

# Exploitation of distant Antarctic waters and close neritic waters by short-tailed shearwaters breeding in South Australia

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**Abstract** Identifying the primary foraging grounds of abundant top predators is of importance in marine management to identify areas of high biological significance, and to assess the extent of competition with fisheries. We studied the search effort and habitat selection of the highly abundant short-tailed shearwater *Puffinus tenuirostris* to assess the search strategies employed by this wide-ranging seabird. During the chick-rearing period 52 individuals were tracked performing 39 short foraging trips (1–2 days), and 13 long trips (11–32 days). First-passage time analysis revealed that 46% of birds performing short trips employed area-restricted searches, concentrating search effort at an average scale of  $14 \pm 5$  km. Foraging searches were more continuous for the other 54%, who travelled faster to cover greater distances, with little evidence of area-restricted searches. The prey returned indicated that continuous searchers consumed similar prey mass, but greater prey diversity than area-restricted search birds. On long trips 23% of birds travelled 500–1000 km to neritic (continental shelf) habitats, showing weak evidence of preference for areas of higher chlorophyll *a* concentration, and foraged at a similar spatial scale to short trips. The other 76% performed rapid outbound flights of 1000–3600 km across oceanic habitats commuting to regions with higher chlorophyll *a*. The spatial scale of search effort in oceanic habitat varied widely with some performing broad-scale searches (260–560 km) followed by finer-scale nested searches (16–170 km). This study demonstrates that a range of search strategies are employed when exploiting prey across ocean basins. The trade-offs between different search strategies are discussed to identify the value of these contrasting behaviours to wide-ranging seabirds.

**Key words:** area-restricted search, first-passage time, foraging, habitat associations, neritic, scale, search effort, tracking.

## INTRODUCTION

Seabirds are potentially valuable bio-indicators of the availability and distribution of prey in the marine environment. One such application is to identify regions where biophysical processes elevate productivity at or near the oceans surface. These ‘hot spots’ are the site of high productivity and biological diversity, and often attract large seabird aggregations (e.g. Cairns & Schneider 1990). Performing at sea surveys, or tracking seabird movements using satellite and archival telemetry, can effectively locate these important foraging areas (e.g. Suryan *et al.* 2006). Studying seabird movements also has the potential to reflect the size, structure and stability of prey patches (e.g.

Fauchald *et al.* 2000; Weimerskirch 2007). This is of value as the marine environment is exceptionally dynamic and heterogeneous (Hunt & Schneider 1987; Hunt 1990), meaning that the distribution and availability of resources is often highly variable in space and time. Yet the widespread use of seabirds as a proxy of prey distribution and availability is limited by our understanding of how search effort is distributed relative to prey density. While this topic has been the focus of much research in recent decades, the motivations underlying seabird movements are largely unresolved.

One of the most common ways to measure search effort in animals is to quantify travel speeds and turning rates (e.g. insects – Crist *et al.* 1992; herbivorous mammals – Rettie & Meisser 2000; Johnson *et al.* 2002; cetaceans – Jaquet & Whitehead 1996; pinnipeds – Bradshaw *et al.* 2004; and seabirds – Fauchald *et al.* 2000; Fritz *et al.* 2003). Reducing travel speed and

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increasing turning rates in an area-restricted search is interpreted as an increase in search effort, and enables animals to reduce the search area and elevate foraging efficiency (Fauchald & Tveraa 2003). In seabirds, increased search effort in an area-restricted search is commonly a response to prey detection (Nevitt & Veit 1999; Fauchald *et al.* 2000; although see Weimerskirch *et al.* 2007). Therefore, the scale of initial and nested searches can reflect the structural distribution of food, where high-density small-scale patches are nested within low-density large-scale patches (Kotliar & Weins 1990; Fauchald 1999).

