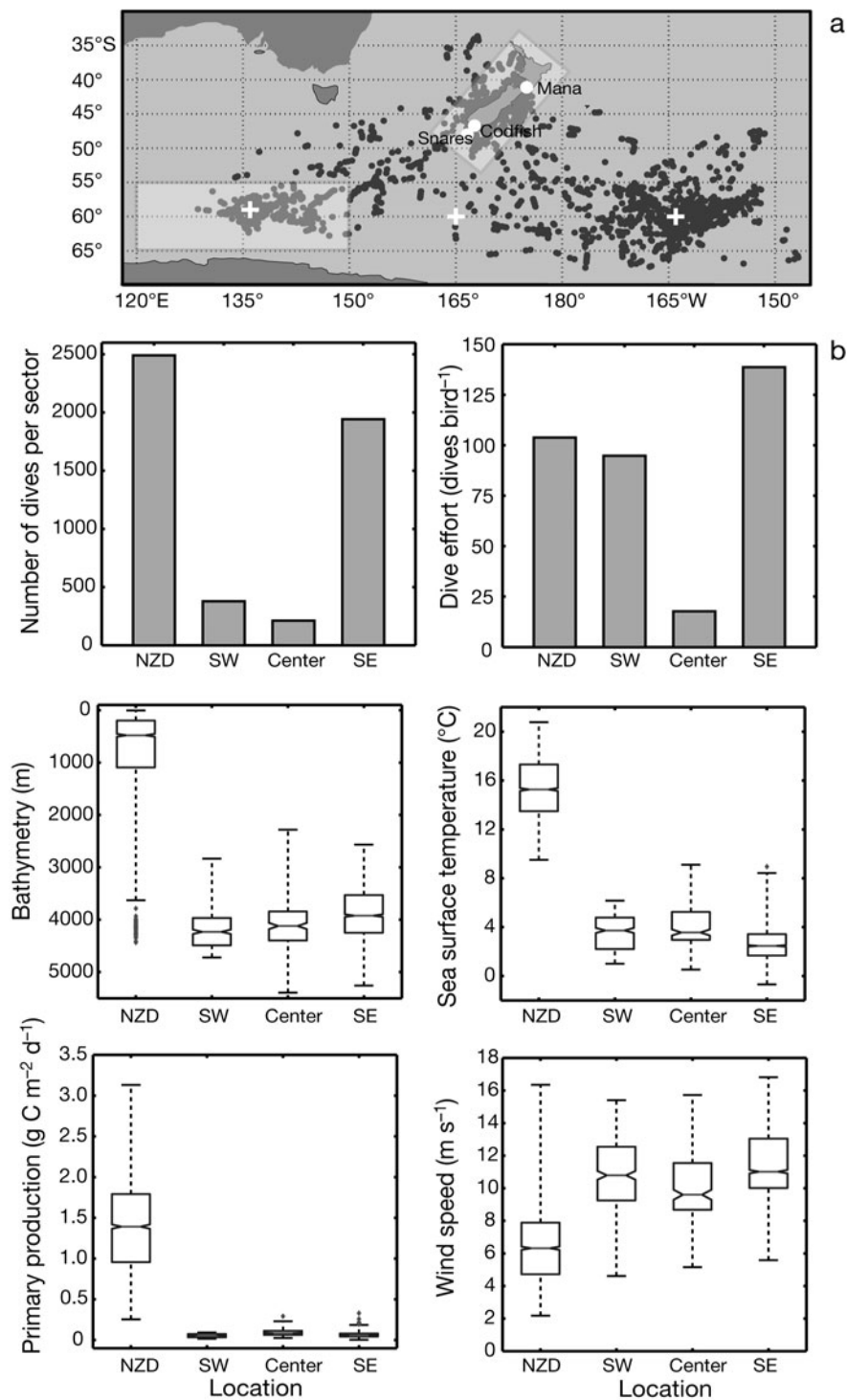


Fig. 4. *Puffinus griseus*. Habitat use of sooty shearwaters based on comparisons of diving activity and complementary environmental data. (a) Dive locations, partitioned into 4 quadrats (1 over neritic waters around New Zealand and 3 of equal size in oceanic waters) that generally encapsulated the core diving areas in oceanic waters (from Fig. 2d). For example, the shaded box (55–65°S × 120–150°E) encapsulates the majority of dives in the southwest (SW) sector. Similar boundaries were created for the center (55–65°S × 150–180°E), southeast (SE) (55–65°S × 180°E–150°W), and New Zealand sectors (NZD; shaded box around main islands). Crosses within each oceanic quadrat denote the 'center' of dive activity or the center of the quadrat, for comparison of distances to the breeding colonies (white dots). (b) Box plots (with the median, 25% and 75% quartiles, error bars representing the 1.5 SD, and points beyond as outliers) of the total number of dives, dive effort, and the values of remotely sensed environmental data for each dive location within a sector

4 to 6 m s⁻¹ slower in New Zealand waters compared to the oceanic sectors to the south (Fig. 4b). The oceanic sectors in Antarctic waters also differed significantly (mixed-effects ANOVA, $p \leq 0.05$) from one another; however, the biological significance of these differences is less clear because the differences were relatively minor (Fig. 4b).

DISCUSSION

Spatial patterns in at-sea distribution

The results of our study confirm that breeding sooty shearwaters do indeed travel to Antarctic waters on long duration bouts, thus supporting our hypothesis. However, we also observed that shearwaters occasionally conducted long duration excursions around New Zealand waters. This may be influenced by colony location, as most shearwaters from the northern colony (Mana Island) remained within New Zealand waters, whereas birds from the 2 southern colonies (Snarres and Codfish Islands) conducted nearly all of their long trips well south of their respective colonies. Tracking studies at the Mana Island colony commenced nearly 1 mo later (but within the same year) than those at Codfish Island, so it is possible that seasonal effects also influenced spatial patterns in habitat use. Further studies would be required to confirm this conclusion.

Given our results that sooty shearwaters will travel well over 2000 km from a breeding colony to forage, how prevalent is this pattern among other seabird species that have been tracked? Short-tailed shearwaters *Puffinus tenuirostris* and white-chinned petrels *Procellaria aequinoctialis* conduct extensive foraging excursions from their breeding colonies to Antarctic waters during the chick-provisioning period (Weimerskirch & Cherel 1998, Berrow et al. 2000, Catard et al. 2000, Klomp & Schultz 2000). For non-procellariiform seabirds, travel to these distant foraging areas over 2000 km away would seem prohibitive during the demanding chick-provisioning period. However, shearwaters and petrels have long slender wings like albatrosses for relatively fast efficient travel (Pennycuik 1987). Based on previous tracking studies (Klomp & Schultz 2000, Shaffer et al. 2006), both short-tailed and sooty shearwaters are capable of traveling over 1000 km d⁻¹. Therefore, under favorable wind conditions, these shearwaters could easily travel several thousand km from a breeding burrow and back in 2 to 4 d and still have ample time (5 to 7 d or more) to forage in more productive Antarctic waters.

In contrast to long duration forays to oceanic (or neritic waters), sooty shearwaters are more constrained to 'local' waters on short bouts (Fig. 2a,d). The bimodal

pattern of long and short foraging bouts in sooty shearwaters (e.g. Fig. 1a), first observed by Weimerskirch (1998), is the probable reason for the cyclic attendance of nests observed in sooty shearwaters by Richdale (1963). This strategy has now been observed in short-tailed and wedge-tailed shearwaters *Puffinus pacificus* (Weimerskirch & Cherel 1998, Congdon et al. 2005). Although we did not monitor colony attendance patterns and chick provisioning during the entire tracking period, the functions of these trips result in different energy intakes and flow between adults and chicks (Weimerskirch 1998, Weimerskirch & Cherel 1998). These results are entirely consistent with our characterization of the environmental conditions of each habitat visited by the shearwaters (discussed below). Thus, the use of a dual strategy may provide adults with greater flexibility in habitat choice to facilitate energy intake or to simply 'bet hedge' in case environmental conditions or food availability are poor in 1 habitat versus another.

One of the more striking results in the foraging patterns and habitat use of sooty shearwaters revealed in our study was the concentration of diving activity in 2 distinct main oceanic regions south of the 3 colonies. The paucity of diving activity between the shelf and oceanic regions suggests that birds were primarily commuting between the colony and each core area to forage. Otherwise, we would have expected shearwaters to engage in diving activity opportunistically along the paths of their trips.

Diving behavior and activity

To our knowledge, the present study is the first to characterize the diving behavior of shearwaters using electronic tags. We are aware of diving studies on at least 6 shearwater species (5 *Puffinus* spp. and 1 *Calonectris* sp.; reviewed by Burger 2001), but these studies all used capillary tubes to measure the single deepest dive of a bird during a trip to sea. Although informative, this method provides no detail of individual diving activity, except maximum depth. In contrast, the time-depth records from our loggers showed that sooty shearwaters are prolific divers, with some birds diving more than 500 times in a single trip to sea (Table 1). The average maximum dive depth of sooty shearwaters measured with data loggers was 16 m, but the deepest dive was 69.9 m, nearly identical to measurements obtained with capillary tube gauges for both sooty (Weimerskirch & Sagar 1996) and short-tailed shearwaters (Weimerskirch & Cherel 1998). Thus, although the deepest dives are consistent with previous records obtained with capillary tubes, it is clear that sooty shearwaters dive more frequently to

shallower depths. Compared to records of diving behavior for other seabirds, *Puffinus* shearwaters can dive deeper than other flying seabirds of comparable body mass (Burger 2001). Given the frequency of diving activity that we measured, our results suggest that shearwaters probably obtain more food from diving than was previously thought (Burger 2001).

We determined that sooty shearwaters dove in discrete bouts of activity, with average durations of 6 h between bouts of diving (Table 1). Although we were not able to accurately determine dive durations or 2-dimensional shape, we were able to resolve temporal associations in diving activity. For example, sooty shearwaters overwhelmingly dove during daylight hours (Figs. 1b & 3). This could partially be explained by the fact that birds experienced short or even non-existent nighttime periods when foraging in the Antarctic summer. However, nearly half of all dives were conducted along the New Zealand shelf (Fig. 1d) at latitudes at or below 50°S. At these latitudes, shearwaters would experience several hours of darkness during nighttime hours, yet <1 % of all dives were conducted in darkness (see Fig. 1b). Some dive activity was also clustered around sunrise and sunset, suggesting that sooty shearwaters possibly capitalized on prey species that migrate to the surface at night and descend during the day (e.g. crustaceans, myctophids, and squids), which is consistent with the observed diet in breeding sooty shearwaters (Kitson et al. 2000, Cruz et al. 2001).

Based on activity levels, we found that sooty shearwaters spend more than 75 % of their time at sea in flight, yet land on the water an average of 27 times d⁻¹ (Table 2). The proportion of time in flight is high compared to several albatross species, which typically spend 50 to 74 % of their time at sea in flight (Shaffer et al. 2001, 2004, Weimerskirch & Guionnet 2002, Phalan et al. 2007). However, Laysan albatrosses *Phoebastria immutabilis* and black-footed albatrosses *P. nigripes* spend even higher proportions of time at sea in flight (80 to 90 %) than sooty shearwaters (Fernández & Anderson 2000). We are unaware of any other comparable data for petrels of a similar size to sooty shearwaters. Given that diving activity of sooty shearwaters is relatively high, we might expect a high frequency of landings, particularly when they are near their foraging grounds.

Patterns of habitat use

The flight paths and spatial proximity of diving activity by sooty shearwaters showed striking and somewhat unexpected variation in habitat use. It was clear that sooty shearwaters used 2 primary habitat types

characterized by (1) temperate waters (13 to 17°C) over the New Zealand shelf and shelf edge, and (2) cold Antarctic waters (2 to 4°C) over deep bathymetric features. When shearwaters foraged on the shelf, diving activity was greatest along the east coast of South Island (Fig. 2d). This region is dominated by localized processes such as wind-driven coastal upwelling, relatively high PP, mixed layer depth, and physical forcing influenced by the shallow bathymetry and numerous seamounts on the New Zealand shelf (Bradford et al. 1991, Vincent et al. 1991, Murphy et al. 2001). Conversely, the distant oceanic regions where shearwaters traveled on long trips were more likely influenced by large-scale oceanic processes driven primarily by strong winds, frontal systems, and prevalence of the Circumpolar Antarctic Current (Huntley & Niiler 1995, Constable et al. 2003). As a result, the physical processes governing each habitat type and the scales over which they occur will influence prey availability, predictability, and composition in different ways (Hunt & Schneider 1987, Hunt et al. 1999). Supporting evidence comes from studies on the diet of breeding sooty shearwaters, which suggest variations in habitat use based on the biogeographical distribution of the prey found in the diet (Kitson et al. 2000, Cruz et al. 2001).

A comparison of habitat use by shearwaters within oceanic sectors revealed a bias towards greater activity within the southeast sector. Nearly twice the number of trips, 5 to 6 times the total number of dives, and overall dive effort was concentrated within a region along the Polar Front between 55 and 65°S (Fig. 4a,b). The geographic center of this core area was approximately 2350 km southeast of Codfish Island compared to the other core area that was ca. 2480 km to the southwest of Codfish Island. Although statistically different, the oceanographic features of each sector were not dramatically different, so it is not clear why diving activity differed between sectors. However, several possible explanations merit further exploration. For example, the trajectories of prevailing wind patterns in relation to movement patterns of birds at certain points along a trip (e.g. departure from the colony or core habitat) influence large-scale movements (cf. Weimerskirch et al. 2000, Felicísimo et al. 2008, Suryan et al. 2008). It is also possible that prey resources could have been greater in the southeast region compared to the southwest, which would explain the greater visitations and activity within the southeast region. Sampling bias could also be a factor in that our sample sizes were not equivalent between the colonies monitored and were small overall compared to the population as a whole. Future studies that combine tracking with colony-based monitoring of food loads brought to the nest and/or body mass changes would undoubtedly resolve this question of habitat use.

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Influence of sea surface winds on shearwater migration detours

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ABSTRACT: To test the potential effects of winds on the migratory detours of shearwaters, transequatorial migrations of 3 shearwaters, the Manx *Puffinus puffinus*, the Cory's *Calonectris diomedea*, and the Cape Verde *C. edwardsii* shearwaters were tracked using geolocators. Concurrent data on the direction and strength of winds were obtained from the NASA SeaWinds scatterometer to calculate daily impedance models reflecting the resistance of sea surface winds to the shearwater movements. From these models we estimated relative wind-mediated costs for the observed synthesis pathway obtained from tracked birds, for the shortest distance pathway and for other simulated alternative pathways for every day of the migration period. We also estimated daily trajectories of the minimum cost pathway and compared distance and relative costs of all pathways. Shearwaters followed 26 to 52 % longer pathways than the shortest distance path. In general, estimated wind-mediated costs of both observed synthesis and simulated alternative pathways were strongly dependent on the date of departure. Costs of observed synthesis pathways were about 15 % greater than the synthesis pathway with the minimum cost, but, in the Cory's and the Cape Verde shearwaters, these pathways were on average 15 to 20 % shorter in distance, suggesting the extra costs of the observed pathways are compensated by saving about 2 travelling days. In Manx shearwaters, however, the distance of the observed synthesis pathway was 25 % longer than that of the lowest cost synthesis pathway, probably because birds avoided shorter but potentially more turbulent pathways. Our results suggest that winds are a major determinant of the migratory routes of seabirds.

KEY WORDS: Migration costs · Wind influence · Bird flight · Shearwaters · Global location sensing · GLS · Geolocator

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INTRODUCTION

Migration is a major activity in the life of many seabird species. Twice a year millions of shearwaters travel 10s of 1000s of kilometres across the equator to move between wintering and breeding areas. Ringing programmes, land-based observers and observations at sea have provided some information on broad-scale migration corridors (Serventy 1953, Alerstam 1990, Brooke 1990, Spear & Ainley 1999, Camphuysen & Van Der Meer 2001). These studies have suggested a

figure-eight pattern, clockwise in the northern and counter-clockwise in the southern hemisphere, but detailed migration pathways remain largely unknown. Currently, tracking devices provide invaluable information on spatial and temporal aspects of the migration at an individual level (Shaffer et al. 2006, González-Solís et al. 2007). These studies have confirmed that shearwaters often do not travel the shortest distance between breeding and wintering areas, but may take longer pathways than expected. Furthermore, the figure-eight pattern of annual movements

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has been confirmed for sooty shearwaters *Puffinus griseus* in the Pacific Ocean (Shaffer et al. 2006). Understanding why shearwaters follow detours in their transequatorial movement is essential in predicting the spatio-temporal passage of shearwaters and will be crucial in defining the main seabird corridors for conservation purposes. Investigating the principles determining migratory detours has been a prime issue in optimal migration studies (Alerstam 2001, Erni et al. 2005). In this regard 2 main currencies have been proposed to be optimised in a migration episode, time and energy (Alerstam & Lindström 1990). Minimising the energy cost of transport may be advantageous because the energy saved can be crucial if food resources or fat reserves are scarce, or it can just be invested in more rewarding activities. Minimising time may compensate potentially greater costs because arriving earlier to the breeding or wintering grounds than other competitors may be advantageous.

One major factor influencing the cost of bird migration is wind conditions (Alerstam 1979, Pennycuik 1982, Richardson 1990, Liechti & Bruderer 1998, Gauthreaux et al. 2004, Liechti 2006). Wind speed can achieve similar values to those of flying birds, and therefore ground speed can be substantially increased or decreased depending on the wind direction with respect to bird heading. This is also true in shearwaters and fulmars, which rely on mixed flap and gliding flight utilising wave uplift and dynamic soaring, both very dependent on the strength of the winds (Alerstam et al. 1993, Furness & Bryant 1996, Rosén & Hedenström 2001). Indeed, several studies have shown shearwaters often follow prevailing winds, during both migration and foraging movements, suggesting that birds optimise the use of winds for gliding (Shaffer et al. 2006, González-Solís et al. 2007, Navarro & González-Solís 2009). When taking into account the costs imposed by winds, the fastest and the shortest distance pathways may not be the same. Shortest pathways, e.g. between breeding and wintering grounds, may be more costly in unfavourable winds. On the contrary, apparently low-cost pathways, e.g. high wind speed in the direction of travel, may save energy, but can be much further.

So far, evidence of wind effects on migrating seabirds has been mainly inferred from local observations and synoptic weather maps (Pennycuik 1982, Alerstam et al. 1993, Nicholls et al. 1997, Spruzen & Woehler 2002, Murray et al. 2003). Although this is the best approach when working at detailed scales, remote-sensing data make it possible to work at broader scales, using concurrent information from winds and migration paths to analyse the responses of birds to wind conditions (Felicísimo et al. 2008). Strength and direction data on sea surface winds are

now available from satellite scatterometers with high spatial and temporal resolution and global coverage. Shearwaters fly low over the sea surface, and therefore information on sea surface winds can be used to build anisotropic 'cost models'. Anisotropic cost analysis is a procedure to estimate the minimum accumulative cost of travelling from a source cell to every other cell on a raster model, which must be considered as a friction surface. Azimuth and speed, the 2 components of a wind vector, are used in the cost calculations. In the case of the azimuth, the minimum resistance to the movement corresponds to the exact wind vector azimuth. Deviations from the actual wind azimuth are penalised through a function in proportion to angle deviation. Regarding wind speed, it enters into the model as a resistance factor; therefore, tail winds reduce cost, while head winds increase it. Using data on wind conditions over the studied migration period, it is possible to calculate the lowest wind resistance pathway connecting specific wintering and breeding areas, which should reasonably reflect the lowest wind-mediated cost pathway for the birds. Pathways with the lowest wind cost can then be compared to the observed pathways followed by the tracked birds. This approach was used to analyse the postnuptial migration of Cory's shearwaters breeding in the northern hemisphere and wintering in the Benguela system (Felicísimo et al. 2008). In the aforementioned study, the authors found that tracked shearwater pathways were very similar to the lowest cost pathway predicted from the analysis of wind conditions experienced by birds during their migration period. However, the suitability of alternative low cost pathways and the time required to travel along the alternative pathways was not considered.

Most optimality models used to understand bird migration have focused on passerines, and they generally obtain predictions assuming either minimisation of total migration time or minimisation of energy. Some recent theoretical approaches have taken both currencies into account, but the inability to track small passerines prevents testing their predictions (Houston 1998, Vrugt et al. 2007). In the present paper, a simple optimality approach is developed relating both potentially conflicting currencies to understand the actual pathway choice made by the shearwaters during migration. Specifically, we tested whether the assistance of sea surface winds makes migration pathways, although of longer distance, less costly (as indicated by less wind resistance) to birds than shorter pathways. Migration routes of 3 Atlantic shearwater species, the Manx shearwater *Puffinus puffinus*, the Cory's shearwater *Calonectris diomedea*, and the Cape Verde shearwater *C. edwardsii* were tracked using geolocators. The migration routes in which the observed path-

ways clearly differed from the shortest path between breeding and wintering grounds were selected for analysis. We also calculated the wind cost of intermediate simulated pathways, including the observed synthesis pathway used by the shearwaters and the synthesis of the daily minimum cost pathways. Finally, we compared the choice made by shearwaters in relation to the simulated pathways with differing costs and distances, in order to understand the dominating factor explaining the pathway choice made by shearwaters.

MATERIALS AND METHODS

Bird tracking and migration pathways. In May and June 2006, we deployed a total of 20 geolocators on Manx *Puffinus puffinus* shearwaters at Heimaey (Iceland). After approximately 1 yr, we recovered data from 10 geolocators. For this study, we use the last portion of 8 prenuptial trajectories, from the Inter-tropical Convergence Zone to Iceland. In June and July 2002, we deployed a total of 50 light level geolocators on Cory's *Calonectris diomedea* shearwaters breeding at Vila Islet (Azores), Veneguera (Gran Canaria, Canary Islands) and Pantaleu Islet (Balearic Islands, Mediterranean). After 1 or 2 yr, we recovered data from 27 geolocators. For this study, we use the postnuptial migration of 20 transequatorial trajectories starting in the Canary Current system. In July 2006, we deployed a total of 40 geolocators on Cape Verde *C. edwardsii* shearwaters at Raso and Curral Velho Islets (Cape Verde). After approximately 1 yr, we recovered complete data from 26 geolocators. For this study, we use 25 prenuptial trajectories from the wintering area (the Brazil and Falklands/Malvinas confluence in front of the Uruguay coast) to Cape Verde.

For the purpose of the present study, we selected migration routes showing detours that allowed us to contrast the hypothesis of long distance detour pathways versus the shortest pathway. Migration routes in which the shortest path did not differ from the observed path were not considered, as they would not allow contrasting of the 2 hypotheses. Synthesis pathways were calculated through a kernel density estimation with the 'linedensity' command on an ArcInfo Workstation 9.1. Alternative pathways to contrast our hypothesis were extrapolated as alternative possibilities between the shortest and the observed pathways, as were similar but intermediate or more extreme detours than the observed pathways.

Birds were tracked using 5 to 10 g geolocators developed by the British Antarctic Survey (BAS; Afanasyev 2004). It has been shown that 10 g geolocators on Cory's shearwaters have no detectable short-term

effects on the birds (Igual et al. 2005). We deployed them on the leg of each bird, mounted on a DARVIC ring. The geolocators had an internal clock and measured the light levels every 1 min, recording the maximum reading within each 10 min interval (Afanasyev 2004). From this information, 2 positions per day (one corresponding to midday and the other to midnight) can be inferred with an average (\pm SD) accuracy of 186 ± 114 km (Phillips et al. 2004). Positions were calculated using BAS software by inspecting the integrity of the light curve day by day and fitting dawn and dusk times. To filter unrealistic positions we removed (1) those obtained from light curves showing interferences at dawn or dusk (mainly due to the bird staying in the burrow); (2) those with a speed index >90 km h⁻¹, as calculated by the root of the square speed average of the segments formed with the 2 preceding and the 2 following positions; (3) those within the equinox periods; and (4) those on land areas.

Wind data. We used free data from SeaWinds on QuikSCAT scatterometer, an instrument developed by NASA JPL (J. P. Laboratory 2001), to measure the speed and direction of ocean surface winds. The QuikSCAT satellite was launched into a sun-synchronous, 803 km, circular orbit on 19 June 1999. The SeaWinds instrument is a specialised microwave radar (scatterometer) that measures near-surface wind speed and direction over the Earth's oceans (J. P. Laboratory 2001). Data are not gathered for the whole ocean surface every day, and, although unobstructed by clouds, measurements are affected by rain. To avoid areas without satellite data and to reduce rain contamination, we calculated wind speed and azimuth daily as the average of that day, the following and the preceding day.

The QuikSCAT HDF (hierarchical data format) files contained a set of 16 scientific data sets (SDS). A HDF SDS is a fixed dimensional array. The QuikSCAT SDS uses a simple 0.25° rectangular latitude to longitude grid that contains 1440 pixels from east to west and 720 pixels from south to north in a standard 'plate carrée' projection. The data used in our study included daily data from January 2002 to December 2007, corresponding to the periods matching the analysed migration trajectories. Wind data were obtained from PO-DAAC (Physical Oceanography Distributed Active Archive Center).

Anisotropic cost analysis. To calculate the cost of travelling over the ocean surface in relation to wind conditions we used an anisotropic cost analysis to create a friction surface. This surface is a grid where the cost to move over each pixel depends on the angle between the movement heading and the azimuth wind, as well as the wind speed, i.e. we used the cost to mean resistance of wind to the movement of the birds,

which we assumed to reflect the energetic costs of the birds to move among pixels.

To model the variation in wind resistance as an estimate of the energy expenditure suffered by a bird in the open ocean in relation to the wind azimuth, we used a cost function inferred from an experimental study on flying albatrosses (Weimerskirch et al. 2000). These authors recorded heart rates of flying albatrosses as an instantaneous index of energy expenditure in relation to wind direction. Although albatrosses may show some slight differences in flight behaviour compared to shearwaters, to our knowledge this is the only available experimental data about the influence of winds on the energy expenditure of a Procellariiform. In our inferred cost function, to calculate the cost to move over a pixel, speed was not considered as an isolated element, but in conjunction with the angle between wind and movement vectors: tail winds were considered a help, and head winds, an obstacle to movement, both proportionally to absolute speed (m s^{-1}) (Fig. 1). In the absence of wind, the cost of moving through the friction surface was set to 31 (arbitrary units) and was held constant with respect to the movement heading (i.e. winds not helping or hindering the movement). In the case of movement following the

exact wind vector azimuth (tail wind corresponding to 0° between vector flight and vector wind) and maximum wind speed (30 m s^{-1} as defined by the sensitivity of the QuikSCAT), we assigned the minimum resistance value of 1 (arbitrary units). Deviations from this minimum cost angle and/or decrease in wind speed were increasingly costly until reaching a maximum of 61 (arbitrary units) at an angle of 180° (head wind, opposite to bird flight) and a wind speed of 30 m s^{-1} (Fig. 1).

An iterative procedure on a cell-by-cell basis from any given source to final points allows the estimation of the accumulated cost of simulated trajectories over the friction surface, as well as the definition of the theoretical minimum cost path between the predefined source and final points. Cost calculations are based on friction surfaces, where the value of each pixel corresponds to the cumulative cost to travel from the origin to that pixel for each day. Cost surfaces were calculated for each day using daily wind conditions during the migration period and year of the tracked birds. Source and final points were set as the breeding colony positions or the core position of a kernel analysis on routes or in wintering areas of the tracked birds. Once the source and the final points and the daily cost surfaces

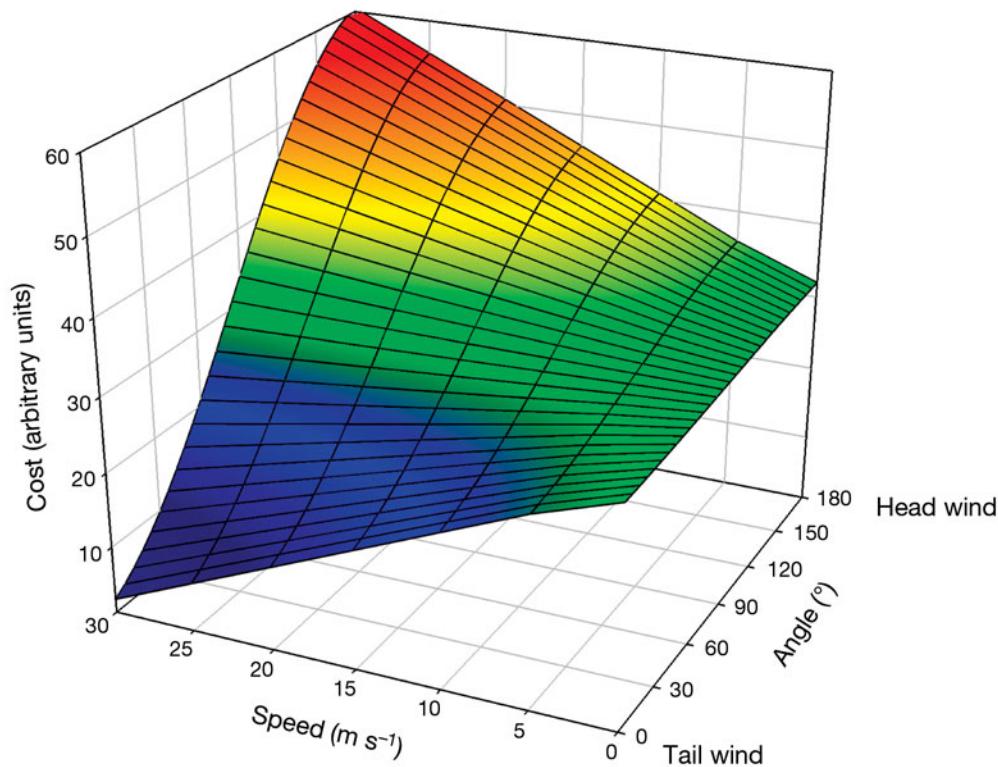


Fig. 1. Cost function used to calculate the cost (arbitrary units) to move over a friction surface depending on wind speed (m s^{-1}) and the angle between the bird heading and the wind azimuth (in degrees). The travelling cost to move over the friction surface in the absence of wind was set at 31 (green); travelling cost decreases with faster tail winds down to 1 (deep blue) and increases with faster head winds up to 61 (red)

corresponding to the migration period were defined, we calculated (1) daily costs for the observed synthesis pathway (obtained from the actual trajectories followed by the tracked birds), (2) daily costs for each simulated alternative path and (3) a synthesis of the daily minimum cost pathways. Based on the daily cost estimations, we then calculated the mean cumulative cost for the whole period, as well as the variability for each path (see Fig. 4), thus integrating the variability of wind conditions among days during the migration period. Calculations were made with the 'pathdistance' command on an ArcInfo Workstation 9.1.

RESULTS

Tracking data

In general, spatio-temporal patterns of the migratory episodes of each species were fairly similar among individuals, showing a general pattern overall, but also with some inter-individual variability. From the 8 Manx *Puffinus puffinus* shearwaters, the first bird started the portion of the analysed trajectory on 6 April and the last started on 1 May. Birds arrived at the end of the considered portion between 23 April and 5 May 2007. On average, trips were 10 400 km long (SD = 1100), and lasted 20 d (SD = 4). In the case of the 20 transequatorial Cory's *Calanectris diomedea* shearwaters included in the analysis, dates of the origin and end of the analysed trajectory were more dispersed; the onset ranging from 24 November 2002 to 8 December and the end ranging from 3 to 29 December. On average, trips were 10 000 km long (SD = 800) and lasted 22 d. Finally, Cape Verde *C. edwardsii* shearwaters showed a greater spatio-temporal cohesion. The 25 tracked shearwaters left the wintering grounds between 11 February and 5 March 2007 and arrived at the breeding colony between 26 February and 21 March 2007. On average, trips were 9100 km long (SD = 1300) and lasted for 13 d (SD = 2) (Figs. 2 to 4).

Wind-mediated cost and path length

In most cases, the cost of each path was strongly dependent on which day this cost was calculated. That is, the range of cost for each path could double or triple depending on the simulated departure day (Fig. 4). Median cost varied substantially depending on the length of the path, but this relationship was not uniform among species. In Manx shearwaters, neighbouring short paths (up to 8000 km) showed disparate average costs (Fig. 4a). Longer paths were increasingly more costly, suggesting that wind assistance did not

favour birds taking longer pathways. The estimated cost and the length of the observed synthesis path was 98 860 cost units and 8890 km, respectively; for the alternative synthesis path with the minimum cost, it was 87 550 cost units and 7100 km, respectively, whereas, for the shortest path, the cost was 105 040 cost units and the distance was 7050 km.

In Cory's shearwaters, shorter paths (<8000 km) were increasingly more costly, being up to 50 % more costly than the lowest cost synthesis path (Fig. 4b). The estimated cost and the length of the observed synthesis path was 102 630 cost units and 9730 km, respectively; for the alternative synthesis path with the minimum cost, it was 90 590 cost units and 11 070 km, respectively, whereas, for the shortest path, the cost was 141 400 cost units and the distance was 6400 km.

In Cape Verde shearwaters, the cost was more uniform regardless of the length of the path. Intermediate length paths (from 8000 to 11 000 km) showed slightly lower costs, but the range of the cost for each path was strongly dependent on the departure day (Fig. 4c). The estimated cost and the length of the observed synthesis path was 122 830 cost units and 8840 km, respectively; for the alternative synthesis path with the minimum cost, it was 109 200 cost units and 10 300 km, respectively, whereas, for the shortest path, the cost was 121 940 cost units and the distance was 6300 km.

DISCUSSION

The trajectories analysed from Manx *Puffinus puffinus*, Cory's *Calanectris diomedea* and Cape Verde *C. edwardsii* shearwaters did not follow the shortest (great circle) trajectory between breeding and wintering areas, rather flyways were from 26 to 52 % longer (Figs. 2 & 4). This result confirms that transoceanic detours are common in long-distance-migrating seabirds. In terrestrial birds, detours are often related to refuelling needs, predator avoidance, or the need to circumvent ecological barriers (Alerstam 2001, Erni et al. 2005, Newton 2008). Although shearwaters do not have major predators at sea, the marine environment also presents potential ecological barriers, such as strong winds and oligotrophic waters. Indeed, refuelling needs could force shearwaters to take longer pathways around low-food-availability areas. Shorter pathways would cross oligotrophic waters in the centre of Atlantic gyres, which are poor in epipelagic fish and cephalopods. There is conflicting evidence on foraging behaviour during migration. Some studies show that shearwaters feed while migrating (Spear et al. 2007, Guilford et al. 2009). On the contrary, the speed of migration suggests that shearwaters do not usually stop over to refuel during migration, and depth loggers

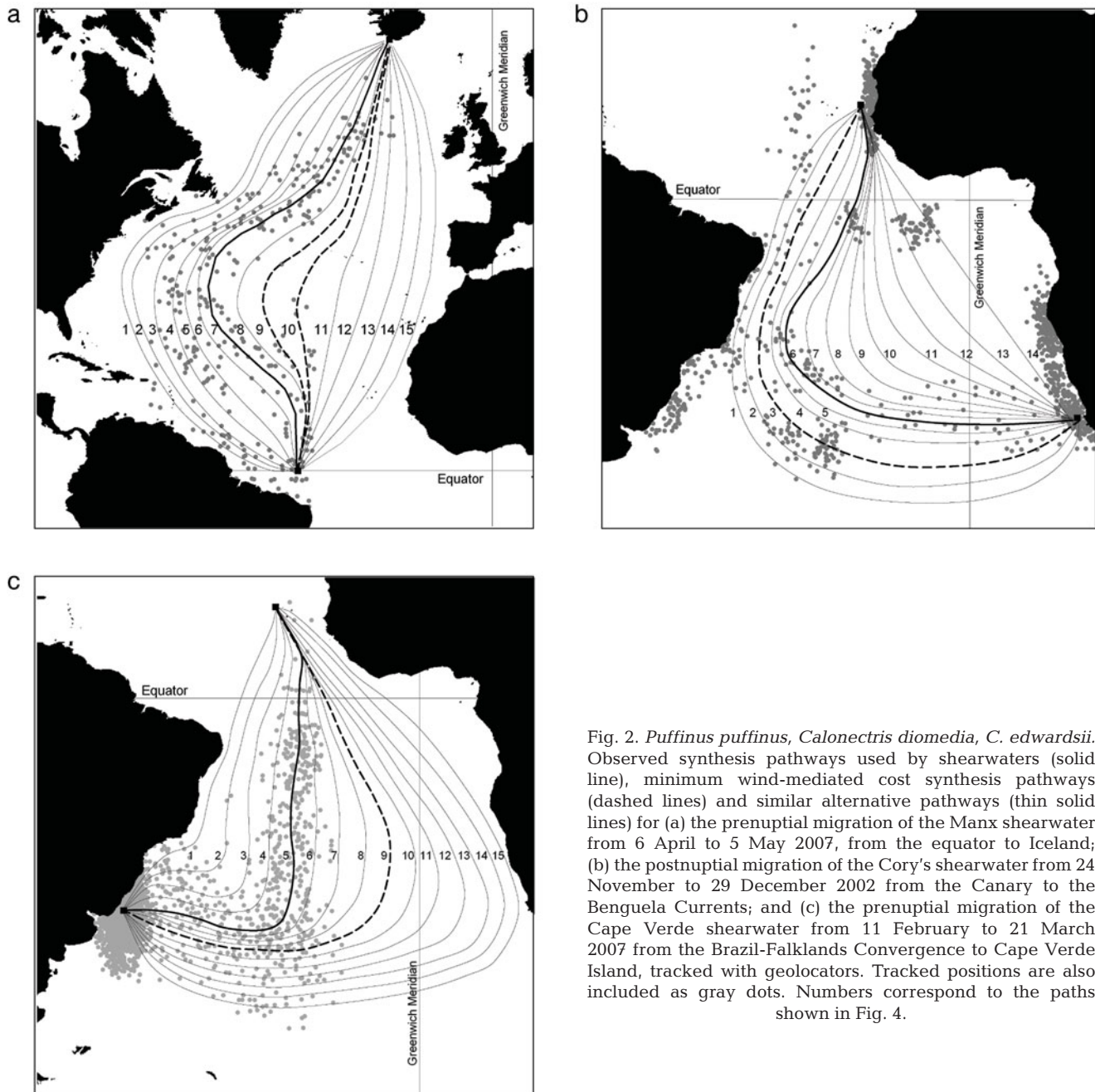


Fig. 2. *Puffinus puffinus*, *Calonectris diomedea*, *C. edwardsii*. Observed synthesis pathways used by shearwaters (solid line), minimum wind-mediated cost synthesis pathways (dashed lines) and similar alternative pathways (thin solid lines) for (a) the prenuptial migration of the Manx shearwater from 6 April to 5 May 2007, from the equator to Iceland; (b) the postnuptial migration of the Cory's shearwater from 24 November to 29 December 2002 from the Canary to the Benguela Currents; and (c) the prenuptial migration of the Cape Verde shearwater from 11 February to 21 March 2007 from the Brazil-Falklands Convergence to Cape Verde Island, tracked with geolocators. Tracked positions are also included as gray dots. Numbers correspond to the paths shown in Fig. 4.

deployed on sooty shearwaters *Puffinus griseus* showed that birds do not generally dive during their transequatorial trips (Shaffer et al. 2006).

In seabirds, detours are probably related to an optimisation of time and energy in relation to differences in wind assistance. In fact, our results show that migration costs are strongly dependent on wind conditions. Wind-mediated costs on the most costly day ranged from being 25 to 150% more expensive than on the least costly day for a given pathway (Fig. 4), using simulated days of departure within the migration period defined by the tracked birds. Variability

in cost was also huge in pathways with very different lengths. For instance, among Cory's shearwaters, pathways varying between 8000 and 13000 km in length showed similar average costs, but each of them ranging from 80000 to 140000 cost units. These results confirm that wind conditions during the journey can have a strong impact on the cost of migrating, and therefore shearwaters should develop strategies to select optimal departure dates. In terrestrial birds, it has been shown that birds tend to depart with tailwinds, which help them to migrate faster and save some energy (Liechti & Bruderer 1998, Åkesson

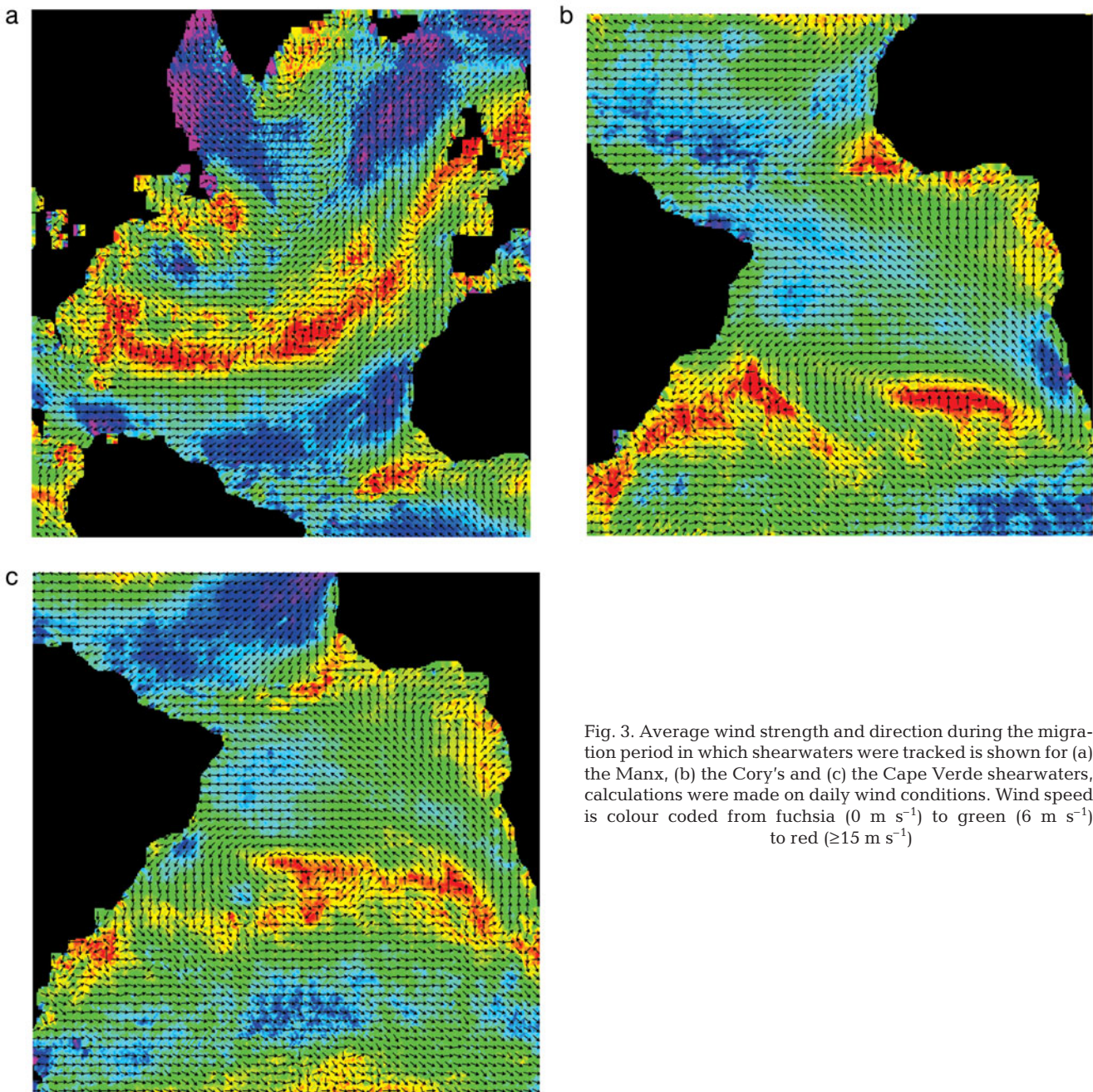


Fig. 3. Average wind strength and direction during the migration period in which shearwaters were tracked is shown for (a) the Manx, (b) the Cory's and (c) the Cape Verde shearwaters, calculations were made on daily wind conditions. Wind speed is colour coded from fuchsia (0 m s^{-1}) to green (6 m s^{-1}) to red ($\geq 15 \text{ m s}^{-1}$)

& Hedenström 2000). Indeed, because pelagic seabirds cannot escape from the influence of unfavourable winds when travelling, coupling migration phenology with winds may be particularly critical. In this regard, it has been suggested that shearwaters may adjust the timing of crossing the equator to avoid the monsoon westerlies associated with the Atlantic intertropical convergence zone during summer months (Felicísimo et al. 2008).

