



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 · Geocator · 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-

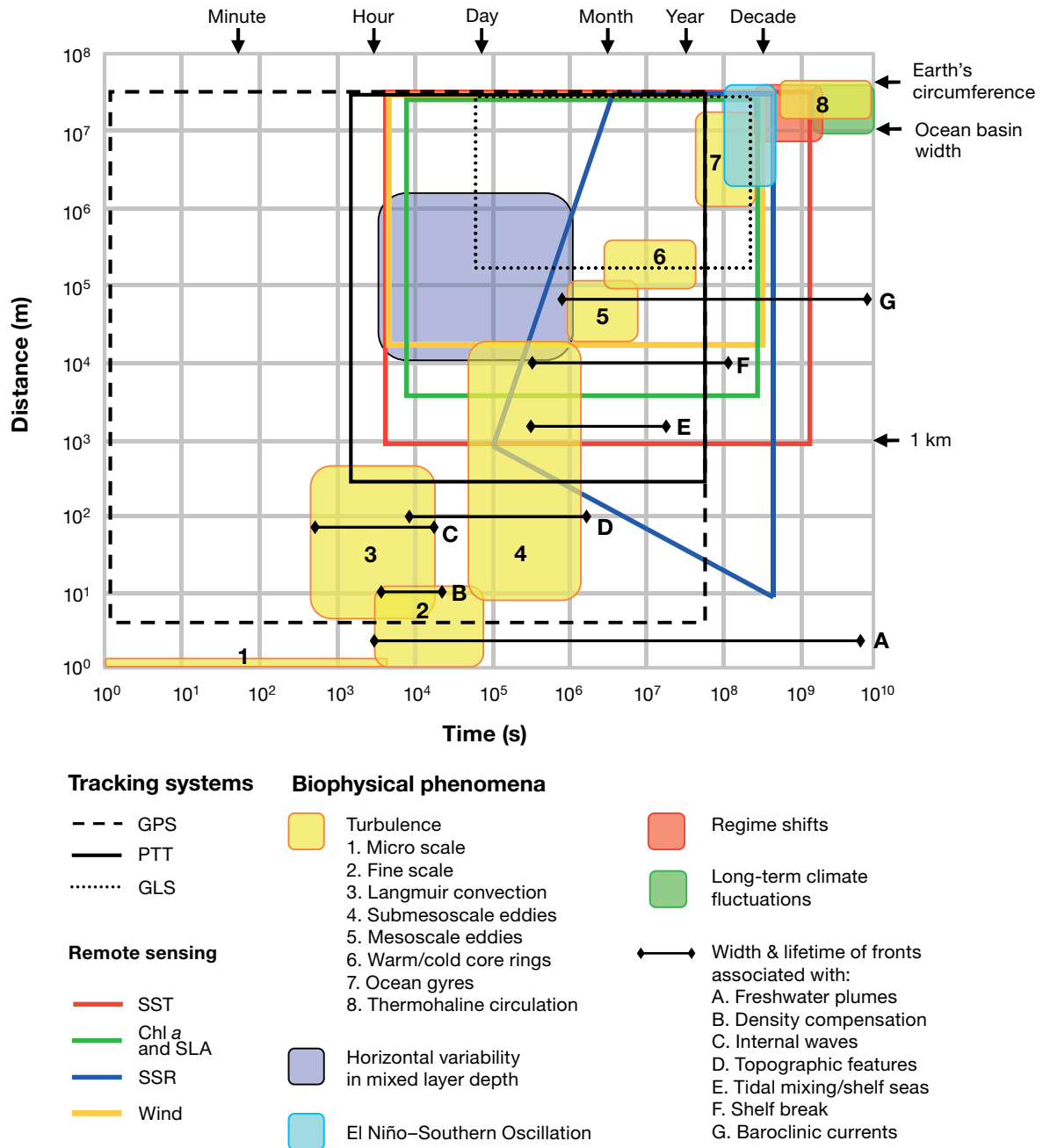


Fig. 1. Spatiotemporal scales of climatic and oceanographic processes compared to the resolution and coverage of human observation in pelagic seabird habitat studies. Tracking systems shown are PTTs (platform terminal transmitters), GPS tags and GLS (global location sensing, geolocator) tags. Remotely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

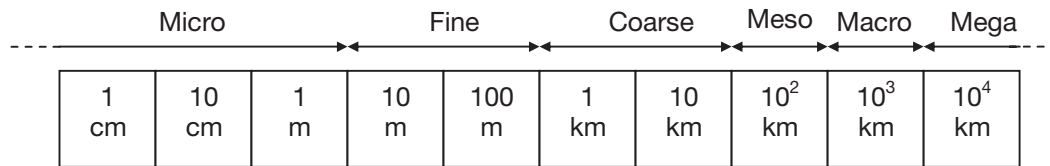


Fig. 2. Definition of terms used to describe spatial scale in habitat studies of pelagic seabirds (after Haury et al. 1977)