Many procellariiform seabirds (albatrosses, shearwaters, petrels) exploit waters of varying productivity, where physical processes operate on a range of spatial and temporal scales. This is achieved through a dual foraging strategy involving the alternation of short trips of 1–3 days with long trips of 5–31 days during their breeding season. On long trips wide-ranging species can travel many thousands of kilometres (e.g. wandering albatross *Diomedea exulans* – Weimerskirch *et al.* 1993; blue petrel *Halobaena caerulea* – Chaurand & Weimerskirch 1994), while short trips are commonly confined to neritic (continental shelf) waters closer to the colony (Baduini & Hyrenbach 2003). Travelling more widely enables individuals to exploit broad-scale physical features (>300 km in diameter) including frontal systems, gyres, mesoscale eddies and large-scale upwellings (Cairns & Schneider 1990; Catard & Weimerskirch 1999; Waugh *et al.* 1999). This is beneficial as prey aggregations associated with broad-scale features are relatively more stable than those of medium- and fine-scale features (<50 km in diameter) (Wu & Louks 1995; Fauchald *et al.* 2000). Thus broad-scale features may provide seabirds with a greater degree of predictability in the location of profitable prey patches (Weimerskirch 2007).

Due to the spatial and temporal scales of Procellariiform foraging they provide a means of exploring the association between scale and predictability in the location of prey. While there is evidence that seabirds use olfactory cues (Nevitt & Veit 1999), and visual cues (e.g. other birds – Silverman *et al.* 2004; other predators – Nevitt & Haberman 2003; or prey) to aid in the location of prey, prior knowledge also plays a role in foraging decisions (Hunt *et al.* 1999). For example, direct flight followed by concentrated area-restricted search is commonly interpreted as birds knowing the location of suitable foraging areas, or following individuals who do (e.g. Waugh *et al.* 1999; Catard *et al.* 2000; Pinaud & Weimerskirch 2005). Directed searches imply there is a degree of stability in the location of prey, at least between one foraging trip and the next. An alternative foraging strategy involves more continuous searching behaviour, with little evidence of area-restricted search (Weimerskirch *et al.* 2007). Continuous searches are considered to reflect an

inability to find a suitable prey patch, and are an effective strategy when birds lack knowledge of current feeding locations, or are feeding on widely dispersed prey. We propose that the prevalence of either search strategy in a population may provide a useful tool for assessing predictability in the location of profitable foraging areas in marine habitats.

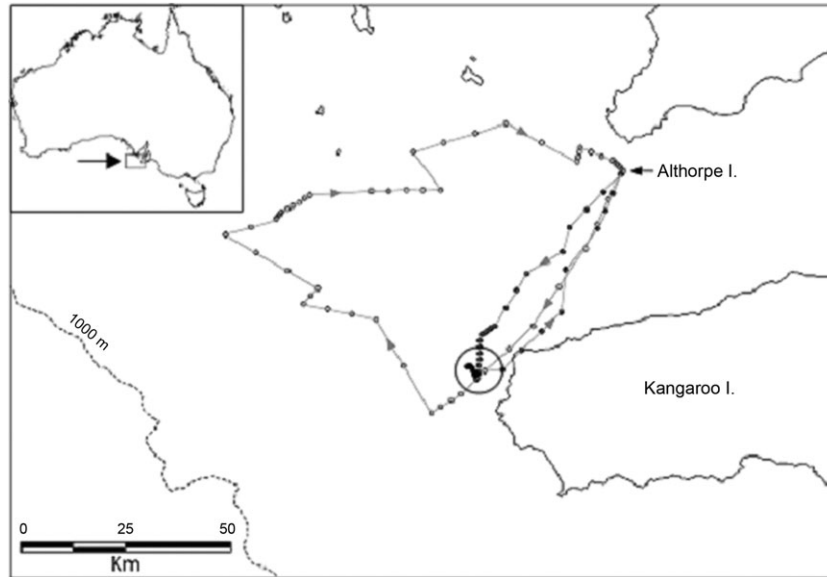
We studied breeding short-tailed shearwaters as they are well known to forage over neritic waters on short trips, and travel many thousands of kilometres across the Southern Ocean on long trips (Klomp & Schultz 2000). First, we hypothesize that the scale of search effort in oceanic waters will be broader than in neritic waters. This is based on the expectation that search effort will reflect the varied scale of biophysical features that influence prey distribution in each region. Second, we hypothesize that direct search strategies will be employed more readily in oceanic compared with neritic habitats. This will reflect that prey distribution and availability is relatively stable in oceanic habitats compared with neritic habitat. We presume that birds performing direct searches are targeting larger more stable prey aggregations, and expect a single prey type to be returned. Whereas continuous searching is considered a more opportunistic mode of foraging (Weimerskirch 2007), so we expect a broader range of prey items and a reduced foraging efficiency.