The optimal migration pathway depends on how shearwaters seek to compromise between wind-mediated costs and travelling time. In general, when

the lowest cost (a synthesis derived from wind resistance models) and the shortest distance pathways between breeding and wintering areas differed, the observed synthesis path for the different shearwater species was relatively close to the lowest cost synthesis pathway (Figs. 2 & 4). Observed synthesis pathways in the 3 species were only about 12 to 13% more costly than the theoretically lowest cost synthesis pathway. In the Cory's and Cape Verde shearwaters, the observed synthesis pathways were 14 to 16% shorter than the lowest cost synthesis pathways, suggesting that the extra cost was somehow compen-

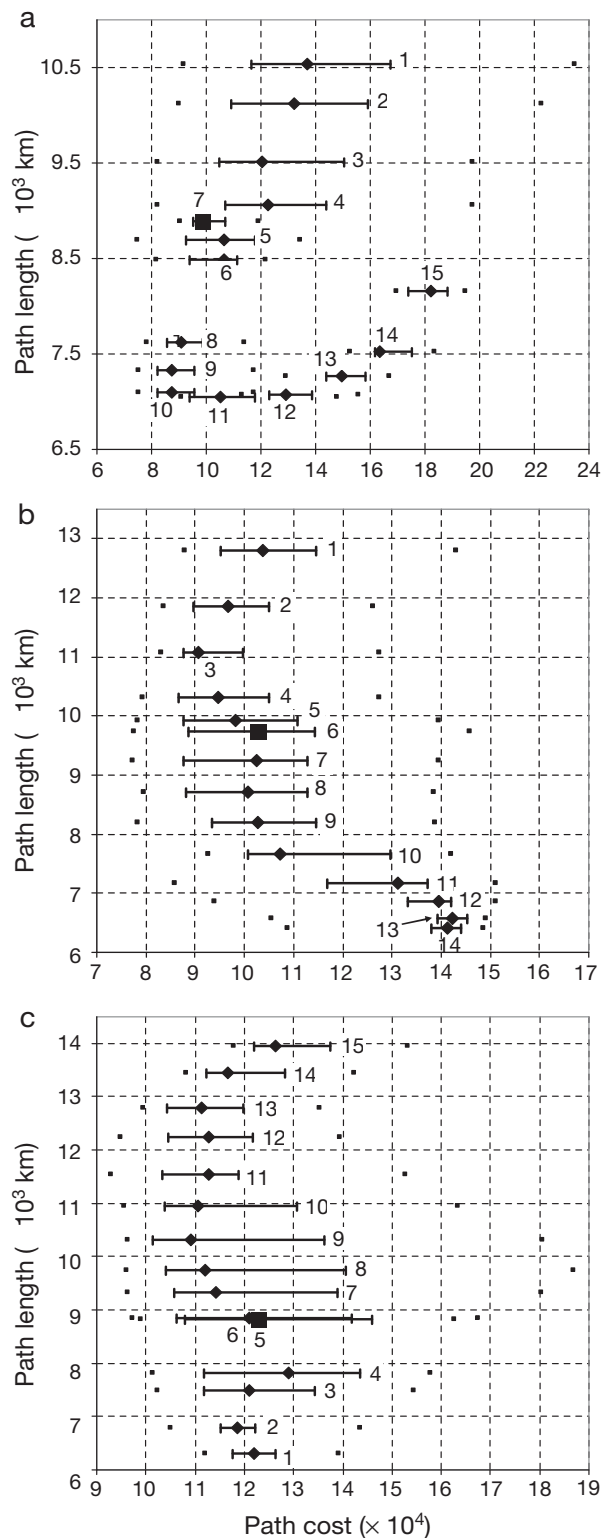


Fig. 4. *Puffinus puffinus*, *Calonectris diomedea*, *C. edwardsii*. Wind-mediated costs (arbitrary units) and path lengths (km) of the trajectories shown in Fig. 2 for (a) Manx shearwaters, (b) Cory's shearwaters and (c) Cape Verde shearwaters. For each path, the cost was calculated every day within the migration period. Results are shown as median, quartile and range values. Numbers correspond to the paths shown in Fig. 2

sated by saving about 2 d of travelling time. In the case of the Manx shearwater, however, the observed path was not only 12% more costly, but also 25% longer. This opposite trend may be a consequence of Manx shearwaters having greater wing-loading compared to Cory's or Cape Verde shearwaters. Manx shearwaters fly with more frequent flapping, much more energetically costly, which may force them to forage during migration, as revealed by a recent study (Guilford et al. 2009). Alternatively, this trend may result from the unpredictability shown by shorter pathways (Fig. 4a; path lengths from 7000 to 8000 km). Manx shearwaters could certainly have taken from 10 to 25% shorter paths, with even lower costs. However, among shorter paths, trajectories of similar length show disparate costs (Fig. 4a; trajectories 8 to 15), suggesting that shearwaters would face the high risk of expending up to double the cost. That is, disparate costs suggest more turbulent and unpredictable weather at the centre of an Atlantic gyre, perhaps deterring shearwaters from crossing it.

In some cases, the trade-off between time and cost in simulated pathways was apparently more optimal than that selected by the birds. For example, the cost of the average observed pathway in Cory's shearwaters was 102 631 cost units and the length 9734 km. However, simulated pathways up to 1500 km shorter showed similar wind-mediated costs, suggesting Cory's shearwaters may have saved about 2 or 3 travelling days. Similar conclusions could be drawn for the Cape Verde shearwater observed synthesis pathway. Discrepancies between optimal and observed synthesis pathways may result from the lack of reliable environmental cues for pathway choice, as well as the influence of prevailing winds on bird migration at an evolutionary scale. As we have shown, migration costs are strongly dependent on wind conditions, but wind patterns may be unpredictable or seabirds may not always have enough information during their migratory episodes to choose the lowest cost pathway. Even if birds have enough information, wind conditions in a single year may not be an adequate scale of study. Shearwaters can live for >30 yr, and therefore pathway choice may depend on the experience gained over many years. Indeed, it has been shown that memory and culture may play an important role in shaping the foraging strategies of seabirds (Grémillet et al. 2004, Camphuysen & Van de Meer 2005). Alternatively, pathways may just have been selected over generations, according to the consistency of wind patterns over the years. Large-scale wind patterns in the Atlantic seem highly predictable, but whether the migratory routes shown in the present study are similar among years is still unknown. In this regard, long-term tracking studies and the analysis of migration pathways over several

years in relation to the changing meteorological conditions would bring new insights into the understanding of the evolution of migration routes. Nevertheless, the fact that birds chose low cost pathways for the transoceanic trips of the 3 shearwater species analysed here suggest that winds are of decisive importance for the evolution of migration systems in seabirds.

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Movements, at-sea distribution and behaviour of a tropical pelagic seabird: the wedge-tailed shearwater in the western Indian Ocean

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ABSTRACT: This is the first study using geolocators (global location sensing, GLS) to track the movements of a pelagic tropical seabird. We used GLS to describe at-sea distribution and activity patterns of wedge-tailed shearwaters *Puffinus pacificus* breeding on Aride Island, Seychelles, in the late chick-rearing, non-breeding and pre-breeding periods. During late chick-rearing and pre-breeding periods, shearwaters foraged relatively close to the colony. In the non-breeding period, shearwaters were found on a west–east gradient along the equator, between 5° N and 10° S. Some of the tracked individuals showed little dispersion, staying as close as 1000 km to Aride Island, while others travelled 3500 km to the Central Indian Ocean Basin. Individual core areas of activity showed little overlap. Overall, wedge-tailed shearwaters showed short-distance movements and exploited relatively unproductive oceanic waters. At-sea distribution largely matched that of yellowfin and skipjack tunas, emphasising the importance of the association with subsurface predators rather than associations with physical oceanographic features that enhance primary productivity. During the non-breeding period, the feeding activity of shearwaters was mainly concentrated in the daylight period, when tunas also forage. A different behaviour, characterised by a much lower proportion of the night sitting on the sea surface, was recorded in the pre-laying exodus of 1 female to more productive waters, suggesting a different feeding strategy and/or targeting of different prey. Knowledge of the at-sea distribution of wedge-tailed shearwaters allows quantification of the overlap with industrial fisheries, which will be crucial to devise fisheries policies for the Indian Ocean with important implications for the conservation of this species.

KEY WORDS: Wedge-tailed shearwater · Activity patterns · At-sea distribution · Foraging behaviour · Pelagic · Habitat preferences · Indian Ocean · Tuna distribution

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INTRODUCTION

Migration is known to be most pronounced in environments in which food supplies vary greatly through the year, enabling animals to exploit periodic abundances and avoid shortages (Newton 2008). In tropical marine environments, food resources have less seasonal variation than in temperate and polar regions (Ashmole 1971, Weimerskirch 2007), which can partly explain why most tropical seabirds, with the exception of populations breeding at the limit of tropical zones, do not perform mi-

grations to the same extent as their temperate or polar counterparts. On the other hand, food resources in tropical oceans are scarcer and more patchily distributed (Ashmole 1971, Weimerskirch 2007), which might impose high foraging costs, either by increasing the proportion of time spent searching or in prey patches, or an extension of the prospected area. For example, dispersal of tropicbirds (*Phaethon lepturus* and *P. aethereus*) outside the breeding season is usually multidirectional (Spear & Ainley 2005). Assuming this is representative of other tropical seabirds, it suggests that their migrations are to

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some extent less predictable than those of many temperate or polar seabirds, where most or all of the population moves to 1 or more distant wintering areas (Phillips et al. 2005, 2006, 2007, Shaffer et al. 2006). Furthermore, whereas temperate and polar seabirds rely mostly on predictable physical oceanographic features (fronts, shelf and ice edges, upwelling zones, etc.), tropical seabird species seem to rely to a much greater extent on fish and squid forced to the surface by diving predators (Ballance & Pitman 1999, Spear et al. 2001, Jaquemet et al. 2004), the location and timing of which is unpredictable (Weimerskirch 2007).

Current knowledge of the at-sea distribution and movements of tropical seabirds is based primarily on shipboard observations (Bailey 1968, Pocklington 1979, Dunlop et al. 2001, Jaquemet et al. 2004), sea-watching from the coast and band recoveries (Rogers 1975). Although at-sea observations provide data on the distribution and multispecific assemblages of seabirds during the non-breeding season, the information is limited given the inability to determine the origin and breeding status of individuals. This can only be achieved by dyeing large numbers of birds at colonies, or by tracking. During the last decade, the development of tracking devices (such as satellite transmitters and light-based geolocators) has enabled much more detailed descriptions of the at-sea distribution and behaviour of pelagic seabirds during the non-breeding period (e.g. Grémillet et al. 2000, Weimerskirch & Wilson 2000, González-Sólis et al. 2007, Phillips et al. 2007, Mallory et al. 2008). Most of these studies have focused on temperate, polar and subtropical species, whereas tropical seabirds have received very little attention (but see Weimerskirch et al. 2006).

Wedge-tailed shearwaters *Puffinus pacificus* have a large breeding distribution and foraging range, extending throughout the tropical and subtropical latitudes of the Indian and Pacific oceans (Harrison 1983). Of these, the tropical populations are thought to be mainly sedentary throughout the year, and the subtropical populations more widely distributed (Harrison 1983). Little is known, however, about the movements and at-sea behaviour of individual wedge-tailed shearwaters. Global population trends of wedge-tailed shearwaters are unquantified but there is some evidence of a population decline due to poaching, predation and over-fishing of tuna (Birdlife International 2007). The knowledge of how pelagic seabirds make use of the marine environment and the identification of core foraging areas may be therefore crucial for understanding their foraging strategies and developing a concerted conservation strategy.

In the present study we used geolocators (also termed global location sensing [GLS] loggers) to describe movements and activity patterns of wedge-tailed shearwaters

breeding on Aride Island, Seychelles, western Indian Ocean. In particular, we aimed to (1) identify the key areas used by wedge-tailed shearwaters during the late chick-rearing, non-breeding and pre-breeding periods, (2) determine habitat preferences (by identifying which oceanographic parameters determine site selection), (3) examine individual variability in site preference and (4) describe activity patterns of non-breeding birds. Our predictions were: (1) Given that ocean productivity in the Seychelles archipelago is low and that wedge-tailed shearwaters are not central-place foragers during the non-breeding season, we expect them to move towards more productive waters, namely to the coastal areas off Arabia, India, Sri Lanka and/or Indonesia. (2) Wedge-tailed shearwaters are the third most abundant seabird in the western Indian Ocean, totalling ca. 145 000 pairs (authors' unpubl. data) and both intra- and inter-specific competition may be especially high in such an unproductive environment. Thus we predict that, despite searching for more productive areas, wedge-tailed shearwaters may show spatial partitioning in their at-sea distribution. (3) In the Indian Ocean, wedge-tailed shearwaters are known to forage in association with subsurface predators, mainly yellowfin tuna *Thunnus albacares* and skipjack tuna *Katsuwonus pelamis* (S. Jaquemet pers. comm.) and thus we expect to find a high overlap in shearwater and tuna fisheries distribution.

This is the first study to present detailed information on the at-sea behaviour, distribution and habitat characteristics of a tropical pelagic seabird during the late chick-rearing, non-breeding and pre-breeding periods. The data were used to discuss the strategies used by tropical pelagic seabirds in general for foraging in an environment of much lower seasonal variability, and with scarcer and more patchily distributed resources than those typical of temperate or polar latitudes. Furthermore, data on the at-sea distribution of wedge-tailed shearwaters will allow the quantification of the overlap with industrial fisheries in the Indian Ocean.

MATERIALS AND METHODS

Oceanography of the Indian Ocean. Fig. 1 shows two large circular currents, one in the northern hemisphere that flows clockwise and one south of the equator that moves anticlockwise, constitute the dominant flow pattern in the Indian Ocean, and are strongly influenced by the Asiatic Monsoon. During the northwest monsoon or austral summer, the wind blows from east to west and induces the development of the North Equatorial Current (NEC; Tomczak & Godfrey 2003; our Fig. 1a). A strong countercurrent, the Equatorial Counter Current (ECC), flows west-east, to the south of the NEC at this time of the year. During the southeast monsoon or austral winter the

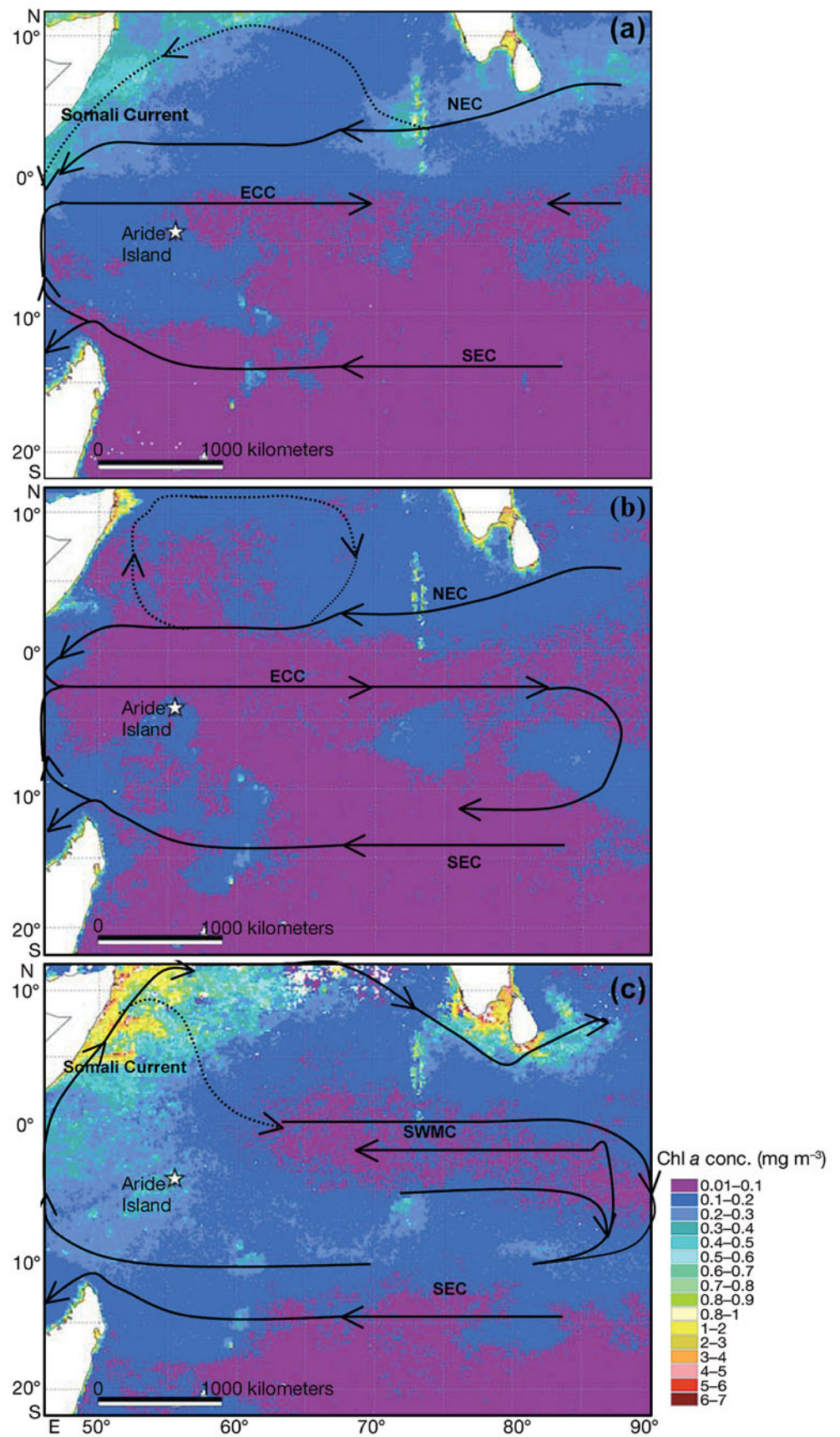


Fig. 1. Chl *a* concentrations and main ocean currents in the study area during 2007: (a) January and February, (b) April and May and (c) June and July. NEC: North Equatorial Current, SEC: South Equatorial Current, ECC: Equatorial Countercurrent, SWMC: Southwest Monsoon Current. Dotted lines: secondary, or weaker currents

NEC reverses and flows west to east as the Southwest Monsoon Current (SWMC; Tomczak & Godfrey 2003; our Fig. 1c). Reversing monsoonal winds are also responsible for changes in the direction of the Somali Current and the latitude of the ECC. Overall, chlorophyll *a* (chl *a*) concentrations are low in the western and central Indian Ocean (Fig. 1a,b), especially in comparison with equatorial regions of the Pacific and Atlantic oceans. The strongest upwelling of the Indian Ocean occurs when the south-east monsoon produces strong Ekman transport away from the coasts of Somalia, Arabia, India and Sri Lanka (Tomczak & Godfrey 2003; our Fig. 1c).

Logger deployment and data analysis. Fieldwork was carried out on Aride Island (4° 10' S, 55° 40' E), the most northerly of the granitic islands of the Seychelles archipelago, where ca. 19 500 pairs of wedge-tailed shearwaters breed (Bowler et al. 2002). Sixteen GLS loggers (MK4, BAS) were deployed on wedge-tailed shearwaters from 20 to 25 January (towards the end of chick-rearing) and recovered from 4 July to 17 August 2007. In the Seychelles, wedge-tailed shearwaters breed during the austral summer, usually between September and February (Burger & Lawrence 2000). After breeding, wedge-tailed shearwaters spend a few months away from Aride Island, and usually return in May or June. Thereafter, visits to the colony become more frequent closer to laying. Each geolocator, weighing 4.5 g, was attached with a single cable tie to a metal ring and deployed on the tarsus (representing ca. 1.6 % of the bird's weight). All shearwaters were captured at the entrance or inside nest-burrows after feeding their chicks, and a single bird per pair was equipped with a logger. Gender was determined by molecular methods using a blood sample collected from the tarsal vein. In order to assess potential negative effects of loggers, all chicks of tracked birds were weighed after logger deployment and ca. 25 d later (or before fledging) and the variation in body mass compared to that of a sample of 12 control chicks of similar age ($t_{26} = 1.069$, $p = 0.295$, based on wing length) in the same period. The devices deployed had light (geolocation), salt-water immersion (activity) and temperature-recording capabilities. Geolocation is the calculation of position from ambient light level readings with reference to time (Wilson et al. 1992, Hill 1994). Latitude and longitude of each bird was estimated (twice d⁻¹) from, respectively, day (night) length, and the time of local midday (midnight) relative to Greenwich Mean Time (GMT) (Phillips et al. 2004). Light data were analysed using MultiTrace software according to Phillips et al. (2004). During processing, locations derived from curves with apparent interruptions around sunset and sunrise, or that required unrealistic flight speeds (>35 km h⁻¹ sustained over a 48 h period), were identified and later excluded if appropriate. Locations were affected and thus excluded for variable periods (2 to 5 wk)

before and after the 21 March equinox. Validated data were smoothed twice (Phillips et al. 2004). Previous studies using geolocators indicate mean accuracies of 186 ± 114 km (Phillips et al. 2004) and of 202 ± 171 km (Shaffer et al. 2005), which seems adequate for studying large-scale movements of pelagic seabirds. However, none of these studies was carried out in equatorial regions, where GLS errors can presumably be larger due to the lower accuracy to determine day length (which is fundamental to estimating latitude). Further studies should investigate GLS accuracy at lower latitudes.

Activity patterns of wedge-tailed shearwaters were derived from immersion data. The immersion data consist of values between 0 and 200 corresponding to the number of instantaneous tests every 3 s for salt-water immersion that were positive within each 10 min period. These data were matched with the timing of civil twilight (when sun is 6° below the horizon) in order to calculate the proportion of time and the total time spent on the water and in flight during darkness and daylight each day.

For the analysis we considered 3 periods: (1) late chick-rearing, the period between logger deployment and the departure on migration, identified either from nest monitoring and/or from location and activity (immersion data), (2) non-breeding, the period between the end of the equinox period (April) and the return to the breeding grounds, identified from location and activity data, and (3) pre-breeding, the period between the first long (>1 d) visit of the bird to land and logger recovery, identified from activity data. Activity patterns of shearwaters were not analysed in the late chick-rearing and pre-breeding periods (except for 1 female during the pre-laying exodus; see 'Results: Pre-breeding period') given the difficulties in differentiating periods of flight and periods in the breeding colony from immersion data.

Locations of birds at sea were examined using ArcView GIS 3.2 (ESRI). Key areas for the 3 periods were identified by generating kernel density maps in an equal-area cylindrical projection using the Animal Movement extension in ArcView (Phillips et al. 2004). We considered the 95 and 50 % kernel density contours to represent the area of active use and the core areas of activity, respectively (Hamer et al. 2007). These areas may be overestimated given the relative inaccuracy of the GLS measurements (see 3 paragraphs above). We used 3 variables to characterise marine habitats: chl *a* concentration, sea surface temperature (SST) and bathymetry. Chl *a* concentrations were derived from the sea-viewing wide field-of-view sensor (SeaWiFS) monthly composites with a 9 km spatial resolution (<http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.seawifs.shtml>). Monthly averages of SST data were Aqua's moderate resolution imaging spectroradiometer (MODIS)-mapped products at 4 km resolution,

downloaded from <http://poet.jpl.nasa.gov/Bathymetry> was determined using ETOPO2 grids (www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html).

Statistical analyses were performed with STATISTICA 6.0. One-way ANOVAs, followed by post hoc Tukey tests, were used to compare oceanographic characteristics (water depth, SST and chl *a* concentrations extracted for each kernel core) of areas used by wedge-tailed shearwaters during the different tracking periods, and between individuals with different at-sea distributions during the non-breeding period. Also, *t*-tests were performed to investigate differences in activity patterns between (1) individuals with different distributions during the non-breeding period and (2) non-breeding and pre-laying exodus periods of 1 tracked female. Values are presented as mean \pm SD. Results were considered significant at $p < 0.05$.

RESULTS

Logger retrieval and device effects

We retrieved all the 16 loggers deployed but 7 of these failed to download. This failure rate reflects the greater age of a number of these loggers that were built for an earlier study. All loggers were retrieved in the pre-breeding period, with the exception of 1 device, deployed on a female, which was recovered while the bird was incubating a recently laid egg. Six female and 3 male wedge-tailed shearwaters were tracked for a mean of 180.1 ± 17.0 d (range: 163 to 206 d). Of the 2149 locations obtained outside the equinox periods, 5.4 and 0.3% were excluded subsequently because of light interference and unrealistic flight speeds, respectively, providing a total of 2025 validated locations.

Variation in body mass was similar for the 16 chicks of tracked birds and 12 control chicks of similar age ($t_{26} = 0.556$, $p = 0.583$). Four of the chicks of tracked birds fledged during the monitoring period.

At-sea distribution and movements

Late chick-rearing period

Wedge-tailed shearwaters were tracked for a mean of 23.9 ± 11.2 d (range: 8 to 37 d) during late chick rearing. Although the area used by the 9 tracked individuals comprised $>1\,500\,000$ km², the core area of activity (50% kernels) was much smaller, at ca. 160 000 km² (Fig. 2a). Foraging areas were exclusively located to the east of Aride Island, with a preference for waters to the northeast. Breeding shearwaters apparently avoided the shallow waters of the Mascarene Plateau,

instead targeting areas with depths ≥ 3500 m. Despite the small sample size (3 males and 6 females), there was some evidence for sex-related differences in the core areas (50% kernels), with females showing a broader distribution than males (Fig. 2a).

Non-breeding period

On average, tracked shearwaters were followed for 37.9 ± 13.7 d (range: 13 to 56 d) during the non-breeding period. Birds dispersed eastwards, occupying the area between Aride Island and the Ninety East Ridge (ca. 80° E; Fig. 2b). We found a west–east distribution gradient in core areas (50% kernels) amongst the 9 birds tracked, and individual movements were classified as either long- or short-distance dispersal (Fig. 2b). The 4 birds that performed short-distance dispersal were distributed between Aride Island and the Chagos-Laccadive Ridge. In contrast, the other 5 wedge-tailed shearwaters travelled further east and were concentrated mainly between the Chagos-Laccadive and the Ninety East Ridge (Fig. 2b). Overall, although individual activity areas (95% kernels) overlapped extensively, core areas overlapped partially only for the 3 individuals that were concentrated in the Central Indian Basin (Fig. 3). There was no evidence of sex-related differences in distribution during the non-breeding period.

Pre-breeding period

Following the exclusively pelagic non-breeding period, wedge-tailed shearwaters returned in May and June to the waters surrounding Aride Island, and most of the birds spent at least 1 long period (2 to 4 d) on land. During the pre-breeding period birds were tracked for a mean of 51.4 ± 24.7 d (range: 22 to 85 d). The distribution of wedge-tailed shearwaters during this time was not very different from that in the late-chick rearing period (Fig. 2c). Core areas (50% kernels) were also located to the east of Aride Island, but whereas during the chick-rearing period birds preferentially foraged on northeast waters outside the Mascarene Plateau, during the pre-breeding period they exploited both the northeast area and the southern shallower waters of the Mascarene Plateau (Fig. 2c). Only 3 birds travelled northwest to the deeper waters of the Somali Basin.

One of the tracked females started breeding unusually early, laying in the 2nd wk of August. Just before laying, this female undertook a pre-laying exodus of 22 d towards the Somali Basin, travelling ca. 7000 km in total (Fig. 4).

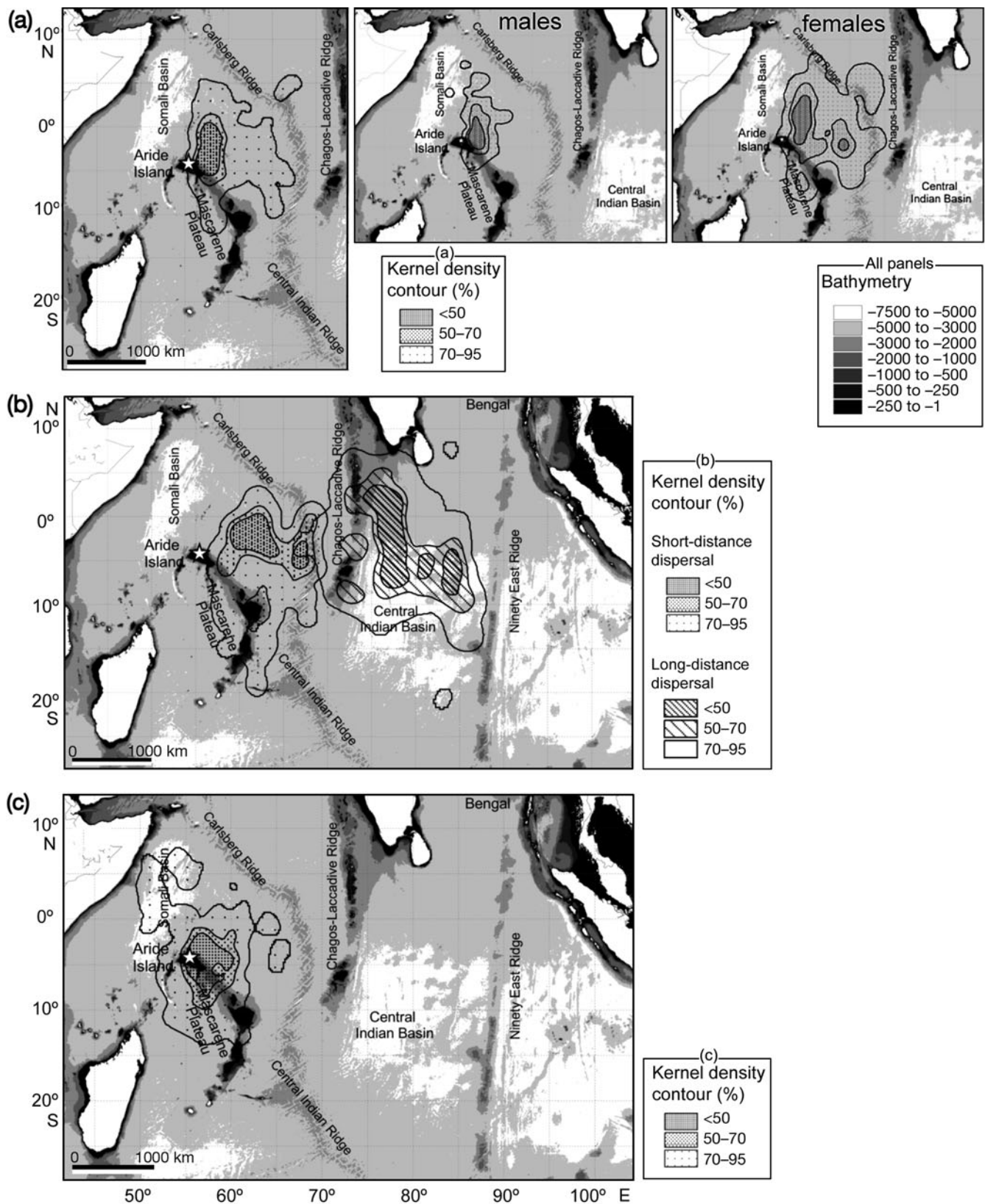


Fig. 2. *Puffinus pacificus*. Density distribution (kernel contours) of 9 birds during the (a) late chick-rearing, (b) non-breeding and (c) pre-breeding periods, with bathymetric details of the study area overlaid. Distinct sex-based distributions were evident only for the late chick-rearing period (a)

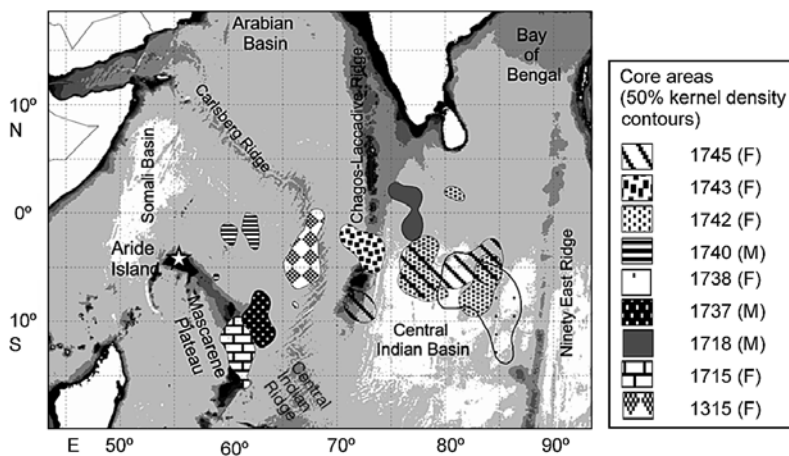


Fig. 3. *Puffinus pacificus*. Individual core areas (50% kernel) of activity of 9 birds during the non-breeding period overlaid on bathymetry. F: female, M: male

At-sea distribution in relation to oceanography

Oceanographic characteristics of the areas used by wedge-tailed shearwaters during the different tracking periods are presented in Table 1. Overall, birds showed an oceanic distribution, exploiting regions of deep water (3500 to 4500 m) and avoiding the shallow waters of both continental and oceanic shelves. Water depth in core areas (50% kernels) was significantly lower during the pre-breeding period than during the late chick-rearing and non-breeding periods ($F_{2,788} = 29.6$, $p < 0.001$, followed by post hoc Tukey tests). Activity areas (95% kernels) of wedge-tailed shearwaters were char-

Table 1. *Puffinus pacificus*. Oceanographic characteristics within the kernel distribution during different tracking periods in 2007. Values are mean \pm SD. SST: sea surface temperature

Kernel density (%)	Chl <i>a</i> concentration (mg m ⁻³)	SST (°C)	Water depth (m)
Late chick-rearing			
50	0.11 \pm 0.05	29.3 \pm 0.4	3965 \pm 660
70	0.12 \pm 0.04	29.3 \pm 0.4	3908 \pm 904
95	0.13 \pm 0.05	29.2 \pm 0.6	3932 \pm 885
Non-breeding			
Long-distance			
50	0.12 \pm 0.03	29.6 \pm 0.9	4581 \pm 849
70	0.13 \pm 0.11	29.6 \pm 1.0	4071 \pm 1218
95	0.12 \pm 0.07	29.7 \pm 1.0	4293 \pm 1152
Short-distance			
50	0.10 \pm 0.03	29.9 \pm 0.8	3411 \pm 1224
70	0.09 \pm 0.02	29.8 \pm 1.0	3735 \pm 979
95	0.10 \pm 0.03	29.9 \pm 1.0	3595 \pm 1108
Pre-breeding			
50	0.21 \pm 0.12	28.3 \pm 1.0	3446 \pm 1468
70	0.21 \pm 0.11	28.2 \pm 1.1	3531 \pm 1366
95	0.20 \pm 0.11	28.2 \pm 1.2	3546 \pm 1327
Pre-laying exodus			
	0.43 \pm 0.29	26.7 \pm 0.7	4662 \pm 1109

acterised by generally low productivity (mean concentration of chl *a* = 0.11 to 0.21 mg m⁻³) and warm water temperatures (mean SST = 28.2 to 29.9°C). Core areas (50% kernels) of tracked birds were significantly more productive and cooler during the pre-breeding period than during the chick-rearing and non-breeding periods ($F_{2,776} = 135.8$, $p < 0.0001$ and $F_{2,788} = 210.7$, $p < 0.0001$, respectively, followed by post hoc Tukey tests).

Individuals that performed long-distance movements spent the non-breeding period in waters that were significantly deeper, more productive and had lower SST than those of birds that stayed closer to Aride Island (for core

areas: $t_{304} = 9.78$, $p < 0.001$; $t_{304} = 5.27$, $p < 0.001$; $t_{304} = 3.32$, $p < 0.01$, respectively).

The area exploited by the female during the pre-laying trip (Somali Basin) was characterised by greater depth and productivity, and lower SST than any other area exploited by tracked shearwaters ($t_{701} = 5.33$, $p < 0.001$; $t_{684} = 11.47$, $p < 0.001$; $t_{701} = 7.86$, $p < 0.001$, respectively).

Activity patterns

During the non-breeding period, wedge-tailed shearwaters spent a high proportion (85.5%) of darkness on the water, and only ca. 1.7 h in total flying (Table 2). In contrast, during daylight, shearwaters spend almost half of their time in flight (mean of 5.2 h d⁻¹). Shearwaters performing short and long dispersals had similar activity patterns (t -tests: $t_7 = 0.76$ to 1.32, $p = 0.27$ to 0.47, for the 6 activity parameters estimated; Table 2) and there was also no evidence of sex-related differences in activity (t -tests: $t_7 = 0.49$ to 1.26, $p = 0.28$ to 0.67). During darkness, the female tracked in the pre-laying exodus spent a significantly lower proportion of time in the water, less time in total in the water and more time in total in flight than in the non-breeding period (t -tests: $t_{55} = 10.17$, $p = 0.000$; $t_{55} = 10.50$, $p = 0.000$; $t_{55} = 9.91$, $p = 0.000$, respectively), whereas during daylight, patterns were similar between the 2 periods (t -tests: $t_{55} = 0.12$, $p = 0.91$; $t_{55} = 0.17$, $p = 0.86$; $t_{55} = 0.38$, $p = 0.70$; Table 2).

DISCUSSION

To our knowledge, this is the first study to use GLS loggers (and one of the few using any tracking device)

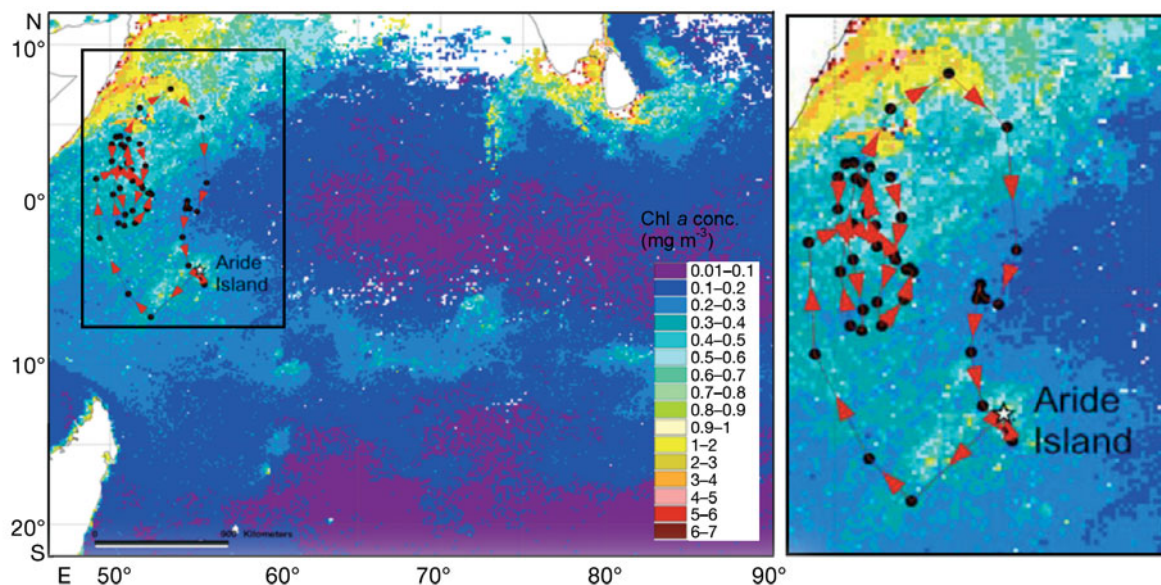


Fig. 4. *Puffinus pacificus*. Pre-laying exodus of 1 female overlaid on productivity (chl *a* concentrations) in the study area in July and August

to describe movements, at-sea distribution and activity patterns of a tropical seabird during the non-breeding and pre-laying periods. GLS loggers had no negative effects on shearwaters: following deployment, chicks were fed for a further month (or until fledging), indicating no desertion as a result of handling of adults. In addition, their growth was similar to that of control chicks. Furthermore, we had an exceptionally high logger recovery rate (100%), which reveals the high nest-fidelity of wedge-tailed shearwaters and supports the absence of any deleterious effects.

Table 2. *Puffinus pacificus*. Activity patterns during the non-breeding period. Values are means \pm SD. F: female, M: male

Tracking no.	Time on water (%)		Total time on water (h)		Total time in flight (h)	
	Daylight	Darkness	Daylight	Darkness	Daylight	Darkness
Non-breeding period						
1315 (F)	58.5 \pm 11.0	89.5 \pm 10.0	7.1 \pm 1.4	10.7 \pm 1.2	5.0 \pm 1.3	1.2 \pm 1.2
1715 (F)	56.4 \pm 14.5	88.9 \pm 7.6	6.6 \pm 1.6	10.9 \pm 1.0	5.1 \pm 1.8	1.4 \pm 0.9
1718 (M)	54.4 \pm 16.5	81.8 \pm 15.2	6.7 \pm 2.1	9.8 \pm 1.8	5.6 \pm 2.0	2.1 \pm 1.8
1737 (M)	52.3 \pm 11.8	80.3 \pm 10.8	6.3 \pm 1.5	9.6 \pm 1.4	5.8 \pm 1.4	2.3 \pm 1.3
1738 (F)	53.0 \pm 11.1	80.4 \pm 13.1	6.3 \pm 1.3	9.7 \pm 1.5	5.6 \pm 1.3	2.4 \pm 1.6
1740 (M)	71.2 \pm 10.6	89.6 \pm 7.7	8.7 \pm 1.3	10.6 \pm 0.9	3.5 \pm 1.3	1.2 \pm 0.9
1742 (F)	51.1 \pm 13.3	87.3 \pm 7.0	6.1 \pm 1.6	10.6 \pm 0.9	5.8 \pm 1.6	1.5 \pm 0.8
1743 (F)	55.8 \pm 20.5	83.8 \pm 19.2	6.7 \pm 2.5	10.1 \pm 2.3	5.3 \pm 2.4	1.9 \pm 2.3
1745 (F)	56.1 \pm 13.5	88.2 \pm 9.7	6.7 \pm 1.6	10.7 \pm 1.2	5.2 \pm 1.6	1.4 \pm 1.2
Mean ^a	56.5 \pm 6.0	85.5 \pm 3.9	6.8 \pm 0.8	10.3 \pm 0.5	5.2 \pm 0.7	1.7 \pm 0.5
Pre-laying exodus						
1743 (F)	56.6 \pm 1.4	31.2 \pm 18.2	7.0 \pm 1.8	3.7 \pm 2.1	5.3 \pm 1.7	8.1 \pm 2.1

^aBased on individual means

At-sea distribution and movements

Late chick-rearing period

During the chickrearing period, most wedge-tailed shearwater chicks are fed every day, and adult foraging trips last on average 1 or 2 d (Berlincourt 2006, Peck & Congdon 2006). This is reflected in the relative proximity of the core foraging areas to the breeding colony. However, and despite the small sample size, females showed a broader distribution

than males during late chick rearing, suggesting possible sex-related differences in foraging and/or provisioning behaviour. This agrees with the results of Peck & Congdon (2006) that described longer foraging trips and lower provisioning rates in females of wedge-tailed shearwaters breeding in the southwestern Pacific Ocean. They suggested that inter-sexual competition (leading to niche/habitat specialisation) at the foraging grounds was the most parsimonious explanation for the sex-specific differences observed in this monomorphic species.