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 & Harty 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

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,

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)

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 (Cstry 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 melanophris* 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

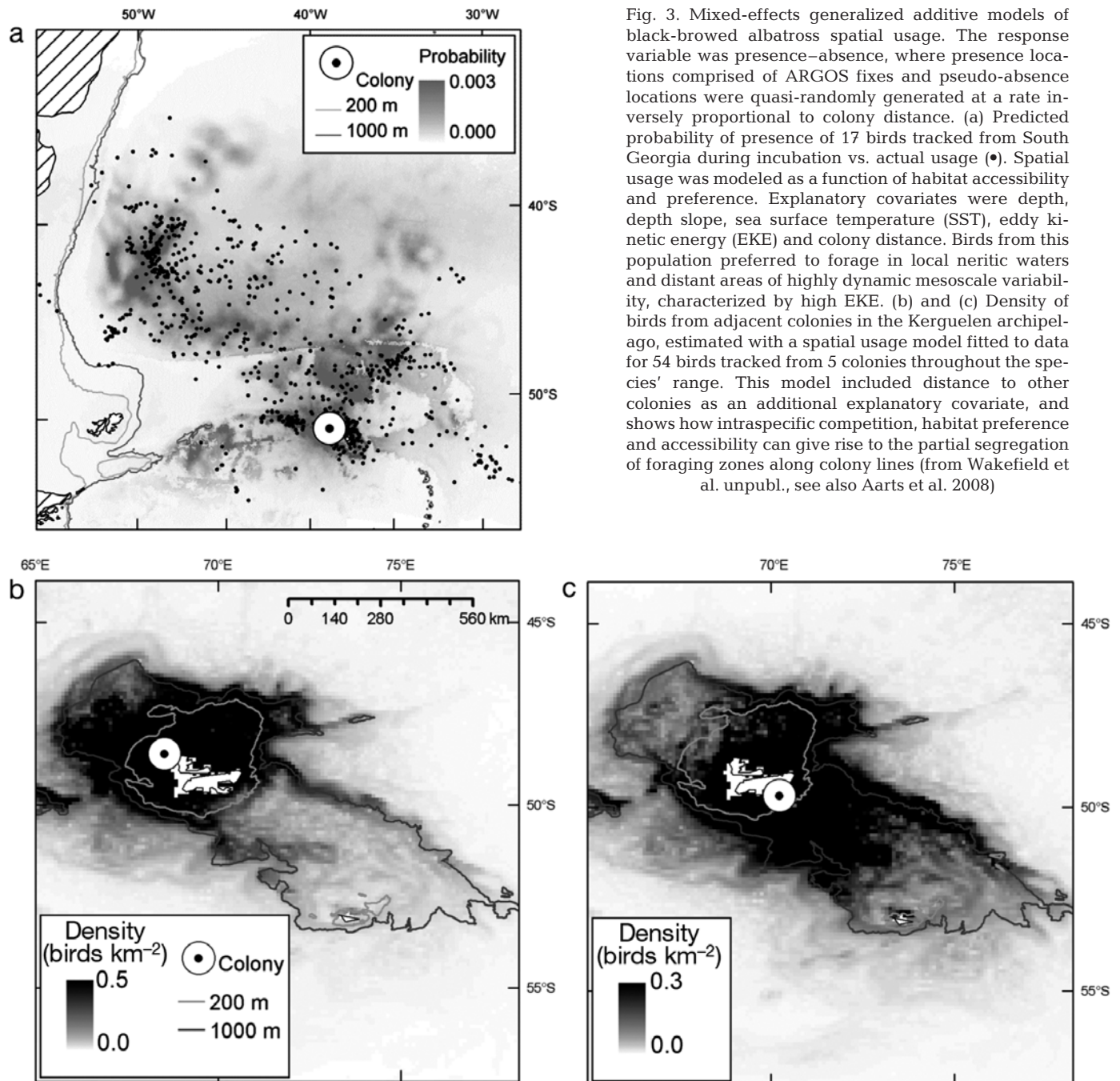


Fig. 3. Mixed-effects generalized additive models of black-browed albatross spatial usage. The response variable was presence-absence, where presence locations comprised of ARGOS fixes and pseudo-absence locations were quasi-randomly generated at a rate inversely proportional to colony distance. (a) 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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