Defining the scale of area-restricted search provides clues as to the most effective scale for investigating the cues to which seabirds respond when foraging. Numerous studies have investigated the association between seabird search effort and either direct measures of food distribution (e.g. prey aggregations – Fauchald *et al.* 2000) or indirect measures (e.g. physical processes in the marine environment – Suryan *et al.* 2006). Trajectories are seldom related to physical or biological parameters. One major limitation involves identifying the optimal spatial scale to draw associations. Many researchers apply an arbitrary scale to the entire population of a species (e.g. Bergman *et al.* 2000; Johnson *et al.* 2002; Mårell *et al.* 2002; Fauchald & Tveraa 2003). However, individuals are expected to modify their movements based upon the size and shape of the prey patches that they encounter, instead of at some arbitrary scale. We hypothesize that modelling seabird habitat features at the scale of each individual will increase the strength of associations compared with a median scale representative of the population.

## METHODS

### Study site and chick capture

This study was conducted on Althorpe Island (35°37'S, 136°86'E), South Australia (Fig. 1) during the austral



**Fig. 1.** Map of corresponding short trips showing flight path of 67354 (hollow circles) with no evidence of area-restricted search, and 67826 (full circles) with an area of area-restricted search at the furthest extent of the foraging trip.

summers of 2005, 2006 and 2007. Each year numbered burrows containing hatched chicks were monitored to identify attendance patterns of parents ( $n = 25$ ). This involved monitoring changes in the mass of chicks by weighing them each night using a spring balance ( $\pm 5$  g). Chicks that increased in mass between weighings were considered to have received a feed, whereas mass loss indicated no visit from adults (as in Weimerskirch & Cherel 1998). Where chicks experienced mass loss over 5 consecutive days both parents were considered to be performing long trips. These burrows were targeted for transmitter deployment as returning parents would likely perform a short trip (repeat long trips were rare). A wooden trapdoor was installed at the burrow entrance. Arriving birds tripped a stick that closed the trapdoor and triggered a flashing red LED light. Upon arrival from a long trip birds were left in the burrow to feed their chick, and captured after 30–60 min, or until chick begging had ceased. Repeat weighing of chicks did not impact overall growth, or the rate of provisioning by adults.

### Transmitter deployment

Satellite transmitters (KiwiSat 202, single AA Cell, Sirtrack Ltd, North Havelock, New Zealand) weighing 30 g were glued to the back feathers of 53 individuals over the 3-year study (following Catard *et al.* 2000) using Loctite 401 glue (Intek Adhesives Ltd, Northumberland, UK). Foraging trips of eight adults were tracked in 2005, 32 in 2006 and 13 in 2007. Transmitter deployments each year were not limited to the same stage of chick rearing, meaning that trip duration was not comparable as long trips are known to increase with chick age (Hamer *et al.* 1997). Midway through the 2006 season, two subcutaneous sutures were added to secure transmitters (Mausser & Jarvis 1991) because some transmitters fell off prematurely. No chick desertion flights occurred,

but trip duration was not recorded for all birds as some avoided recapture upon return to their burrow. The impact of tracker attachment was assessed by comparing trip duration of tracked adults with a control group ( $n = 70$ ), recorded at the same time as transmitter deployment, from adults in surrounding burrows. A Wilcoxon rank sum test was chosen due to the unequal sample variances in the treatment and control groups, and an inability to accurately compare distribution and normality because of low sample size.

### Foraging success

We studied the 'foraging success' of adults performing short trips, being the combined measure of adult mass loss (i.e. depletion of energy reserves) and the mass of the meal returned (as in González-Solis *et al.* 2000). At the colony adults were weighed after they had fed their chicks, and before transmitter attachment. Upon their return from a tracked short trip some adults avoided capture so were recaptured and reweighed after they had completed feeding their chicks. If captured before feeding had commenced their stomachs were emptied by water offloading (Wilson 1984), before reweighing. Diet samples were collected from 20 of the 39 tracked short trips, and were stored in plastic vials and frozen until analysis. After flushing adults were re-fed 60 mL of minced sardines, and 60 mL of Vitrate formula to reduce the chances of dehydration. Most adults began feeding their chicks 30–60 min after re-feeding. Where a diet sample was collected the mass of the solid fraction collected was considered meal mass (see below). If adults fed chicks then pre- and post-feeding chick weights were used to estimate meal mass (Hamer *et al.* 1997). Diet samples were not collected, nor mass changes recorded, for long trips.