Non-breeding period

Wedge-tailed shearwaters showed 2 distinct strategies during the non-breeding period. Most birds were found on a distribution gradient along the equator, between 5°N and 10°S. Some of the tracked individuals showed little dispersion, staying as close as 1000 km to Aride Island, while others commuted 3500 km to the Central Ocean Basin. Individual variation in distribution of foraging areas during the non-breeding season has been described for several species of Procellariiformes (Croxall et al. 2005, Phillips et al. 2005, 2006, Shaffer et al. 2006, González-Sólis et al. 2007). Although this is intriguing, there is no evidence that even dramatic variation in dispersal tactics within a population reflects short- or long-term variation in success, or has any implication for timing of return or subsequent success of the individuals concerned (Croxall et al. 2005, Phillips et al. 2005, 2006).

Pre-breeding period

Although most wedge-tailed shearwaters start breeding in late September or October, adults return to Aride Island in mid-May or June. The first visits to land after the non-breeding period took place in a temporal window of ca. 3 wk for all tracked birds. An early return to the breeding colony is a way to avoid the occupation of nests by intruders and seems to be common among burrow-nester seabirds (Phillips et al. 2006). In our case, this early return is also probably related to the increase in primary productivity of the surrounding waters, which is an indicator of the abundance of food resources for seabirds (see next subsection). The distribution of wedge-tailed shearwaters during the pre-breeding period largely overlapped that during late chick rearing. Given that during the pre-breeding period, shearwaters are not nearly as tied to central-place foraging as they are when provisioning chicks, although they do attend the colony to mate and prospect or defend nest sites, this suggests that foraging conditions within a relative short range of Aride Island are adequate for the needs of shearwaters during this time.

The only individual followed during a pre-laying foraging trip (exodus) of 22 d spent about 15 d of this in the Somali Basin. This was the only bird to spend a considerable proportion of time in this productive region. Although more coastal, this area is characterised by very deep waters, and is located at the edge of the continental shelf, which is commonly associated with strong upwelling. Egg formation is an energetically costly process in birds (Ricklefs 1974) and this result suggests that the exploitation of more productive waters by females may be particularly important dur-

ing the pre-laying period. Nevertheless, more data from a larger sample size would be essential to confirm these results.

At-sea distribution in relation to oceanography and abundance of subsurface predators

Overall, and despite some individual variation, the tracked wedge-tailed shearwaters utilised deep, warm and relatively unproductive oceanic waters. Food availability in tropical marine environments is usually described as low and unpredictable, and considered to show limited seasonal variation (Harrison & Seki 1987, Weimerskirch 2007). Nevertheless, in the Seychelles archipelago there is a clear seasonality in food availability, which seems to be directly related to phytoplankton blooms (Monticelli et al. 2007). Two blooms occur with some predictability each year: a small one from December to February, and the main one from May to August (Monticelli et al. 2007). These 2 periods of enhanced ocean productivity around the archipelago seem to play an important role in determining the breeding phenology and movements of wedge-tailed shearwaters. During both these periods, corresponding to chick rearing and pre-breeding, core areas of the distribution of wedge-tailed shearwaters are centred on Aride Island. In contrast with most other seabirds on the island (Bowler et al. 2002), wedge-tailed shearwaters breed during the austral summer, rearing their chicks at the time of the smaller phytoplankton bloom. At the end of the breeding season, and from March to at least mid-May, mean chl *a* concentrations are extremely low in most of the tropical Indian Ocean and it is then that wedge-tailed shearwaters disperse over a wider area. The early return to the colony, in late May to June, although also conditioned by the need to arrive early to defend nest sites, seems to be highly synchronised with this second peak in primary productivity in the surrounding waters.

During the non-breeding period, individual variation in distribution and habitat preferences was marked, and suggests a lack of specialisation on specific habitats or oceanographic features by tracked birds. This is likely to be because compared with temperate or polar seabirds that are often associated with oceanographic features such as fronts, eddies, shelf edges or upwelling, tropical seabirds seem to rely to a much greater extent on subsurface predators (Ballance & Pitman 1999, Spear et al. 2001, Jaquemet et al. 2004). Previous studies in the western Indian Ocean have shown that wedge-tailed shearwaters usually associate in large flocks with yellowfin tuna *Thunnus albacares* and skipjack tuna *Katsuwonus pelamis* (S. Jaquemet pers. comm.), which facilitate feeding on juvenile goatfish (Mullidae) and flying squid

(Ommastrephidae; Catry et al. in press). The distribution of wedge-tailed shearwaters, which is mostly restricted to between 5° N and 10° S in the area of influence of the ECC, corresponds closely to the distribution of catches of yellowfin and skipjack tuna by human fisheries (IOTC 2005, SFA 2006), which agrees with our predictions. As Spear et al. (2001) found for tropical piscivore seabirds in the Pacific Ocean, the affinity of shearwaters for the ECC is probably related to the distribution of surface-feeding tuna, which are associated with areas of deeper and well-stratified thermocline (Brill et al. 1999). Previous shipboard transects in the western and central Indian Ocean also recorded higher concentrations of wedge-tailed shearwaters (between March and May) within the ECC (Bailey 1968).

Although some tracked shearwaters travelled >3000 km to exploit the relatively deep, cooler and more productive waters of the Central Indian Basin (in relation to the western areas), contrary to our prediction, no bird travelled to the much more nutrient-rich waters of the Arabian Sea. Overall, the distribution of tracked individuals during the non-breeding and pre-breeding periods suggests that wedge-tailed shearwaters do not take advantage of foraging in very productive waters, such as the upwelling region off Somalia and Arabia. During the pre-breeding period, however, 3 ind. (including the one performing the pre-laying exodus) exploited the more nutrient-rich waters of the Somalia Basin. Nonetheless, these birds did not show fidelity to the area. Several authors consider that differences in water clarity drive differences in seabird foraging behaviour and that different adaptations may be needed for feeding in the clear blue water of the mid-ocean compared with more turbid, plankton-rich upwelling areas (Bailey 1968, Spear et al. 2001, 2007). In tropical marine environments, prey are concentrated in the water column during the day, avoiding the upper layer where high water clarity makes them highly susceptible to predators. Subsurface predators are therefore crucial for driving prey upwards and making them available to seabirds. In contrast, in highly productive waters where prey frequently aggregate near the sea surface in any case, such an association with subsurface predators is no longer necessary. Furthermore, upwelling regions usually concentrate high densities of foraging seabirds in which inter-specific competition tends to be higher (Ballance et al. 1997), which might be another reason the tracked birds tended to avoid the Somalian and Arabian coasts.

Activity patterns

The risk of predation, mainly by sharks, was previously pointed to as an important selective pressure for tropical seabirds not spending the night sitting on the

sea surface (Weimerskirch et al. 2005). The presence of sharks has also been proposed as one of the factors explaining the absence of an important niche of pursuit divers among tropical seabirds (Spear et al. 2007). In the present study, during the non-breeding period, wedge-tailed shearwaters spent a very high proportion of the night resting on the water, suggesting that the risk of predation may be much lower than previously proposed. The higher feeding activity during the day is somewhat unsurprising given that tuna activity, which seems to be important for shearwater foraging, is limited to daylight (Roger 1994). Furthermore, foraging efficiency may be reduced at night because it is harder to see and catch prey at low light levels (Catry et al. 2004, Phalan et al. 2007). Paradoxically, the female tracked during the pre-laying exodus spent a much lower proportion of the night sitting on the sea surface. This suggests that females increase their foraging effort during the pre-laying period, although the fact that activity patterns during daylight remained unchanged does not support this explanation. It is possible, however, that foraging activity is limited by physiological processes, e.g. digestion, requiring periods of inactivity. Nevertheless, the use of a different feeding strategy and/or the targeting of different prey may be the most plausible explanation for the differences recorded, and could be an adaptation to the different characteristics of the area exploited—deeper waters, lower SST and significantly higher productivity. The lack of studies on activity patterns of Procellariiformes during the non-breeding period precludes direct comparisons. Grémillet et al. (2000) showed that non-breeding black-browed albatrosses *Diomedea melanophrys* spent more time on the water than breeding individuals in the Falkland Islands; however, no data on activity during daylight and darkness periods were presented. Four species of albatrosses studied during different phases of the breeding period at South Georgia spent less time on the water during daylight (14.3 to 39.8%; Phalan et al. 2007) than did wedge-tailed shearwaters in the present study.

Foraging strategies of tropical pelagic seabirds

Previous studies on the at-sea distribution of albatrosses and petrels during the non-breeding period in both temperate and polar environments have described relatively long migrations from breeding grounds towards areas of high primary productivity associated with coastal ocean currents and/or continental shelves (Croxall et al. 2005, Phillips et al. 2005, 2006, Shaffer et al. 2006, González-Sólis et al. 2007). By comparison, wedge-tailed shearwaters from Aride Island showed short-distance movements and ex-

exploited relatively unproductive oceanic waters. The distribution of shearwaters largely matched the distribution of yellowfin and skipjack tunas, emphasising the importance of the association with subsurface predators rather than associations with physical oceanographic features that enhance primary productivity. The present study therefore highlights the differences in foraging ecology of tropical versus temperate and polar seabird species during the little-known non-breeding season.

Implications for conservation

Tuna catches in the Indian Ocean have dramatically increased since the early 1980s (IOTC 2005). The main impact of fisheries on tropical shearwaters in the Indian Ocean, in contrast to the situation for subtropical, temperate and polar Procellariiformes (e.g. Skillman & Flint 1997, Baker & Wise 2005, Phillips et al. 2005, 2006), is probably not the risk of incidental mortality on longlines. Stock assessments suggest that if current fishing effort and catches are maintained, tuna populations will soon fall to levels below those of sustainable yield (IOTC 2005). If tuna populations are depleted, prey availability to tropical seabirds associated with tuna schools will decrease accordingly. Therefore, current and future fisheries policies and practices in the Indian Ocean have important implications for the conservation of tropical wedge-tailed shearwaters.

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Effects of hydrographic and meteorological factors on seasonal seabird abundance in the southern North Sea

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ABSTRACT: We examined the influence of both season and hydrographic and meteorological factors on seabird abundance in the southern North Sea. Seabirds were counted from ships in a study area of 27.8×32.8 km on 407 d from 1990 to 2007. Two hydrographic and 5 meteorological parameters were taken from archived data. The relationships between bird abundance and abiotic parameters were investigated by generalised additive models for 3 distinct seasons. The species in the study area exhibited different seasonal patterns. While some species were present year-round, others occurred only at certain periods. Despite these substantial changes in abundances, the nature of the interactions between bird abundances and abiotic parameters did not vary much between seasons. All 5 meteorological and 2 hydrographic parameters significantly influenced the abundance of seabird species, though to a different degree. The single factors that most often had a significant influence in the single models were wind field, sea surface temperature anomaly, sea surface salinity anomaly and air pressure change. The quantitative composition of the seabird community differed significantly between onshore wind and offshore wind conditions. It is assumed that hydrographic parameters are relevant for the birds by determining their foraging habitats and that atmospheric parameters influence flight conditions during foraging and migration.

KEY WORDS: Seabird · Hydrography · Meteorology · Phenology · Wind · Monitoring

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INTRODUCTION

Various studies have investigated the influence of abiotic and biotic factors on the distribution and abundance of seabirds at sea (for reviews see Hunt 1990, Schneider 1991). Processes involved vary from 100s of metres to 1000s of kilometres in spatial ranges and from hours to years in temporal ranges, reflecting the influence of different oceanographic features and processes affecting prey availability to seabirds (Hunt & Schneider 1987). Less attention has been paid to the influence of meteorological factors, except for wind direction and wind speed (Furness & Bryant 1996, Weimerskirch et al. 2000). Recent advances in global weather data availability have enabled analyses of how seabirds cope with large-scale weather patterns,

e.g. the use of low and/or high pressure systems for movements and foraging flights (Nicholls et al. 1997, Spruzen & Woehler 2002). However, at small temporal and spatial scales, little is known about the respective effects of hydrographic and meteorological factors on seabird abundance, namely in coastal areas with high environmental variability, such as the southeastern North Sea (Markones et al. 2008). There, in particular, *Larus* spp. gulls often show highly divergent patterns on a day to day basis. This could be expected, to some degree, since the study area in question, the Inner German Bight, is an area of very high hydrographic variability, comprising the transition zone between the less saline and turbid Continental Coast Water Mass and the more saline and transparent Central North Sea Water Mass (Becker et al. 1983). In this system, fresh-

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water influx is enhanced during offshore easterly and southerly winds, while seawater influence is increased when westerly winds occur. Garthe (1997) and Markones (2007) showed that the distribution of several seabird species correlated with the occurrence of these 2 main water masses. The nearshore-dominating Continental Coast Water Mass was the preferred habitat of common gulls *Larus canus*, while northern fulmars *Fulmarus glacialis*, black-legged kittiwakes *Rissa tridactyla* and common guillemots *Uria aalge* were significantly associated with the Central North Sea Water Mass, which becomes dominant in the deeper north-western part of the study area. Changes in bird assemblages may be a consequence of sometimes rapid

variations in hydrographic and/or meteorological parameters. Also, species may differ in their response to these changes, as well as in their choice of habitat, especially pelagic versus coastal seabirds. Furthermore, habitat requirements of seabirds undergo a seasonal pattern. During the breeding period, the activity range of birds is restricted by the availability of suitable nest sites and parental duties (incubation shifts and chick provisioning). During spring and autumn, distribution patterns are often influenced by moulting, migration, or dispersal (Stone et al. 1995). In winter, movements are generally less pronounced, though, e.g., cold spells may induce some movement, especially in waterfowl species (Elkins 1988, Ridgill & Fox 1990). In consequence, different influences of abiotic factors on the distribution and abundance patterns of seabirds among the different seasons may occur (Markones 2007).

In the present paper, we thus investigate to what degree seasonal, hydrographic and meteorological factors influence seabird abundance in the Inner German Bight (southern North Sea). We concentrate our efforts on an intensively surveyed study site at the transition between coastal and marine influences. A high level of survey effort has been carried out under variable environmental conditions. We relate key hydrographic and atmospheric parameters to bird abundance to assess which factors predominantly influence the abundance of the different seabird species during different seasons. We also investigate whether these factors may influence seabird community composition. Finally, we evaluate the consequences of our findings for seabird monitoring programs, processes of selection and delineation for marine protected areas and climate change predictions.

MATERIALS AND METHODS

Study area. The study area is a 27.8×32.8 km rectangular area located to the east of the island of Helgoland in the Inner German Bight (hereafter 'HELBOX'; Fig. 1). Both bird and environmental data were assembled for each day of ship-based observations, which covered at least 5 km^2 within the box area (5 km^2 as a minimum equals 1 h of counts at a ship speed of 9 knots and with 17 km of linear survey effort).

Bird data. Birds at sea were counted from ships, following the current international standard (Tasker et al. 1984, Camphuysen & Garthe 2004). All species were recorded within a transect strip of 300 m width set perpendicular to one or both sides of the steaming vessel. The width of 300 m was estimated according to the range-finding method of Heinemann (1981) using callipers. For swimming individuals, the transect strip was

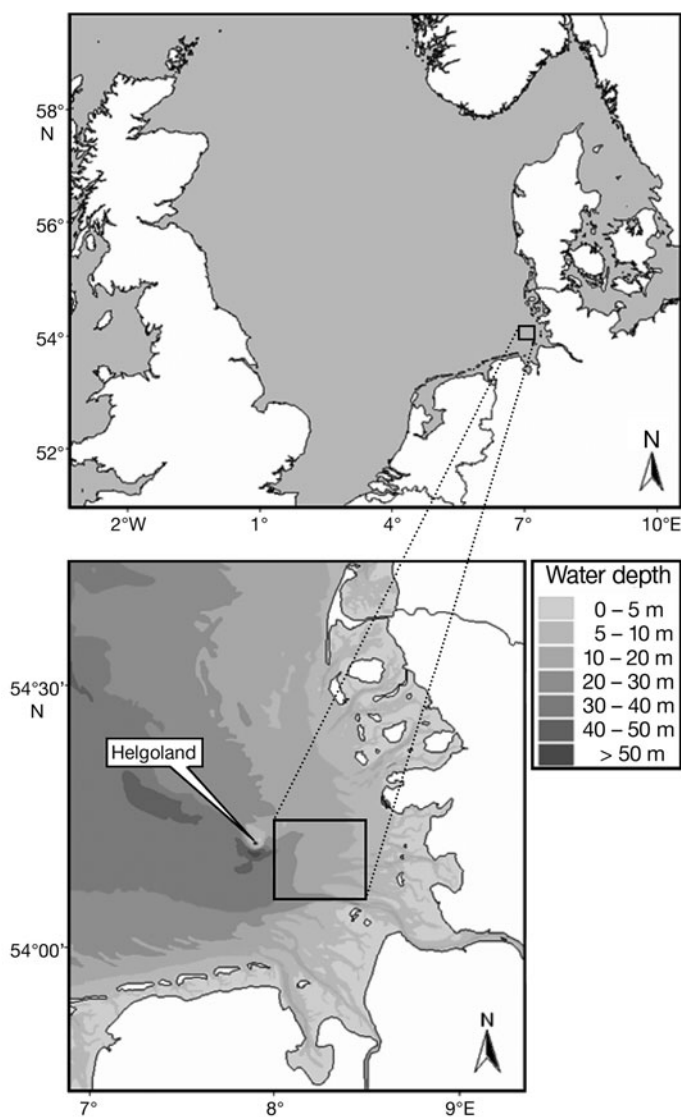


Fig. 1. Location of the study area 'HELBOX' (Helgoland box). The upper panel shows the location in the North Sea; the lower panel shows more details from the southeastern North Sea. The label 'Helgoland' represents both the island and the station 'Helgoland Roads'

subdivided into 4 bands (0 to 50, 50 to 100, 100 to 200 and 200 to 300 m) to allow for distance corrections. As flying birds move faster than the observation vessel, we used the snapshot method described by Tasker et al. (1984) to avoid overestimation of particularly mobile species. According to this technique, flying birds are, by convention, only recorded as within the transect when they fly over the area of the transect strip at the time of a snapshot count. Flying birds crossing the transect strip at other times and birds sighted outside the transect area were usually also recorded, but their numbers were not used for density calculations. During all surveys, geographic positions were automatically recorded every minute with a hand-held GPS (global positioning system)-recorder. Counts were only conducted and used for analysis when visibility was good enough to survey the entire transect area and beyond (minimum visibility: 1 km) and when other weather conditions such as wind, rain and spray did not influence the counts.

To account for birds that were overlooked, especially in the outer transect area on the water, we applied the distance sampling methodology and calculated species-specific correction factors to estimate detection probability. To take into account clustering of birds (group sizes per observation), the time unit for analysis was set at a 1 min counting interval. We applied the half-normal function with cosine adjustment using the software Distance 5.0 (Thomas et al. 2006). Only for this analysis, were data based on all records from within the German Bight (not only from the HELBOX) since 1993. As the detectability of birds on water (i.e. birds that are swimming, resting, preening, etc.) changes with wave heights and white crests on the water (Duffy 1983), correction factors were calculated separately for each sea state. Sea states are coded to describe wave height and white water conditions

(Beaufort scale; Dietrich et al. 1975). As sea state is recorded continuously during all bird counts, such a correction procedure takes into account the frequently changing conditions at sea. For species with low sample sizes and for sea states experienced rarely or with similar effects on detectability, correction factors were summarised for >1 sea state value. Common guillemot *Uria aalge* and razorbill *Alca torda* were combined because razorbill sample sizes were relatively low. Table 1 shows all correction factors applied for the analyses in the present paper. Correction factors were calculated by dividing the 300 m transect band by the estimated 'effective strip width' (in m; Buckland et al. 2001), as analysed by the software Distance 5.0. Abundances of flying birds were not corrected for distance as we assumed that, in contrast to swimming birds, all flying individuals within the area surveyed had been recorded completely.

Data on seabird abundance in the study area were analysed from the German Seabirds at Sea Database, Version 5.12, as of October 2008. In total, data for 407 d from July 1990 to May 2007 were available, summing to 4786.5 km² of survey effort (Table 2). Although days were not sampled on an exact schedule every year, data effectively covered the different years and months over the whole study period, so possible biases due to unequal distribution of observation days should have been minimised. The unit for analysing bird data was the 'day'. For each day, and separately for all species, abundance values were obtained by: (1) summing the total number counted in the transect, (2) dividing this number by the survey effort (km²), and (3) multiplying this value by the correction factor (see above). We thus obtained species-specific density values.

As the (variable) influence of abiotic parameters was much more of interest than the seasonal cycle, we chose 3 distinct 'seasons' and pooled all data within

Table 1. Correction factors calculated by distance sampling methods for birds on water for different seabird species at different sea states (Beaufort scale). See 'Materials and methods' for procedure. Correction factors in bold were used for analyses. Seasonal patterns of the species present in the study area are also given (see Fig. 2)

Species	Taxon	Seasonal pattern	Sea state						
			0–1	2	3	4–7	0–2	3–7	0–7
Red-throated diver	<i>Gavia stellata</i>	c	–	–	–	–	1.4	1.8	1.7
Northern gannet	<i>Sula bassana</i>	a	–	–	–	–	–	–	1.5
Little gull	<i>Hydrocoloeus minutus</i>	d	–	–	–	–	1.7	1.7	1.7
Black-headed gull	<i>Larus ridibundus</i>	a	1.6	1.8	1.9	2.3	–	–	1.8
Common gull	<i>Larus canus</i>	b	1.5	1.8	1.8	2.2	–	–	1.7
Lesser black-backed gull	<i>Larus fuscus</i>	a	1.4	1.5	1.6	1.8	–	–	1.6
Herring gull	<i>Larus argentatus</i>	b	1.5	1.6	1.7	2.2	–	–	1.7
Great black-backed gull	<i>Larus marinus</i>	b	–	–	–	–	1.7	1.9	1.8
Black-legged kittiwake	<i>Rissa tridactyla</i>	b	1.7	1.8	1.8	2.2	–	–	1.9
Sandwich tern	<i>Sterna sandvicensis</i>	a	–	–	–	–	1.8	1.8	1.8
Common/Arctic tern	<i>Sterna hirundo/paradisaea</i>	a	–	–	–	–	1.8	1.8	1.8
Common guillemot	<i>Uria aalge</i>	b	1.6	2.0	2.0	2.2	–	–	2.1
Razorbill	<i>Alca torda</i>	c	1.6	2.0	2.0	2.2	–	–	2.0

Table 2. Number of observation days (upper value) and survey effort (lower value, in km²) per month and year in the study area from 1990 to 2007

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1990	–	–	–	–	–	–	3	3	1	–	–	1	8
	–	–	–	–	–	–	24.4	34.5	19.4	–	–	17.1	95.4
1991	4	3	1	2	3	3	3	1	1	2	4	1	28
	43.9	35.0	08.3	19.1	34.0	47.6	30.8	21.7	05.9	17.6	37.1	08.9	309.9
1992	4	2	2	2	6	4	3	2	4	6	1	2	38
	44.8	15.4	21.0	16.4	67.4	38.8	32.7	25.3	37.5	52.0	06.8	26.6	384.7
1993	2	1	4	2	5	2	2	8	1	2	5	1	35
	23.5	08.3	43.4	29.1	62.6	16.4	32.6	93.3	08.4	28.2	55.1	9.0	409.9
1994	2	2	2	1	2	3	5	5	5	–	1	–	28
	16.3	15.4	21.3	09.5	19.4	29.1	80.3	49.0	56.3	–	9.0	–	305.6
1995	–	1	–	–	–	2	1	–	–	–	2	–	6
	–	09.2	–	–	–	24.3	08.3	–	–	–	14.4	–	56.2
1996	–	–	–	2	2	2	–	5	3	–	–	–	14
	–	–	–	16.6	20.3	21.4	–	52.9	38.2	–	–	–	149.4
1997	2	4	–	4	7	8	11	10	2	–	3	1	52
	16.3	29.7	–	29.2	75.9	71.8	135.7	112.6	19.8	–	25.1	08.5	524.6
1998	3	4	4	–	3	2	–	5	–	–	–	2	23
	25.5	32.3	38.7	–	66.5	19.5	–	51.2	–	–	–	17.9	251.6
1999	–	–	2	–	–	–	–	2	–	–	1	1	6
	–	–	16.0	–	–	–	–	92.7	–	–	08.9	08.6	126.2
2000	2	–	3	2	2	4	1	2	–	1	2	3	22
	16.8	–	24.2	26.6	26.2	44.7	06.5	17.0	–	07.8	16.3	25.0	211.1
2001	1	–	2	4	2	3	3	–	–	–	–	3	18
	08.5	–	20.7	42.2	61.8	25.4	32.7	–	–	–	–	27.9	219.2
2002	–	–	–	3	5	5	3	2	3	2	–	–	23
	–	–	–	27.5	51.6	42.9	26.0	16.6	26.6	20.6	–	–	211.8
2003	–	1	3	4	1	3	1	11	–	–	–	1	25
	–	11.0	34.5	79.4	07.7	26.0	05.9	194.4	–	–	–	8.0	366.9
2004	–	–	–	1	–	2	1	3	2	–	2	–	11
	–	–	–	12.2	–	23.7	19.5	44.7	25.3	–	36.2	–	161.6
2005	–	–	1	3	7	7	3	5	3	2	1	2	34
	–	–	07.6	29.2	93.1	109.5	50.0	90.5	50.7	38.4	08.5	18.3	495.8
2006	1	1	2	2	3	5	3	4	2	2	1	1	27
	08.8	14.8	17.1	28.7	38.3	75.0	52.8	54.0	39.6	15.2	09.1	09.8	363.2
2007	1	1	2	3	2	–	–	–	–	–	–	–	9
	07.1	15.7	31.3	49.5	39.8	–	–	–	–	–	–	–	143.4
Total	22	20	28	35	50	55	43	68	27	17	23	19	407
	211.5	186.8	284.1	415.2	664.6	616.1	538.2	950.4	327.7	179.8	226.5	185.6	4786.5

these. Seasons were defined to match the species presence in the study area (for species-specific seasons see Garthe et al. 2007). The periods of the year not covered by our analyses were eliminated, due either to insufficient sample sizes (i.e. the number of days at sea with sufficient coverage, e.g. spring) or because these were transient months associated with different 'seasons' for the different species (e.g. the second half of July partly represents the breeding period, and partly, autumn migration).

For each season, we included in the analysis those species that were present on at least 15 % of the observation days. The only exceptions were common eider

Somateria mollissima and common scoter *Melanitta nigra*, which were excluded from the analysis in winter, as the study area is located clearly outside their foraging and resting areas and recordings were only from migrating birds. For the seasonal analyses, the species analysed in detail comprised 39 % (winter), 94 % (autumn migration) and 94 % (reproductive period) of overall seabird abundance. Ignoring the 2 sea duck species mentioned above, the values increased to 96 % (winter), 98 % (autumn migration) and 99 % (reproductive period). Divers (i.e. loons *Gavia* spp.) were defined as red-throated divers *Gavia stellata*, because 93 % of all divers identified to species and registered in the

transect were of that species (69% of all divers were identified to species; $n = 363$ individuals). Common terns *Sterna hirundo* and Arctic terns *Sterna paradisaea* were pooled as common terns. A total of 57% of all common terns was identified to species ($n = 1202$ individuals). Although common terns were more numerous and made up 83% of all common terns registered in the transect and identified to species, a relatively high percentage of non-identified individuals occurred on some observation days (in contrast to the case of the divers), so that simple species allocation was not regarded as adequate. In all other cases, proportions of unidentified birds were very small and therefore negligible (0.7% of common guillemot and razorbill and 0.03% of large gulls). Scientific names of the bird species follow Bauer et al. (2005).

Environmental data. In spite of having a large set of hydrographic and meteorological parameters, only those that were considered meaningful from a seabird biology and marine ecology point of view (Table 3) were selected. Thus, e.g., precipitation and visibility

were neglected because, to the best of our knowledge, they do not generally affect seabird abundance directly. Also, strongly correlated factors were avoided, e.g. multiple measurements of the same or a similar parameter on a specific day. The variables finally selected for analysis were only weakly correlated, with a maximum Pearson correlation coefficient of 0.4 (Table 4). Furthermore, it was considered that the temporal resolution (e.g. 1 measurement per day) of some environmental parameters (e.g. air pressure) might not be appropriate, as they are fast changing. In such cases, ratios or means were calculated (see below).

Two hydrographic parameters, sea surface temperature (SST) and sea surface salinity (SSS; Table 3), were analysed from the Helgoland Roads time series (Franke et al. 2004, Wiltshire & Manly 2004) provided by the Alfred-Wegener Institute for Polar and Marine Research. These parameters were measured from a boat at a fixed place near the island of Helgoland once a day on working days. We interpolated values for days not sampled (weekends and public holidays). Helgo-

Table 3. Environmental parameters and their time scales as used in this study. The measurement frequency for each parameter is one value per day. SST: sea surface temperature; SSS: sea surface salinity; CET: Central European Time. ΔT : Temperature difference

Parameter	Unit	Explanation
SST anomaly	$^{\circ}\text{C}$	Deviance of the SST value on a specific date (e.g. 1 April 2000) from its long-term mean for that date (e.g. mean for 1 April from 1990 to 2007)
SSS anomaly	psu	Deviance of the SSS value on a specific date (e.g. 1 April 2000) from its long-term mean for that date (e.g. mean for 1 April from 1990 to 2007)
Absolute air pressure	hPa	Mean of measurements from 07:00, 14:00 and 21:00 h CET on the observation day
Preceding air pressure change	hPa	Difference between 07:00 h CET on the day before the observation day and 07:00 h CET on the observation day
Concurrent air pressure change	hPa	Difference between 07:00 and 21:00 h CET on the observation day
Wind field	–	Combination of wind direction and wind speed on the observation day For wind directions (measured at 07:00 h CET) from the sea (SW, W, NW), the Beaufort-scaled wind speeds (measured at 07:00 h CET) were taken as positive values, while for wind directions from land (N, NE, E, SE, S), the Beaufort-scaled wind speeds were multiplied by -1
ΔT : water–atmosphere	$^{\circ}\text{C}$	Difference between the SST value and the mean atmospheric temperature value on the observation day

Table 4. Cross correlations between the environmental parameters used for analysis. Correlation coefficients shown are based on Pearson correlations for the whole data set (407 observation days; see Table 1). SST: sea surface temperature; SSS: sea surface salinity. ΔT : Temperature difference

	SST anomaly	SSS anomaly	Absolute air pressure	Preceding air pressure change	Concurrent air pressure change	Wind field	ΔT : water–atmosphere
SST anomaly	–						
SSS anomaly	–0.137	–					
Absolute air pressure	0.028	0.025	–				
Preceding air pressure change	–0.073	0.118	0.404	–			
Concurrent air pressure change	–0.055	0.083	–0.117	0.147	–		
Wind field	0.005	0.055	0.024	0.130	0.120	–	
ΔT : water–atmosphere	–0.098	–0.008	0.061	0.042	0.104	0.020	–

land Roads is located only 6.5 km west of the study area. As we were not interested in the annual cycle of these parameters but rather in their deviance from the means, we calculated daily means for both, and used 'SST anomaly' and 'SSS anomaly' as the deviations from the long-term mean on the respective day. SST anomalies should indicate warmer or colder years; SSS anomalies should indicate influence of Continental Coast Water Mass (if SSS values are lower than on average) or Central North Sea Water Mass (if SSS values are higher than on average; see also Loewe et al. 2006). These different causes for changes in SST and SSS are also supported by the fact that SST and SSS were not correlated ($r = -0.003$, $df = 4187$, $p = 0.846$, Pearson correlation; data from 1 January 1990 to 31 May 2007).

Meteorological data were obtained from the German Weather Service (DWD). They were selected to reflect important atmospheric parameters possibly influencing seabird behaviour, e.g. when foraging and migrating (all times are given according to Central European Time; Table 3): (1) absolute air pressure (means of measurements from 07:00, 14:00 and 21:00 h on the observation day), (2) preceding air pressure change (from 07:00 h on the day before the observation day to 07:00 h on the observation day), (3) concurrent air pressure change (from 07:00 to 21:00 h on the observation day), (4) wind field (see below) and (5) the temperature difference between SST and the atmospheric temperature on the observation day. The last parameter was based on observations by Haney & Lee (1994), who suggested that air–sea heat flux and ocean wind fields may have a strong influence on offshore dispersal of gulls by facilitating energy-efficient flying under certain conditions. For the wind field, the selected variable includes a quantitative combination of direction and speed, scaled to highlight an onshore/offshore axis. For wind directions (measured at 07:00 h) from the sea (SW, W, NW), the Beaufort-scaled wind speeds (measured at 07:00 h) were taken as positive values, while for wind directions from land (N, NE, E, SE, S), the Beaufort-scaled wind speeds were multiplied by -1 .

Statistical analysis. The comparison of bird abundance and abiotic parameters was done on a daily basis; bird abundance was obtained from our own data set on seabirds at sea (see 'Bird data' above), and abiotic parameters were gleaned from archived materials (see 'Environmental data' above and Table 3). The relationships between bird abundance and abiotic parameters were investigated using generalised additive models (GAMs; Hastie & Tibshirani 1990, Wood 2006). Influences of the hydrographic and meteorological parameters on seabird abundance in the study area were tested separately for each species and season. GAMs with quasi-Poisson error distribution were performed

using the MGCV package (Wood 2008) of the open source software package R 2.8.1 (R Development Core Team 2008). As the data set was based on counts, the Poisson function should usually form the basis of the analysis (Zuur et al. 2007). However, to prevent over-dispersion, an underlying quasi-Poisson function was selected in the model frame. Models were selected using backward selection and exclusion of non-significant predictor variables (applying the ANOVA function with F -statistics). To avoid over-fitting of models (Meynard & Quinn 2007), only seasons with an adequate sample size were used (≥ 80 observation days), rare species were disregarded (see 'Bird data' above) and the degrees of freedom for curve smoothing were restricted to 4. Models were validated applying 10-fold cross-validations, which were repeated 10 times. We calculated the root mean-squared error of prediction (RMSEP) and the correlation between observed values and the values predicted during the cross-validation procedure (r^2) to obtain measures of model performance.

As the wind field is considered a central element responsible for the distribution of water masses and also influencing bird flight behaviour, we investigated whether onshore wind versus offshore wind conditions may lead to differences in the quantitative composition of the seabird community. Analysis was performed for winter only, as this is the period during which the least migratory movements are expected and when no birds commute between colonies and feeding grounds. We tested whether the (daily) species abundance values differed between 52 d with offshore conditions (wind from land towards the sea) and 32 d with onshore conditions. We conducted a Monte Carlo permutation test with 1000 permutations, based on a detrended correspondence analysis (DCA). A dummy variable wind (0 for onshore wind, 1 for offshore wind) was introduced and tested for significance to the quantitative species data. This test was undertaken using the package 'vegan' (Oksanen et al. 2008) in R. Significance levels were set to 0.05 for all analyses.

RESULTS

Seasonality

The species in the study area exhibited different seasonal patterns. While some species were present year-round, others occurred only at certain periods. Principally, all species can be divided into 4 groups as exemplified in Fig. 2: (a) species that occur from spring to autumn and breed on islands or along the coast near the study area, but leave the study area in winter, e.g. *Larus fuscus*; (b) species that occur year-round and breed nearby, e.g. *L. canus*; (c) species that occur from

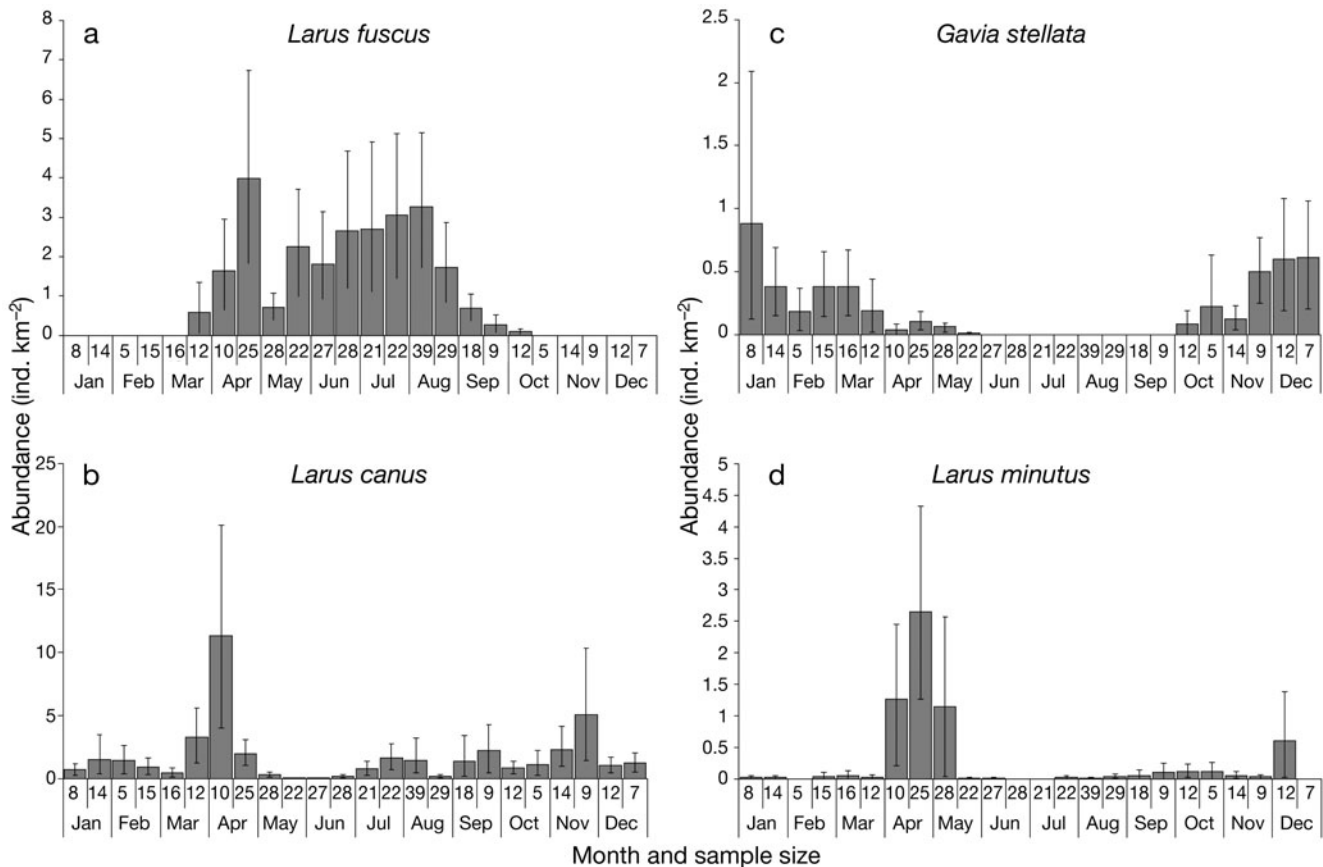


Fig. 2. Abundance patterns of 4 seabird species over the annual cycle. Each month is split into 2 halves, with the number of days from 1990 to 2007 as sample size indicated below the x-axis. Means and 95% confidence intervals are based on bootstrapping the original values 10 000 times: (a) lesser black-backed gull *Larus fuscus*, (b) common gull *L. canus*, (c) red-throated diver *Gavia stellata*, (d) little gull *L. minutus*

autumn to spring, including the winter period, but leave the area for breeding, e.g. *Gavia stellata*; and (d) species that predominantly occur during the autumn and spring migration periods and have a clear bimodal distribution, e.g. *L. minutus*.

Influence of hydrographic and meteorological parameters on seabird abundance

All 5 meteorological and 2 hydrographic parameters significantly influenced the abundance of seabird species in the study area in the southeastern North Sea, though to a different degree (Table 5). Except for the common guillemot during the reproductive period, the GAMs found at least 1 abiotic parameter explaining considerable variance in species abundance. Overall, the 2 hydrographic parameters were significant in 54% of all species/season combinations, while the 5 atmospheric parameters were significant in 44% of these combinations. The single factors that most often had a significant influence in the single models were

wind field, SST anomaly, SSS anomaly and preceding air pressure change (Table 5).

Two typical patterns are explained in more detail. Species responded differently to the wind field, with species such as the common gull *Larus canus* being significantly less abundant during onshore wind conditions, while the opposite was true for the black-legged kittiwake *Rissa tridactyla* (Fig. 3). Especially during autumn migration, but also during the 2 other periods, species were often significantly more abundant when air pressure was high and/or increased, as shown for the black-headed gull *L. ridibundus* (Fig. 4). These responses were apparent in several species.

For all models the results of the cross-validation were characterized with a low r^2 (<0.1) and a large RMSEP.

Seabird community and wind field

The quantitative composition of the seabird community in the HELBOX area differed significantly between onshore wind and offshore wind conditions in winter

Table 5. Influence of 5 atmospheric and 2 hydrographic variables on abundances of the most common seabird species in the study area based on generalised additive models. Analyses are shown for winter (November to February; n = 84 observation days; total effort = 809.9 km), autumn migration (August to September; n = 95 observation days; total effort = 1277.8 km) and the reproductive period (mid-May to mid-July; n = 99 observation days; total effort = 1189.8 km). -: non-significant results; *p < 0.05, **p < 0.01, ***p < 0.001; SST: sea surface temperature; SSS: sea surface salinity; ΔT: temperature difference

Taxon	Species presence (% of days)	Total ind. seen (n)	Deviance explained (%)	Absolute air pressure	Air pressure change Preceding	Wind field	ΔT water-atmosphere	SST anomaly	SSS anomaly
Winter									
<i>Gavia stellata</i>	67	239	17.7	-	•	-	-	-	-
<i>Hydrocoloeus minutus</i>	18	56	78.8	•	•	-	•	•	•
<i>Larus canus</i>	80	1140	31.2	-	•	•	•	•	-
<i>Larus argentatus</i>	71	914	71.5	-	•	•	•	•	-
<i>Larus marinus</i>	69	500	25.1	-	•	•	•	•	-
<i>Rissa tridactyla</i>	50	329	73.4	-	•	•	•	•	-
<i>Uria aalge</i>	63	457	47.5	-	-	-	-	-	-
<i>Alca torda</i>	17	24	14.4	-	-	-	-	-	-
Autumn migration									
<i>Larus ridibundus</i>	46	1491	69.1	•	-	•	•	•	•
<i>Larus canus</i>	56	827	29.7	•	-	-	•	•	•
<i>Larus fuscus</i>	85	1797	42.6	•	-	-	•	•	•
<i>Larus argentatus</i>	77	1685	20.1	-	-	•	•	•	•
<i>Larus marinus</i>	54	276	41.6	-	•	•	•	•	•
<i>Rissa tridactyla</i>	62	1191	65.2	-	•	•	•	•	•
<i>Sterna sandvicensis</i>	53	247	46.7	•	-	•	•	•	•
<i>Sterna hirundo/paradisaea</i>	73	692	23.8	-	-	-	-	-	-
Reproductive period									
<i>Sula bassana</i>	16	33	28.4	•	•	-	•	•	•
<i>Larus ridibundus</i>	33	129	60.2	•	•	•	•	•	•
<i>Larus canus</i>	24	173	51.7	•	•	•	•	•	•
<i>Larus fuscus</i>	93	1744	49.7	•	-	-	-	-	-
<i>Larus argentatus</i>	72	951	42.3	-	-	-	•	•	•
<i>Larus marinus</i>	24	47	55.4	-	-	-	•	•	•
<i>Rissa tridactyla</i>	60	659	12.5	-	-	-	•	•	•
<i>Sterna sandvicensis</i>	54	196	25.0	•	•	-	•	•	•
<i>Sterna hirundo/paradisaea</i>	43	214	37.1	-	-	-	-	-	-
<i>Uria aalge</i>	57	306	0	-	-	-	-	-	-

($r^2 = 0.27$, $n = 84$ d, $p = 0.033$, detrended correspondence analysis with Monte Carlo permutation). During onshore wind situations, common guillemots *Uria aalge* and black-legged kittiwakes constituted much higher percentages than during offshore wind situations, while common gulls and herring gulls *Larus argentatus* occurred in higher percentages during offshore wind situations (Fig. 5).