The solid fraction of stomach samples was separated through a 0.25-mm sieve (Connan *et al.* 2005), and the wet

weight of solids gained using an electronic balance ( $\pm 0.001$  g). Species contribution was based on the reconstructed biomass of each prey component after identifying cephalopod beaks (Lu & Ickeringill 2002), crustacean bodies (Ritz *et al.* 2003), and fish otoliths (Williams & McEldowney 1990). To estimate the length and mass of fish, otolith length was applied to species-specific regressions (Hindell 1988; Williams & McEldowney 1990; Cullen *et al.* 1992), and cephalopods from the upper or lower rostral length of beaks (Lu & Ickeringill 2002). Prey diversity was calculated as a percentage of the total number of meals that contained fish, squid or crustaceans. The variability in prey types returned from area-restricted search and non-area-restricted search short trips was assessed using a Kruskal–Wallis test.

### Flight parameters

Movement of tracked birds was monitored by Argos satellites. Argos locations were filtered by excluding locations below Class 0 (1–1.25 km accuracy), and by deleting records involving travel speeds above  $60 \text{ km h}^{-1}$  using the program ‘TimeTrack’ (version 1.0–9, M. D. Sumner, University of Tasmania, Hobart, following McConnell *et al.* 1992). Both short trip and long trip data were linearly interpolated in the R Statistical Package V2.6.2 (R Development Core Team, 2008), using the extension ‘adehabitat’, by adding a point every 15 min (time) between satellite-derived locations (Guinet *et al.* 1997). Total distance travelled was the cumulative distance between interpolated points, and maximum distance was the straight-line distance from the colony to the most distant point (Guinet *et al.* 1997). Foraging parameters on short trips were compared between years using ANOVAs or Mann–Whitney *U*-tests, and parameters were transformed where necessary.

### First-passage time and area-restricted search

To test if direct searches were more readily used in oceanic compared with neritic habitat, the search strategy of each individual was determined using first-passage time analysis. First-passage time, defined as the time required for an animal to cross a circle of a given radius, is particularly valuable for assessing hierarchical scales of movement (Fritz *et al.* 2003; Certain *et al.* 2007). A low first-passage time identifies areas along a trajectory where birds travelled rapidly, and high first-passage time signifies the slow travel speed and high sinuosity associated with area-restricted search. Relative consistency in the travel speed along an entire track indicates that birds were performing a more continuous foraging strategy, with no obvious areas of area-restricted search. To identify where fine-scale searches were performed inside broader-scale area-restricted search areas (nested area-restricted search) first-passage time was analysed within the most intensively searched area (Fauchald 1999; Fauchald & Tveraa 2003).

The occurrence of area-restricted search and the scale at which it was most evident were identified by examining the variance in log first-passage time at radii between 1 and 50 km at 2-km increments for each location for each short

trip, between 2 and 1000 km at 2-km increments for each long trip. A peak in first-passage time variance (denoted by an increase in variance beyond that recorded at the minimum scale) signifies the spatial scale where area-restricted search behaviour is most apparent (following Fauchald & Tveraa 2003). The absence of a peak (denoted by an instant drop in first-passage time variance from the minimum scale) signifies that birds travelled at a relatively continuous speed. Where a peak occurs (i.e. the scale of maximum first-passage time variance) the location of areas of area-restricted search along each track was identified by plotting first-passage time values for that corresponding scale as a function of time. A threshold first-passage time value was identified above which an animal was considered to be performing an area-restricted search, and below which it was assumed to be travelling (Pinaud & Weimerskirch 2007). This procedure also identified the: (i) number of area-restricted search zones; (ii) distance from the colony where area-restricted searches were performed; and (iii) time in area-restricted searches as a percentage of the total foraging trip time.

Area-restricted searches can be misinterpreted as periods when birds are not flying, but possibly resting on the sea surface. The presence of resting behaviour was assessed by inspecting the timing of first-passage time *versus* travelling behaviour for all foraging trips (Pinaud & Weimerskirch 2007). Where periods of area-restricted search were identified to be occurring at night time, location data were removed from the analysis.

### Marine habitat characterization

To investigate the correspondence between indirect measures associated with prey aggregation (i.e. habitat features) and seabird search effort, marine habitats exploited during short trips were characterized by: depth, chlorophyll *a* (Chl *a*), sea surface temperature and the gradients of each. For long trips, sea surface height and sea surface height gradient variables were also included. To examine whether changes in sea surface temperature were an artefact of location, latitude was also included in long trip analysis. Data for depth were obtained from the GEBCO 1-min grid. Chl *a* concentration and sea surface temperature data were obtained from SeaWiFS MODIS satellites (<http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.seawifs.shtml>). For short trips, 8-day averages of Chl *a* and sea surface temperature were obtained at a resolution of 0.1 degree. For long trips, monthly averages of both variables were obtained at 0.3 degrees. Monthly averages of sea surface height anomalies were obtained from AVISO Live Access Server V7 (<http://las.aviso.oceanobs.com/las/servlets/dataset>) at a resolution of 0.1 degree. All mapping was in MapInfo version 8.0, and gradients of habitat variables were calculated using the Vertical Mapper extension.

### Habitat associations

Habitat associations for long trips were assessed using two methods. First, correspondence between search effort and broad habitat features was analysed from the proportion of a foraging trip that was spent in different habitats. Depth

classes included neritic (<500 m), slope (500–1500 m) and oceanic waters (>1500 m; Waugh & Weimerskirch 2003). Sea surface temperature classes were defined as: temperate (>18°C), subtropical (14–18°C), subtropical front (12–14°C), sub-Antarctic (11–12°C), sub-Antarctic Front (9–11°C), Polar Frontal Zone (6–9°C) and Polar Front (<6°C) (Pinaud & Weimerskirch 2005). Chl *a* was assigned a category A–E to include five groups, each representing 20% of the range between the highest and lowest Chl *a* (Pinaud & Weimerskirch 2005). This method was not applied to short trips as the habitat categories were mainly applicable to larger scale movements in oceanic regions.

Second, a more detailed analysis was performed on long and short trips to assess the influence of spatial scale on habitat associations. This approach identifies the habitat features that influence search effort at a chosen scale. Generalized linear mixed-effects models were used, with first-passage time the response variable.

Habitat use was compared between different search strategies, and between large and nested scales in hierarchical searches. Trip types were also modelled separately to allow comparisons between short trips and long trips. A multi-scale modelling approach involved modelling habitat variables and first-passage time first at the scale of each individual, and then at a median scale representative of the entire sample. At each spatial scale first-passage time was recalculated. Habitat variables were extracted from the area defined by the circles of first-passage time along each track, and were recalculated to present averages at the appropriate scale for each model set. Bird identity was included as a random factor in each approach to account for intra-individual trends in first-passage time.

For short trips, the habitat variables used as independent predictors were: depth, depth gradient, sea surface temperature, sea surface temperature gradient, Chl *a* and Chl *a* gradient. The additional variables of sea surface height, sea surface height gradient and latitude were included in the long trip analysis. Meaningful interactions between habitat variables were also added to the analysis but kept to a minimum (Burnham & Anderson 2002). Where errors were non-Gaussian we used Gamma error distributions in the models. First-passage time was log-transformed, and the independent predictors were transformed where appropriate. Sea surface temperature was highly correlated with latitude so removed from the analysis. We used the methods of Suryan *et al.* (2006) to subsample first-passage time data and thereby avoid temporal autocorrelation (Legendre *et al.* 2002).