DISCUSSION

Influence of season and abiotic parameters

The different seabird species exhibit different seasonal patterns in the southern North Sea. Interestingly, despite substantial changes in abundances, the nature of the relations between bird abundances and abiotic parameters did not vary much between seasons. However, the highest deviances explained by the GAMs were only achieved in winter and during autumn migration. This substantiates that breeding birds are restricted in their spatial distribution, as they have to commute regularly to their breeding colonies for territorial and nest defence, incubation and chick provisioning. Thus, they are bound to stay within their foraging range, thereby possibly masking 'ideal' habitat relationships (Garthe 1997, Markones 2007).

The seabird assemblage in the study area consists mostly of highly mobile and frequently flying species. It can consequently be expected that, on the one hand, hydrographic parameters are relevant for the birds, determining the foraging habitats and options, and, on the other hand, atmospheric parameters, influencing flight conditions during foraging and migration. Flying in adverse conditions is energetically expensive, and birds may avoid extensive movements under such conditions (Haney & Lee 1994). The significant influence of air pressure was revealed in several species. High air pressure per se generally coincides with 'good weather', i.e. clear skies and good visibility, which facilitates orientation, whereas low pressure

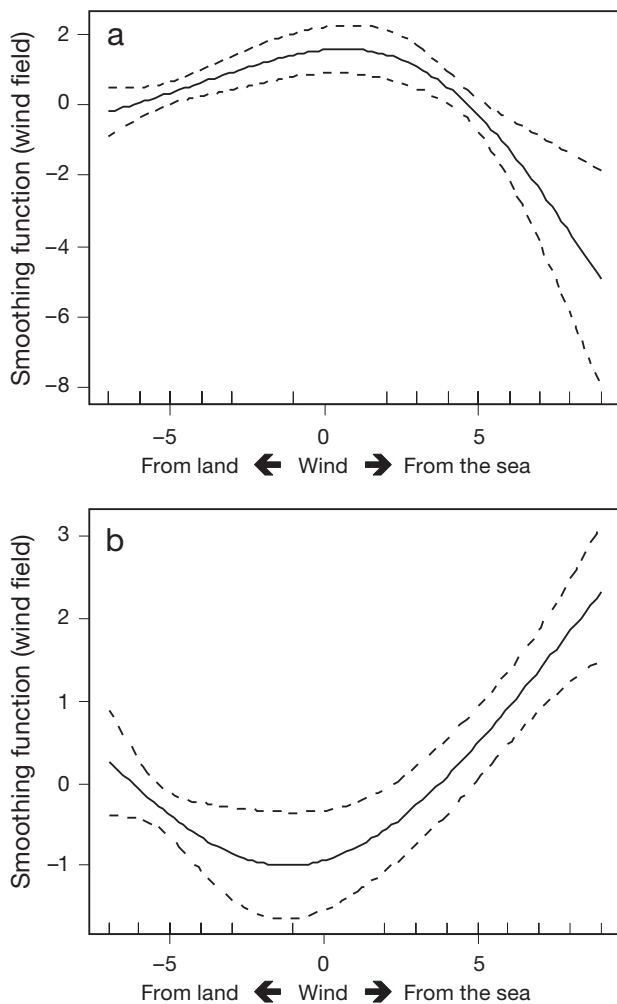


Fig. 3. Generalised additive model (GAM) smoothing curve fitted to partial effects of explanatory variables on abundance of (a) common gulls *Larus canus* and (b) black-legged kittiwakes *Rissa tridactyla* in winter. Density is represented as a function of the variable 'wind field'. Dashed lines show 95% confidence intervals around the main effects. Common gull: $F = 6.368$, $p < 0.001$; black-legged kittiwake: $F = 18.572$, $p < 0.0001$

is associated with precipitation and poor visibility. Periods of high pressure are thus often characterized by high migration intensities, though some species are observed migrating beneath, above, or even in clouds (Richardson 1990). Others migrate only when all orientation cues are available (Nilsson et al. 2006). This may hold true not only for birds on migration, but also for offshore foraging flights of coastal birds, such as gulls and terns, during the breeding season. Our variable 'wind field' is a particularly important factor for 2 reasons. First, wind speed and wind direction are known to influence or determine when and where birds are able to fly (Woodcock 1940, Manikowski 1971, Furness & Bryant 1996). Although we did not sample many days with wind speeds >7 on the Beaufort scale (i.e.

$>17 \text{ m s}^{-1}$), even wind speeds of 10 to 15 m s^{-1} may have strong effects on field metabolic rates (Gabrielsen et al. 1987) and flight performance (Spear & Ainley 1997). Strong winds also reduce foraging options (Dunn 1973, Finney et al. 1999). In the southeastern North Sea strong winds reduce commercial fishing activity and thus the availability of discards for scavenging seabirds and, for gulls, are correlated with high proportions of resting (Markones et al. 2008). Second, the wind regime steers the distribution of the water masses in the German Bight and is thus a proxy for maritime versus coastal/freshwater conditions. Consequently, this factor significantly changed the composition of the community in the study area, with pelagic species, such as common guillemot and black-legged kittiwake, dominating during sea wind conditions, while coastal species, such as common and herring gull, dominated during land wind conditions. It is somewhat surprising that the 2 hydrographic parameters were not significant in more models. A possible reason is that the Helgoland Roads station is only partly a good indicator for the study area; unfortunately, no other stations or data sets were available throughout our time series. Sea surface salinity may also be an important indicator of fronts (Skov & Prins 2001, Markones 2007), but frontal occurrence and related bird distribution are much smaller scale processes in space and time and thus were not detectable by our analysis.

Responses to the environmental parameters varied between species, but also between seasons within the same species. There was a tendency for the diving species (divers, auks) to respond to fewer atmospheric parameters than the other species that forage in flight. This would make sense as flying is much more vulnerable to adverse weather conditions than diving. On the other hand, most species showed stronger responses to atmospheric conditions during the main migration period from August through September than, e.g., during the breeding period (see the discussion above).

Methodology

There are constraints when studying seabird distributions at sea from ships in relation to environmental conditions, as adverse conditions affect the ability to detect and census certain species. We tried to circumvent this problem by only using count data when visibility was good enough for overlooking the transect area and substantially beyond, and when other weather conditions such as wind, rain and spray were not affecting the counts. We calculated sea-state-dependent correction factors to adjust counts for birds overlooked in the outer transect area. However, Ron-

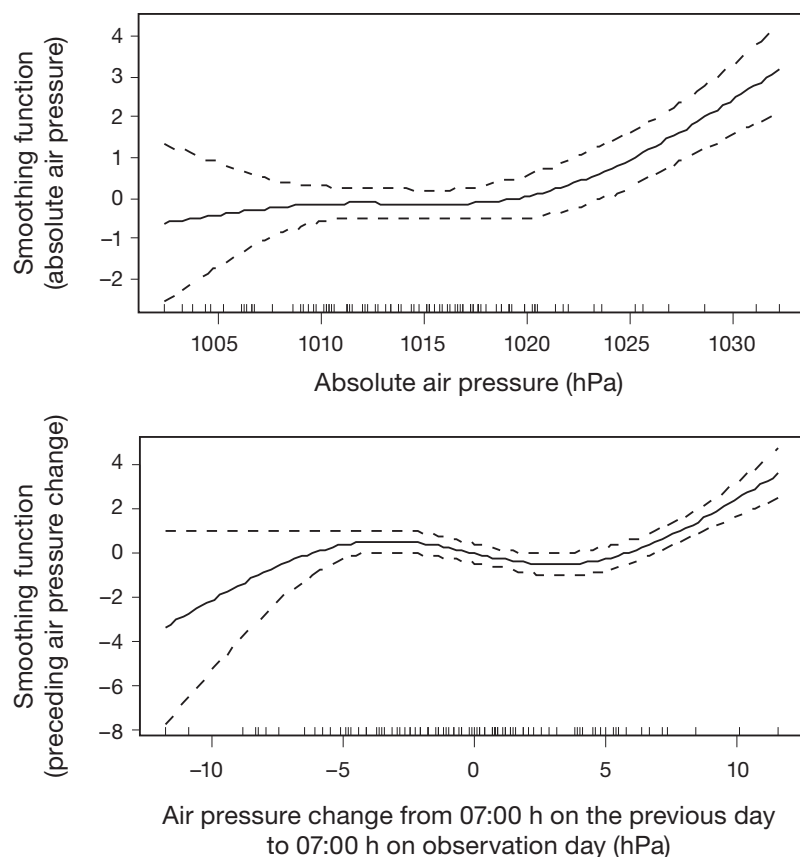


Fig. 4. Generalised additive model (GAM) smoothing curve fitted to partial effects of explanatory variables on abundance of black-headed gulls *Larus ridibundus* during autumn migration. Density is represented as a function of the variables (a) 'absolute air pressure' and (b) 'preceding air pressure change'. Dashed lines show 95% confidence intervals around the main effects. Absolute air pressure: $F = 14.702$, $p < 0.0001$; preceding air pressure change: $F = 18.309$, $p < 0.0001$

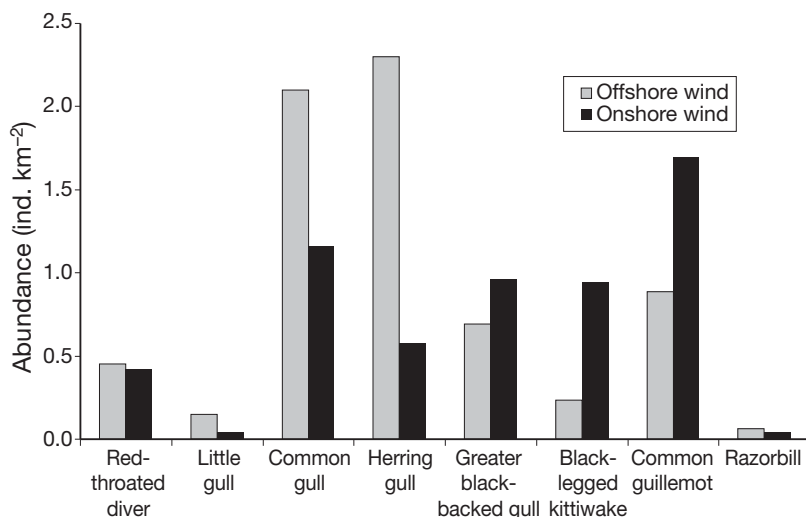


Fig. 5. Composition of the seabird community in winter during offshore and onshore wind conditions. For taxonomic names, see Table 1

coni & Burger (2009) point out that the basic assumption for this methodology, seeing all birds in front of the boat near the transect line, may be violated in some species that are difficult to detect. Fortunately, no such species (e.g. small auks) occurred in considerable quantities in our study area. Hyrenbach et al. (2007) highlight the need to test survey techniques for different survey platforms, as the latter provide different advantages and disadvantages for detecting birds. The authors also showed that cloud cover and sea state may affect census properties. We accounted for the latter effect by calculating different correction factors for different sea states.

This analysis focused on the influence of major hydrographic and atmospheric parameters on the abundance of seabird species during 3 different seasons. Such comprehensive analyses are associated with advantages and disadvantages. To establish a baseline of the influence of abiotic conditions on seabird abundance, it is advantageous to investigate the influence of these factors on all species during different periods of the annual cycle. However, sample sizes could never be large enough to test the whole suite of possible factors, interacting effects and their combinations. Thus, a pre-selection of pertinent parameters is unavoidable, in our analyses as well as in others.

Some important parameters were not included in this analysis, although they are known to affect seabird abundance and distribution patterns. Fish trawler abundance data were not available at the required temporal and spatial resolution. Previous analyses have shown that trawler distribution may influence the distribution of some seabird species feeding on discards (Camphuysen et al. 1995, Garthe 1997), but more complex analyses revealed that this factor is not related in a straightforward manner to seabird abundance and that it interacts strongly with various other factors (Markones et al. 2008). The influence of tides (Becker et al. 1993, Schwemmer & Garthe 2008) and the time of day (Burger 1983, Markones et al. 2008)

were excluded, as they are also very complex. Furthermore, in an 18 yr data set, trends in numbers over time do occur. Although such trends were detected for the German Bight (Garthe & Schwemmer 2005), they did not appear to be strong enough to affect our analyses. Generally, results of GAMs have to be treated with care, as indicated by high prediction errors and low correlation between observed values and values predicted during cross-validation procedures. Thus, they may be sufficient to explain the factors causing the observed variance in seabird abundance, but not to enable predictions. Further species-specific analyses would be required focussing on certain parameters in more detail.

Implications for monitoring programmes, marine protected area delineation and climate change predictions

The findings from our analyses have some strong implications for other issues. First, seabird at sea monitoring programmes need to take different weather scenarios into account to obtain the full picture, not only patterns from high-pressure, low-wind scenarios. This is particularly relevant for aerial surveys that can only be conducted when the sea state is very low, as birds otherwise cannot be distinguished from wave crests (Camphuysen et al. 2004). Such conditions often occur during passages of (ridges of) high pressure systems, often in combination with easterly winds, that in turn enhance the abundance of coastal species, such as black-headed gulls and common gulls, and may also trigger migration (Hüppop et al. 2006). Furthermore, it needs to be considered how representative such surveys are, especially for certain species that respond strongly to atmospheric parameters.

Similar implications hold true for the identification and delineation of marine protected areas, especially those designated for seabirds that are not related to fixed bottom structures but to hydrographic features such as water masses and fronts. The preferred habitats of such species vary in location and extent with changing hydrographic and meteorological parameters (Markones 2007); thus, habitat models need to be incorporated into recommendations for locations of protected areas (Louzao et al. 2006). Protected areas for seabirds in the Exclusive Economic Zone of Germany have recently been designated, as demanded by the EU Birds Directive (Garthe 2006), but such approaches assume that the distribution of birds does not change over time. Changes in seabird abundance and distribution may, however, occur as a consequence of substantial changes in the North Sea ecosystem (Beaugrand 2004, Edwards & Richardson 2004).

Finally, statistical models such as those developed in the present paper will enable predictions, for example on the consequences of climate change. Scenarios will consider future changes in environmental parameters, such as wind fields, pressure systems and SST (Christensen et al. 2007). From the data shown here we can expect substantial effects of future climatic changes on the composition of the seabird community in the southern North Sea, due to the link between relevant environmental parameters and seabird distribution. This prediction is further supported by the fact that climatic and hydrographic parameters are known to significantly affect seabird demography (Sandvik et al. 2008).

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Individual migratory schedules and wintering areas of northern gannets

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ABSTRACT: Individual migratory schedules and wintering areas of northern gannets *Morus bassanus* were studied over 2 consecutive winters by deploying geolocation data loggers on breeding adults from the Bass Rock, UK. Northern gannets attended the breeding colony on Bass Rock until between 24 September and 16 October (median: 5 October). Afterwards, individual birds engaged in different migratory behaviour. Of the 22 birds tracked until at least December, 18% wintered in the North Sea and the English Channel, 27% in the Bay of Biscay and the Celtic Sea, 9% in the Mediterranean Sea and 45% off West Africa. Individual winter home ranges as measured by the 75% kernel density contours varied between 8100 and 308 500 km² (mean = 134 000 km²). Several northern gannets migrated northwards from Bass Rock after leaving the colony for a stay of a few days to a few weeks, independent of whether they migrated to Africa or other southern areas later. Birds wintering off West Africa migrated to their wintering areas mostly within 3 to 5 wk, usually starting between early and late October. Most of these birds stayed off West Africa for a period of about 3 mo, where they remained in a relatively restricted area. Return migration was initiated between the end of January and mid-February, and took about as long as autumn migration. We conclude that individual gannets display very variable migratory behaviours, with discrete winter home ranges, and we infer that the migration habits of gannets may be changing in response to human impacts on marine ecosystems.

KEY WORDS: Seabird · Migration · Winter · Geolocation · Home range · Fisheries

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INTRODUCTION

Bird migration is a well-known and widespread phenomenon occurring on all continents and involving most bird taxa (Berthold 2001). While passerine and shorebird species perform well-defined migrations from distinct breeding areas to wintering areas, such migration habits are less obvious for many seabirds. Studying migration and winter distribution in seabirds is difficult, as these phenomena take place at sea and often involve huge distances, and are logistically very challenging. Most information on seabird migration has so far been based on ring recoveries and thus mainly on land-based recoveries of dead birds, or on

ship-based surveys with mostly patchy survey effort. Ring recoveries give a valuable overview of the migration of species, but suffer from strongly varying spatial and temporal effort during re-sightings. Most ring recoveries originate from dead birds, informing us of the places where the birds died, rather than where they were living successfully. Recoveries may also be from places where the carcasses have been washed ashore and not necessarily where the birds died. Systematic studies of coastal seabird migration ('sea-watching'; e.g. Camphuysen & van Dijk 1983) and seabirds at sea censuses (e.g. Tasker et al. 1984) tend to give a biased pattern of the migratory behaviour because observation effort cannot be kept similar over

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vast areas, especially in the open sea, and seawatching data may be very weather dependent. Furthermore, the status and origin of individuals cannot be assessed, which could mean that birds found at sea in winter could breed in any colony of the respective species. Recent studies using data loggers have provided new insights into the migratory behaviour of large- and medium-sized seabirds such as penguins (e.g. Wilson et al. 1998), albatrosses (e.g. Grémillet et al. 2000, Phillips et al. 2005), shags (Daunt et al. 2006), shearwaters (Shaffer et al. 2006), petrels (Phillips et al. 2006, Rayner et al. 2008) and skuas (Phillips et al. 2007). The advantages of these devices is that geographic positions and behavioural parameters can be obtained without the need to watch the birds directly. Such devices have also substantially increased our knowledge on the individual behaviour of birds. Grémillet et al. (2000) and Weimerskirch & Wilson (2000) found that albatrosses may exhibit distinct home range preferences during the non-breeding seasons that may or may not overlap with those of other individuals. Phillips et al. (2005) determined a high degree of site fidelity in grey-headed albatrosses *Thalassarche chrysostoma*, thus confirming winter site philopatry. Likewise, at much smaller spatial scales, consistent individual preferences for specific foraging areas or departure directions were found for black-legged kittiwakes *Rissa tridactyla* (Irons 1998) and northern gannets *Morus bassanus* (Hamer et al. 2001) during the breeding season. In Cory's shearwaters *Calonectris diomedea*, breeding populations clearly differed in their preference amongst their 3 major wintering areas, but showed substantial mixing (González-Solís et al. 2007).

Northern gannets are long-lived seabirds for which distribution and migratory movements have been documented from different data sources. Ring recoveries indicate that European adult northern gannets winter within a range from the North Sea, close to their main breeding sites, to southern Europe, with a high proportion of ring recoveries in winter in the North Sea, Celtic Sea and Bay of Biscay (Wernham et al. 2002). The Mediterranean Sea is also visited regularly in autumn and winter (Nelson 2002). Seawatching studies have revealed seasonal patterns in migratory and local movements of gannets at a few, selected coastal sites. These migratory patterns show periods of high migration intensity in autumn and spring and much smaller movements at other times of the year (Camphuysen & van Dijk 1983), suggesting that migration is concentrated in certain periods of the year, but also that it varies over a few weeks among individuals and between years. Line transect surveys of seabird densities at sea have described the distribution of gannets over large areas of NW Europe, with particular focus on the

North Sea (Stone et al. 1995). These at-sea surveys demonstrate that adult gannets occur regularly in winter in the North Sea (e.g. Tasker et al. 1985), but also on the small continental shelf off (North-) West Africa (Camphuysen & van der Meer 2005). Distribution patterns in the North Sea suggest alternative migratory routes in autumn and spring (Tasker et al. 1985). From observations in their principal North Sea breeding colony, the Bass Rock, Nelson (2002) found that northern gannets depart from late October to mid-November (Nelson 2002) and return there 'over a short period in mid-March' (J. Nelson pers. comm. in Tasker et al. 1985), although some individuals may return as early as January (Nelson 2002). The mean laying date is around mid-April, incubating takes about 6 wk, and chick-rearing, 13 wk (Nelson 2002).

Whilst data from ringing recoveries and at-sea surveys have provided useful insights into the winter distribution of gannets, a detailed understanding of individual migration and wintering strategies can only be achieved by attaching data loggers to individual birds over the non-breeding period. The wide range of wintering areas suggests that adult individuals show differences in their wintering areas and movements even when originating from the same breeding colony. We thus hypothesised that northern gannets from Bass Rock: (1) use different sea areas in winter, (2) spend the winter in rather restricted individual areas instead of migrating larger distances, and (3) exhibit individual routes and timing of migration. We investigated these hypotheses by deploying miniaturised electronic data loggers on chick-rearing adult gannets late in the breeding period at Bass Rock. Loggers were recovered early in the subsequent breeding season, yielding detailed information on individual over-winter movements. We discuss why gannets chose different wintering areas and how these are related to natural and anthropogenic variables.

MATERIALS AND METHODS

Data logger description. To study the movements over the non-breeding period, we deployed geolocation data loggers (GeoLT; Earth & Ocean Technologies) on breeding adult northern gannets *Morus bassanus* from Bass Rock. The device was housed in a pressure-tight, seawater-resistant casing (diameter: 14 mm; length: 45 mm; weight: 8.2 g, equivalent to ca. 0.3% of the bird body mass) and attached to a custom-built leg band. Times of dawn and dusk were determined from a light sensor, allowing geographic position to be calculated from day length and time of local midday and midnight (e.g. Wilson et al. 1992, Hill 1994, Ekstrom 2004). The device's maximum sensitiv-

ity was optimized for wavelengths penetrating deepest into clear coastal water, which minimizes the influence of submergence or atmospheric conditions, such as clouds or dust. Light levels were measured every 30 s, allowing the device to operate for 1 yr while providing 2 positional fixes per day. In addition to the light measurement, the GeoLT recorded ambient temperatures, (every 120 s) throughout deployment.

Data logger deployment and working period. Chick-rearing adult northern gannets on Bass Rock, Firth of Forth, Scotland (56.078° N, 2.639° W) were equipped with geolocation loggers over 2 winter seasons; 15 devices were deployed in August 2002, and 26 devices were deployed on different individuals in August 2003. Of these, 13 were retrieved in April and May 2003 (first season), and 21 in April and May 2004 (second season). Tags were only recovered in accessible areas of the colony, but this allowed a high recovery rate, because almost all birds that were re-trapped nested at the same site in successive seasons (see Nelson 2002 for nest site fidelity).

Not all of the 34 loggers recovered functioned throughout the whole period of deployment. For both years combined, 65, 32 and 18 % of the devices worked until 30 November, 31 January and 31 March, respectively.

For all birds recaptured after the second season, sex was determined from blood samples using standard molecular methods (Griffiths et al. 1998).

Data logger analysis. The light data were analysed using MultiTrace Geolocation from Jensen Software Systems. Light levels were calibrated for sunrise and sunset from known locations (colony) and then applied to the whole dataset. Since our focus was on migratory movements rather than at-colony activity, analysis was restricted to the period from colony departure to colony return. Colony attendance was derived from logger temperature profiles, since they differ between birds on land and those in air or on water (for details see e.g. Wilson et al. 1995, Garthe et al. 2003).

Conventional geolocation analysis by light curves is hampered by inaccuracy of latitude estimation during equinoxes (e.g. Wilson et al. 1992, Hill 1994), such that reliable position determination during these periods is not directly possible. Also, latitude estimates are usually less accurate than longitude estimates. The achievable accuracy of this technique essentially depends on season and actual latitude and lies, for flying seabirds, in the order of 200 to 400 km (Phillips et al. 2004, Shaffer et al. 2005). To improve or generate latitude estimates we compared logger-measured sea surface temperatures (SSTs) with remotely sensed satellite SSTs using methods described by Teo et al. (2004) that have been validated for applications on

seabirds (Shaffer et al. 2005). These methods work well in areas featuring north–south temperature gradients. Using these procedures, many positions from the equinox period were recovered. Furthermore, positions from other periods of the year were evaluated as well, and SST-corrected positions were taken where appropriate. The method of SST correction worked well in all areas except off West Africa due to strong east–west temperature gradients on the narrow continental shelf. In these cases, the original latitude values were retained. Furthermore, we filtered all datasets by excluding all positions that were >700 km apart from the previous position based on the average flight speed of long-distance gannet flights of 58.4 km h⁻¹ (Garthe et al. 2007) and unpublished data showing that our birds flew during <50 % of the 24 h day. As latitude values vary more than longitude values, even after the correction procedures mentioned above (the present analysis), we smoothed latitude values (see e.g. Pütz 2002) for migration and home range analysis (see below) by averaging data over 5 consecutive measurements. The 5 positions were weighted by a ratio of 3:2:1 for the current:last/next:previous-to-last/subsequent-to-next positions, respectively, to balance between the characteristics of the current day and possible improvements of the location by the adjacent measurements.

Latitude was chosen as the best indicator of migratory movements, since all birds migrated more or less due south. A smoothed latitude value was determined for each bird, for each 5 d period from the moment of colony departure until colony return or logger failure.

December was chosen as the most suitable time for 'winter', as basically all larger scale movements of gannets had ceased by the end of November and sample sizes decreased over time due to logger failures. Mean winter region position was defined as the mean of all locations obtained during the period 1 to 31 December ($n = 22$ individuals). We also calculated winter home ranges for each of the birds that yielded at least 40 positions from 1 to 31 December ($n = 18$ individuals). This number of positions was chosen both to cover the major part of the month and to guarantee a good sample size for each of the birds, but also to include some birds where the logger stopped working in late December. Because of the low accuracy of the positional calculations, we decided to use the 75 % fixed kernel density for all positions in that period, using the Animal Movement Extension for ArcView (Hooge & Eichenlaub 1997). Data were normalised between birds by always taking the first 40 positions in December of each individual for which these were available. Cell size for home range analysis was 10 km. We used the ad hoc calculation of a kernel smoothing parameter provided by the Animal Movement Extension, as rec-

ommended by Hooge & Eichenlaub (1997). We also compared the individual home range with the combined home ranges for all 18 birds.

Generalised linear models (GLMs) were run to test for differences in direct distances from colony location to mean winter region position between years and sexes, as well as for home range sizes between winter regions using R 2.7.1 (R Development Core Team 2008).

RESULTS

Device effects

Recovery rates of devices from northern gannets *Morus bassanus* after 3 quarters of a year were very high (87% after the first winter and 81% after the second winter), despite difficulties of landing on Bass Rock, which limited our search effort. Furthermore, these return rates were likely underestimates, as only a small part of the colony could be checked for birds with loggers, and at any single visit we could expect about half of the birds with loggers to be at sea rather than at the nest. Re-sightings were made only during 5 visits, each lasting 1 to 3 h, in the early summers of 2003 and 2004. All birds with loggers that were seen breeding in the season after first capture were recaptured easily, and only 1 bird showed minor abrasions on the foot/leg where the device was attached. Only 1 gannet equipped with a logger was seen in the colony but not recaptured, and that individual was the only one (out of 35 known to be alive; 2.9%) that was not breeding in the second season and did not seem to be holding a nest site. There is no reason to think that this bird was not breeding due to the presence of the logger, as a non-breeding rate of 2.9% is low compared to rates found among many long-lived seabirds (Catry et al. 1998). All 34 birds that were recaptured had an egg or a chick in the nest when recaptured. These recapture rates are substantially lower than the average annual adult survival rate. It cannot be resolved at this stage whether this is due to overlooking birds, due to device loss, due to relocation of nest sites of birds, or possibly due to elevated mortality. However, complete loss of a device plus attachment has been confirmed for an identical attachment procedure from 1 bird on Helgoland (in 2009; S. Garthe unpubl. data).

Wintering areas and winter home ranges

Northern gannets demonstrated individual variability in wintering areas. A few birds stayed in the North Sea, but most of them travelled further south (Table 1), with several birds going as far south as West Africa or as far east as the Mediterranean Sea (Fig. 1). From the 22 birds for which the winter region could be determined, 18% wintered in the North Sea and the English Channel; 27%, in the Bay of Biscay and the Celtic Sea; 9%, in the Mediterranean Sea; and 45%, off West Africa (Table 1). Northern gannets travelled highly variable distances between colony and winter area (Table 1). The shortest direct distance between Bass Rock and the mean winter region position of a bird was 343 km and the largest distance was 4654 km, with mean (\pm SD) distances of 2171 ± 1722 km in 2002/2003 ($n = 10$) and 2766 ± 1658 km in 2003/2004 ($n = 12$). Differences between the 2 years were not significant (GLM; $t = 0.814$, $p = 0.425$). Although there was a tendency for females to winter further away from the breeding colony than males (mean \pm SD: male = 2485 ± 1931 km, $n = 6$; females = 3024 ± 1629 km, $n = 5$; see also Table 1), the difference could not be established statistically (GLM; $t = -0.487$, $n = 11$, $p = 0.638$), possibly due to the small sample size.

Table 1. *Morus bassanus*. Winter region, direct distance from colony to mean winter region position (km) winter home range size (as measured by the 75% kernel density contour line) and sex of individual northern gannets equipped with geolocation data loggers on Bass Rock over the winter periods 2002/2003 and 2003/2004

Year	Bird ID	Sex	Winter region	Distance to winter region (km)	Winter range (km ²)
2002/2003	18	?	West Africa	4654	288 300
	19	?	Bay of Biscay	773	–
	20	?	Bay of Biscay	994	91 800
	24	?	Mediterranean Sea	2244	13 800
	25	?	North Sea	387	–
	26	?	North Sea	477	69 500
	27	?	Mediterranean Sea	2422	36 400
	28	?	West Africa	4371	116 100
	29	?	West Africa	4378	31 900
	30	?	Bay of Biscay	1014	81 400
2003/2004	03	?	Bay of Biscay	1044	139 700
	35	Male	West Africa	3167	55 500
	36	Female	West Africa	4467	70 000
	37	Male	North Sea	343	308 500
	42	Male	West Africa	4521	–
	43	Female	West Africa	3941	82 400
	45	Male	North Sea	608	8 100
	47	?	West Africa	4288	62 400
	48	Female	Bay of Biscay	1474	225 900
	49	Male	West Africa	3824	–
	50	Female	West Africa	4196	167 800
	51	Male	Bay of Biscay	1324	132 600
All birds					1 619 000

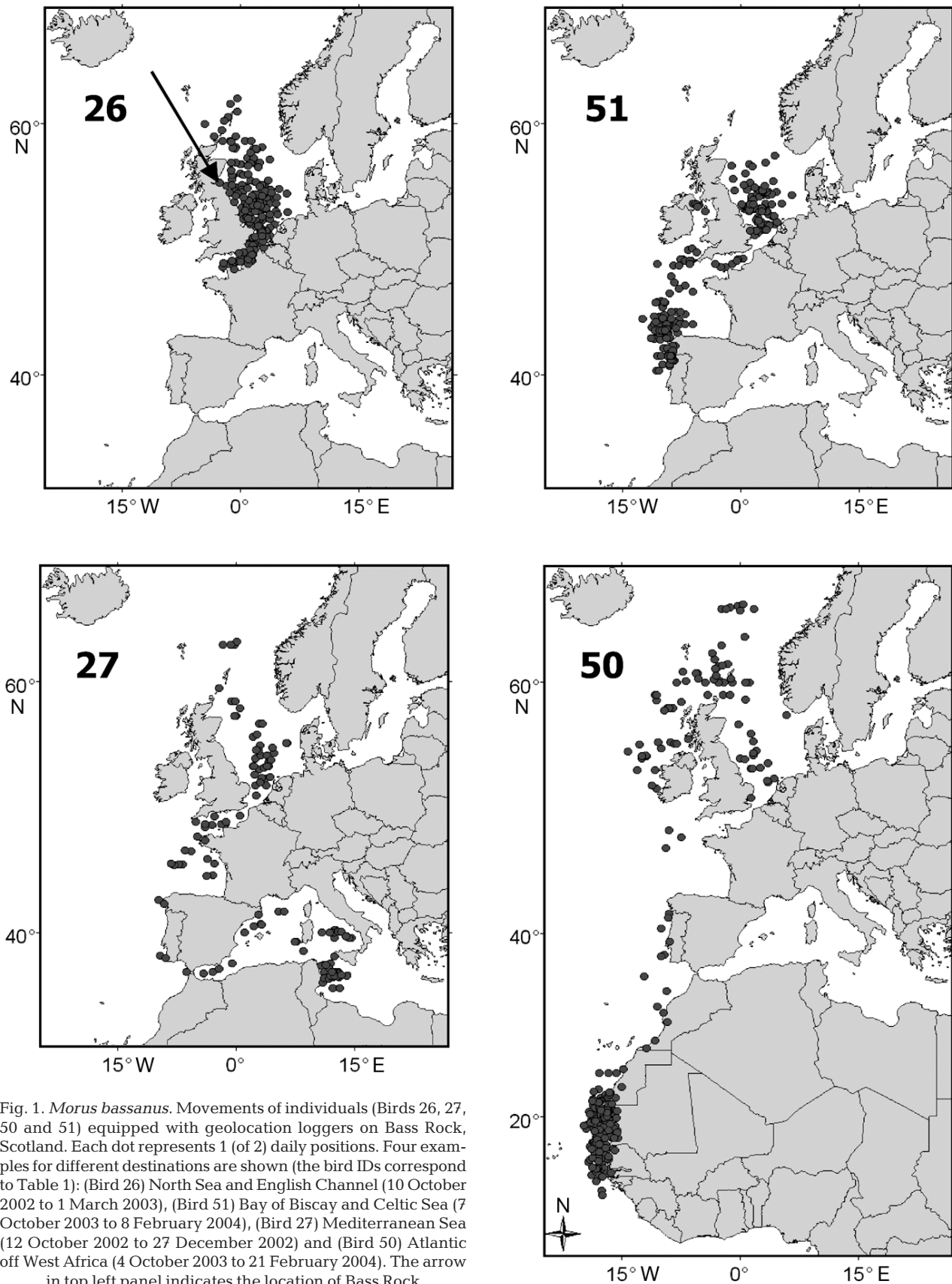


Fig. 1. *Morus bassanus*. Movements of individuals (Birds 26, 27, 50 and 51) equipped with geolocation loggers on Bass Rock, Scotland. Each dot represents 1 (of 2) daily positions. Four examples for different destinations are shown (the bird IDs correspond to Table 1): (Bird 26) North Sea and English Channel (10 October 2002 to 1 March 2003), (Bird 51) Bay of Biscay and Celtic Sea (7 October 2003 to 8 February 2004), (Bird 27) Mediterranean Sea (12 October 2002 to 27 December 2002) and (Bird 50) Atlantic off West Africa (4 October 2003 to 21 February 2004). The arrow in top left panel indicates the location of Bass Rock

Individual winter home ranges as measured by the 75% kernel density contour line varied between 8100 and 308 500 km², with a mean (\pm SD) of 134 000 \pm 87 800 km² (Table 1). Differences between the different winter regions (Table 2) were not significant (GLM; $t = -0.122$, $p = 0.905$), likely because of the small sample sizes. Individual home ranges of the 18 birds comprised $6.8 \pm 5.4\%$ (range: 0.5 to 19.1%) of the overall area of the 18 birds combined. This range is reduced to 0.1 to 4% when considering the whole biogeographic sea area from the North Sea to West Africa that is visited by the birds on migration and in winter.

Migratory schedule and migratory routes

Northern gannets attended the breeding colony on Bass Rock until between 24 September and 16 October ($n = 24$, median: 5 October). Medians differed slightly between autumn 2002 (7 October, $n = 10$) and autumn 2003 (3 to 4 October, $n = 14$). Afterwards, individual birds engaged in different migratory behaviours. Birds that migrated south started their main migration on different dates (Fig. 2). Birds that were in the Bay of Biscay region in December showed variable approaches to the area, with one bird going to the northern North Sea first and another bird moving first to the more southerly Iberian Peninsula (as early as October). Birds wintering off West Africa migrated to their wintering areas mostly within 3 to 5 wk, usually starting between early and late October (Fig. 2). Most of these birds stayed off West Africa for a period of about 3 mo and remained in a relatively restricted area. Return migration was initiated between the end of January and mid-February and took about as long as autumn migration (Fig. 2). There was not much variation in the timing when birds returned from the different winter regions: 2 March for 1 bird from the North Sea, 9 and 12 March for 2 birds from the Bay of Biscay, and 4, 6 and 15 March for 3 birds from West Africa.

Several northern gannets migrated northwards from Bass Rock after leaving the colony to stay in the northern North Sea and Norwegian Sea for a few days to a few weeks, independent of whether they migrated to Africa or other southern areas later (Fig. 2). Similarly, in spring, most birds with functioning loggers migrated to more northerly latitudes than their colony

before returning to breed (Fig. 2). Of the 20 birds that migrated to West Africa, the Mediterranean Sea and the Bay of Biscay/Celtic Sea, 12 left the North Sea through the English Channel, while the remaining 8 migrated through the seas west of Scotland. In spring, 3 of the 9 gannets with functioning loggers came through the English Channel and the other 6 flew along the west coast of Scotland. Looking at the 9 individuals for which both periods could be tracked, individual responses are apparent: 2 birds using the channel in autumn also used the channel in spring; 3 birds using the area west of Scotland used the same area in spring; 1 bird flying south west of Scotland returned north through the channel, and the remaining 3 birds were birds that left the North Sea through the channel and came back west/north of Scotland.

DISCUSSION

Methodology

The method of geolocation involves relatively high inaccuracies compared to satellite telemetry and GPS logger technology, with lower errors for non-volant species (Wilson et al. 2002). Pütz et al. (1998) calcu-

Table 2. *Morus bassanus*. Sizes of winter home ranges per winter region. See Table 1 for data on individual birds; n: no of birds

Wintering region	n	Mean (km ²)	SD (km ²)	Minimum (km ²)	Maximum (km ²)
North Sea/English Channel	3	128 700	158 700	8 100	308 500
Bay of Biscay/Celtic Sea	5	134 300	57 100	81 400	225 900
Mediterranean Sea	2	25 100	16 000	13 800	36 400
West Africa	8	109 300	83 500	31 900	288 300

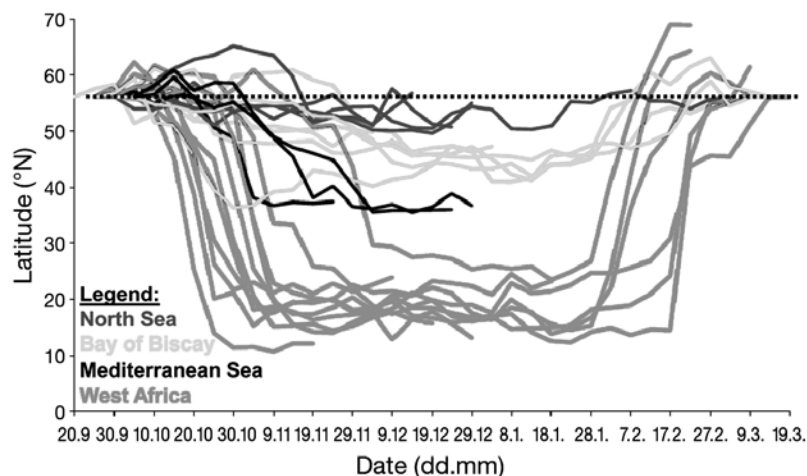


Fig. 2. *Morus bassanus*. Timing of movements of individuals showing smoothed mean latitude for each bird during standardized 5 d periods. The dotted line indicates latitude of the Bass Rock colony

lated an error of 31.3 ± 30.6 km when comparing light-based locations and satellite-derived locations for king penguins *Aptenodytes patagonicus*. Phillips et al. (2004) determined, for black-browed albatrosses *Thalassarche melanophrys*, an average error without data smoothing of 186 ± 114 km for trials on birds and 85 ± 47 km for static trials. Shaffer et al. (2005) found even higher errors working with 2 albatross species in the North Pacific. The mean (\pm SD) difference between light-based location and satellite-based location was 400 ± 298 km. Errors in geolocation positions were reduced to 202 ± 171 km when light-based longitude and SST-based latitude were combined to establish locations (Shaffer et al. 2005). Large inaccuracies were also visible in our raw data sets, and both SST correction and data filtering are likely to have improved our position estimates based on findings from Phillips et al. (2004) and Shaffer et al. (2005).

Winter distribution and home ranges

The large number of birds migrating from Bass Rock to West Africa is surprising, especially when compared to the very small number of ring recoveries from that part of the world (Nelson 2002, Wanless 2002), although numerous recoveries exist for other species from the area (Wernham et al. 2002). This also indicates possible changes in the wintering behaviour of Bass Rock gannets *Morus bassanus*. Although our sample sizes are relatively small, the similar results in both study years support the conclusion that these patterns are representative of the large breeding colony on Bass Rock in recent years.

Despite some local movements, most individuals spent the winter period in relatively small, well-defined winter home ranges. This was particularly true for the period from early December to mid-January. In November some birds were still migrating (Fig. 2) (but at a slower rate than in October), while several birds had already reached their final destination. These birds might have sampled other areas for possible wintering. The wide range of distinct wintering regions and the relatively small winter home ranges in comparison to the overall wintering area, confirm our first 2 hypotheses: that different gannets migrate to different areas and tend to stay in discrete wintering areas.

Migration

Gannets that migrated furthest showed a general pattern of flying from slightly north of 50°N latitude to $20\text{--}23^\circ\text{N}$ latitude fairly quickly and at a relatively constant speed of 250 to 450 km d^{-1} . However, the timing

of this migration varied between individuals by almost a month. Individuals also exhibited individual migratory routes. Several individuals flew north for variable periods after leaving Bass Rock, while others departed south. Also, while birds tended to leave the North Sea through the English Channel (rather than west of Scotland) and tended to return through the seas off western Scotland (rather than through the English Channel), an observation that is confirmed from distribution patterns of birds at sea (Tasker et al. 1985) and from seawatching studies in the Netherlands (Camphuysen & van Dijk 1983), there were individual differences that were independent of their final wintering area. These findings all confirm our third hypothesis that routes and timing of migrations vary among individuals.