The multi-scale approach involved presenting a number of candidate model sets that were contrasted using Akaike's information criterion corrected for small samples (AIC<sub>c</sub>) and the Bayesian information criterion (BIC) (Burnham & Anderson 2002; Link & Barker 2006). AIC<sub>c</sub> favours more complex models when tapering effects exist and samples are large, whereas BIC identifies the principal drivers of complex relationships within larger datasets (Link & Barker 2006). The strength of evidence for each model relative to the model set was assessed by calculating relative model weights ( $w_{AIC_c}$  and  $w_{BIC}$ ). Weightings vary from 0 (no support for relationship between first-passage time and habitat variables) to 1 (complete support) (Burnham & Anderson 2002).

## RESULTS

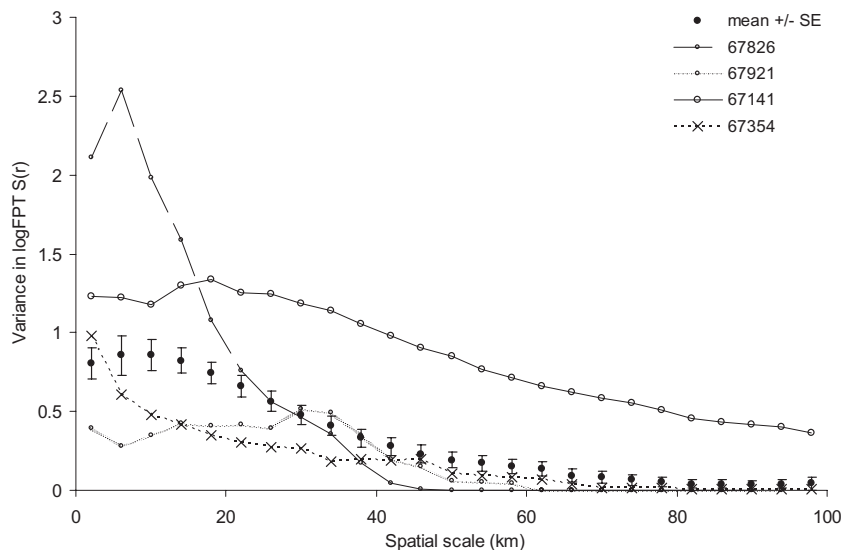
### Foraging strategies employed in neritic versus oceanic habitats

All short trips were performed in neritic waters. A direct search strategy, involving at least one distinct period of area-restricted search, was performed by 46% of individuals (18/39) on short trips (e.g. Fig. 1). The number of area-restricted search zones performed varied from 1 to 5. The general pattern of direct searches involved direct flight to an area followed by a bout of increased search effort (Fig. 1). A second mode of foraging performed by 54% of birds (21/39) involved a more continuous 'searching' strategy with no detectable periods of area-restricted search. This was identified by the absence of a variance peak (e.g. Bird 67354, Figs 1,2), indicating that there was low variance in travel speed along the entire flight path (i.e. relatively continuous movement). Continuous searching flights were faster both in terms of average and maximum speed (Table 1). While the average distance travelled by continuous searchers was greater than direct searches, this was not significant due to the extent of inter-individual variation within groups (Table 1).

The duration of long trips performed by tracked birds (mean = 19.7 ± 7.4 days (standard deviation; SD),  $n = 9$ ) was longer, but did not differ significantly from the control group (mean = 15.2 ± 5.9 days (SD),  $n = 70$ ) ( $Z = -1.8267$ ,  $P = 0.0677$ ). This suggests that tracked birds were not impacted by carrying a transmitter, and were behaving normally.

Of all 13 long trips, 10 were performed in oceanic waters, and the remaining three were largely restricted to neritic waters. Oceanic foraging trips reached a maximum of 6952 km from the colony (Table 2, Bird 52459, Fig. 3), whereas neritic trips reached 990 km (Table 2, Bird 52478, Fig. 3) (Table S1). Despite oceanic area-restricted search foragers travelling much further from their colony, a similar proportion of the tracked component of their long trip was engaged in area-restricted searches (37 ± 5%) compared with neritic foragers (40 ± 7%) (Table 3). This was due to the faster maximum travel speed of oceanic foragers, which enabled them to reach foraging sites more quickly ( $t = 6.27$ , d.f. = 7,  $P = 0.03$ , Table 2).