Distribution, prey resources and anthropogenic pressures

The winter distribution of gannets as well as their migratory corridors match well with areas of high productivity (e.g. Mann & Lazier 2006). The area used most commonly in our study is a near-coastal area off (North-)West Africa. This area is part of a large upwelling zone extending along the coast of NW Africa (van Camp et al. 1991, Nykjær & van Camp 1994). As large pelagic fish comprise the most important prey of gannets (Nelson 2002), it is of little surprise that the shelf sea and the shelf break areas off West Africa may offer a rich food supply of such energy-rich fish. This is also apparent due to the occurrence of intense pelagic fisheries off West Africa, targeting *Sardinella aurita*, *Sardinella maderensis*, *Sardina pilchardus*, *Scomber japonicus* and *Trachurus trecae* (ter Hofstede & Dickey-Collas 2006).

Earlier studies have shown that gannets may also use fishery discards to a substantial degree (e.g. Tasker et al. 1987, Camphuysen et al. 1995, Käkälä et al. 2007). The availability of discards may thus be another important factor influencing their winter distribution. Crane (2005) investigated how much food may be made available to seabirds as fishery discards in different regions, mainly from demersal fisheries. He reviewed the literature and analysed the Food and Agricultural Organisation's database to find information on discard rates in different fisheries and regions. Overlaying our winter regions with the discard data shown in Crane (2005) revealed that remarkably high proportions of northern gannets stayed in areas of elevated discard rates. This is strongly corroborated by the observations of Camphuysen & van der Meer (2005), who found that 88.8% of the northern gannets wintering off the western Sahara and Mauritania were

associated with commercial fishing vessels. West African fisheries have developed strongly over the last 2 decades and produce substantial amounts of discards (Kaczynski & Fluharty 2002, Alder & Sumaila 2004, Crane 2005).

Altogether, these data and observations suggest that areas outside the North Sea offer sufficient food for northern gannets from natural and anthropogenic sources. If, as a consequence of the current high fishing effort, fish stocks off West Africa become depleted, it is to be expected that the attractiveness of the West African winter region for gannets may diminish in the future—directly by overfishing of pelagic fish stocks and indirectly by reducing the amounts of discards due to regulations that reduce fishing effort.

Perspectives

Further investigations are needed to elucidate the advantages and disadvantages for gannets to stay close to their breeding site (i.e. in the North Sea) or to undertake migratory movements to distant wintering areas. This may include comparisons of diets (e.g. Phillips et al. 2007), activity rhythms (e.g. Daunt et al. 2006), and food availability (e.g. Hamer et al. 2001). Additionally, studies of individual consistency in migratory schedules and wintering areas would help to further unravel the migratory strategies of northern gannets.

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Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California

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ABSTRACT: When 2 closely related species co-occur, each exhibiting sex-specific differences in size, resource partitioning is expected. We studied sex-specific foraging behaviour of 2 sympatric seabird species in the Gulf of California to disentangle the respective influence of species and sex, but also mass and size of individuals, on observed foraging behaviour. We used highly accurate data loggers to study movements, diving behaviour and activity of brown and blue-footed boobies rearing young chicks. Interspecific differences were limited; brown boobies had longer foraging trips and spent less time on the water than blue-footed boobies. The major differences observed were sex-specific; females of each species tended to have longer foraging trips, foraged farther from the colony, flew greater distances and had larger zones of area-restricted search. These sex-specific differences were more prominent in brown than in blue-footed boobies. Diet and stable isotope analyses showed that, during the study period, both species fed mainly on sardines, at similar trophic levels and in similar zones; outside the breeding season, the carbon and nitrogen signatures from feathers were also similar on average. In these sympatric species that feed on a superabundant prey, sex-specific differences appear to have a greater role than species-specific differences. We suggest that sex-specific differences may be mainly related to breeding involvement, as males are more involved in nest attendance and defence and females are greater provisioners. However, we show that several sex-specific differences in observed foraging behaviour were partly or totally explained by body size (flight speeds, foraging range, flapping frequency) or by body mass (depths attained during diving, duration of dives), which are parameters influenced by biomechanical constraints such as flight and diving.

KEY WORDS: Accelerometers · GPS tracking · *Sula leucogaster* · *Sula nebouxii* · Area-restricted search · Fractal landscape method · Diet · Isotopes

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INTRODUCTION

Understanding how closely related species can coexist has been a long-lasting subject of research (e.g. Pianka 1981, Ricklefs 1990). When species breed sym-

patrically, niche differentiation is expected at equilibrium. Partitioning of food sources can occur in sympatric species by differential selection of foraging habitat, foraging strategy or prey choice. Body size differences between species may also favour niche dif-

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ferentiation (Bowers & Smith 1979, Clutton-Brock et al. 1987, Andersson 1994, LeBoeuf et al. 2000). Within species, body size differences between sexes are common, and the extent of the difference in size varies extensively according to the taxa considered (Andersson 1994). Three major hypotheses have been proposed to explain the evolution of sexual size dimorphism: (1) sexual selection, (2) intersexual food competition, and (3) reproductive role division, and empirical studies have demonstrated that each of the 3 mechanisms operates in natural populations (Hedrick & Temeles 1989). Sex differences in food and foraging ecology have often been proposed as important factors leading to the evolution of size dimorphism between sexes (Andersson & Norberg 1981, Shine 1989, Mueller 1990), and many empirical studies have highlighted such differences (e.g. Selander 1966, Schoener 1967, Pierotti 1981, Le Boeuf et al. 2000, Cook et al. 2007). Apart from diet, it is often difficult to study foraging behaviour in many fast-moving or wide-ranging animals under natural conditions. Therefore, we generally lack information on the way sexes or species can differ in their foraging behaviour, such as movement, techniques or effort, which limits our ability to relate foraging and body size differences.

In birds, where flight is strongly constrained by physics, and in particular by structural size and mass, body size differences between sexes are less exaggerated than in mammals and reptiles (Andersson 1994). Although not as prominent, sexual dimorphism occurs in many bird taxa where males are larger than females, and the differences have most often been related to sexual selection. Reversed size dimorphism (referred to as reversed sexual dimorphism, RSD) also exists among several avian taxa. In species exhibiting sexual size dimorphism, significant differences in foraging behaviour have been found (e.g. Newton 1979). Within a particular taxonomic family, the extent of sexual dimorphism can vary according to species, suggesting that mechanisms leading to the evolution of dimorphic patterns within a family should vary in their extent. In the hypothesis that sexual dimorphism is related to foraging behaviour, the extent of niche partitioning and congruent differences in foraging behaviour between 2 species are expected to differ in proportion to sexual dimorphism. Thus, when examining the evolution of size dimorphism and its relationship with foraging behaviour, it is of particular interest to compare the respective influence of species, sex and the degree of size difference on the foraging behaviour of closely related species. However, this has rarely been done (e.g. Paredes et al. 2008).

In seabirds, males and females have similar roles when breeding, plumage characteristics are generally similar between the sexes, and sexual dimorphism is

not extensive compared to other species of birds. Nevertheless, sex-specific differences in foraging behaviour have been found in several species with pronounced sexual dimorphism (Weimerskirch et al. 1993, 2006, Kato et al. 1999, González-Solís et al. 2000a,b, Phillips et al. 2004), but also in species with no size dimorphism (Gray & Hamer 2001, Lewis et al. 2002). These latter examples suggest that differences in foraging behaviour may not always be related to the maintenance of sexual size dimorphism (Lewis et al. 2005). RSD is also found in several seabird families such as boobies, frigatebirds and skuas. In boobies, sex differences in foraging behaviour have been found in several species (Lewis et al. 2005, Weimerskirch et al. 2006, Zavalaga et al. 2007), and the degree of difference appears to match the extent of sexual dimorphism for some foraging parameters such as dive depths or foraging duration (Lewis et al. 2005).

In the present study, we examined sex differences in the foraging behaviour of 2 sympatric booby species of different body size, each species presenting RSD with extensive size dimorphism. We studied brown boobies *Sula leucogaster brewsteri* and blue-footed boobies *S. nebouxii* breeding on an island in the Gulf of California, using (1) highly accurate miniaturised GPS data loggers to examine the spatial distribution and foraging movements of each species and sex, and (2) data loggers that measured diving depth and acceleration to study the details of the diving behaviour and time-budget activity. In addition, diet differences between study groups were examined by collecting regurgitated stomach contents, and stable isotopes were studied from blood and feather samples. Our primary objective was to examine whether both species differed in their foraging behaviour, and whether foraging behaviour differed between sexes within each species. Because one species is smaller than the other, and in contrast to the approach of Lewis et al. (2005), who tested sexual differences within 2 species, one with a higher degree of sexual dimorphism than the other, we chose to investigate differences along a gradient of individuals ranging from small male brown boobies, medium-sized female brown and male blue-footed boobies, and larger female blue-footed boobies. This setting allowed us to disentangle the respective roles of each species–sex combination in foraging behaviour at this breeding colony, while taking into account the influence of size and mass on foraging parameters.

MATERIALS AND METHODS

The study was carried out on Isla San Ildefonso (111.4° W, 26.6° N) in the Gulf of California, Mexico, between 3 and 12 March 2006. San Ildefonso is a 1 km

long island located ca. 10 km from the eastern coast of the Baja California Peninsula. The island has mixed colonies of blue footed boobies (BFB) and brown boobies (BB) that breed in similar numbers, which we estimated to be 1000 to 2000 pairs for each species during our stay (see also W. G. Anderson in Nelson 1978, p. 520, who reported 800 to 1000 pairs in 1973 for blue-footed, but only a few pairs of brown boobies, which was supposedly abnormal for the species on this island). In March 2006, individuals of both species were mainly rearing small to large chicks, although some birds were still incubating eggs, which is in accordance with the winter breeding of the 2 species reported for the Gulf of California region (Nelson 1978, Mellink 2000). Our main study plot was located on the western side of the island, where most booby colonies occurred. Nests were localised during the day, but birds were captured only at night and solely when the moon was below the horizon to avoid predation of eggs and small unattended chicks by yellow-footed gulls *Larus livens*. Captures of birds for logger attachment or recovery upon completion of a foraging trip were made by hand or using a net. The exact duration of foraging trips was measured from GPS or accelerometer recordings.

At first capture, each bird was banded with a stainless steel identification band, measured (culmen length [Cl] in mm using dial callipers and wing length [Wl] in mm using a ruler), and weighed in a bag using a Pesola balance (± 20 g). Upon recapture for recovery of the data loggers, boobies were only weighed. An additional sample of 20 individuals was captured specifically to measure wingspan (Ws, in cm) and wing area (Wa, in cm^2) according to the methods developed by Pennycuik (1989), Hertel & Ballance (1999) and Shaffer et al. (2001). From these measurements and the body mass (BM, in g), we calculated the wing loading (an index of force per unit wing area in g cm^{-2}) as $W_{\text{load}} = \text{BM} \times g$ (gravitational acceleration, 9.81 m s^{-2})/Wa, and the wing aspect ratio (an index of wing shape), as $W_{\text{ar}} = \text{Ws}^2/\text{Wa}$. Brown boobies were sexed by plumage characteristics (Nelson 1978), and BFB, whose sexes are similar in terms of plumage, were sexed by vocal call (when captured, males have a higher pitched call than females; Nelson 1978). An index of size was calculated as the first principal component (PC1) of a principal component analysis performed on wing length and culmen length (78.9% of the variance explained).

To study the foraging movements of boobies, we fitted 34 individuals (9 male BFB, 11 female BFB, 8 female BB and 6 male BB) with a GPS receiver with integrated antenna and a 1 Mbyte flash memory operated by a rechargeable battery (Newbehavior; Steiner et al. 2000) recording at 10 s intervals. The loggers

were sealed into small polyethylene bags. The overall weight of the device and its waterproof package was 32 g and measured ca. 38×70 mm. Loggers were deployed for 1 to 2 d on each bird before being retrieved, recording a total of 48 foraging trips. Activity patterns like flight and diving behaviour were studied using cylindrical, 4 channel data-loggers (M190-D2GT, 12 bit resolution, 60×15 mm, 20 g, Little Leonardo) on 15 birds (9 BFB and 6 BB) for 1 to 3 trips each. The devices simultaneously monitored depth (every second), temperature (every minute) and acceleration (16 Hz) along 2 axes. The units contained a tilt sensor capable of measuring both dynamic (i.e. vibration) and static accelerations (i.e. gravity). Both types of loggers were attached to the birds' tail feathers so that acceleration was measured along the following 2 axes: surging acceleration was measured along the longitudinal body axis of a bird and heaving acceleration was measured dorso-ventrally (Watanuki et al. 2003, see also Ropert-Coudert et al. 2004). The relative accuracy of the depth sensor was 0.1 m. GPS and accelerometers were taped under the 3 central tail feathers using Tesa[®] tape. Only one logger type was attached to a bird (either accelerometer or GPS), and the maximum added weight reached by an attached logger was 3% of the bird's body mass (in the case of a GPS). The locations and duration of time spent on the water were derived from GPS data when flight speeds were $< 10 \text{ km h}^{-1}$ (see Weimerskirch et al. 2005 and 'Results'). To estimate the foraging areas of boobies, we searched the tracks for the zones of area-restricted search (ARS, generally considered an indication of prey searching), when birds decreased flight speed and increased sinuosity, by using the fractal landscape method (Tremblay et al. 2007). This method allowed us to precisely quantify each ARS separately, in addition to estimating the size of each ARS and time spent within each ARS zone.

Boobies spontaneously regurgitate their stomach contents when handled, so 31 food samples were obtained from breeding adults caught at the nest after returning from sea. Samples were stored in plastic containers and frozen until identification of material in the laboratory. Samples were carefully inspected to identify fish or crustacean prey. Most of the material was digested, but some samples had fish in good enough shape to be identified or contained hard parts such as otoliths and urohial bones that were used to determine fish species. Otolith identification was made to the lowest possible taxon using photographs and diagrams (Fitch 1966, Fitch & Brownell 1968) as well as the reference collection from the Centro Interdisciplinario de Ciencias Marinas (CICIMAR, La Paz, B.C.S., Mexico), which includes more than 100 species of fish from around Baja California.

In addition to diet, we also collected feathers and blood samples for isotopic analyses. Blood was collected into a heparinised syringe by venipuncture of a brachial or tarsal blood vessel. Ethanol (70 %) was then added to whole blood as a preservative, which does not alter the isotopic composition of tissues (Hobson et al. 1997). The extremity (2 to 4 cm) of 2 cover feathers was also collected and stored dry in plastic bags. Feathers were non-abraded fully-grown feathers, indicating they had been synthesised during the weeks/months before breeding. Blood and feather samples were subsequently kept at -20°C and returned to the laboratory in La Paz, Mexico, for analysis. Feathers were rinsed with distilled water and then fully dried at 80°C for approximately 12 h. Lipids were removed following the microwave-assisted extraction (MAE) protocol using a mixture of chloroform and methanol (1:1) (Bligh & Dyer 1959). Feathers were subsequently dried and ground into a homogeneous fine powder. Serum samples were lyophilised and stored in a freezer prior to weighing sub-samples of 1.2 ± 0.01 mg of homogenised tissue. Both feather and serum samples were loaded into tin cups heated to CO_2 and N_2 at 1000°C in an on-line elemental analyser (PDZ Europa ANCA-GSL; Stable Isotope Laboratory, University of California, Davis) and analysed using a continuous flow isotope ratio mass spectrometer (20-20 PDZ Europa). The gases were separated on a Carbosieve G column (Supelco) before introduction to the IRMS. Ammonium sulphate ($\delta^{15}\text{N} = 1.33\text{‰}$) was used as a secondary standard for nitrogen, and sucrose ($\delta^{13}\text{C} = -23.83\text{‰}$) was used for carbon.

Differences in isotopic composition were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation: $\delta^{15}\text{N}$ or $\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is the ratio of $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ for the sample and the standard, respectively. The international standards for stable isotope ratio analysis are atmospheric N_2 (AIR) ($\delta^{15}\text{N} = 0.004\text{‰}$) for nitrogen and Vienna Pee Dee Belemnite (V-PDB) ($\delta^{13}\text{C} = 0.011\text{‰}$) for carbon. The analytical error indicated by replicate measurements of secondary standards was $\pm 0.2\text{‰}$ for both nitrogen and carbon.

Statistical analyses were performed with STATISTICA 8 (Stat-Soft). Mean values are given ± 1 SD. Because some individuals were tracked for multiple successive trips, we analysed foraging parameters using mixed-model analyses of variance (ANOVAs;

module VEPAC in STATISTICA) to consider issues of pseudoreplication. Foraging parameters were taken as dependent variables, sex and species were added to the model as fixed factors and individual bird was included as a random factor. In a second step, we included the size (PC1) and body mass of individuals as a covariate in all analyses to examine whether individual size or mass was important after controlling for sex. Values for variables representing percentage were arcsine-transformed before performing ANOVAs.

RESULTS

Body size and mass

Within each species, females were 5 to 7 % larger than males according to body measurements (except for tail length), and 18 to 21 % according to body mass (Table 1). Between species, there was a gradient, with large female BFB at one end, small male BB at the opposite end, and intermediate and overlapping male BFB and female BB (Fig. 1, Table 1). There were no significant differences in wing loading or aspect ratio between the different categories; however, sample sizes were small.

Foraging movement and habitat

Foraging movements were similar between species, with a straight outward movement to one (or two in some individuals) sector considered a foraging zone, where birds changed flight direction regularly, followed by straight return movements (Fig. 2). Birds

Table 1. *Sula leucogaster* and *S. nebouxii*. Mass and morphometric measurements of male and female blue-footed and brown boobies. Values are mean \pm SD (sample size)

	Males	Females	df	F	p
Blue-footed booby					
Culmen length (mm)	106.7 \pm 4.6 (22)	113.1 \pm 3.6 (22)	42	25.5	<0.001
Wing length (mm)	412.7 \pm 9.0 (17)	433.1 \pm 10.2 (17)	32	37.6	<0.001
Tail length (mm)	238 \pm 3.0 (2)	232 \pm 17 (2)	3	0.37	0.585
Wing loading (N m^{-2})	75.5 \pm 5.4 (3)	72.9 \pm 3.2 (7)	8	0.9	0.365
Aspect ratio	12.3 \pm 0.4 (3)	12.2 \pm 0.6 (7)	8	0.1	0.742
Wing span (cm)	1576 \pm 29 (3)	1705 \pm 39 (7)	8	25.4	<0.001
Mass (g)	1430 \pm 131 (22)	1811 \pm 105 (22)	42	112.5	<0.001
Brown booby					
Culmen length (mm)	96.2 \pm 2.2 (19)	102.1 \pm 3.3 (20)	37	42.2	<0.001
Wing length (mm)	393.5 \pm 15.7 (15)	419.1 \pm 8.1 (14)	27	29.6	<0.001
Tail length (mm)	226 \pm 10 (6)	210 \pm 17 (3)	7	3.2	0.104
Wing loading (N m^{-2})	69.1 \pm 11.4 (4)	70.6 \pm 7.7 (5)	7	0.1	0.818
Aspect ratio	11.5 \pm 0.5 (4)	11.9 \pm 0.6 (5)	7	1.0	0.349
Wing span (cm)	1431 \pm 11 (4)	1560 \pm 65 (5)	7	14.9	0.006
Mass (g)	1194 \pm 85 (19)	1448 \pm 86 (20)	37	86.2	<0.001

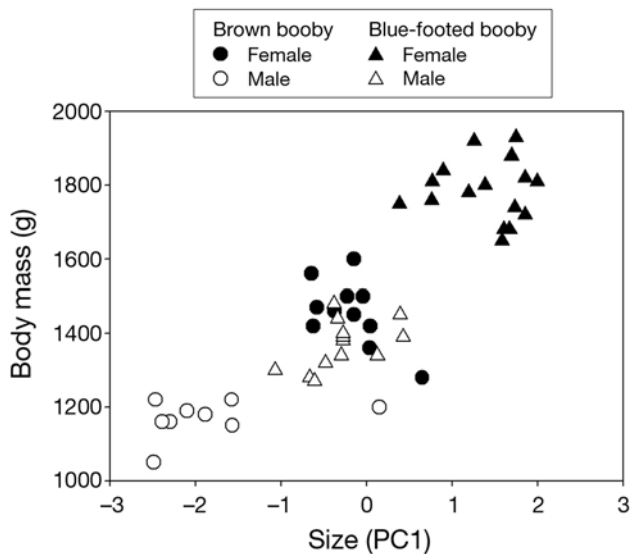


Fig. 1. *Sula leucogaster* and *S. nebouxii*. Relationship between size and body mass of male and female brown boobies and blue-footed boobies

moved mainly to the west of the colony in 2 distinct manners: (1) short trips to a large gulf between Isla San Ildefonso and Baja California (hereafter called the Gulf of San Ildefonso; Fig. 2b,d), or (2) longer trips along the northern or southern coastal region of Baja California (Fig. 2a,c). All birds remained in waters shallower than 500 m, and none moved to deeper waters east of the colony. Within a foraging zone, birds engaged in ARS as detected by fractal landscape analysis (Fig. 3). Several ARS of various sizes occurred within a foraging zone (Fig. 3). Although individuals spent only ~13% of their at-sea time in small-scale ARS, 42% of landings were made within ARS, and 68% of the remaining landings were within 5 min of an ARS, i.e. at close distance.

There was high spatial overlap in foraging zones of both species (Fig. 4). For each species, ARS zones of males and females were mainly concentrated in the Gulf of San Ildefonso, but ARS zones of females were found much farther away from the colony in places never visited by males (Fig. 4).

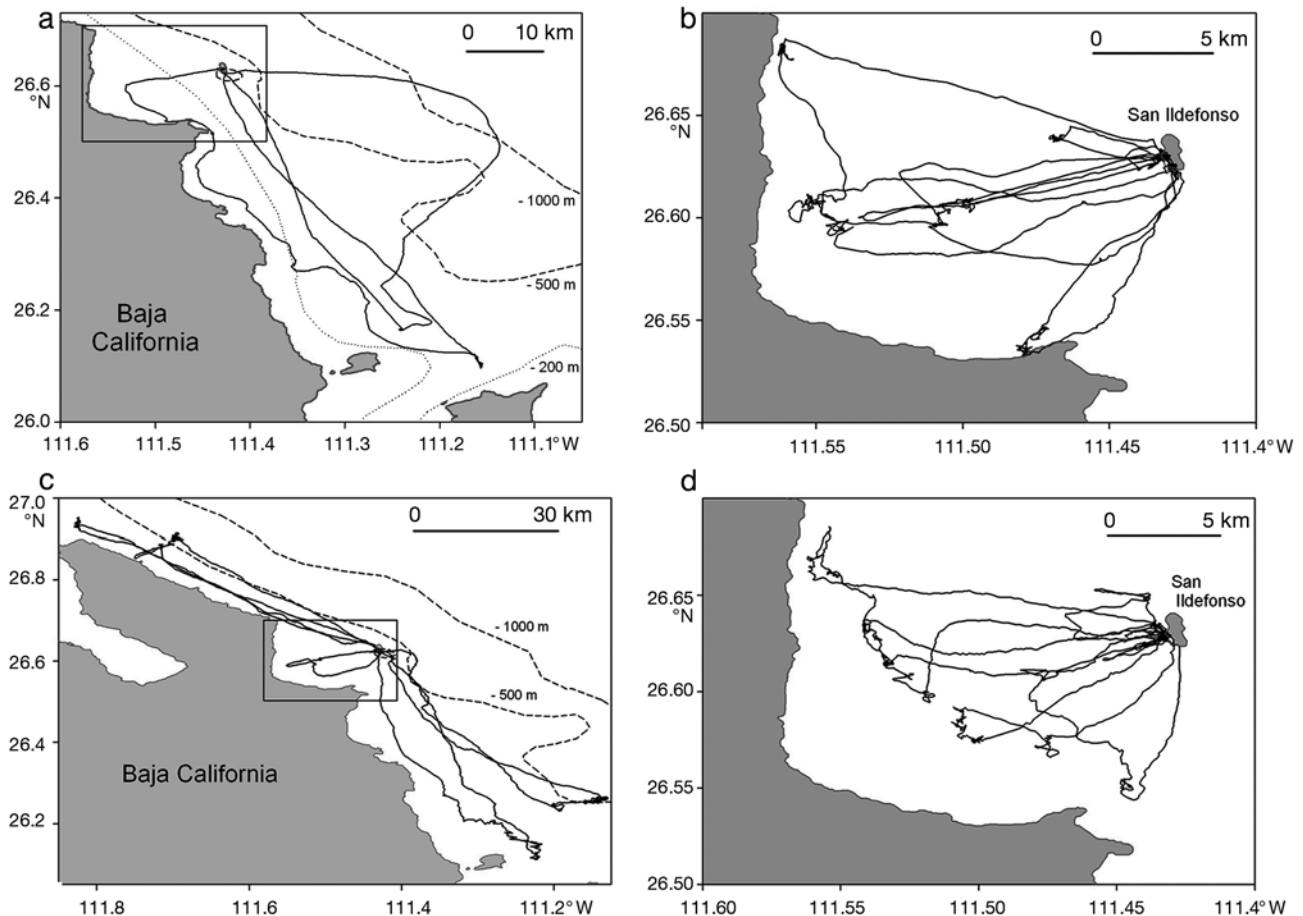


Fig. 2. *Sula leucogaster* and *S. nebouxii*. Foraging movements recorded by GPS at 10 s intervals: (a) long foraging trips of 2 female blue-footed boobies, and (b) short trips of 3 female and 1 male blue-footed boobies; (c) long trips of 3 female and 1 male (the longest trip to the north) brown boobies, and (d) short trips of male brown boobies. All birds were foraging from Isla San Ildefonso

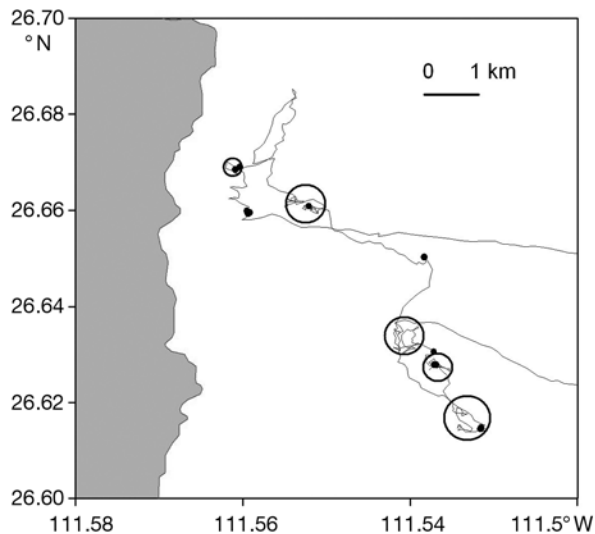


Fig. 3. Enlargement of a track of a female brown booby, showing the zones where area-restricted search was detected using the fractal landscape method. Black dots indicate when the bird was sitting on the water

Foraging duration and range

The duration, distance covered and maximum range of foraging trips were not different between species (Tables 2 & 3). Females had longer foraging trips in both duration and distance travelled, as well as longer foraging ranges (Tables 2 & 3). Similarly, distance to ARS zones from the colony were similar between species, but were longer in females than males for each species (Tables 2 & 3). Female BB had larger ARS zones than males; however, time spent within an ARS or the number of ARS zones per trip did not differ between groups (Tables 2 & 3). When body mass and size were included as covariates, foraging range and distance covered were positively related to size, but not to mass (Tables 2 & 3).

Flight speed, flight pattern, activity and diving

Flight speeds were not significantly different between species, but they were significantly higher in females compared to males, and this difference was due to variation in body size (Tables 2 & 3). Stroke (flapping) frequency was higher for BB than for BFB and was mainly related to the size of individuals (Tables 2 & 3). The percentage of time spent on water during a complete trip was higher for BB than for BFB, but there were no differences between sexes or an influence of body mass or size (Tables 2 & 3). The number of landings per hour, an index of activity, was sim-

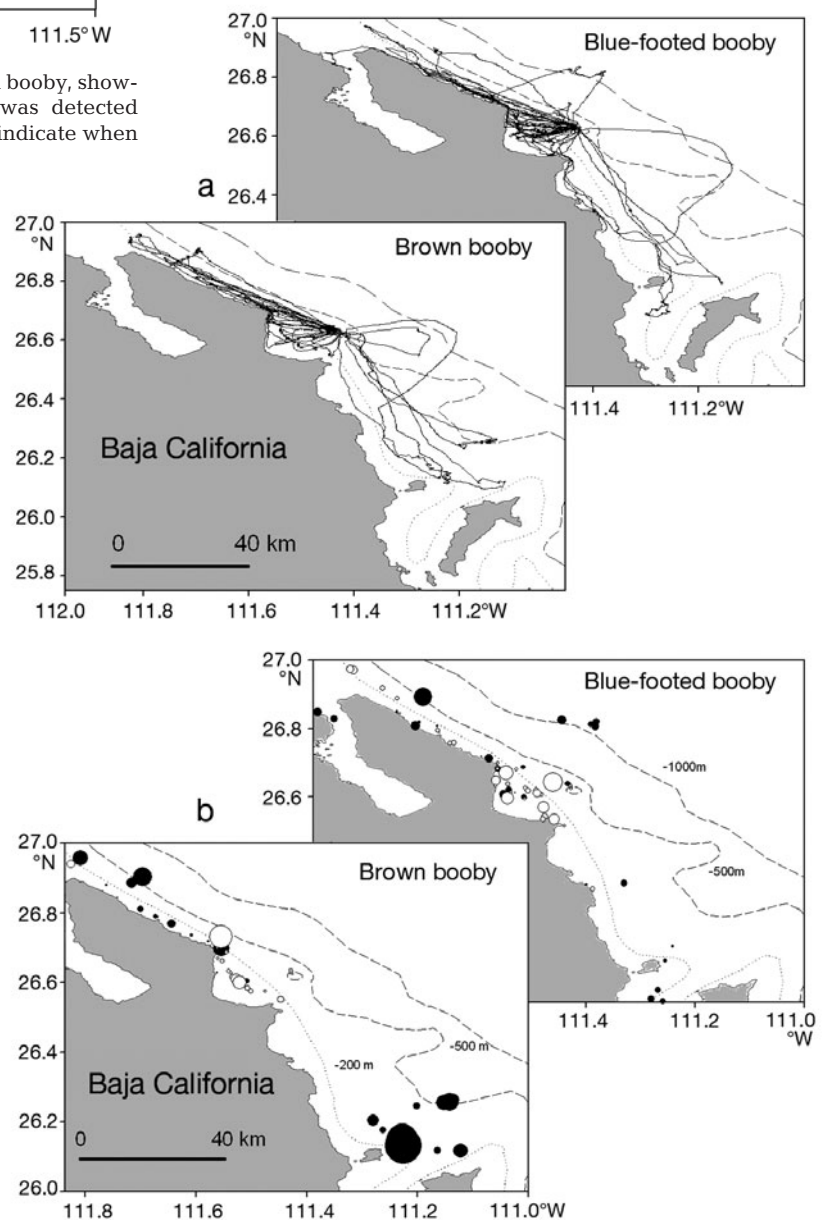


Fig. 4. *Sula leucogaster* and *S. nebouxii*. (a) Tracks and (b) zones of area-restricted search (ARS) for male (white circles) and female (black circles) blue-footed and brown boobies. The size of the circles is proportional to the size of the ARS zone, but to be visible in the figure, the circle diameters have been multiplied by 5

Table 2. *Sula leucogaster* and *S. nebouxii*. Foraging parameters of male and female blue-footed and brown boobies. Values are mean \pm SD (sample size). ARS: area-restricted search

	Blue-footed boobies		Brown boobies	
	Males	Females	Males	Females
Time of departure (local time)	12.6 \pm 3.6 (18)	11.4 \pm 3.3 (20)	10.9 \pm 3.6 (15)	11.8 \pm 3.4 (17)
Trip duration (h)	1.8 \pm 1.3 (17)	2.3 \pm 1.3 (18)	2.0 \pm 1.0 (14)	3.0 \pm 1.3 (17)
Maximum foraging range (km)	22.2 \pm 15.9 (13)	32.0 \pm 22.7 (14)	16.6 \pm 14.3 (9)	39.2 \pm 16.6 (11)
Distance covered (km)	55.6 \pm 35.6 (12)	85.3 \pm 61.5 (13)	50.9 \pm 31.5 (8)	105.6 \pm 45.9 (11)
Average flight speed during trip (km h ⁻¹)	31.7 \pm 6.5 (13)	37.8 \pm 4.7 (14)	27.7 \pm 6.5 (9)	34.4 \pm 8.2 (11)
Stroke frequency (power spectral density; Hz)	3.64 \pm 0.04 (6)	3.55 \pm 0.06 (6)	3.93 \pm 0.12 (6)	3.84 \pm 0.12 (6)
Number of ARS per trip	2.2 \pm 1.9 (13)	2.1 \pm 1.8 (14)	1.4 \pm 1.4 (9)	1.8 \pm 0.8 (11)
Distance of ARS from colony (km)	16.9 \pm 13.6 (25)	32.2 \pm 22.0 (29)	12.2 \pm 11.4 (14)	35.7 \pm 17.1 (19)
ARS diameter (km); fractal landscape method	0.7 \pm 0.4 (31)	0.6 \pm 0.4 (35)	0.7 \pm 0.6 (16)	1.2 \pm 0.9 (26)
% foraging time in ARS	19.7 \pm 8.6 (12)	9.0 \pm 7.1 (13)	12.7 \pm 12.3 (11)	11.9 \pm 8.3 (11)
Fractal dimension	1.22 \pm 0.09 (31)	1.18 \pm 0.09 (35)	1.21 \pm 0.11 (16)	1.18 \pm 0.13 (26)
Effort within ARS (distance covered/ARS surface; km km ⁻²)	8.4 \pm 5.1 (31)	8.8 \pm 7.1 (35)	9.4 \pm 7.2 (16)	6.8 \pm 7.1 (26)
% time foraging on water	11.4 \pm 12.4 (18)	8.5 \pm 8.1 (20)	3.5 \pm 6.7 (15)	2.7 \pm 4.2 (17)
Number of landings per hour	6.3 \pm 1.8 (12)	4.4 \pm 2.4 (13)	6.1 \pm 4.7 (11)	4.1 \pm 1.4 (11)
Number of dives per hour	31.4 \pm 9.9 (6)	19.3 \pm 12.7 (6)	24.0 \pm 15.0 (6)	21.4 \pm 8.2 (6)
Maximum dive depth (m)	2.5 \pm 1.4 (261)	4.4 \pm 1.7 (223)	1.3 \pm 0.5 (364)	1.1 \pm 0.71 (258)
Duration of dives (s)	3.5 \pm 1.6 (261)	4.8 \pm 2.6 (223)	2.0 \pm 0.8 (364)	1.9 \pm 1.3 (258)

ilar between species, but different between sexes; males landed more often per unit of time than females, and this parameter was influenced by body mass (Tables 2 & 3). Diving depths were deeper (Fig. 5) and dive durations longer in BFB compared to BB; this difference was mainly the result of body mass differences between individuals (Tables 2 & 3). The number of dives per hour, a measure of foraging effort, was similar between sexes and species (Tables 2 & 3).

Diet and isotopic signatures

The diet of both species was dominated by one prey species, the sardine *Sardinops caeruleus*, with 90.4 % of the samples containing this species. Of all samples, 77.4 % contained only sardines, and the rest contained sardines and the fish species *Selar crumenophthalmus* or *Etrumeus teres*. In some samples, either or both of these 2 species were found exclusively, and in 1 female

Table 3. Results of general linear mixed models investigating the effects of sex and species, and body mass and size (as covariates) on foraging parameters of male and female blue-footed and brown boobies shown in Table 2. ARS: area-restricted search. Significant results in **bold**

	df	Effect							
		Species		Sex		Body mass		Size	
		F	p	F	p	F	p	F	p
Time of departure	38	2.3	0.201	0.4	0.593	4.0	0.144	0.2	0.757
Trip duration	36	1.8	0.180	4.6	0.039	0.8	0.367	0.9	0.346
Maximum foraging range	26	0.1	0.796	5.4	0.030	0.4	0.530	6.1	0.022
Distance covered	24	0.4	0.529	6.8	0.017	0.8	0.590	5.1	0.046
Average flight speed during trip	24	3.3	0.100	11.5	0.004	3.5	0.101	12.8	0.004
Stroke frequency (power spectral density)	8	45.8	<0.001	4.3	0.076	3.0	0.126	31.0	0.002
Number of ARS per trip	24	1.6	0.229	0.7	0.418	0.1	0.959	0.2	0.646
Distance of ARS from colony	23	0.4	0.424	4.2	0.045	2.9	0.218	7.1	0.012
ARS diameter; fractal landscape method	24	4.7	0.044	0.6	0.444	1.0	0.332	0.2	0.628
% foraging time in ARS	24	0.8	0.403	8.9	0.020	2.1	0.137	5.1	0.061
Fractal dimension	24	0.1	0.771	1.8	0.201	0.4	0.546	0.2	0.683
Effort within ARS (distance covered/ARS surface)	24	1.9	0.179	0.1	0.762	2.0	0.199	0.3	0.556
% time foraging on water	38	12.1	<0.001	1.4	0.253	0.1	0.773	2.5	0.134
Number of landings per hour	24	0.4	0.603	24.4	0.041	8.0	0.024	2.5	0.158
Number of dives per hour	19	0.2	0.637	2.2	0.201	0.5	0.488	1.5	0.360
Maximum dive depth	12	44.1	<0.001	3.8	0.062	58.2	<0.001	0.4	0.521
Duration of dives	12	42.8	<0.001	3.5	0.072	42.0	<0.001	1.5	0.317

BFB stomach, an unidentified scombrid species alone was found. There was no significant difference ($\chi^2_3 = 2.2$, $p = 0.517$) in the percentage of sardines in the diet of male BFB (66.6%), female BB (75%), female BFB (88.8%) or male BB (92.8%).

Isotopic analyses showed that the stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic compositions of blood during the breeding season were similar for male and female BB and BFB ($\delta^{13}\text{C}$: $F_{1,27} = 0.2$, $p = 0.656$ species effect, and $F_{1,27} = 2.1$, $p = 0.158$ sex effect; $\delta^{15}\text{N}$: $F_{1,27} = 0.4$, $p = 0.153$ species effect, and $F_{1,27} = 1.9$, $p = 0.173$ sex effect; Fig. 6). Similarly, the analysis of feathers produced during moult indicates that the 2 sexes and species were feeding at similar trophic levels and in similar water masses (Fig. 6: $\delta^{13}\text{C}$: $F_{1,56} = 0.1$, $p = 0.932$ species effect, and $F_{1,56} = 0.4$, $p = 0.510$ sex effect; $\delta^{15}\text{N}$: $F_{1,56} = 2.8$, $p = 0.098$ species effect, and $F_{1,56} = 0.1$, $p = 0.797$ sex effect; Fig. 6). The high vari-

ance observed (Fig. 6) was due to the existence of groups with distinct isotopic signatures, suggesting variability in the prey consumed.

DISCUSSION

This study is the first to simultaneously compare the detailed foraging behaviour of both sexes in 2 closely related sympatric species of boobies, and in seabird species in general where only some foraging parameters have been studied in a few species before (e.g. González-Solís et al. 2000b, Lewis et al. 2005, Paredes et al. 2008). In addition, it is also the first to take into account size and body mass of individuals as covariates in a study on foraging parameters of seabirds. Although our study was based on small sample sizes due to logistic constraints, several clear results have emerged. The most important result is that differences between the sexes explained variation in foraging behaviour better than differences between species, and

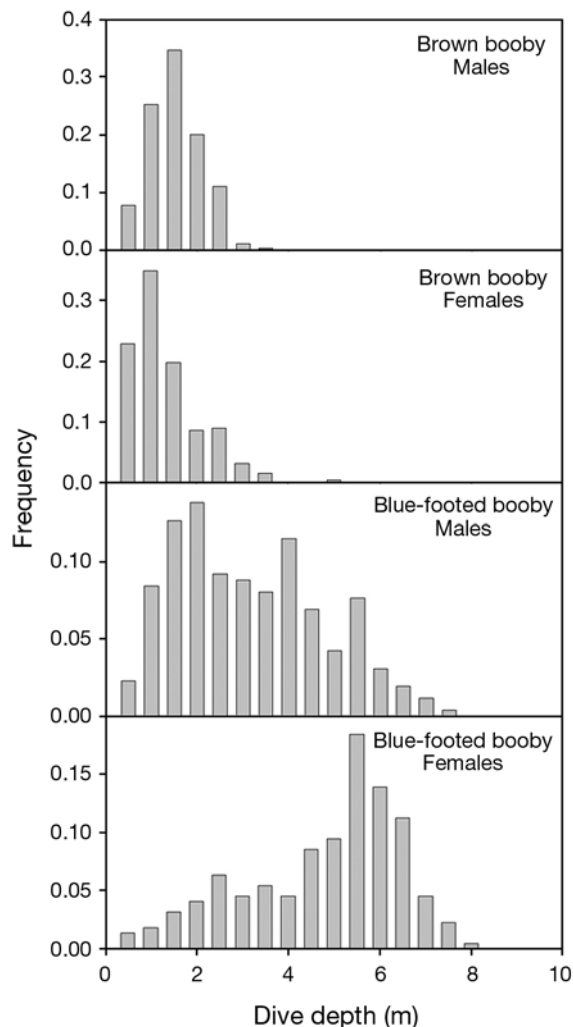


Fig. 5. *Sula leucogaster* and *S. nebouxii*. Frequency distribution of maximum diving depths of male and female brown and blue-footed boobies

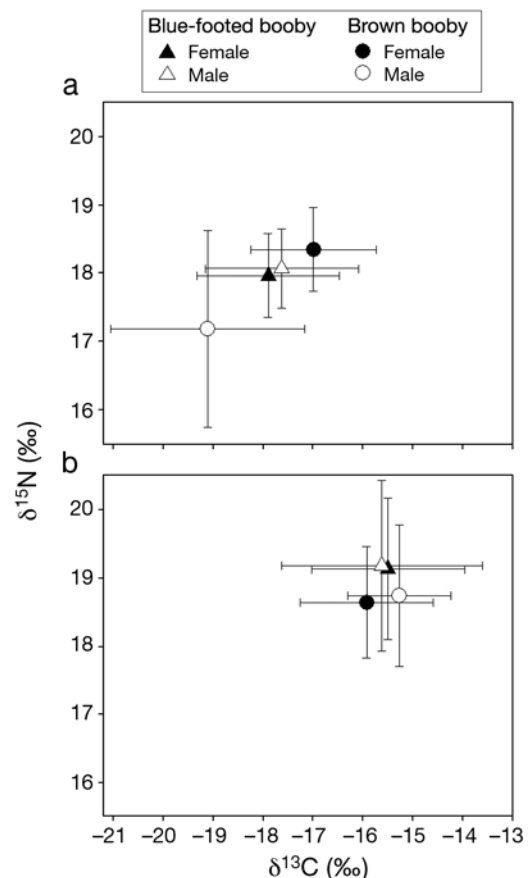


Fig. 6. *Sula leucogaster* and *S. nebouxii*. Stable carbon and nitrogen isotope values of (a) blood and (b) feathers of male and female blue-footed and brown boobies from Isla San Ildefonso. Values are mean \pm SD

that several differences between sexes or species can be explained by differences in body size or body mass.

Foraging context

Both booby species breed in winter, when sea-surface temperatures are coldest and chlorophyll (chl) *a* concentrations are highest in the Gulf of California, favouring the presence of large populations of sardines (Lluch-Cota et al. 2007). Nutrient enrichment within this geographic region is produced mainly by vertical mixing from tidal currents and wind-driven coastal upwelling (Roden & Groves 1959). Overwhelmingly, sardines were the principal prey available and were consumed by both booby species, although anchoveta *Cetengraulis mysticetus* have been observed in the diets of BB in previous studies at Isla San Ildefonso (Mellink et al. 2001). The overlap in foraging zones of both species was extensive, as both BB and BFB concentrated their foraging effort in the Gulf of San Ildefonso. The relatively short foraging trip durations, compared to more pelagic booby species (red-footed and masked boobies, Weimerskirch et al. 2005, 2008) or even the same species at different locations (BFB: Nelson 1978, Anderson & Ricklefs 1992, Zavalaga et al. 2007; BB: Nelson 1978, Lewis et al. 2005) suggests that food availability was relatively high close to the colony. Thus, the absence of clear segregation between species at Isla San Ildefonso was likely related to prey abundance; competition between species would have been stronger if food had been more limiting.

In the Gulf of California, coastal upwelling—forced by local wind conditions that are particularly strong in winter—creates important habitat for many top predators like large predatory fish, marine mammals and seabirds (Lluch-Cota 2000). During our study, boobies were often seen feeding in association with bottlenose dolphins *Tursiops truncatus gilli* that probably pushed sardines to the surface. The upwelling front was clearly visible from the surface, and the locations of ARS zones within the Gulf of San Ildefonso appeared to coincide with the location of the front (e.g. in Fig. 2d where ARS zones are aligned, presumably along the upwelling front). Boobies foraged mainly in these narrow upwelling fronts along the coast, which explains why their ARS zones were so tightly clustered just offshore. Within ARS zones, landings are probably associated with plunging (Fig. 3). Isolated landings may represent plunge dives on isolated prey or on small schools of fish that are rapidly disrupted by the plunging birds. In contrast, repeated plunging in ARS zones may represent foraging in larger, more stable schools, which are eventually maintained at depths reachable by marine mammals.

Species differences

In closely related species that breed sympatrically, it is generally expected that ecological segregation occurs to reduce competition (Ricklefs 1990). Several mechanisms have been found in seabird communities that allow ecological segregation, such as differences in foraging areas at sea (Croxall & Prince 1980, Weimerskirch et al. 1986, 1993), or diving depths (Mori & Boyd 2004), selection of different prey or prey of different size (Ashmole & Ashmole 1967, Kato et al. 1996), timing of foraging (Cook et al. 2007) or time of reproduction (Harrison 1990). At Isla San Ildefonso, BFB and BB forage at sea during daylight hours, and both feed on average at similar trophic levels under the same oceanographic conditions. Isotopic feather analyses indicated that, during moult, which occurs in boobies outside or at the end of the breeding season (Nelson 1978), no difference in average trophic level or oceanographic conditions between sexes and species occurs. However, average values show high variance during breeding and during moult. This high variance is not due to the small sample size, but to the existence of distinct groups with distinct isotopic signatures both in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, indicating that some individuals are feeding in different water masses on different prey, suggesting a specialisation of some individuals that is not apparent in the tracking data.

Although some foraging behaviours differed between species, the most noticeable difference was the maximum diving depths attained by BFB compared to BB (Fig. 6). The difference between both species is probably not related to their body mass differences alone, because there was little overlap in the depths attained by male BFB and female BB, which have a similar body mass (Table 1, Fig. 5). Behavioural differences may also play a role in the depths attained, because we observed that BFB fly at a higher altitude than BB and plunge dive from greater heights, which—combined with heavier bodies—provides greater momentum when entering the water (Ropert-Coudert et al. 2004). Another clear significant difference in foraging behaviour between species was the percentage of time spent on the water. BFB spent proportionally more time on the water than BB, suggesting some behavioural differences in foraging between species.

Sex differences

We expected interspecific differences to be greater than intersexual differences within a species. However, differences in foraging behaviour between sexes within the same species were more marked than the differences between species (Table 3). The major dif-

ference between male and female boobies was that females foraged farther from the colony, had longer trip durations, flew greater distances at higher flight speeds, and travelled to more distant zones of ARS than males in both species. The differences in foraging behaviour between sexes were always more significant for BB than for BFB, whereas the differences in body mass and size between males and females were similar for both species, suggesting that there is no linear relationship between morphology and its effect on behaviour.

Previous studies have shown that BFB males and females had similar foraging trip durations in the Galapagos Islands (Anderson & Ricklefs 1992) and in Peru (Zavalaga et al. 2007), and that females dove deeper and had different dive patterns than males (Zavalaga et al. 2007). In addition, female BB at Clipperton Island (Eastern Tropical Pacific) were observed at greater distances from the colony than males (Gilardi 1992), but in the Hawaiian Islands, females had shorter trips than males (Lewis et al. 2005). In San Pedro Martyr Island, another island in the Gulf of California, foraging trip duration of male and female BB were similar during the chick-feeding period, but females delivered heavier food loads (and more food overall) to chicks (Tershy 1998, Tershy & Croll 2000). Sex-specific differences in foraging were also noted in red-footed boobies, where females foraged farther from the colonies (Weimerskirch et al. 2006) and were less active than males (Lewis et al. 2005, Weimerskirch et al. 2006). Conversely, there were no sex differences in most foraging parameters of masked boobies, except that females had higher foraging effort (i.e. dives per hour) and spent more time foraging than males (Weimerskirch et al. 2009). Overall, results of previous research as well as our study indicate that, in most localities, female boobies tend to forage farther from the nest and have longer foraging trips than males, but considerable variations exist between sites, which is likely due to variability in prey resources. Certainly, biological productivity is higher in the Gulf of California, given its more temperate oceanic conditions, compared to tropical and subtropical conditions where other booby species breed and where previous studies have been carried out (e.g. Europa Island, Northwest Hawaiian Islands, Clipperton Atoll).

During our study, we were not able to monitor nest attendance, which would have allowed us to relate foraging parameters and breeding involvement. Farther north, in the Gulf of California, female BB delivered more food overall to chicks than males (Tershy 1998, Tershy & Croll 2000). Other studies have shown that larger females bring larger meals to chicks (Anderson & Ricklefs 1992, Weimerskirch et al. 2006, 2009), which can be attributed in part to greater food storage capac-

ity (Pierotti 1981, Shaffer et al. 2001), but also to shorter time spent with the chick compared to males. Since one parent always guards the small chick(s) when the other is at sea, the longer foraging trips of the partner results in longer periods on the nest, reducing further provisioning by the male to the chick(s). Thus, the longer foraging trips and larger size of females of both species suggest that, at our study site, females are probably the main provisioners, whereas males spend more time in nest attendance and nest defence (Guerra & Drummond 1995, Tershy 1998, Tershy & Croll 2000, Weimerskirch et al. 2006, 2009, see also Paredes et al. 2008 for alcid). Thus, the evolution of sexual size dimorphism in boobies may be related to the differences in roles that each parent plays in nest attendance and provisioning, and this may have led to differences in foraging strategies between the sexes. However, more studies relating detailed foraging behaviour and breeding duties are needed to validate this hypothesis.

Similar results whereby sex differences are more important than species differences have been shown in 2 sibling species of giant petrels, where males of both species forage over land whereas females are offshore feeders (González-Solís et al. 2000b). In that study, males and females occupied very distinct niches, with larger males foraging on seal carcasses on land and smaller females feeding on marine organisms, whereas differences between species within a particular sex were more subtle, with species foraging in slightly different water masses (González-Solís et al. 2000b). Similarities in foraging ecology between sexes of both species suggest that intersexual differences in trophic ecology probably evolved before the speciation of the 2 taxa (González-Solís et al. 2000b). However, it is important to point out that the similar results observed in boobies and in giant petrels, i.e. more extensive differences between sexes than between species in sympatric species, have probably evolved from completely different proximal causes.

Influence of size and mass

We used size and mass as covariates to examine whether they may explain part of the differences in foraging behaviour observed between individuals. Differences observed between sexes were explained by size for several parameters, in particular flight speed, foraging range and distance covered. As predicted by flight theory (Pennycuik 1989), flight speed was higher in larger individuals. The longer foraging range and distance covered could partly be the consequence of size differences. However, females fly 7 to 9 % faster than males, but forage 32 to 59 % farther than males, indicating that size accounts only for a small part of the

variation in range and distance covered. In flying birds, stroke or flapping frequency are lower in larger individuals (Sato et al. 2007), and we indeed found a significant influence of size on stroke frequency in boobies. Body mass is also directly related to biomechanical constraints, and we showed that dive depths and time spent diving were positively related to the body mass of individuals. This is a logical result for a plunge-diving animal such as a booby that uses only the momentum of its plunge to attain depths, with heavier individuals attaining deeper depths when plunge diving (Ropert-Coudert et al. 2004).

CONCLUSIONS

We have shown that the differences in foraging behaviour in these 2 sympatric species are more prominent between the sexes than between species, and that size, and to a lesser extent body mass, explain several of the differences between individuals, in particular several sex differences. This underlines the importance of taking into account size as a covariable when sex-specific differences are examined in size-dimorphic species. In the case of our study on boobies, the greater differences in foraging behaviour observed between sexes than between species may be related to the superabundance of sardines consumed by both sexes and both species, which does not lead to niche differentiation between species. It would be interesting to test this hypothesis by comparing other populations of boobies breeding in sympatry, but in situations where food is scarce; in this case, we would predict that differences in foraging ecology between species would be at least as important as differences between sexes.

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Albatross foraging behaviour: no evidence for dual foraging, and limited support for anticipatory regulation of provisioning at South Georgia

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ABSTRACT: Many pelagic seabirds are thought to regulate reproductive effort by adopting a dual foraging strategy, alternating or mixing short foraging trips over local shelf waters (maximising provisioning rates) with longer trips over distant oceanic water (allowing restoration of lost condition). Many species also respond to chick condition, decreasing food supply to over-fed, and sometimes increasing it to under-fed chicks. Analysis of tracking data from 4 albatross species breeding at South Georgia provided evidence that adults responded to prevailing environmental conditions, but did not provide evidence for a dual foraging strategy. Trip durations and maximum foraging ranges tended to follow a positively skewed, unimodal distribution, with the exception of the light-mantled albatross for which no significant modes were apparent. Individual distributions deviated from this, but none were strongly bimodal or showed regular alternation of trip lengths, trip distance or predominant bathymetric regime. There were significant relationships between meal mass and trip duration, time since the last feed and chick condition on return, reflecting responses to current rather than predicted chick needs. On average, adults returned with smaller meals after 1 to 2 d trips, but otherwise stayed away until a threshold payload was obtained; consequently, provisioning rate (g d^{-1}) was much greater after shorter trips. Lack of dual foraging may reflect the diversity of foraging zones available in this highly productive region. By inference, this would mean that adoption of dual foraging elsewhere is a consequence of greater heterogeneity in resource availability in waters surrounding those colonies.

KEY WORDS: Foraging behavior · Parental investment · Provisioning · Regulation · Satellite-telemetry

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INTRODUCTION

Numerous studies have examined parental effort in long-lived, iteroparous species that, according to life-history theory, should not over-invest in a particular breeding episode if this is likely to jeopardise their subsequent survival or reproductive potential (Stearns 1992). Seabirds are amongst the most *K*-selected of any bird group, yet several unpredictable aspects of

their environments handicap their capacity to easily regulate foraging effort and control reproductive investment: many forage in the open ocean where prey is considered to be patchy and ephemeral, and adults are unable to gauge feeding success of their partner in the long intervals between nest visits. Nonetheless, there would be considerable theoretical advantages to regulating provisioning effort, channelling more resources into adult condition if the chick is well-

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nourished, and increasing effort if it is underweight (assuming sufficient body reserves to buffer extra costs).

Although early work concluded that pelagic seabirds fed chicks according to an inherent internal rhythm (Ricklefs 1992, Hamer & Hill 1993, Ricklefs & Schew 1994), more recent studies have shown reduced food delivery to overweight chicks and, much more rarely, increased food supply to under-fed offspring (Bolton 1995, Weimerskirch et al. 1995, Hamer & Hill 1997, Granadeiro et al. 1998, Tveraa et al. 1998, Quillfeldt et al. 2004). These studies indicate a surprising degree of variability: responsiveness is usually greater in species with higher feeding frequencies, and in some cases, adults of only 1 sex, at 1 colony, or in 1 year, are capable of increasing provisioning rates. Explanations for this vary from differential investment, resource availability or parental condition constraining the options available, or methodological inconsistencies and the difficulty in detecting often quite subtle biological effects.

Balancing offspring requirements with those of self-maintenance is clearly not straightforward, particularly given the continuous changes in nutritional status and gut fullness (hence capacity for ingestion) of both parent and chick (Ropert-Coudert et al. 2004). One solution is for adults to alternate one or more short trips to the local shelf that maximise energy delivery per unit time, with often one, but sometimes several long trips to deep, oceanic water that result in reduced provisioning rates, but enable adults to restore their own reserves (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, Weimerskirch 1998). In some species that use this strategy, adults do not respond to chick condition, and in others they do, but not necessarily in every year (Granadeiro et al. 1998, 2000, Weimerskirch 1998, Weimerskirch et al. 2001). The dual foraging strategy was described initially in 4 of 6 procellariiform species breeding in the southwest Indian Ocean based on 2 modes in the frequency distribution of trip duration and on data on mass of adults and meals fed to chicks. Its occurrence has subsequently been postulated for at least a further 9 other species, and it appears to be increasingly accepted as the default (Weimerskirch et al. 1999, Baduini & Hyrenbach 2003, Congdon et al. 2005). A few studies indicate that its usage differs between populations, or between years (Granadeiro et al. 1998, Peck & Congdon 2005), and it is not clear what proportion of birds need to show trip characteristics akin to dual foraging before it can be assumed to be the dominant mode.

Dual foraging as a strategy is often inferred either: (1) solely from the frequency distribution of trip duration, despite the potential for a second (spurious) mode (because some rare frequency classes are under- and others over-represented simply by chance), or because of the pooling of data from individuals that tend to per-

form either long or short trips; or (2) from tracking data that indicate foraging in 2 different habitats without any information on how this relates to chick feeding rates, meal mass or adult condition. Only rarely are provisioning and tracking (or diet) data presented that confirm not only the utilisation of the requisite 2 disjunct foraging habitats, but also that these are exploited in turn leading to regulation of adult reproductive effort *sensu* Weimerskirch et al. (1994). Otherwise adults on long trips could just as easily be feeding close to the colony, or the long trips could simply reflect contingent switches to alternative (distant) feeding grounds because of prevailing environmental conditions or low prey ingestion rates in nearby waters. The purpose of the present study was to use comprehensive tracking data collected from the 4 albatross species breeding at South Georgia to test for the existence of dual foraging strategies at this site. We also examined evidence for regulation of provisioning (in terms of foraging destination, trip duration and meal mass) according to chick condition, and for synchronicity in foraging patterns, to determine to what extent adults respond to extrinsic factors such as natural variation in the environment and in the needs of their offspring.

MATERIALS AND METHODS

Fieldwork was carried out during the post-brood period (when both adults feed at sea, returning at irregular intervals to feed the chick) at Bird Island, South Georgia (54° 00' S, 38° 03' W) on wandering albatross *Diomedea exulans* (austral winters, April–December 1996, April–October 1997, July–October 2002 and April–October 2004), black-browed albatross *Thalasarche melanophris* (austral summers, January–May 1990, January–May 1992–1994 and January–March 2002), grey-headed albatross *T. chrysostoma* (austral summers, January–May 1993–1996 and January–March 2001) and light-mantled albatross *Phoebastria palpebrata* (austral summer, January–May 2003). Typically, 16 to 46 birds in each year were fitted with a 17 g radio transmitter attached to a plastic band (Darvic) on one tarsus which allowed exact arrival and departure times to be determined using a remote radio-receiver logger system (Televilt) (Huin et al. 2000, Berrow & Croxall 2001, Phillips et al. 2003).

In at least 1 season for each species, 4 to 26 adults were also tracked using a 20 or 30 g satellite-transmitter (Platform Terminal Transmitter or PTT-100; Microwave Telemetry), or (wandering albatross only in 2004) a 68 g GPS logger (BGDL-II; Shizuoka University, Japan) attached using sticky tape (Tesa) to mantle feathers for 1 to 29 foraging trips (Fukuda et al. 2004, Phillips et al. 2004, 2005a). These birds were usually fitted con-

currently with a radio transmitter; otherwise, arrival and departure times were estimated from satellite fixes and visual observations. Attachment of devices took <10 min. Instrument loads (0.2 to 2.0% of body mass) were well below the threshold where deleterious effects might be expected, and there was no indication that mean foraging trip duration or chick meal mass was affected (Phillips et al. 2003, 2005a).

All satellite-transmitter locations in ARGOS Sytem Location Class 3,2,1,0, A and B were filtered using an iterative forward/backward averaging filter (McConnell et al. 1992) to remove any that indicated unrealistic flight speeds (filter velocity >90 km h⁻¹ to allow for occasional rapid flights that were clearly genuine based on visual examination). Hourly locations were estimated by linear interpolation, and maximum range (furthest distance from the colony) and total (cumulative) travel distance along the route were then calculated, using great-circle distances (Phillips et al. 2005a,b).

Following Wakefield et al. (in press) tracks were then divided into commuting and foraging phases. Briefly, for each interpolated location, the great circle distance from the colony as a proportion of the maximum reached ($d_{\text{col}}/d_{\text{max}}$) and the proportion of the trip time elapsed (t/t_{max}) were calculated. Plots of $d_{\text{col}}/d_{\text{max}}$ vs. t/t_{max} showed that trips made by all species comprised an outward and return commuting phase, during which birds flew rapidly away from or towards the colony, and a foraging phase during which birds moved slowly with respect to the colony. Plots of the variance of $d_{\text{col}}/d_{\text{max}}$ vs. t/t_{max} showed that on average the foraging phase occurred when between 20 and 81% of the total trip time had elapsed. Hence, locations occurring between these values were classified as foraging.

Trips were classified as 'local' if the majority of recorded foraging locations were ≤ 500 km from Bird Island; otherwise they were classified as 'distant'. This division ensured that trips made to shelf and slope waters surrounding South Georgia and Shag Rocks—as well as those to the Antarctic Polar Frontal Zone (APFZ), where this is closest to South Georgia—were classified as local (Fig. 1). The depth and distance from the 1000 m depth contour were obtained from the Terrain Base digital atlas. The predominant bathymetric regime was classified as follows—neritic: depth at foraging locations predominantly ≤ 1000 m; slope: either, depth >1000 m and ≤ 2500 m, or, depth >1000 m and distance from the 1000 m depth contour ≤ 150 km; oceanic: all other cases. In addition the mean positions of foraging locations during each trip were calculated. Plots of trip length, foraging range and bathymetric regime for consecutive trips by individuals were examined to check for relationships that might represent

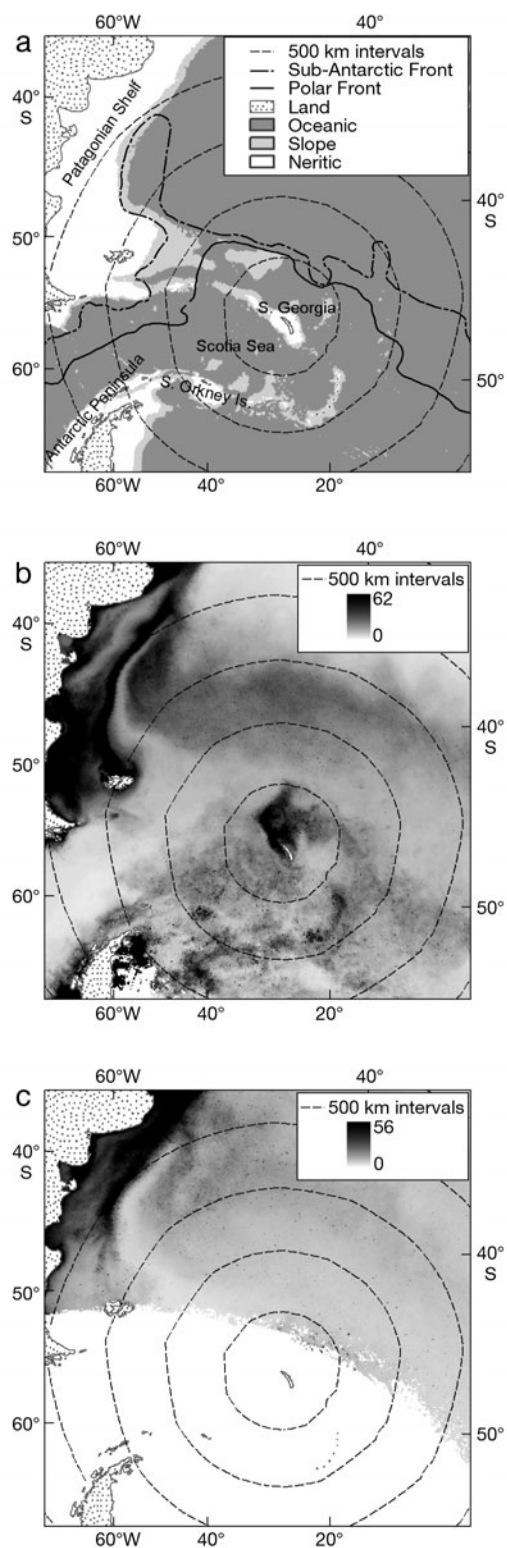


Fig. 1. Study area and places mentioned in the text, showing (a) bathymetric regime, distance from Bird Island (South Georgia) in 500 km increments, and mean location of the Antarctic Polar Front (Moore et al. 1999); mean chlorophyll concentration (mg m⁻³) in (b) January to March, and (c) July to August (Feldman & McClain 2008)

dual foraging, *sensu* Weimerskirch et al. (1994). There were insufficient consecutive trips from individual wandering albatrosses to examine the behaviour of this species in detail. The spatial distribution of areas of elevated primary productivity in the study area was investigated using seasonal mean chlorophyll *a* (chl *a*) images (Feldman & McClain 2008). These corresponded to the early-middle part of the chick-rearing period for black-browed, grey-headed and light-mantled albatrosses (January to March), and the middle of the chick-rearing period for the wandering albatross (July to August).

Automated nest balances were deployed shortly after the end of brood-guard in 2002 (black-browed albatross) and 2003 (light-mantled albatross) (Phillips et al. 2003, 2005a). These record chick mass to the nearest 10 g every 10 min, allowing the timing of feeding and mass of meals to be determined from mass increments. Measurements were very accurate, as rain drained freely through holes in the cover, and accumulated soil or other material was removed daily. Similar information on provisioning was available in 2001 for a sample of grey-headed albatross chicks weighed twice daily for a period of 30 d (Phillips & Croxall 2003). Comparable data were not collected for wandering albatross. Indices of condition were estimated as residuals from linear, quadratic or cubic regressions (whichever was the best fit) for individual chicks of mass upon age (Phillips & Croxall 2003, Phillips et al. 2005a). Adult attendance was monitored independently, and meals allocated to the parent visiting the colony at the time. Occasionally an adult would feed the chick, depart, then return and feed again within the course of a few hours. During this time, the bird was probably close to the colony but not actively foraging, and we therefore only considered absences of >6 h as foraging trips (following Weimerskirch et al. 1997, Phillips & Croxall 2003). Meal mass was only calculated when a feed could be allocated unequivocally to a particular adult. These factors, and whether other tracking information was available, account for variation in sample sizes.

Frequency distributions of trip duration and maximum range were examined. The shape of such distributions when presented as histograms may be sensitive to bin size (Venables & Ripley 2002), so we calculated the kernel density (KD), using a fixed bandwidth of 1 d (duration) or 100 km (distance). We then tested the significance of KD slopes using the 'feature' package (Duong et al. 2008), identifying significant modes as features preceded by a significant positive slope and followed by a significant negative slope. As the apparent modality of distributions may vary with bandwidth (Venables & Ripley 2002), we examined modality across a wide range of plausible bandwidths using SiZer plots

(Chaudhuri & Marron 1999). As dual foraging may be evident only in some years (Granadeiro et al. 1998), separate frequency distributions were plotted if multiple years of data were available, but conclusions were the same. We examined relationships between satellite-trip characteristics using mixed-effects linear models fitted by Maximum Likelihood, treating individual bird as a random effect (Pinheiro & Bates 2000), and transforming the data where necessary. In each case we fitted one model with a first order serial autocorrelation term, and one without, selecting the most parsimonious by comparing the Akaike Information Criterion (Crawley 2007). Relationships between meal mass, previous and subsequent trip duration and maximum range, time since the previous feed by either parent and chick condition at departure and at return were examined in the same way. All statistical tests were carried out in R (R Foundation for Statistical Computing, Vienna).

RESULTS

The bathymetric regime of waters accessible to albatrosses breeding at South Georgia is complex (Fig. 1). Although the neritic zone around South Georgia and Shag Rocks is relatively narrow, it is surrounded by extensive areas of shelf slope. At intermediate distances from the colonies are oceanic waters and areas of elevated productivity associated with the APFZ. Within 1000 km of South Georgia, extensive tracts of slope and neritic waters of the Patagonian Shelf, South Orkney Islands, South Shetland Islands and Antarctic Peninsula are available, which are all areas of high primary productivity. Satellite-tracked birds of all 4 species undertook trips both to local and more distant areas (Fig. 2).

In all species, correlations between trip duration, maximum foraging range and cumulative travel distance were highly significant (Table 1). KD and 'feature' analysis of the distributions of trip duration indicated that they were positively skewed and unimodal, with the majority of trips short in duration in wandering, black-browed and grey-headed albatrosses (Fig. 3). No clear mode was apparent in the distribution of trip durations in light-mantled albatross. None of the distributions provided any indication of significant bimodality, and SiZer plots showed that this conclusion was consistent across a range of plausible bandwidths (Fig. 4). Although visual examination of histograms suggested the possibility of bimodality in maximum foraging ranges of black-browed, grey-headed, and particularly wandering albatross, with only 3 % of trips of 400 to 900 km (Fig. 3), KD and SiZer plots showed that in all species and at all bandwidths, distributions were unimodal (Figs. 3 & 4).

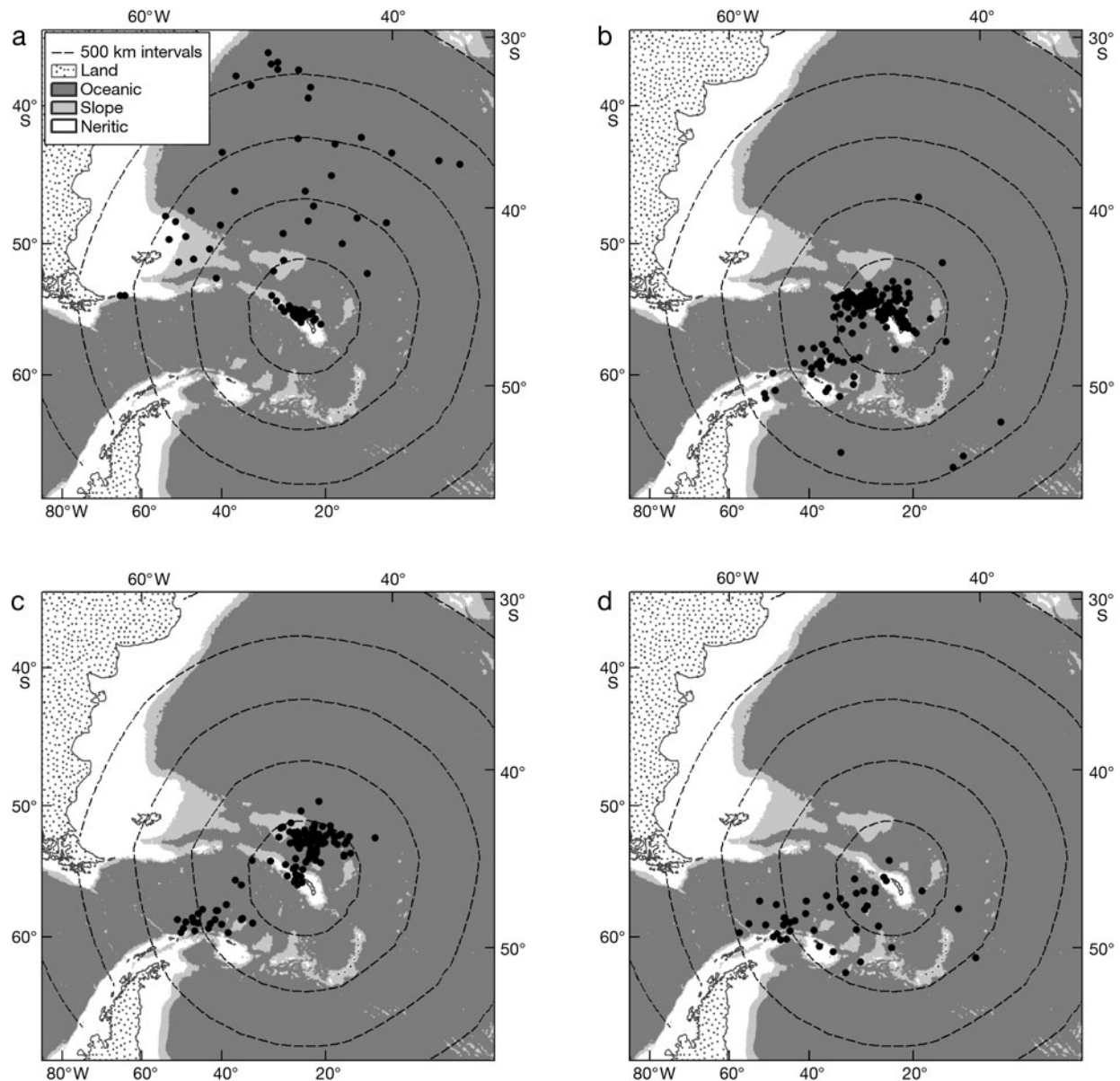


Fig. 2. Mean positions of foraging phases of trips made by (a) 49 wandering albatrosses ($n = 74$ trips from 2002 and 2004), (b) 12 black-browed albatrosses ($n = 237$ trips from 2002), (c) 10 grey-headed albatrosses ($n = 123$ trips from 2001), and (d) 4 light-mantled albatrosses ($n = 38$ trips from 2003) tracked from Bird Island, South Georgia (see 'Materials and methods' for details)

Histograms of trip durations for individual black-browed, grey-headed and light-mantled albatrosses are indicated in Fig. 5. Although the small sample sizes preclude statistical analyses, it is clear that while distributions from some individuals deviated from the pattern typical of the population as a whole (cf. Fig. 3), none were strongly bimodal. With the exception of one grey-headed albatross, none of the satellite-tracked individuals showed any regular pattern in the sequence of trip lengths, trip distance or predominant bathymetric regime visited (Fig. 5). Some black-browed albatrosses carried out only relatively short,

local trips (Birds 1 & 4), while another (Bird 11) spent most of its time carrying out longer trips, to distant areas. However, very long trips ($\sim 3 \times$ the mean trip length or more) never occurred consecutively. Some birds apparently favoured a particular type of habitat (e.g. black-browed albatross no. 1 spent all of its time in neritic and slope waters, whereas black-browed albatross no. 8 spent the majority of its time in oceanic and slope waters; grey-headed albatross no. 1 spent all of its time in oceanic waters). Local trips by black-browed and wandering albatrosses tended to be to neritic and slope waters (92 and 100 % of trips, respec-

Table 1. Summary of goodness of fit (r^2 values) and gradient (+ve, -ve or non-significant) for fixed effects in linear mixed-effects models of foraging and provisioning characteristics of albatrosses from South Georgia. Models account for serial autocorrelation and individual (as random) effects. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Variable	No. adults	No. trips	r^2	p	Gradient
Black-browed albatross (Jan–Mar 2002)					
Duration (h) vs. Cumulative distance (km)	12	237	0.91	***	+
Duration (h) vs. Max. range (km)	12	237	0.68	***	+
Cumulative distance (km) vs. Max. range (km)	12	237	0.88	***	+
Duration (h) vs. Meal mass (g)	46	867	0.08	***	+
Max. range vs. Meal mass (g)	12	195	0.06	***	+
Interval ^a (h) vs. Meal mass (g)	46	863	0.05	***	+
Chick condition on arrival ^b vs. Meal mass (g)	46	867	0.09	***	–
Chick condition on arrival ^b vs. Interval ^a	46	842	0.45	***	–
Chick condition on departure ^b vs. Duration ^c (h)	46	832	0.01	**	+
Chick condition on departure ^b vs. Max. range ^c (km)	12	185	0.00	0.25	n/a
Chick condition on departure ^b vs. Meal mass ^c (g)	46	832	0.01	*	–
Grey-headed albatross (Jan–Mar 2001)					
Duration (h) vs. Cumulative distance (km)	10	123	0.85	***	+
Duration (h) vs. Max. range (km)	10	123	0.66	***	+
Cumulative distance (km) vs. Max. range (km)	10	123	0.89	***	+
Duration (h) vs. Meal mass (g)	46	182	0.09	***	+
Max. range vs. Meal mass (g)	10	27	0.00	0.34	n/a
Interval ^a (h) vs. Meal mass (g)	46	164	0.11	***	+
Chick condition on arrival ^b vs. Meal mass (g)	46	205	0.01	0.21	n/a
Chick condition on arrival ^b vs. Interval ^a	46	194	0.01	0.10	n/a
Chick condition on departure ^b vs. Duration ^c (h)	46	213	0.01	0.05	n/a
Chick condition on departure ^b vs. Max. range ^c (km)	10	34	0.01	0.28	n/a
Chick condition on departure ^b vs. Meal mass ^c (g)	46	70	0.02	0.13	n/a
Light-mantled albatross (Jan–May 2003)					
Duration (h) vs. Cumulative distance (km)	4	38	0.95	***	+
Duration (h) vs. Max. range (km)	4	39	0.55	***	+
Cumulative distance (km) vs. Max. range (km)	4	38	0.69	**	+
Duration (h) vs. Meal mass (g)	8	66	0.15	0.12	+
Max. range vs. Meal mass (g)	4	29	0.05	**	n/a
Interval ^a (h) vs. Meal mass (g)	8	66	0.10	0.14	+
Chick condition on arrival ^b vs. Meal mass (g)	8	66	0.02	***	n/a
Chick condition on arrival ^b vs. Interval ^a	8	67	0.29	0.25	–
Chick condition on departure ^b vs. Duration ^c (h)	8	67	0.01	0.37	n/a
Chick condition on departure ^b vs. Max. range ^c (km)	4	30	0.00	0.18	n/a
Chick condition on departure ^b vs. Meal mass ^c (g)	8	66	0.01	***	n/a
Wandering albatross (Jul–Oct 2002, Apr–Oct 2004)					
Duration (h) vs. Cumulative distance (km)	45	74	0.92	***	+
Duration (h) vs. Max. range (km)	45	74	0.84	***	+
Cumulative distance (km) vs. Max. range (km)	45	74	0.93	***	+

^aInterval since last meal by either adult, ^bresiduals from separate regressions of mass upon age for each chick, ^con subsequent trip

tively; Fig. 2). In contrast, local trips by grey-headed and light-mantled albatrosses were to oceanic waters (67 and 62 %, respectively). Distant trips by the smaller species were most often to shelf or neritic waters (56 to 79 % of trips) but those made by wandering albatrosses were most often to oceanic (68 %) or slope waters (26 %).

Both black-browed and grey-headed albatrosses showed some synchronicity in trip characteristics across individuals (Fig. 6). Black browed albatross trips commencing in the 5 d before Day 35 (01 March 2002) tended to be short and to local waters, while those commencing in the subsequent 5 d were most frequently long and to distant waters. This reflected a switch from trips predominantly to the west of South

Georgia in local neritic and slope waters around Shag Rocks, to trips to distant slope and neritic waters around the South Orkney Islands and the Antarctic Peninsula (Fig. 6a,b). Similarly, grey-headed albatrosses tended to make short to long oceanic trips, predominantly to APFZ waters north of South Georgia before Day 23 (28 February 2001), then longer trips to slope waters of the South Orkney Islands and the Antarctic Peninsula thereafter (Fig. 6c,d).

Relationships among provisioning characteristics having accounted for serial autocorrelation and individual (as a random effect) in mixed-effects linear models are indicated in Table 1. In black-browed, grey-headed and light-mantled albatross, meal mass showed a sig-

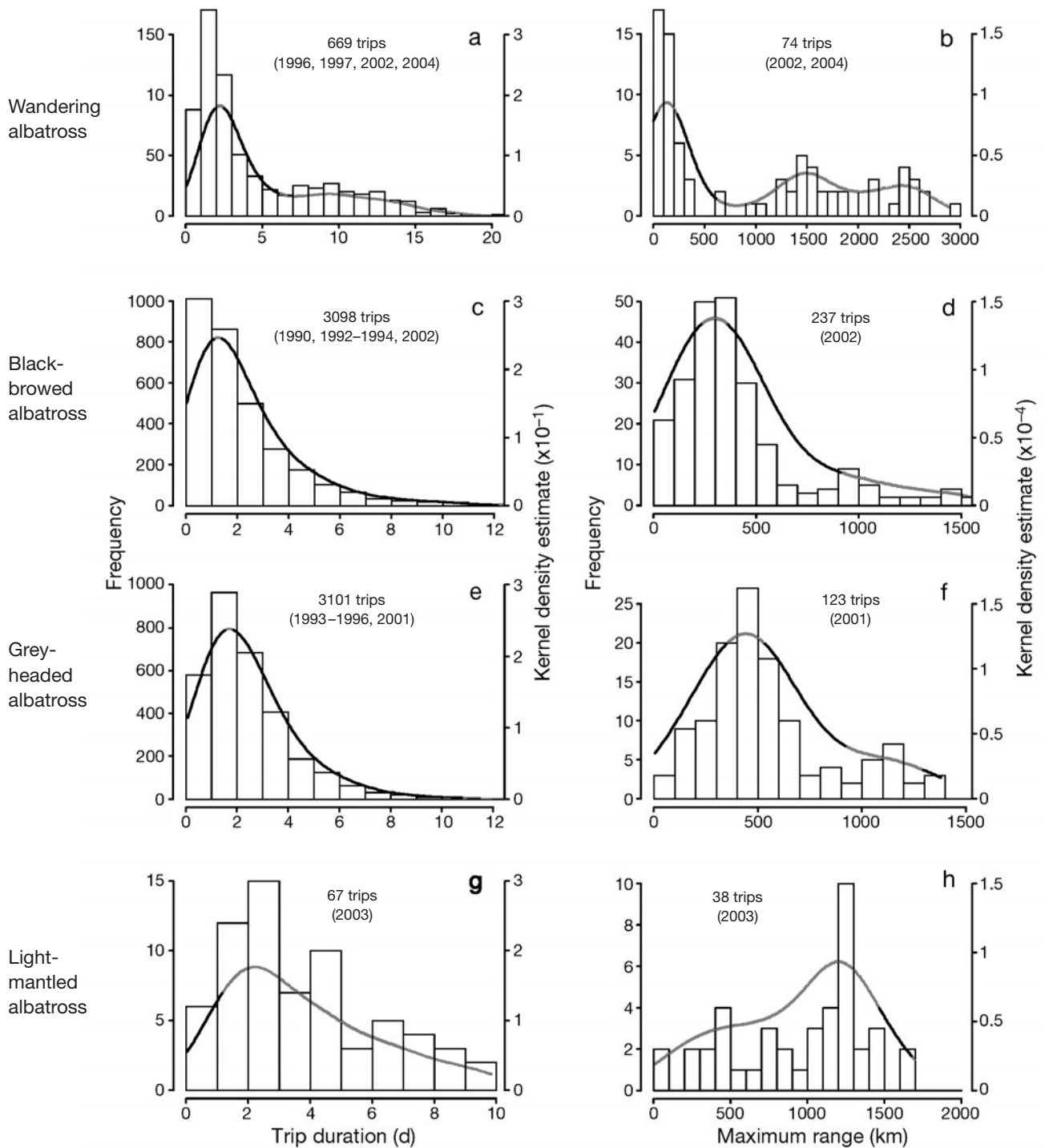


Fig. 3. Foraging trips of 4 albatross species from Bird Island, South Georgia. Frequency histograms showing trip duration (left) and maximum range (right). Black/grey lines: kernel density estimate (bandwidth 1 d or 100 km)—black: significant slope, grey: non-significant slope (see 'Materials and methods' for details)

nificant positive correlation with the duration of the foraging trip and the interval since the previous meal delivered by either adult ($r^2 = 0.08$ to 0.15). There was also a significant, negative correlation between meal mass and the condition of the chick on arrival in black-

browed albatross. Chick condition was closely related (negatively) with the interval since the last meal in black-browed ($r^2 = 0.45$) and light-mantled albatross ($r^2 = 0.29$). Closer examination indicated curvilinear asymptotic relationships between meal mass and trip

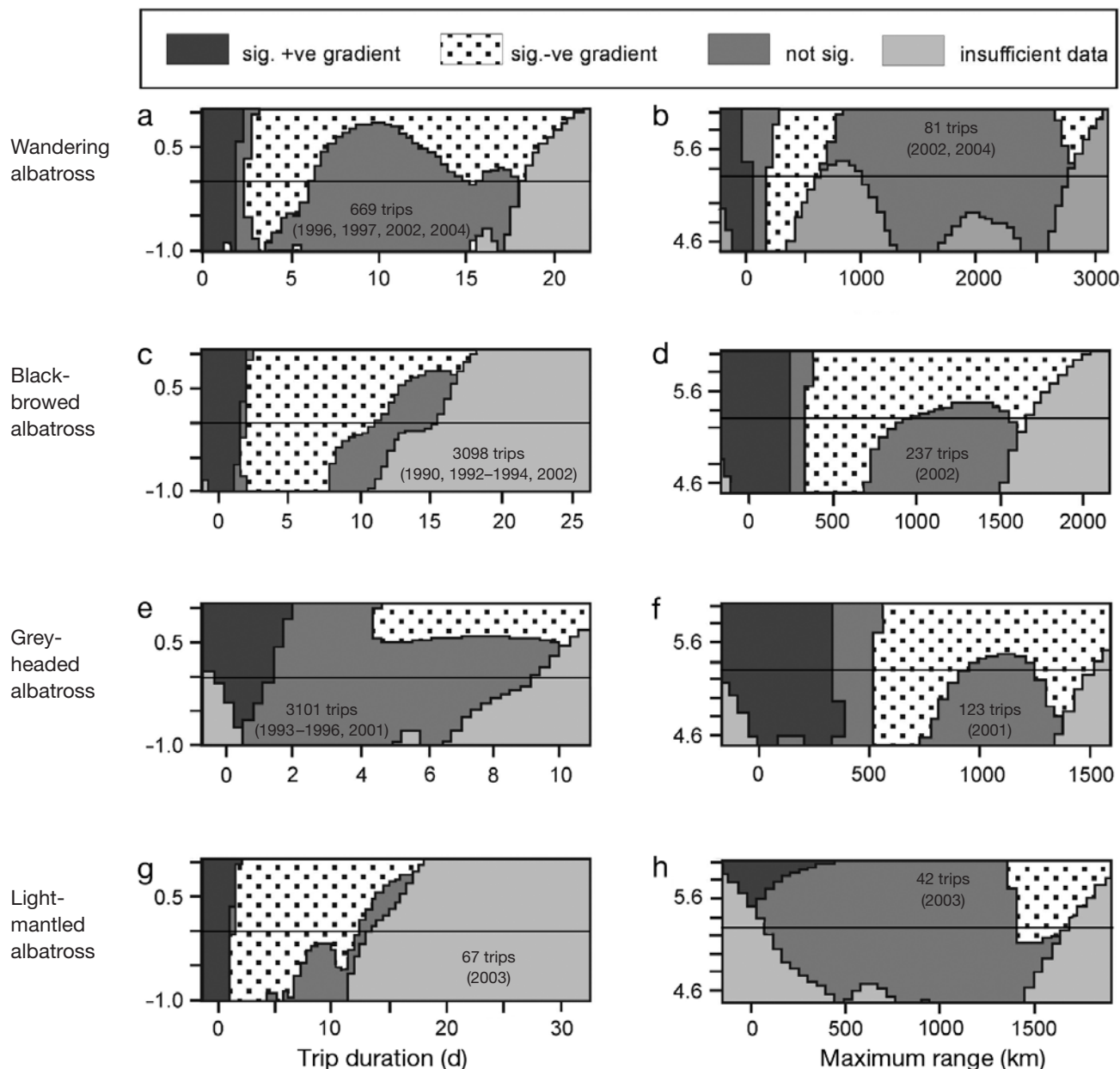


Fig. 4. Foraging trips of 4 albatross species from Bird Island, South Georgia. SiZer plots (Chaudhuri & Marron 1999) of trip duration (left) and maximum range (right). Horizontal lines indicate a bandwidth of 1 d (a,c,e,g) or 100 km (b,d,f,h). In all cases, a single instance of a significantly positive gradient followed by a significantly negative gradient occurs at the majority of bandwidths, indicating that all distributions are unimodal

duration, with smaller than average meals delivered after shorter periods (1 to 2 d) spent at sea (Fig. 7). Based on these data, prey delivery rates were far higher after trips of 1 d than of 2 d (means of 515 vs. 281, 517 vs. 320 and 416 vs. 227 g d⁻¹ for black-browed, grey-headed and light-mantled albatross, respectively), and were even lower thereafter. Meal mass showed a significant positive, albeit relatively weak relationship with maximum range in black-browed albatross only ($r^2 = 0.06$). Only in black-browed albatross were there

relationships between chick condition at departure and the subsequent trip duration (significant, positive) and meal mass (significant, negative). However, these were very weak ($r^2 = 0.01$).