Compared with short trips, continuous search strategies were less prevalent on long trips, with no area-restricted searches detected for 23% (3/13) of birds (non-area-restricted search birds). With no evident area-restricted search these birds were considered to be adopting a continuous search strategy in oceanic waters, travelling to between 1854 and 2667 km from the colony (Table 2). Direct search strategies were more prevalent on long than short trips, with area-restricted searches on 77% (10/13) of long trips. Direct searches



**Fig. 2.** First-passage time analysis results, showing the variance in log first-passage time (FPT) (i.e. identifies areas of more variable travel speeds) as a function of spatial scale (km). The mean and standard error (SE) for all 19 individuals, which showed a pattern of area-restricted search is shown (black dots). Peaks in variance indicate an increase in search effort at that corresponding scale. Four examples of different types of trips are also shown. Bird 67354 shows no evidence of area-restricted search.

**Table 1.** Foraging parameters of short trips showing comparison between area-restricted search (ARS) *versus* non-ARS foraging parameters

| Parameter                           | ARS     |     | Non-ARS |     | ARS <i>versus</i> non-ARS      |             |
|-------------------------------------|---------|-----|---------|-----|--------------------------------|-------------|
|                                     | Average | SE  | Average | SE  | $U^{\dagger}$ , $F^{\ddagger}$ | $P$         |
| $n$                                 | 19      |     | 20      |     |                                |             |
| Trip duration (h)                   | 17      | 2   | 21      | 2   | 163.5 <sup>†</sup>             | 0.47        |
| Average speed (km h <sup>-1</sup> ) | 13      | 1   | 15      | 1   | 0.1 <sup>‡</sup>               | <b>0.03</b> |
| Maximum speed (km h <sup>-1</sup> ) | 51      | 3   | 66      | 3   | 4.2 <sup>‡</sup>               | <b>0.05</b> |
| Maximum distance from colony (km)   | 64      | 7   | 97      | 20  | 175.5 <sup>†</sup>             | 0.70        |
| Total distance travelled (km)       | 200     | 19  | 266     | 45  | 166 <sup>†</sup>               | 0.52        |
| Average bearing (degrees)           | 216     | 6   | 223     | 5   | 0.2 <sup>‡</sup>               | 0.63        |
| Meal mass (g)                       | 36.3    | 5.2 | 39.5    | 4.6 | 0.17 <sup>†</sup>              | 0.68        |

<sup>†</sup>Mann-Whitney  $U$ -test. <sup>‡</sup>ANOVA. Bold  $P$ -values denote significance at the 0.05 level.

were performed on all three long trips to neritic waters, and on seven of the 10 to oceanic waters.

Foraging success was comparable on both modes of short trip foraging as the mass of meals returned, and the body mass loss of foraging birds, did not differ (area-restricted search meal mass =  $39 \pm 4$  g ( $n = 10$ ), non-area-restricted search meal mass  $36 \pm 5$  g ( $n = 10$ ):  $F_{1,12} = 0.16$ ,  $P = 0.61$ ; area-restricted search mass loss =  $47.6 \pm 25.2$  g d<sup>-1</sup>, non-area-restricted search mass loss =  $39.9 \pm 29.7$  g d<sup>-1</sup>:  $F_{1,12} = 0.71$ ,  $P = 0.41$ ). Meal composition did differ, with 85% of meals returned from area-restricted search birds containing a single prey type, and 14% contained two prey types. In contrast, only 23% of the meals of non-area-restricted search birds contained a single prey type, 61% contained two prey types, and 15% three prey

types. There were also differences in the relative proportion of each major prey type (% mass). Area-restricted search meals contained a higher proportion of fish compared with non-area-restricted search meals ( $\chi^2 = 4.2$ ,  $P = 0.01$ ), which contained more cephalopod and krill (Fig. 4).