DISCUSSION

There was no evidence of significant bimodality in frequency distributions of trip duration and maximum foraging range of any species in this study (Fig. 3). This

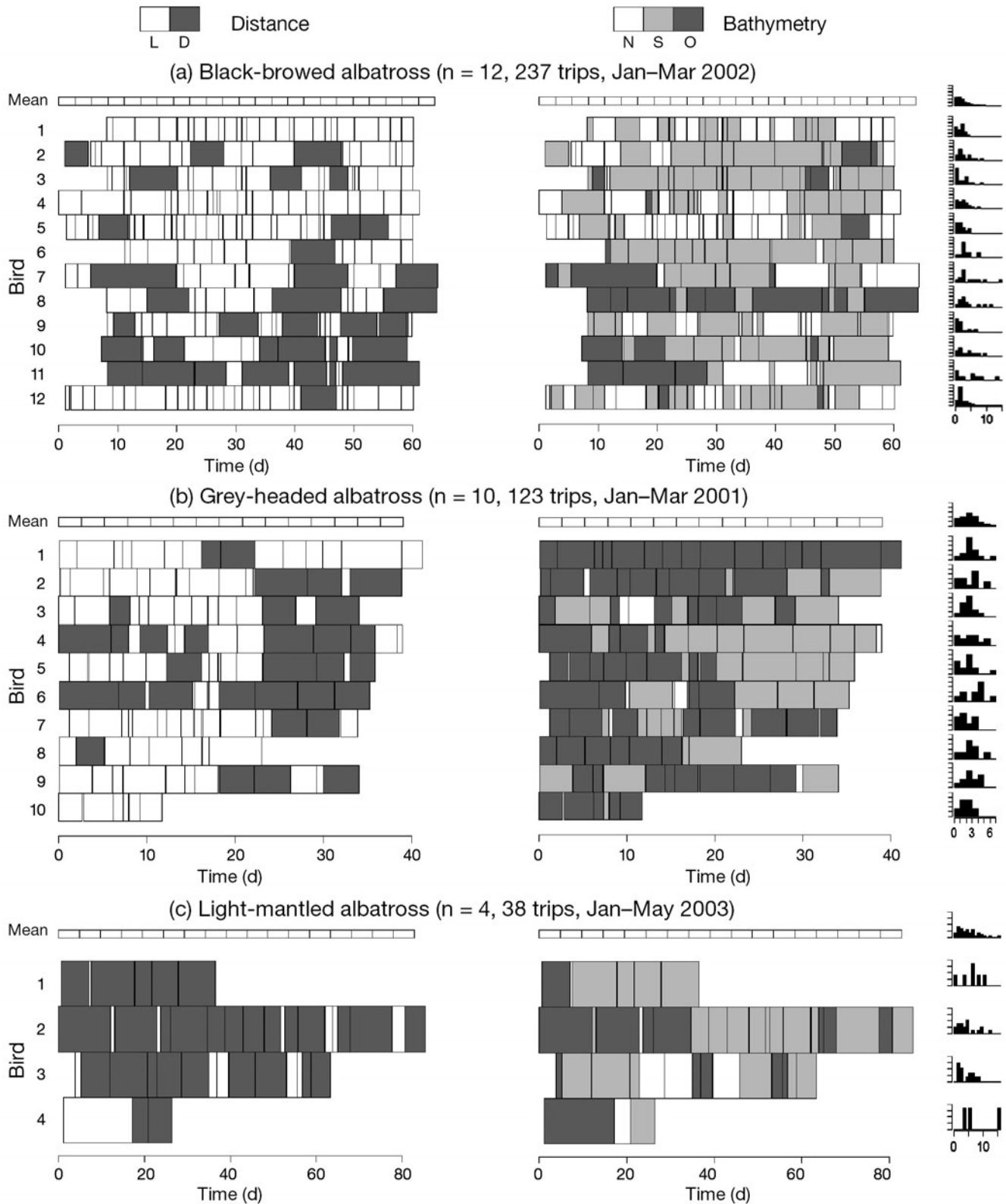


Fig. 5. Foraging trips of 3 albatross species from Bird Island, South Georgia. Length of consecutive trips classified by predominant distance to the colony (left) during the foraging phase (L = local, ≤ 500 km; D = distant, > 500 km), and predominant bathymetric regime (right) (N = neritic, S = slope, O = oceanic; see 'Material and methods' for details). Mean trip lengths indicated by scale bar. Histograms show mean and individual trip length distributions

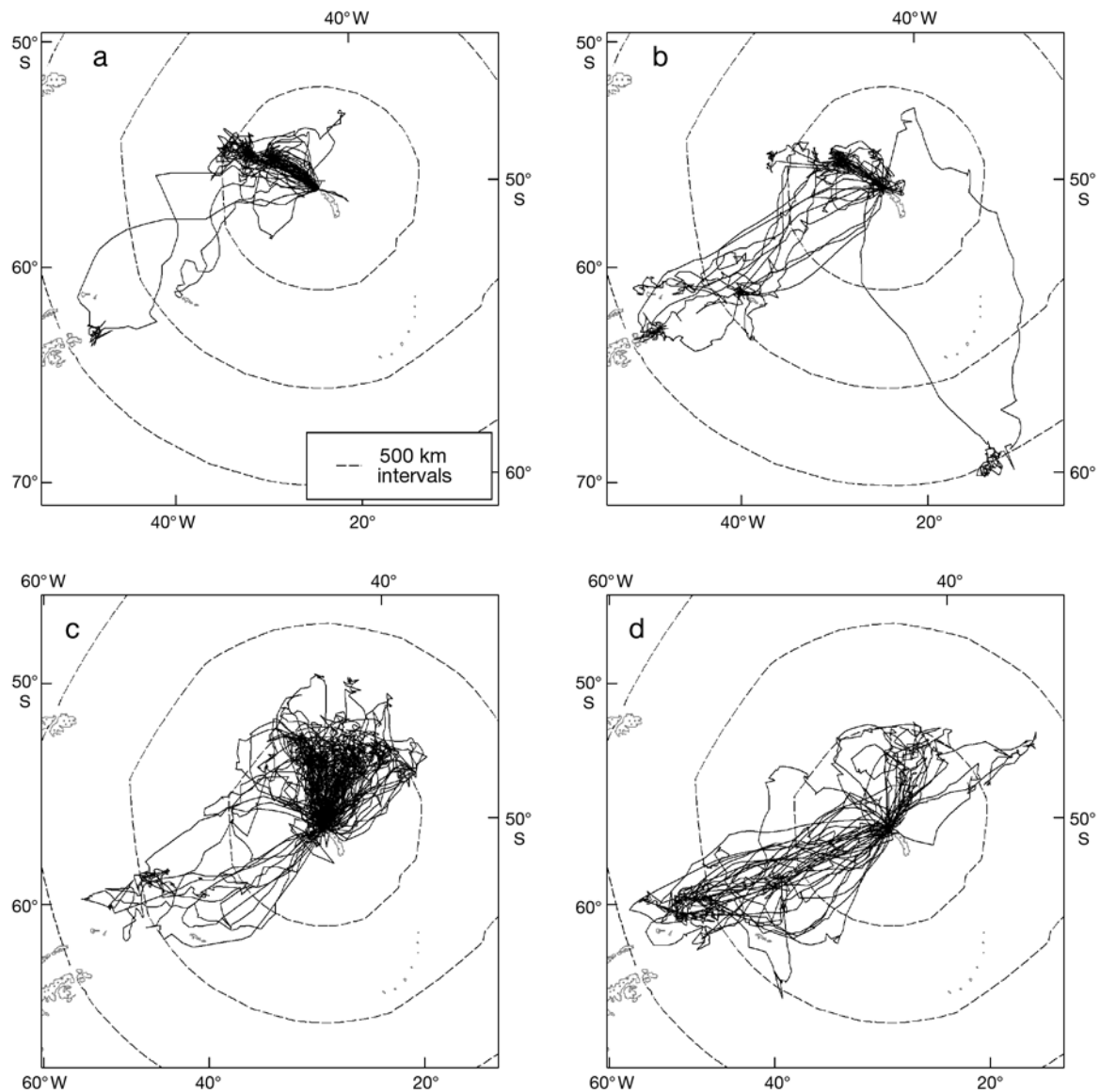


Fig. 6. Consecutive foraging trips by 12 black-browed albatrosses, commencing in the 5 d either (a) before or (b) after 1 March 2002, and by 10 grey-headed albatrosses, commencing in the 5 d (c) before or (d) after 28 February 2001

was despite visual examination of histograms suggesting that 2 modes might be a possibility, particularly for the wandering albatross, which had a somewhat disjunct distribution of maximum foraging range, with few trips between 400 and 900 km away from the colony (Fig. 3b). In addition, in a previous study involving a subset of the data presented here, there was some suggestion of bimodality in the frequency distribution of trip durations in 1 of 2 years (Berrow & Croxall 2001). However, none of these suspicions were borne out by our rigorous statistical analysis. Nor was there evidence of bimodality in trip durations of any of the individuals satellite-tracked for an average of 10 to 20 consecutive foraging trips (Fig. 5).

The existence of a dual foraging strategy was superficially supported by the observation that it was relatively rare for most birds to perform 2 consecutive very long trips (although a few black-browed albatrosses and some grey-headed albatrosses did so; Fig. 5). In addition, examination of consecutive foraging tracks from the same individuals indicates that after a variable number of shorter trips some birds did switch to longer trips, to more distant destinations. The critical question is therefore, whether these results are sufficient grounds for concluding that birds adopt a general dual foraging strategy *sensu* Weimerskirch et al. (1994), comprising short foraging trips over the nearby shelf that maximise energy delivery rate to the chick,

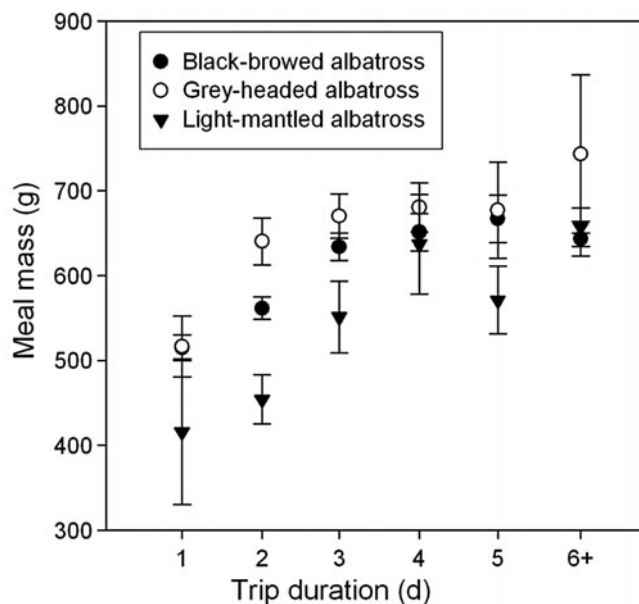


Fig. 7. Relationships between foraging trip duration and meal mass in black-browed ($n = 867$), grey-headed ($n = 182$), and light-mantled albatross ($n = 66$) at South Georgia in 2002, 2001 and 2003, respectively. Data are means \pm SE

alternated with longer trips over distant oceanic water that allow the restoration of the adult's body condition.

Particularly for the smaller albatrosses at South Georgia, most evidence runs contrary to the dual foraging hypothesis as stated: (1) no species exhibited 2 modes in the frequency distributions of trip durations; (2) although these species exploit 2 or more discrete foraging grounds, the longest trips (>1000 km) are to distant shelf and shelf-slope rather than oceanic waters. However, note that subsequent interpretation of the dual foraging theory (e.g. Granadeiro et al. 1998, Peck & Congdon 2005) is that adults feed either in nearby and relatively unproductive waters, or in distant, more productive areas, and water depth per se is not considered important; (3) mixing of short and long trips was far from a universal characteristic—indeed, 2 of 12 black-browed albatrosses tracked for >50 d spent the entire period commuting to feeding areas within 500 km of the colony and never engaged in a longer trip. To be sustained for such long periods, it follows that short trips are profitable for both adults and chicks.

Other results emphasised the importance of environmental factors in foraging decisions. We observed incidences of trip synchronicity in both black-browed and grey-headed albatrosses (Fig. 6). Given the timescale of a few days, the most likely explanation is that these resulted from variation in the environment (such as a change in prey abundance or availability, or in the wind field). It is important to note that there are no significant changes in mean trip duration while chicks are between ca. 35 and 95 d old in black-browed or grey-

headed albatrosses (Huin et al. 2000), and therefore these sudden switches do not have an ontogenetic origin. In addition, detailed analysis of tracks indicates that individuals sometimes first fly to a nearby foraging area and only if ingestion rate is low will they switch to an alternative, more distant foraging ground (Xavier et al. 2003, Catry et al. 2004). Therefore, longer trips are sometimes triggered by poor feeding conditions encountered in the initial time at sea (also see Kato et al. 2008). Such results do not refute the dual foraging hypothesis, as it could be argued that the final trip destination was influenced by the adult's dwindling reserves in the first few days (indeed, this is almost impossible to disprove). However, they do emphasise that extrinsic factors have a major influence.

So, why do albatrosses at South Georgia apparently not use a dual foraging strategy, and is this unusual? As far as we are aware, only one penguin species and only a proportion of albatrosses and petrels (and none of the storm or diving petrels, or other pelagic seabirds such as gannets, boobies and frigatebirds) use such a strategy during post-brood, and it is sometimes facultative, varying spatially (between populations) or temporally (between years), relative to resource distribution and abundance (Clarke et al. 1998, Granadeiro et al. 1998, Baduini & Hyrenbach 2003, Peck & Congdon 2005). In general, the incidence of dual foraging is greater (although not significantly) in populations breeding in tropical-subtropical and temperate areas compared with higher latitude subpolar-polar regions, and where the adjacent shelf is small-intermediate in size (Baduini & Hyrenbach 2003). Hence, our results are less exceptional than could be supposed.

Baduini & Hyrenbach (2003) also found that in species with a dual strategy, chl *a* concentrations were significantly higher (but not less variable) in the distant compared with the nearby foraging areas. Differing diets, prey biogeography and habitat accessibility may explain why albatrosses breeding at South Georgia do not exhibit the marked bimodality in trip characteristics reported for other populations. During post-brood, South Georgia albatrosses make extensive use of nearby neritic waters (wandering and black-browed albatrosses), the APFZ (black-browed and grey-headed albatrosses), and the central Scotia Sea and distant shelf-slope and shelf of the South Orkneys and Antarctic Peninsula (black-browed, grey-headed and light-mantled albatross) (Prince et al. 1998, Phillips et al. 2004, 2005a, Xavier et al. 2004). These regions are within a 500 km radius of the colony, with the exception of the southern Scotia Arc (600 to 1400 km to the south).

Few fishing vessels operate within the foraging ranges of the 3 smaller albatrosses during chick-rearing, therefore, only in wandering albatross (which is a

winter breeder) is at-sea distribution potentially influenced by fishing effort. Within the broad range of Antarctic waters exploited by the 3 smaller albatrosses, primary productivity and prey availability may be sufficiently high and predictable, and the choice of foraging locations sufficiently diverse, for there to be no selective advantage in the adoption of a dual strategy. This is particularly so for the south-west Atlantic, which is one of the most productive regions of the Southern Ocean, supporting >50% of global stocks of Antarctic krill *Euphausia superba*, a major prey item of the smaller South Georgia albatrosses (Sullivan et al. 1993, Atkinson et al. 2004). Although the wandering albatross raises its chick during the Antarctic winter when oceanic productivity has dropped, and feeds very little on krill, instead visiting the Patagonian Shelf and shelf-break, or engaging in long, looping journeys far to the north to feed on the large squid *Kondakovia longimana* in temperate and subtropical waters (Prince et al. 1998), it too may have widespread feeding opportunities, which would explain its routinely high breeding success (Croxall et al. 1998). By inference, we might therefore expect that where other species or populations adopt a dual foraging strategy, this reflects greater heterogeneity in resource availability in the waters surrounding those colonies.

In black-browed but not grey-headed or light-mantled albatross, chick condition at departure showed a significant but weak ($r^2 = 0.01$) relationship with subsequent trip duration and meal mass. Hence, in black-browed and Indian yellow-nosed *Thalassarche carteri* albatross at colonies in the Indian Ocean, but only 1 of 3 species at South Georgia and neither grey-headed nor Campbell albatross *T. impavida* at Campbell Island, is there evidence that adult albatrosses actively modify their foraging behavior in this way (Waugh et al. 2000, Weimerskirch et al. 2001, this study). By comparison, all 3 studies found stronger relationships between meal mass and the length of the foraging trip, the period since the last feed by either parent, and chick condition on arrival. Certainly for black-browed, grey-headed and light-mantled albatross breeding at South Georgia, regulation of provisioning is primarily a reactive process according to immediate chick requirements, rather than a proactive anticipation of future needs. Without experimental manipulation it is difficult to determine whether parents reduce the amount fed to chicks in good condition and/or increase that fed to those that are recently underfed, although the former seems more likely. Either could be based on an assessment of chick status through some visual or auditory cue such as begging, or result from the incapacity of a chick that has been well-fed to ingest the adult's entire stomach contents (Tveraa et al. 1998, Phillips & Croxall 2003).

Our results suggest that adults have either little or no capacity or inclination to actively change their foraging patterns in response to chick requirements. Certainly, the foraging destination is not dictated by chick condition. Although in theory adults might elevate work rates by increasing the number of landings and take-offs, flying faster, making longer commuting flights and spending less time resting etc., the extremely strong relationships ($r^2 = 0.55$ to 0.95) between trip duration, cumulative travel distance and maximum range indicate more or less the same average travel speed irrespective of the number of days at sea or distance to the furthest destination. This is suggestive of relatively uniform foraging effort, but would need to be confirmed by analysis of activity patterns.

Asymptotic relationships between meal mass and trip duration (Fig. 7) indicate that if adults can gather a sizeable meal relatively quickly (i.e. within 1 to 2 d), they may return with a less than maximum payload. If at sea for longer, however, which usually means that they have travelled further afield, they do not return until an optimal mass of prey has been collected, presumably because of the inefficiency of commuting with a small load. This threshold almost certainly derives from wing loading or other structural considerations limiting payload (Phillips & Hamer 2000). In addition, the adult has no knowledge of how well its partner has been feeding in the meantime (feeding success is highly variable as a consequence of the patchy nature of marine prey) and therefore cannot risk returning with a small payload. Results indicate that benefits to the chick were almost certainly greater after short trips. Although energy density of meals delivered after longer periods could be higher because of increased oil content (e.g. Chaurand & Weimerskirch 1994), this would be insufficient to compensate for the substantial reduction in prey delivery rate (g d^{-1}) of at least 60 to 80% after trips of 2 or more days.

To conclude, we suggest that adult albatrosses at South Georgia do neither utilise a dual foraging strategy *sensu* Weimerskirch et al. (1994), nor actively regulate provisioning according to chick condition. No information on adult mass was collected because of the unacceptable level of disturbance that would have resulted from repeated weighing of albatrosses that were typically tracked for 10 to 25 foraging trips, and so we were unable to assess the importance of adult condition in determining foraging destinations and durations. Although it is highly likely that foraging behaviour and strategies were also modulated by current adult condition, as in many other seabirds (Tveraa et al. 1998, Weimerskirch 1998, Kato et al. 2008), at least at South Georgia it would appear that many of the decisions about foraging destination are also strongly influenced by exogenous, stochastic processes. While

we would not dispute the compelling evidence for dual foraging in many species and populations, our results underline that it is a facultative rather than an obligate strategy. We therefore caution against the assumption of dual foraging in other studies without robust statistical testing of frequency distributions and other supporting evidence.

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Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean

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ABSTRACT: We determined the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of individual amino acids (AAs) isolated from chick blood of 4 penguin species that forage in different oceanic regions (from the subtropics of the Indian Ocean to Antarctica) to test if: (1) the $\delta^{15}\text{N}$ values of phenylalanine ($\delta^{15}\text{N}_{\text{phe}}$) revealed different foraging areas among the species; (2) the difference between glutamic acid and phenylalanine $\delta^{15}\text{N}$ values ($\Delta\delta^{15}\text{N}_{\text{glu-phe}}$) accurately predicted trophic levels; and (3) the $\delta^{13}\text{C}$ value of AAs could resolve species foraging locations, similar to bulk $\delta^{13}\text{C}$ values. The $\delta^{13}\text{C}$ values of all AAs decreased with latitude, were positively correlated with bulk $\delta^{13}\text{C}$ data, and, therefore, tracked the isotopic baseline. However, we were not able to discern additional ecological information from these $\delta^{13}\text{C}$ values. In contrast, the $\delta^{15}\text{N}$ values of AAs distinguished the isotopic value of the nitrogen at the base of the food web from the trophic level of the consumer, providing new insight for the study of the trophic ecology of seabirds. The difference in the bulk $\delta^{15}\text{N}$ values of northern and southern rockhopper penguins *Eudyptes chrysocome* ssp. was due to both a difference in their foraging location (different $\delta^{15}\text{N}_{\text{phe}}$) and their trophic levels (different $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$). The $\delta^{15}\text{N}_{\text{phe}}$ values of king *Aptenodytes patagonicus* and Adélie penguins *Pygoscelis adeliae* were higher than those of rockhoppers, which could reflect a foraging on mesopelagic prey for king penguins and, in the highly productive Antarctic shelf waters, for Adélie penguins. The $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ accurately reflected the relative trophic level of penguins, but further work is required to determine the trophic enrichment factors for compound-specific isotope analysis.

KEY WORDS: $\delta^{15}\text{N}$ · $\delta^{13}\text{C}$ · Compound specific · Isotopic niche · Trophic level

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INTRODUCTION

Determining dietary preference together with foraging habitat of marine predators can be challenging because of the extent of their pelagic environment and their long-distant movements. Traditionally, the diet of predators has been determined by stomach content,

bulk stable isotopes, and fatty acid analyses (Hyslop 1980, Michener & Schell 1994, Iverson et al. 2004). Foraging habitat can be investigated with tagging technologies (Wienecke et al. 2000, Charrassin & Bost 2001, Bost et al. 1997) or by linking a predator's stable isotope compositions with the isotope values of the local environment (Lee et al. 2005, Cherel et al. 2006,

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2007, Wallace et al. 2006). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of phytoplankton at the base of marine food webs can vary greatly due to different factors including phytoplankton community composition, nutrient utilization, differences in nutrient sources (e.g. denitrification vs. N_2 fixation) and the subsequent biological transformations of these nutrients (Altabet 2001, Sigman & Casciotti 2001, Karsh et al. 2003, Tamelander et al. 2009). The resulting spatial gradients in phytoplankton or zooplankton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (e.g. inshore/offshore, pelagic/benthic, latitudinal) have been shown to propagate up to consumers and have served as proxy values for the foraging habitat of consumers (Best & Schell 1996). For example, bulk $\delta^{13}\text{C}$ values have been used to determine the foraging habitats of cetaceans and seabirds (Best & Schell 1996, Cherel et al. 2006, 2007, Quillfeldt et al. 2005), and bulk $\delta^{15}\text{N}$ values have been used to delineate temporal changes in the foraging regions of marine mammals (e.g. Burton & Koch 1999, Newsome et al. 2007). However, only a few of these studies directly compare the baseline and predator isotope values (Lee et al. 2005). Instead, the spatial variation in the isotopic baseline is inferred by knowledge of the local oceanography and from previous studies that characterized variations in the isotopic baseline from isotopic analyses of, e.g., particulate organic matter (POM) or zooplankton (Cherel & Hobson 2007, Ménard et al. 2007). A spatial knowledge of baseline isotope variations and an understanding of the physiology and ecology of the marine predator are required for interpretation of the bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of predators. However, characterizing the isotopic baseline at the scale of ocean basins is logistically challenging (Jennings & Warr 2003) and speculative for historical periods when archived specimens are examined.

Recent evidence suggests that compound-specific isotopic analyses (CSIA) of individual amino acids (AAs) isolated from marine consumers could distinguish the isotopic value of the nitrogen at the base of the food web from the trophic level (TL) of the consumer (McClelland & Montoya 2002, Chikaraishi et al. 2007, Popp et al. 2007, Hannides et al. 2009). Results of the laboratory experiments by McClelland & Montoya (2002) showed that the $\delta^{15}\text{N}$ value of 'trophic' AAs (e.g. glutamic acid) can be enriched by as much as ~7‰ in the marine rotifer *Brachionus plicatilis* relative to the $\delta^{15}\text{N}$ value in the alga *Tetraselmis suecica*, whereas other 'source' AAs (e.g. phenylalanine) are little affected by trophic status and retain the $\delta^{15}\text{N}$ values of the phytoplankton or cyanobacteria at the base of this food web. The implication of these results are that both TL and the nitrogen isotopic baseline where predators foraged can be determined by analyzing only the $\delta^{15}\text{N}$ values of individual AAs isolated from a predator's

tissue (see also Schmidt et al. 2003, Popp et al. 2007, Hannides et al. 2009). However, to date, CSIA of individual AAs has mainly been applied to low TLs (McClelland & Montoya 2002, Schmidt et al. 2004, Chikaraishi et al. 2007, Hannides et al. 2009), with only one vertebrate predator study (tuna; Popp et al. 2007), and no work has yet been conducted on birds or mammals. Carbon CSIA on individual AAs has mainly focused on the metabolic pathways of animals (e.g. O'Brien et al. 2005), but the results of Fantle et al. (1999) on blue crabs suggested that the $\delta^{13}\text{C}$ values of individual AAs (both essential and non-essential AAs) could complement bulk isotopic results to decipher a consumer's food sources.

In the present paper, we analyzed the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of individual AAs isolated from chick blood of 4 Southern Ocean penguin species: northern rockhopper (NRP, *Eudyptes chrysocome moseleyi*), southern rockhopper (SRP, *Eudyptes chrysocome chrysocome*), king (KP, *Aptenodytes patagonicus*) and Adélie (AP, *Pygoscelis adeliae*) penguins. These Southern Ocean penguins could be ideal species to test the efficacy of AA $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analyses to determine the ecological niches of seabirds, as their food habits and foraging regions are diverse and well documented (details in Cherel & Hobson 2007). Both bulk stable isotope and stomach content analyses showed different foraging strategies among these species (e.g. fish vs. crustaceans, see Table 1). Furthermore, their foraging habitats differ (see Table 1 and related references), and their breeding colonies are located at sites encompassing a large latitudinal range, from the subtropical Amsterdam Island north of the Subtropical Front, over the Crozet Islands in the Polar Frontal Zone to Adélie Island, Antarctica (Table 1). These regions exhibit different oceanographic characteristics (temperature, chlorophyll *a* concentrations, sea-ice extent) that could lead to spatial variations in the carbon and nitrogen isotopic compositions at the base of the food web (see Fig. 1; Altabet & François 1994, Trull & Armand 2001). In the southwest Indian Ocean, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of POM show an abrupt decrease between 40 and 45° S (François et al. 1993, Altabet & François 1994), leading to a north–south gradient across the subtropical frontal zone. This latitudinal gradient can, however, be complicated by inshore–offshore productivity gradients (Cherel & Hobson 2007), the influence of blooms and nutrient utilization (Karsh et al. 2003, Tamelander et al. 2009), the mixing of water masses across the frontal zone, and the contribution of sea-ice phytoplankton to the food web (Hobson et al. 1995, Gibson et al. 1999, Norkko et al. 2007).

The present study is the first to analyze carbon and nitrogen isotopes of individual AAs in seabirds, and also the first to analyze AAs isolated from whole blood.

It should be noted that adult penguins can segregate their diet from the food they feed their chicks (Cherel 2008). Our study is limited to the chicks' diet and the adults' foraging areas when they feed their chicks, but does not cover the adult's diet. Based on our current knowledge of this species, 3 predictions were tested:

1. NRP chicks have $\delta^{15}\text{N}$ values 2.4‰ higher than those of SRP chicks (Cherel & Hobson 2007). We expect this bulk isotopic difference to be mainly due to isotopic baseline differences in the areas where penguins feed. NRP forage in the Subtropical Zone, where $\delta^{15}\text{N}$ values of POM are higher than in the Polar Frontal Zone (Altabet & François 1994), where SRPs feed. Since phenylalanine is a source AA and should reflect the isotopic baseline, the $\delta^{15}\text{N}$ values of phenylalanine ($\delta^{15}\text{N}_{\text{phe}}$) in the blood of NRP should be higher than those of SRP (Cherel & Hobson 2007).

2. KP feed heavily upon fish compared to SRP, NRP and AP, which mainly eat crustaceans. Thus, KP should have the highest TL (Cherel et al. 2007, 2008); we, therefore, predict that KP will show the greatest difference between source and trophic AA $\delta^{15}\text{N}$ values.

3. High-latitude oceanic ecosystems (without considering onshore–offshore gradients) typically have much lower POM $\delta^{13}\text{C}$ values than subtropical regions (François et al. 1993, Goericke & Fry 1994) and reflect the $\delta^{13}\text{C}$ values of phytoplankton (Popp et al. 1999). The bulk $\delta^{13}\text{C}$ values of these penguins decreased with increasing latitude, which was attributed to the difference in the $\delta^{13}\text{C}$ values of the baseline in their respective foraging areas (Cherel & Hobson 2007). If some AAs provide information about the carbon source incorporated in food webs, the $\delta^{13}\text{C}$ values of these AAs should also track spatial variations in the $\delta^{13}\text{C}$ values and we expect the $\delta^{13}\text{C}$ value of some specific AAs to decrease with increasing latitude, similar to the bulk $\delta^{13}\text{C}$ values.

MATERIALS AND METHODS

Sample collection. A detailed description of breeding colony sites, collection methods and bulk isotope analyses for these penguin samples can be found in Cherel & Hobson (2007) and in our Table 1. We present here only a brief description of the methods used to collect blood samples from penguin chicks. Four species of penguins were sampled from 3 different breeding areas during the austral summer 2001/2002 (Fig. 1). NRP and SRP chicks were collected from Amsterdam Island and the Crozet Islands, respectively. KP chicks were also collected from the Crozet Islands, while AP chicks were collected at Pointe Géologie Archipelago in Adélie Land, Antarctica. The chicks were sampled at the end of the chick-rearing period, after most growth has already occurred, to minimize any growth effect on blood $\delta^{15}\text{N}$ values (Sears et al. 2009). During this period, food is only provided by the adults, and therefore the isotopic values of chick blood will reflect their diet and the foraging locations of adults. Chicks were selected at random from each site and whole blood was collected via venipuncture, stored in 70 % ethanol, and then at -20°C until analysis. Storage in 70 % ethanol does not alter the bulk $\delta^{15}\text{N}$ values of blood (Hobson et al. 1997, Bugoni et al. 2008), while some studies reported a slight increase in bulk $\delta^{13}\text{C}$ values of blood. Lipids were not removed from these samples, as it has been shown that the low lipid content of blood does not require lipid extraction prior to isotopic analysis (Cherel et al. 2005).

Sample preparation for CSIA. Prior to CSIA, ethanol was evaporated and the whole blood samples were freeze-dried. Blood samples from 3 chicks from each species were selected for CSIA. Preparation of blood samples for CSIA followed previous protocols for muscle samples (e.g. Popp et al. 2007, Hannides et al. 2009). Only an overview of the CSIA method is pre-

Table 1. Foraging characteristics and blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (means \pm SD) of penguin species during the chick-rearing period

Species	Locations	Foraging areas	Foraging range (km)	Chick diet	$\delta^{13}\text{C}$ (‰) ^a	$\delta^{15}\text{N}$ (‰) ^a	References
<i>Eudyptes chrysocome moseleyi</i> , northern rockhopper penguin	Amsterdam Island (37.8°S)	Subtropical Zone	<10	Squid & crustaceans	-19.5 ± 0.3 (n = 10)	9.2 ± 0.3 (n = 10)	Tremblay & Cherel (2003)
<i>Eudyptes chrysocome chrysocome</i> , southern rockhopper penguin	Crozet Islands (46.42°S)	Polar Frontal Zone	<10	Crustaceans	-21.2 ± 0.1 (n = 10)	6.8 ± 0.3 (n = 10)	Tremblay & Cherel (2003)
<i>Aptenodytes patagonicus</i> , king penguin	Crozet Islands (46.42°S)	Polar Front (50°S)	340–450	Pelagic fish	-22.6 ± 0.1 (n = 10)	10.3 ± 0.2 (n = 10)	Cherel et al. (1993), Charrassin & Bost (2001)
<i>Pygoscelis adeliae</i> , Adélie penguin	Adélie Land (66.7°S)	Antarctic Zone	<50	Crustaceans (fish)	-24.8 ± 0.5 (n = 9)	10.1 ± 0.8 (n = 9)	Wienecke et al. (2000)

^aBulk values of whole blood of penguin chicks during the austral summer in 2001 and 2002 from Cherel & Hobson (2007)

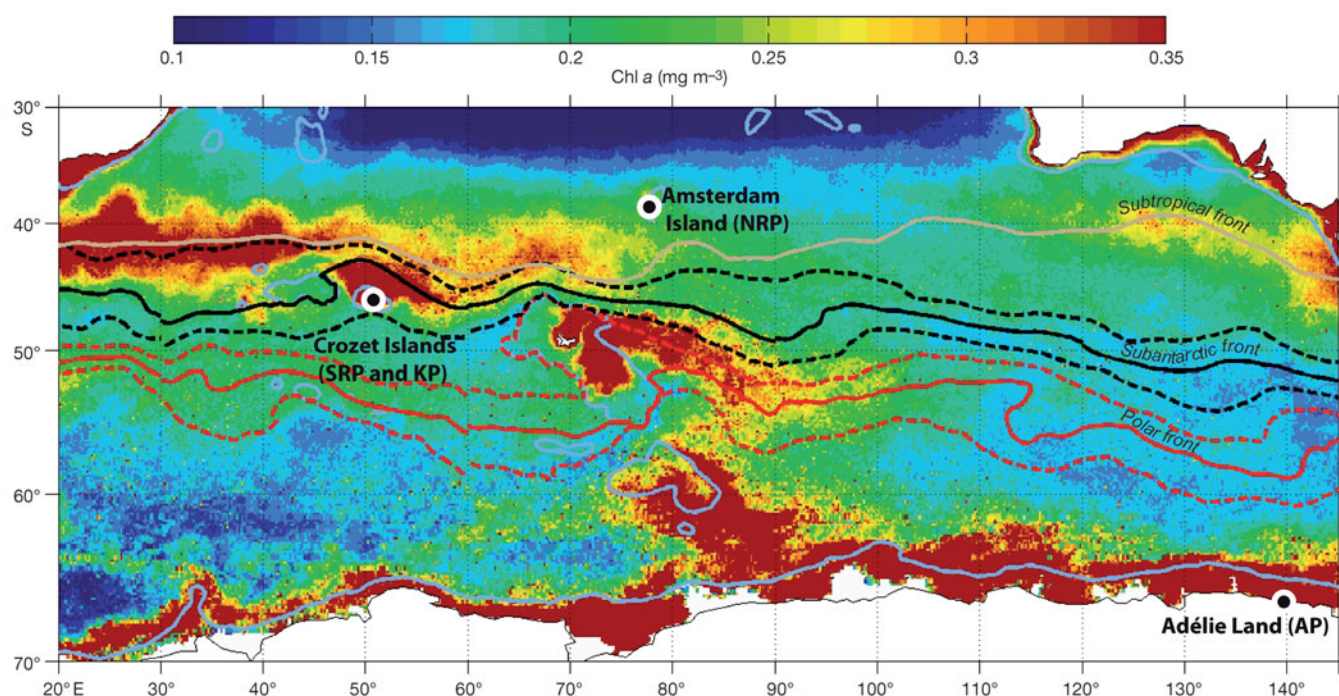


Fig. 1. Sampling locations (●) of the 4 penguin species in the Southern Ocean: northern rockhopper penguins (NRP, *Eudyptes chrysocome moseleyi*), southern rockhopper penguins (SRP, *Eudyptes chrysocome chrysocome*), king penguins (KP, *Aptenodytes patagonicus*), and Adélie penguins (AP, *Pygoscelis adeliae*). Mean chlorophyll distribution averaged over the period from October 1997 to October 2002 (mg m^{-3} , color scale) in the Southern Ocean overlaid with the Southern Ocean fronts. Mean ocean front positions (subantarctic and polar) are mapped using sea surface height (SSH) observations (adopted from Sokolov & Rintoul 2007, in press). The Subtropical front position (light brown line) is based on the temperature criteria in Sokolov & Rintoul (2002) and is mapped using WOCE global hydrographic climatology (Gouretski & Koltermann 2004). The 2000 m bathymetric contour is indicated by a light blue line

sented here; we refer the reader to Popp et al. (2007) and Hannides et al. (2009) for specific details on materials and methods. To hydrolyze the samples, 4 to 6 mg of dried (whole) blood were transferred to high-temperature reaction vials, ~1 ml 6 N HCl added, heated to 150°C for 70 min, and cooled. These hydrolysates were evaporated and the residue re-dissolved in 1 ml 0.01 N HCl and the solution filtered (0.2 μm). The solution was further purified using the cation-exchange method of Metges et al. (1996). Prior to the derivatization, samples were re-acidified.

AA derivatization included esterification of the carboxyl terminus followed by trifluoroacetylation of the amine group. Samples were esterified using 4:1 isopropanol:acetyl chloride and by heating at 110°C for 60 min. Samples were dried and acylated by the addition of 3:1 methylene chloride:trifluoroacetic anhydride (TFAA) and heating at 100°C for 15 min. The derivatized samples were further purified using the method of Ueda et al. (1989). Finally, to ensure complete derivatization of the samples, the TFAA acylation step was repeated. The resulting trifluoroacetic (TFA) derivatives were stored in 3:1 methylene chloride:TFAA at 4°C.

Compound-specific $\delta^{15}\text{N}$ stable isotope analyses.

The $\delta^{15}\text{N}$ values of individual AAs were analyzed by isotope ratio monitoring gas chromatography–mass spectrometry (IRMS) using a ThermoFinnigan Delta-Plus XP mass spectrometer interfaced to a Trace GC gas chromatograph through a GC-C III combustion furnace (980°C), reduction furnace (680°C), and liquid nitrogen cold trap. L-2-aminoacidipic acid (AAA), for which the $\delta^{15}\text{N}$ value was known, was co-injected as an internal reference. Samples plus the AAA reference compound were dried and diluted with ethyl acetate prior to injection (1 to 3 μl , split/splitless, 5:1 split ratio) onto a 50 m HP Ultra-2 column (0.32 mm inner diameter, 0.5 μm film thickness) at an injector temperature of 180°C and a constant helium flow rate of 2 ml min^{-1} . The column oven was initially held at 50°C for 2 min, ramped to 190°C at 8°C min^{-1} and then to 280°C at 10°C min^{-1} , and finally held at 280°C for 10 min. The irmGCMS method allowed isotopic determination of alanine, glycine, leucine, isoleucine, proline, aspartic acid, glutamic acid, phenylalanine, and histidine. Samples were analyzed at least in triplicate, and the measured isotopic ratios were normalized to the $\delta^{15}\text{N}$ value of the AAA reference peak in each chromatogram.

Reproducibility associated with these isotopic measurements averaged 0.8‰ and ranged from 0.1 to 1.8‰. All $\delta^{15}\text{N}$ values are reported relative to atmospheric N_2 (air).

Sample preparation for compound-specific carbon isotope analysis. For $\delta^{13}\text{C}$ measurements of individual total hydrolyzable AAs (THAA), 2.3 to 7.5 mg of freeze-dried blood was homogenized and hydrolyzed at 110°C in 1 ml 6 M HCl in screw-cap vials with a N_2 headspace. After addition of an internal standard (Norleucine), the hydrolysate was evaporated under a gentle N_2 flow at 60°C. The dried THAA extracts were re-dissolved in MQ water and stored frozen (−20°C). Prior to analyses on the HPLC-IRMS, samples were centrifuged at 3000 rpm (1603 g) for 10 min.

Compound-specific $\delta^{13}\text{C}$ stable isotope analyses. The $\delta^{13}\text{C}$ values of specific AAs were analyzed using a modified HPLC-IRMS method, based on the protocol suggested by McCullagh et al. (2006). A Surveyor HPLC was coupled to a Finnigan Delta V IRMS via the LC Isolink interface (Thermo Electron). AA separation was performed using a Primesep A column (3.2 × 250 mm, particle size 5 μm , pore size 100 Å, SIELC Technologies) by applying a gradient program with 2 mobile phases (100% H_2O [Milli-Q] and 0.2% [v/v] H_2SO_4 , respectively), supplied by a pump with high precision proportioning valves to control mobile phase composition. Pure H_2O was used for the first 22 min, after which the mobile phase was switched to linearly increase to 0.2% H_2SO_4 after 75 min. The mobile phase then remained at 0.2% H_2SO_4 for 40 min and switched back to 100% H_2O until the end of the run (138 min). All mobile phase and reagent solutions were ultrasonically degassed under reduced pressure prior to use, and stock solutions were continuously purged with He during analysis. The column flow rate was kept stable at 500 $\mu\text{l min}^{-1}$ at 22°C. All samples were analyzed with 10 μl partial loop injections using a 50 μl injection loop.

Separated AAs eluting from the HPLC were oxidized online with a mixture of 0.67 M sodium peroxodisulfate (Merck, Darmstadt) and 1.5 M phosphoric acid (Fluka Sigma Aldrich) at 99.9°C. The flow of both reagents was kept at 30 $\mu\text{l min}^{-1}$. The resulting CO_2 was extracted from the liquid in a phase separator with a 1 ml He flow (see Krummen et al. 2004). The He containing the CO_2 from the individual AAs was dried over a Nafion tube and subsequently transferred to the IRMS through an open split.

To calibrate $\delta^{13}\text{C}$ values of AAs, a mixture of individual AA laboratory reference compounds was used. The $\delta^{13}\text{C}$ values of these compounds were determined independently with an EA (elemental analysis)-IRMS using IAEA-CH-6 and an internal laboratory reference compound (Schimmelmann acetanilide). The $\delta^{13}\text{C}$ value of each of these compounds was previously calibrated

using NBS 19 and L-SVEC on the VPDB (Vienna PeeDee Belemnite) scale, where NBS-19 and L-SVEC are defined as exactly +1.95 and −46.6‰, respectively (Coplen et al. 2006). Individual AA calibration was required because the offset in $\delta^{13}\text{C}$ values between measurements made on the HPLC-IRMS and those obtained on the EA-IRMS were different for some AAs (corrections ranged between −3.8‰ for glycine and +5.7‰ for threonine). Repeated analyses of glycine over a range of concentrations (200 to 1000 ng C) showed excellent reproducibility, with the $\delta^{13}\text{C}$ value averaging $-39.8 \pm 0.15\text{‰}$ ($n = 15$).

The Primsep A column is a mixed-mode column, with negatively charged functional groups due to the embedded anionic ion-pairing reagent. AAs with >1 charge state within the pH range (e.g. aspartic acid and glutamic acid) have retention times that shift as a function of the mobile phase pH, which can result in co-elution of AA peaks. Unfortunately these analytical conditions resulted in co-elution of glutamic acid, cysteine and serine, as well as isoleucine, norleucine and leucine. Therefore isotopic values of these compounds were considered in the present study. Six AAs were analyzed for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (alanine, aspartic acid, histidine, glycine, phenylalanine, and proline).

Statistical modeling of AA $\delta^{15}\text{N}$ values. Statistical analyses must account for the different sources of variation induced by the sampling strategy, and for the small number of samples analyzed. First, blood samples were collected from several individuals per species (2 or 3 individuals selected at random). Secondly, several replicates were performed on each blood sample (at least 3 replicates, but some AA isotope data were removed because of peak co-elution). Simple averages cannot account for the within-individual variability and for the between-individual variability. On the contrary, linear mixed-effects models (LME model; Pinheiro & Bates 2000) are well suited to deal with unbalanced sampling schemes, and they allow different sources of variation to be included. In the present study, we had to consider several replicates per blood sample and several individuals per species. Therefore, LME models were fitted to the $\delta^{15}\text{N}$ values of individual AAs, and data were grouped by individuals (measurement replicates) and by species. The individual effect was treated as random variation around a population mean. The species effects represent average characteristics of the populations of the 4 penguin species (i.e. the fixed effect in LME terms). These models allowed us to predict population values of AA $\delta^{15}\text{N}$ for each penguin species. These predicted values were then used as the best estimates, as they accounted for the different sources of variation. Parameter estimation used the maximum-likelihood method, and all computations and tests were performed in S-PLUS.

Comparison of source AA $\delta^{15}\text{N}$ values and TL estimates. These LME models were used to predict population $\delta^{15}\text{N}$ values of glutamic acid ($\delta^{15}\text{N}_{\text{glu}}$) and phenylalanine ($\delta^{15}\text{N}_{\text{phe}}$) for each species. We assumed: (1) that phenylalanine does not fractionate between TLs (i.e. a source AA), (2) that glutamic acid demonstrates a step-wise trophic enrichment (i.e. a trophic AA) from one TL to the next above the primary producers, and therefore (3) that the difference between glutamic acid and phenylalanine ($\Delta\delta^{15}\text{N}_{\text{glu-phe}} = \delta^{15}\text{N}_{\text{glu}} - \delta^{15}\text{N}_{\text{phe}}$) can be considered as an index of TL for each penguin species (see Schmidt et al. 2004, Hannides et al. 2009). We computed $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ for each replicate and calculated population values of this parameter using a supplementary LME model. These population-predicted values of $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ were used to compare the relative TLs of each penguin species.

The TL for each penguin ($\text{TL}_{\text{penguin}}$) species can be estimated from the equation of Hannides et al. (2009):

$$\text{TL}_{\text{penguin}} = \left[\frac{(\Delta\delta^{15}\text{N}_{\text{glu-phe}})_{\text{penguin}} - (\Delta\delta^{15}\text{N}_{\text{glu-phe}})_{\text{phytoplankton}}}{\text{TEF}} \right] + 1 \quad (1)$$

where TEF is the trophic enrichment factor that results from a shift in 1 TL. Eq. (1) has 3 unknown variables: $\text{TL}_{\text{penguin}}$, $(\Delta\delta^{15}\text{N}_{\text{glu-phe}})_{\text{phytoplankton}}$, and TEF. The TEF has been determined directly and indirectly to be $\sim 7\text{‰}$ for samples of fish, mollusk and crustacean muscle tissue and whole organisms (McClelland & Montoya 2002, McClelland et al. 2003, Schmidt et al. 2004, Chikaraishi et al. 2007, Popp et al. 2007). The value of $(\Delta\delta^{15}\text{N}_{\text{glu-phe}})_{\text{phytoplankton}}$ is assumed to be equal to 4‰ . A $(\Delta\delta^{15}\text{N}_{\text{glu-phe}})_{\text{phytoplankton}}$ value of $\sim 4\text{‰}$ has been found for marine green microalgae (McClelland & Montoya 2002), cyanobacteria (McClelland et al. 2003), and brown and red macroalgae (Chikaraishi et al. 2007),

suggesting that these AAs are biosynthesized and metabolized by similar pathways in these diverse photoautotrophs. Although the TEF has not yet been rigorously tested, a value of 7 has produced reasonable TL estimates for marine zooplankton (Hannides et al. 2009), krill (Schmidt et al. 2004), yellowfin tuna (Popp et al. 2007), and gastropods (Chikaraishi et al. 2007). Notably none of these studies has examined the isotopic compositions of AAs in blood.

RESULTS

Patterns in $\delta^{15}\text{N}$ AA values

Bulk $\delta^{15}\text{N}$ values ranged 3.7‰ among all the penguin blood samples (Table 2; Cherel & Hobson 2007). The $\delta^{15}\text{N}$ values of AAs isolated from penguin chick blood ranged from -0.2 to $+26.0\text{‰}$ (Figs. 2 & 3, Table 2). The trophic AAs (glutamic acid, alanine, aspartic acid, isoleucine, leucine and proline; mean: $17.9 \pm 3.0\text{‰}$) were enriched in ^{15}N relative to the source AAs (glycine, phenylalanine and histidine; mean: $5.1 \pm 3.5\text{‰}$) (Table 2). Aspartic acid (mean: $14.7 \pm 2.1\text{‰}$) showed the least ^{15}N enrichment of the trophic AAs. Among the source AAs, glycine (gly) (mean: $9.2 \pm 2.8\text{‰}$) was enriched in ^{15}N relative to phenylalanine (mean: $2.5 \pm 1.2\text{‰}$), and $\delta^{15}\text{N}_{\text{gly}}$ values did not reflect the species-specific patterns observed in $\delta^{15}\text{N}_{\text{phe}}$ values (Table 2, Fig. 2). Except for glycine and aspartic acid, the patterns observed in AA $\delta^{15}\text{N}$ values of penguin chicks followed previous trends in trophic and source AAs isotopic values measured in marine invertebrates and fish (McClelland & Montoya 2002, McClelland et al. 2003, Schmidt et al. 2004, Chikaraishi et al. 2007, Popp et al. 2007, Hannides et al. 2009).

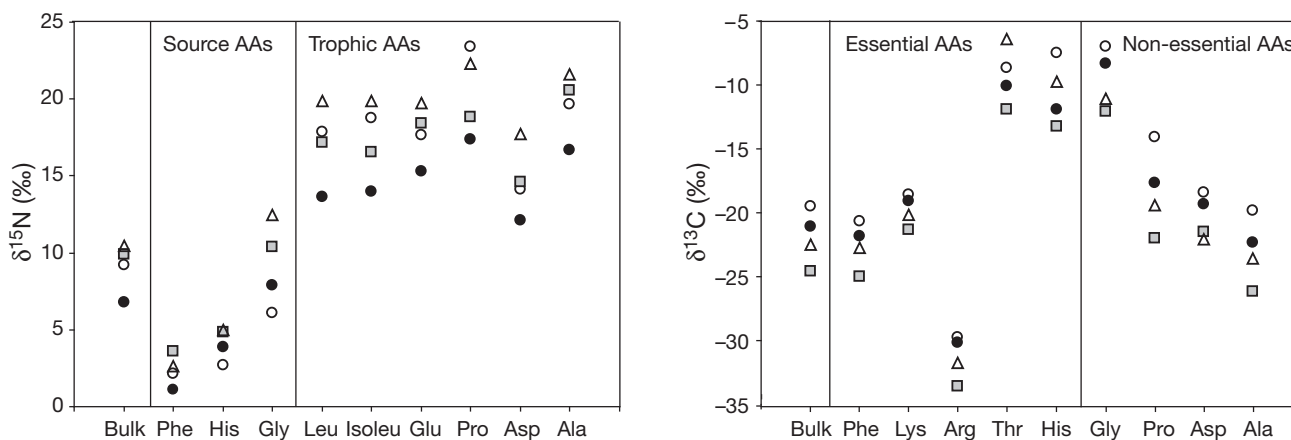


Fig. 2. Stable isotope values ($\delta^{15}\text{N}$ to the left and $\delta^{13}\text{C}$ to the right) of bulk and individual amino acids (AAs) of the 4 penguin species. ○: northern rockhopper penguin *Eudyptes chrysocome moseleyi*; ●: southern rockhopper penguin *Eudyptes chrysocome chrysocome*; △: king penguin *Aptenodytes patagonicus*; ▣: Adélie penguin *Pygoscelis adeliae*. Note: for N, mean values are predicted values (see Table 2). Phe: phenylalanine; His: histidine; Gly: glycine; Leu: leucine; Isoleu: isoleucine; Glu: glutamic acid; Pro: proline; Asp: aspartic acid; Ala: alanine; Lys: lysine; Arg: arginine; Thr: threonine

Table 2. $\delta^{15}\text{N}$ values of the bulk sample and isolated amino acids (full designations, see Fig. 2 legend) of blood collected from penguin chicks from the Southern Ocean. Data for the different individuals per species are indicated (2 ind. for both NRP and SRP; 3 for both KP and AP). Source amino acids are indicated by bold print. NC: not considered because of peak co-elution. Linear mixed-effect (LME) estimates for each species (mean \pm SE) were calculated with LME models that accounted for the heterogeneity of the data set (see 'Materials and methods')

Bulk $\delta^{15}\text{N}$ (‰)		Amino acid $\delta^{15}\text{N}$ values (‰)								
		Phe	His	Gly	Leu	Isoleu	Glu	Pro	Asp	Ala
<i>Eudyptes chrysocome moseleyi</i>, northern rockhopper penguin (NRP), 37.8° S										
NRP 1	9.2	2.5	3.0	6.9	18.5	19.7	19.0	23.9	14.6	20.3
		3.1	2.9	5.6	17.2	17.4	18.3	22.4	14.0	19.8
		1.6	0.9	3.9	16.1	17.7	16.0	20.4	13.8	18.7
		1.7	2.2	4.7	17.2	18.1	16.3	23.6	13.0	19.8
NRP 2	9.2	2.4	1.2	5.7	18.4	19.5	17.5	21.8	13.3	18.5
		1.5	2.9	5.5	18.3	19.4	18.0	23.8	14.1	19.3
		2.6	3.6	7.7	18.2	17.8	16.2	25.4	14.7	20.1
		1.7	5.1	8.8	18.8	20.4	19.9	26.0	15.4	20.7
LME	Estimate	2.1 ± 0.5	2.7 ± 1.4	6.1 ± 0.8	17.8 ± 0.5	18.8 ± 0.7	17.7 ± 0.6	23.4 ± 0.7	14.1 ± 0.5	19.7 ± 0.4
<i>Eudyptes chrysocome chrysocome</i>, southern rockhopper penguin (SRP), 46.7° S										
SRP 1	6.8	1.1	2.7	9.6	12.8	12.8	14.8	16.4	12.0	16.8
		1.7	1.0	7.9	12.7	13.2	14.0	16.5	12.9	16.3
		1.4	1.3	7.8	13.1	14.4	14.9	17.4	11.9	15.8
		1.1	2.2	7.9	12.7	12.6	15.8	16.0	11.1	16.4
SRP 2	6.8	−0.2	4.7	6.4	13.5	14.4	15.5	19.0	12.0	16.6
		1.8	5.9	8.6	15.0	15.2	16.1	18.0	12.4	17.3
		1.2	7.6	7.3	14.8	14.4	15.5	17.5	12.4	17.3
LME	Estimate	1.1 ± 0.5	3.9 ± 1.4	7.9 ± 0.8	13.6 ± 0.5	13.9 ± 0.8	15.2 ± 0.6	17.3 ± 0.7	12.1 ± 0.5	16.6 ± 0.4
<i>Aptenodytes patagonicus</i>, king penguin (KP), 50.0° S										
KP 1	10.4	2.8	NC	13.6	19.8	21.5	20.2	22.4	18.4	22.3
		3.0	NC	14.5	NC	NC	22.0	24.6	19.3	22.9
		4.1	7.7	12.2	20.0	21.8	21.5	23.2	18.0	21.3
		2.5	5.3	11.5	20.1	20.4	21.4	22.1	18.2	21.0
KP 2	10.5	2.5	5.0	NC	19.6	NC	19.7	23.1	NC	NC
		2.0	4.5	NC	20.1	NC	19.5	23.1	18.1	NC
		1.0	3.0	NC	19.9	NC	17.4	21.2	NC	NC
		2.7	4.4	NC	19.3	18.6	18.8	20.7	15.9	20.6
KP 3	10.5	2.3	2.3	11.2	18.9	18.4	18.7	21.2	16.4	21.2
		3.8	5.9	12.8	20.9	NC	20.0	22.4	17.8	22.3
LME	Estimate	2.6 ± 0.5	4.9 ± 1.3	12.6 ± 0.9	19.8 ± 0.4	20.0 ± 0.8	19.9 ± 0.6	22.4 ± 0.7	17.7 ± 0.5	21.7 ± 0.4
<i>Pygoscelis adeliae</i>, Adélie penguin (AP), 66.7° S										
AP 1	9.5	3.1	9.0	8.8	16.7	15.8	18.6	18.6	14.4	21.0
		3.8	5.7	9.7	17.2	15.4	18.3	18.7	13.6	21.8
		2.9	5.7	7.9	16.4	16.2	18.2	18.3	13.8	20.1
AP 2	10.0	1.4	1.7	10.9	16.5	16.0	17.4	17.3	14.0	19.4
		3.7	3.6	13.2	18.2	17.9	20.1	19.5	15.3	21.9
		2.8	3.8	11.5	17.3	17.6	18.2	18.2	15.0	20.3
		2.9	2.7	11.0	17.0	16.3	18.6	18.0	14.8	21.1
AP 3	10.3	4.7	5.7	9.4	17.3	17.0	17.9	19.1	15.5	19.4
		4.3	6.5	11.3	17.8	17.1	19.7	20.9	16.1	20.9
		5.1	5.4	11.5	17.4	16.3	17.8	19.3	14.6	20.1
LME	Estimate	3.5 ± 0.5	5.2 ± 0.9	10.5 ± 0.5	17.2 ± 0.3	16.5 ± 0.5	18.5 ± 0.4	18.8 ± 0.5	14.7 ± 0.3	20.6 ± 0.2

The LME models fitted to the $\delta^{15}\text{N}_{\text{phe}}$ and to the $\delta^{15}\text{N}_{\text{glu}}$ data indicated that the species effect was significant ($p = 0.022$ and $p = 0.002$, respectively) and that these values differed then by penguin species (Table 2). LME values with their standard errors (SE) for the 4 penguin species are shown graphically in

Fig. 3 and are listed in Table 2. AP had the highest LME estimated $\delta^{15}\text{N}_{\text{phe}}$ values ($3.5 \pm 0.3\text{‰}$), whereas SRP had the lowest LME estimated values ($1.1 \pm 0.5\text{‰}$). NRP had LME predicted $\delta^{15}\text{N}_{\text{phe}}$ values ($2.1 \pm 0.5\text{‰}$) higher than SRP ($1.1 \pm 0.5\text{‰}$), while KP had moderate $\delta^{15}\text{N}_{\text{phe}}$ values ($2.6 \pm 0.5\text{‰}$).

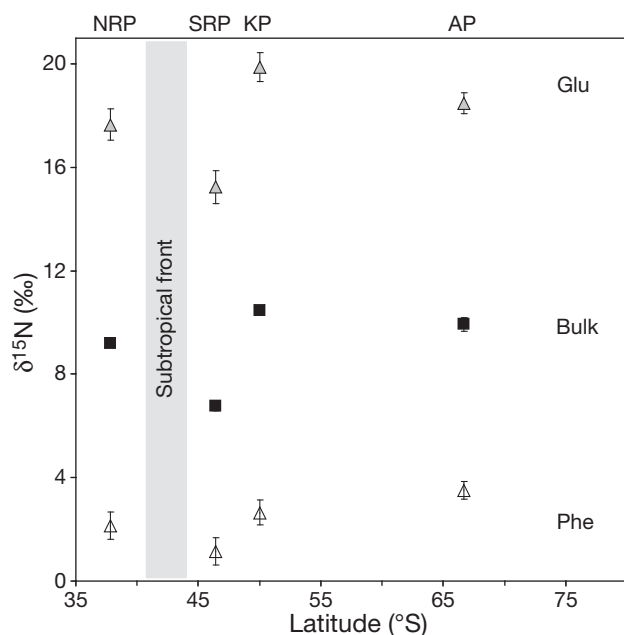


Fig. 3. Variations of $\delta^{15}\text{N}$ values for bulk (■, mean \pm SE), phenylalanine (Δ , Phe), and glutamic acid (Δ , Glu) (predicted values \pm SE, see 'Materials and methods') with latitude for 4 penguin species: northern rockhopper penguin (NRP, *Eudyptes chrysocome moseleyi*), southern rockhopper penguin (SRP, *Eudyptes chrysocome chrysocome*), king penguin (KP, *Aptenodytes patagonicus*) and Adélie penguin (AP, *Pygoscelis adeliae*)

Trophic level of Southern Ocean penguins

Table 3 displays the LME estimated values for the index of TL $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ for the 4 species. The species effect was significant ($p = 0.018$). Among penguin species, KP had the highest $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ value (17.2‰, Table 3), and SRP had the lowest (14.1‰). Estimates for NRP and AP were close, with a slightly higher $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ for NRP (15.5 vs. 15.0‰).

Using Eq. (1) with a TEF of 7‰ and a $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ in phytoplankton of 4‰ provided consistent underestimates of TL (2.6, 2.4, 2.9, and 2.6 for NRP, SRP, KP, and AP, respectively) relative to independent TL estimates based on bulk stable isotope analyses for 3 of the 4 spe-

cies (4.0, 4.5, and 3.9 for SRP, KP, and AP, respectively; see Table 3, Cherel et al. 2008) and stomach content analyses for all the species (Table 1). Assuming that the TL estimates based on bulk stable isotope analysis are correct, a TEF for penguin chick blood was calculated. This TEF estimation is based on the LME model estimated differences ($\Delta\delta^{15}\text{N}_{\text{glu-phe}}$, see Table 3) and a $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ of 4‰ for phytoplankton. Given these assumptions (which will be addressed in the 'Discussion'), the new TEF would be 3.4, 3.8, and 3.8‰ for SRP, KP, and AP, respectively (3.6‰ on average), which is less than the 7‰ cited in previous studies.

Patterns in $\delta^{13}\text{C}$ AA values

While bulk $\delta^{13}\text{C}$ values showed a range of 5.5‰ among the penguin samples (see Tables 1 & 4), the $\delta^{13}\text{C}$ values of AAs isolated from the blood of penguin chicks ranged from -5.0 to -34.0 ‰ (Table 4, Figs. 2 & 4). There was no clear pattern of ^{13}C enrichment related to essential (arginine, histidine, lysine, phenylalanine, and threonine) or non-essential AAs (alanine, aspartic acid, glycine, and proline) (Table 4, Fig. 2). Instead, there were 3 general $\delta^{13}\text{C}$ groups of AAs, in which 2 of the 3 groups included both essential and non-essential AAs: (1) a group of AAs with high ^{13}C enrichment (threonine, glycine, and histidine; mean: -9.9 ± 2.3 ‰), (2) an intermediate group of AAs with $\delta^{13}\text{C}$ values similar to bulk $\delta^{13}\text{C}$ values (proline, alanine, phenylalanine, aspartic acid, and lysine; mean: -22.2 ± 4.3 ‰), and (3) a final group of only essential AAs that were very depleted in ^{13}C (arginine; mean: -31.3 ± 1.6 ‰). The bimodal pattern observed in the $\delta^{15}\text{N}$ values of source and trophic AAs was not seen in the $\delta^{13}\text{C}$ values. Instead, the $\delta^{13}\text{C}$ values of all AAs decreased with increasing latitude, which mirrored the trend in bulk carbon isotope (Fig. 4a). A covariance analysis showed that a model with separate slopes for bulk and all the AAs was justified compared to a model with parallel regressions ($p = 0.006$). Slopes varied between -0.10 ± 0.03 (lysine) and -0.26 ± 0.03 (proline), with 1 group of 4 AAs having parallel slopes with bulk (phenylalanine,

Table 3. Trophic position estimates from the literature, linear mixed-effect model predictions of the difference between glutamic acid and phenylalanine $\delta^{15}\text{N}$ values ($\Delta\delta^{15}\text{N}_{\text{glu-phe}}$) for 4 penguin species, and estimated trophic enrichment factor (TEF) between source and trophic transfer amino acids for penguin chick's blood using Eq. (1) (see 'Materials and methods' for more details). Trophic positions are from Cherel et al. (2008). NA: not available; ND: not determined

Species	Trophic position	Predicted $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ (‰)	Estimated TEF (‰)
<i>Eudyptes chrysocome moseleyi</i> , northern rockhopper penguin	NA	15.5	ND
<i>Eudyptes chrysocome chrysocome</i> , southern rockhopper penguin	4.0	14.1	3.4
<i>Aptenodytes patagonicus</i> , king penguin	4.5	17.2	3.8
<i>Pygoscelis adeliae</i> , Adélie penguin	3.9	15.0	3.8

Table 4. $\delta^{13}\text{C}$ values of the bulk sample and isolated amino acids (full designations, see Fig. 2 legend) of blood collected from penguin chicks from the southern Indian Ocean. Normal font indicates essential amino acids and bold print indicates non-essential amino acids. NC: not considered because of peak co-elution

Bulk $\delta^{13}\text{C}$ (‰)	Amino acid $\delta^{13}\text{C}$ values (‰)								
	Phe	Lys	Arg	Thr	His	Gly	Pro	Asp	Ala
<i>Eudyptes chrysocome moseleyi</i>, northern rockhopper penguin (NRP), 37.8° S									
−19.4	−20.7	−18.8	−29.8	−8.4	−7.9	−7.0	−13.4	−18.8	−19.8
−19.5	−20.6	−18.4	−29.5	−8.4	−7.9	−7.9	−13.3	−18.0	−18.7
−19.7	−20.8	−18.4	−29.9	−9.1	−6.7	−6.1	−15.7	−18.5	−19.9
<i>Eudyptes chrysocome chrysocome</i>, southern rockhopper penguin (SRP), 46.7° S									
−21.3	−21.9	−19.2	−30.4	−10.5	−12.7	−8.2	−16.8	−19.3	−22.8
−21.0	−21.9	−19.0	−30.0	−9.3	−11.0	−9.9	−18.1	−19.7	−22.4
−21.0	−21.8	−19.1	−30.2	−10.4	−12.0	−6.9	−18.2	−19.1	−21.8
<i>Aptenodytes patagonicus</i>, king penguin (KP), 50.0° S									
−22.5	−22.7	−20.1	−31.8	−7.9	−9.2	−10.4	−18.5	−20.9	−24.2
−22.6	−22.6	−19.9	−31.7	NC	−10.0	NC	−19.6	−20.7	−24.7
−22.5	−22.9	−20.4	−31.9	−5.0	−10.0	−11.7	−20.2	−24.8	−21.7
<i>Pygoscelis adeliae</i>, Adélie penguin (AP), 66.7° S									
−24.5	−25.2	−21.2	−33.4	−11.5	−14.9	−12.2	−22.2	−21.5	−26.3
−24.9	−24.7	−21.2	−33.3	−12.7	−14.3	−12.0	−21.9	−22.0	−26.4
−24.4	−25.2	−21.6	−34.0	−11.6	−10.6	−12.0	−22.0	−21.1	−25.7

histidine, arginine, and glycine; Fig. 4a). In addition, the links between the $\delta^{13}\text{C}$ values of all AAs and bulk were investigated with an extra covariance analysis: the model with separate slopes was significant ($p = 0.002$; Fig. 4b). Slopes varied between 0.52 ± 0.18 (threonine) and 1.51 ± 0.18 (proline). For 6 AAs (proline, alanine, glycine, arginine, lysine and phenylalanine), the correlation between bulk and AA-specific $\delta^{13}\text{C}$ was highly significant ($R^2 > 0.8$ and $p < 0.01$), but there were clearly different patterns in the slope of the relationship (Fig. 4b). For those AAs with good correlation between bulk and AA-specific $\delta^{13}\text{C}$, all non-essential AAs, except aspartic acid, had slopes > 1 , i.e. the range in $\delta^{13}\text{C}$ -AAs was higher than in the bulk. In contrast, for all essential amino acids the slope was < 1 . From all AAs that show good correlation with both bulk and latitude, the isotopic composition of phenylalanine was closest to that of the bulk.

DISCUSSION

Penguin $\delta^{15}\text{N}$ values and foraging habitat (Hypothesis 1)

Small but significant differences were found in $\delta^{15}\text{N}_{\text{phe}}$ values among penguin species (maximum range: 3‰). These results suggest then that phenylalanine $\delta^{15}\text{N}$ values can be used as a source AA to study the foraging habitat of penguins. NRP $\delta^{15}\text{N}_{\text{phe}}$ values were higher—even if the difference was relatively small—than SRP $\delta^{15}\text{N}_{\text{phe}}$ values (2.1 ± 0.5 ‰ vs. 1.1 ± 0.5 ‰), which is consistent with the hypothesis of Cherel & Hobson (2007) i.e. that the observed differ-

ence in their bulk $\delta^{15}\text{N}$ value (2.4‰) relates in part to differences in the isotopic baseline of their foraging regions. The nitrogen isotopic composition of particulate matter is higher in the Subtropical Frontal Zone north of 40 to 45° S where NRP forage (Table 1; Tremblay 2003) than at latitudes south of 45° S in the SW Indian Ocean (from 5 to –2‰; see Altabet & François 1994), i.e. where SRP forage close to the Crozet Islands (Table 1). These north–south $\delta^{15}\text{N}$ gradients have also been found in modern sediments collected from the northeast Indian Ocean, which indicates that this trend has persisted for long periods of time (Altabet & François 1994).

The highest $\delta^{15}\text{N}_{\text{phe}}$ values were observed for KP and AP, which forage at the highest latitudes in the Southern Ocean. Previous tagging and observational data suggest that these penguins forage at the Polar Front (~50° S) and over the Antarctic shelf (~66° S), respectively (Wienecke et al. 2000, Charrassin & Bost 2001). Both of these oceanic regions are south of the Subtropical front where one would have expected low baseline $\delta^{15}\text{N}$ values (–1 to –2‰; Altabet & François 1994, Lourey et al. 2003). However, several factors can lead to elevated $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values at the base of the food web. The elevated $\delta^{15}\text{N}_{\text{phe}}$ values observed in these penguins could be explained by different processes: (1) a local increase in the $\delta^{15}\text{N}$ value of the isotopic baseline (neritic vs. oceanic waters, high seasonal nutrient utilization by phytoplankton, or sea ice influence) or (2) a difference in the vertical foraging habitat, with penguins foraging on a greater proportion of mesopelagic prey that have elevated $\delta^{15}\text{N}$ values. A local region can have high baseline $\delta^{15}\text{N}$ value because

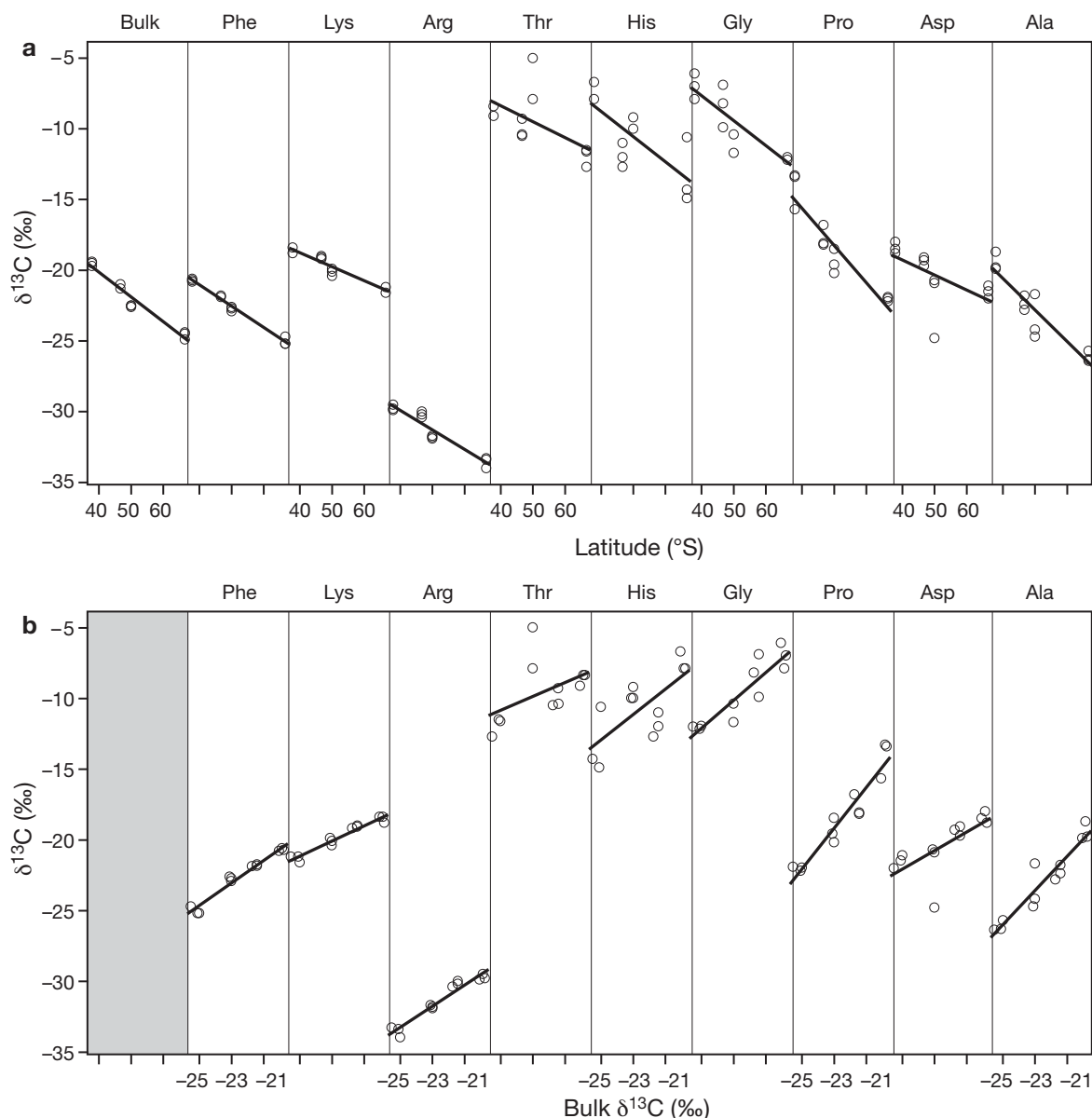


Fig. 4. Variations of (a) bulk and individual amino acid (AA) $\delta^{13}\text{C}$ values (full designations, see Fig. 2 legend) with latitude and (b) of AA $\delta^{13}\text{C}$ values with bulk for the 4 penguin species: northern rockhopper penguin, southern rockhopper penguin, king penguin and Adélie penguin

of extensive NO_3^- utilization after a large phytoplankton bloom (Tamelander et al. 2009). From Fig. 1, high chlorophyll *a* concentrations are commonly found near the Crozet Islands and Adélie Land. However, the waters close to the Crozet Islands are deep and well-mixed and the injection of new NO_3^- to the surface waters will not produce high POM $\delta^{15}\text{N}$ values because the NO_3^- pool size is already large. On the other hand, over the Antarctic shelf, the water column is stratified, and nitrogen delivery to the surface waters and the subsequent uptake by phytoplankton will lead to high

$\delta^{15}\text{N}$ values of the POM. Trull et al. (2008) showed a 2‰ increase in the $\delta^{15}\text{N}$ values of POM on Kerguelen Plateau relative to $\delta^{15}\text{N}$ values of POM collected off the plateau. The higher $\delta^{15}\text{N}$ values of POM were attributed to an increase in the uptake of NO_3^- by phytoplankton on the Kerguelen Plateau. The isotopic baseline of the waters directly surrounding the Antarctic shelf may be higher than offshore waters. AP forage within 50 km of their Antarctic colonies (Cherel et al. 2008). Therefore, the relatively high $\delta^{15}\text{N}_{\text{phe}}$ values observed in AP could reflect their neritic foraging

behavior in waters above the Antarctic shelf. Finally, the high $\delta^{15}\text{N}$ values of AP could be explained by feeding in a food web supported in part by sea-ice phytoplankton, which has been shown to have elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Hobson et al. 1995, Norkko et al. 2007).

The high $\delta^{15}\text{N}_{\text{phe}}$ values of Ks that forage in the polar front could be explained by the relative importance of mesopelagic prey in their diet (prey living around 300 to 500 m). Previous studies have suggested there is a positive depth gradient in the $\delta^{15}\text{N}$ value of particulate nitrogen in the open ocean (Saino & Hattori 1980, 1987, Dore et al. 2002, Trull et al. 2008). Saino & Hattori (1980) found an overall increase of 9‰ in POM $\delta^{15}\text{N}$ values between 0 and 1000 m in the northeast Indian Ocean, and Trull et al. (2008) found +0.5‰ enrichment in ^{15}N with depth on Kerguelen Plateau up to 140 m. If this nitrogen is incorporated and conserved in the food web, then prey that forage at depth (below 100 to 200 m) can have higher $\delta^{15}\text{N}$ values than similar prey in the surface waters (Rau et al. 1989, Graham et al. 2007). Mintenbeck et al. (2007) showed a significant increase in the $\delta^{15}\text{N}$ values of benthic suspension feeders with water depth on the Weddell Sea shelf (up to 1000 m). Thus, if predators forage on a greater proportion of mesopelagic prey, their $\delta^{15}\text{N}_{\text{phe}}$ values could potentially be higher than those of consumers feeding in the same region, but on a more epipelagic resource. KP make deep dives to forage, regularly exceeding 150 m depth (Kooyman et al. 1992), and feed almost exclusively on mesopelagic fish of the family Myctophidae, while other penguins (including AP, NRP, SRP) dive to shallower depths and mainly prey upon crustaceans (Cherel et al. 1993, 2007, Rodary et al. 2000, Tremblay & Cherel 2003, Cherel 2008).

The $\delta^{15}\text{N}_{\text{phe}}$ values of SRP and NRP suggest that they do not forage in the same oceanic regions and that the difference in their bulk $\delta^{15}\text{N}$ values is due, in part, to baseline differences. These results also revealed that KP and AP have higher $\delta^{15}\text{N}_{\text{phe}}$ values than do rockhoppers, which could be explained by the foraging of KP on mesopelagic prey and of AP in the highly productive Antarctic shelf waters.

Penguin $\delta^{15}\text{N}$ values and TLs (Hypothesis 2)

Results of previous stomach content and bulk stable isotope analyses suggest that KPs have a higher TL than SRP and AP (Cherel et al. 2008). The compound-specific isotope data support these observations, as the difference between the $\delta^{15}\text{N}$ values of trophic (glutamic acid) and source (phenylalanine) amino acids was greatest in KP (17.2‰; Table 3). If bulk isotope $\delta^{15}\text{N}$ values (Table 1) are interpreted only in the context of variations in trophic ecology, NRP (9.2‰) were at a

lower TL than AP (10.1‰), and SRPs (6.8‰) were at the lowest TL. The AA $\delta^{15}\text{N}$ data, however, indicated that NRP had a higher $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ value, or TL, than both SRP (15.5 vs. 14.1‰) and AP (15.5 vs. 15.0‰). These conclusions are consistent with stomach content analyses, which indicate that NRP feed on squids and crustaceans, whereas SRP and AP forage mostly on crustaceans (Table 1). The bulk $\delta^{15}\text{N}$ difference (2.4‰) between NRP and SRP is, therefore, not only due to a baseline difference, as discussed previously, but also to a difference in their TLs.

Our study thus suggests that the $\delta^{15}\text{N}$ analyses of individual AAs, such as glutamic acid and phenylalanine, can provide an opportunity to distinguish the relative influence of baseline variations and TL on the bulk $\delta^{15}\text{N}$ values of penguins. However, using Eq. (1) and a TEF of 7‰ (cf. McClelland & Montoya 2002), the TL of penguin chicks ranged from 2.6 to 2.9. A TL <3 is inconsistent with what we know about these penguins, as they are strictly carnivorous (Cherel et al. 1993, 2008). For example, the KP is a myctophid-eater, and myctophids forage mainly on meso- and macrozooplankton, including some herbivorous, omnivorous, and even carnivorous species. Consequently, a TL of KP cannot be <4. To match the expected TLs for penguins, and considering that the 4‰ phytoplankton $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ is correct, a TEF of 3.6‰ (see 'Results') has been used. Assuming this TEF_{blood} of 3.6‰ is correct for all penguin blood samples and 4‰ for the $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ value of phytoplankton, we estimate for the first time the TL for NRP chicks (4.2) and determine TLs for SRP, KP, and AP of 3.8, 4.6, and 4.0, respectively. Although our results suggest that the 7‰ TEF is inconsistent when $\Delta\delta^{15}\text{N}_{\text{glu-phe}}$ is used in penguin blood to determine TL, uncertainty exists in the universal applicability of our lower TEF for samples of blood in organisms. The TEFs, particularly for tissues other than muscle, should be subjected to further experimental work conducted on a diverse assemblage of consumers.

The $\delta^{15}\text{N}$ values of glutamic acid and phenylalanine in penguin blood ($\Delta\delta^{15}\text{N}_{\text{glu-phe}}$) allowed successful estimation of the relative TLs of the different species of penguins. However, before absolute TLs can be calculated, controlled experiments should be performed on seabirds and their diets to better constrain TEF for blood samples.

Penguin $\delta^{13}\text{C}$ values and foraging habitat (Hypothesis 3)

Variations in bulk $\delta^{13}\text{C}$ values have been interpreted as differences in the foraging habitats of the 4 penguin species and to spatial differences in the $\delta^{13}\text{C}$ values at the base of the food web (Cherel & Hobson 2007). Strong spatial gradients have been observed in the Southern Ocean, with a ~9‰ decrease in the $\delta^{13}\text{C}$ val-

ues of POM from low to high latitudes (François et al. 1993, Popp et al. 1999, Trull & Armand 2001). The laboratory and field results of Fantle et al. (1999) showed that the essential AAs valine, leucine and phenylalanine did not exhibit significant $\delta^{13}\text{C}$ enrichment from the diet and had lower $\delta^{13}\text{C}$ values than the non-essential AAs. Based upon these observations we predicted that essential AAs would mirror the latitudinal bulk isotopic trends exhibited in Southern Ocean phytoplankton, i.e. the $\delta^{13}\text{C}$ values of essential AAs in penguins that forage in lower latitude areas would be higher than those that forage at higher latitudes.

The $\delta^{13}\text{C}$ values of 6 AAs (phenylalanine, lysine, arginine, glycine, proline, alanine) showed very good correlation with bulk $\delta^{13}\text{C}$ values ($R^2 > 0.8$) and decreased with increasing latitude, suggesting that these AAs track $\delta^{13}\text{C}$ baseline variations. In contrast to what has been found in blue crabs (Fantle et al. 1999), the $\delta^{13}\text{C}$ values of essential AAs do not segregate relative to non-essential AAs in penguin's blood. Both essential AAs and non-essential AAs had higher $\delta^{13}\text{C}$ values than bulk $\delta^{13}\text{C}$ values. Interestingly, all essential AAs exhibited lower slopes relative to bulk $\delta^{13}\text{C}$ values, indicating that the range of variation in these AA-specific $\delta^{13}\text{C}$ values was lower relative to bulk $\delta^{13}\text{C}$ values, while non-essential AAs (except for aspartic acid) had higher ranges. We are unable to interpret this pattern with our current understanding of carbon isotope fractionation of specific AAs in seabirds. As such, applying carbon CSIA to determine the foraging ecology and location of marine consumers is not straightforward, and may not even be applicable. Without baseline or prey $\delta^{13}\text{C}$ data, it is not possible to determine whether some essential AAs fractionate or not relative to their diet. In an experimental study conducted on fish, McCullagh et al. (2008) also found that there was no clear pattern in ^{13}C fractionation relative to the essentiality of AAs. Instead, these authors found that phenylalanine alone showed no isotopic difference between the $\delta^{13}\text{C}$ value of the consumer and its diet. In our study, phenylalanine had $\delta^{13}\text{C}$ values close to the bulk values for all penguin species, which suggests that it may be the most appropriate AA for tracking changes in the baseline $\delta^{13}\text{C}$ values and determining a marine consumer's foraging habitat. If one specific AA has to be chosen for simultaneous C and N isotope analysis, we propose phenylalanine, which has the closest values relative to bulk and is also a source AA for nitrogen.

Conclusions

Few studies have been conducted on carbon and nitrogen isotope analyses of individual AAs, and none of them examined seabirds. The present study shows

for the first time that the $\delta^{15}\text{N}$ values of individual AAs, such as glutamic acid as a trophic AA and phenylalanine as a source AA, reflect the TL and the foraging regions of penguins. These results further support the use of compound-specific $\delta^{15}\text{N}$ isotope analysis to determine the foraging areas and TLs of marine consumers, from primary consumers to top predators. Previous analyses, however, focused on muscle and whole body, while the present study examined blood. Our results suggest that blood can be used to estimate relative TLs, but that the TEF reported in previous studies (i.e. 7‰) might not be appropriate to calculate absolute TL in penguin blood and, perhaps, in general, for seabirds. Controlled experiments are therefore needed to better constrain the TEF value for penguin blood. The $\delta^{13}\text{C}$ values of 6 individual AAs followed the $\delta^{13}\text{C}$ isotopic baseline, but without additional CSIA data on the diet or base of the food web, we were unable to further interpret the $\delta^{13}\text{C}$ values of specific AAs isolated from penguin blood. Our study, however, suggests that glutamic acid ($\delta^{15}\text{N}$) and phenylalanine (for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) could be key individual AAs in the study of foraging habitat and the behavior of marine consumers.

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