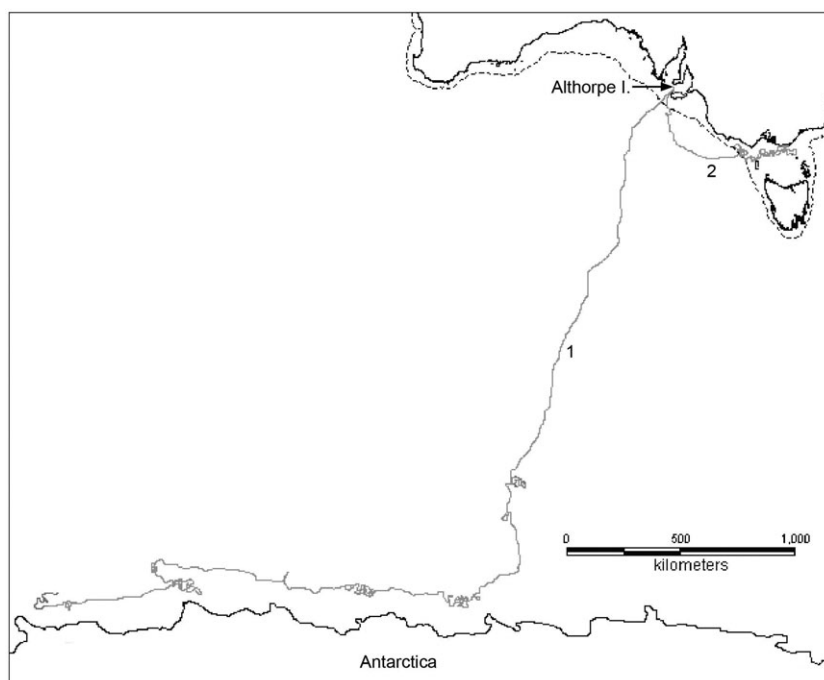
### Spatial scale of searches in neritic *versus* oceanic habitats

Of the 18 birds that performed area-restricted searches on their short trips the average scale was  $14 \pm 5$  km. Nearly half of these short trip foragers concentrated searches at a consistently fine spatial scale of 6 km, producing a narrow peak of high first-passage time

**Table 2.** Flight parameters of long trip foragers performing different search patterns (hierarchical area-restricted searches (ARSs), small-scale ARSs or no-ARSs), showing trip duration (days), distance (km) and speed of travel (km h<sup>-1</sup>)

| Search pattern                        | Mean         |      | Mean        |      | Mean   |     | Mean  |     |
|---------------------------------------|--------------|------|-------------|------|--------|-----|-------|-----|
|                                       | Hierarchical | SE   | Small-scale | SE   | No-ARS | SE  | Total | SE  |
| Trip duration                         | 26.3         | 1.7  | 12.7        | 0.7  | 20.3   | 2.3 | 19    | 1.9 |
| Days tracked                          | 13.8         | 1.0  | 9.0         | 0.4  | 7.7    | 0.7 | 10.9  | 1.4 |
| Total distance tracked                | 5862         | 439  | 2645        | 524  | 3900   | 324 | 4419  | 697 |
| Minimum total trip distance           | 10 023       | 1430 | 3638        | 1397 | 5897   | 556 | 7106  | 306 |
| Distance from colony when signal lost | 4161         | 224  | 993         | 182  | 1998   | 116 | 2687  | 486 |
| Maximum distance from colony          | 4087         | 669  | 1469        | 526  | 2334   | 246 | 2877  | 131 |
| Maximum speed                         | 66.4         | 1.2  | 50.7        | 2.2  | 65     | 2   | 61.3  | 0.6 |
| Average speed                         | 23           | 3    | 15          | 7    | 32     | 2   | 22.6  | 0.7 |
| <i>n</i>                              | 6            |      | 4           |      | 3      |     | 13    |     |

SE, standard error.

**Fig. 3.** Map showing the long trips of: (1) Bird 52463 and (2) Bird 52478. Note that Bird 52463 travels into oceanic habitat, and concentrates foraging activity in Antarctic waters, while Bird 52478 focuses foraging activity in neritic waters to the east of Althorpe I. Dashed lines show the continental shelf (>1000 m).

variance ( $n = 10/18$ , e.g. Bird 67826, Fig. 2). The remaining birds intensified their search effort at broader spatial scales (range 8–40 km), signified by a less distinct (i.e. flatter) peak in their first-passage time variance (e.g. Bird 67141, Fig. 2).

Of the 10 long trip foragers that conducted area-restricted searches a hierarchical search pattern was performed by 6. Hierarchical searches involved an increase in search effort first at a broad scale of  $269 \pm 84$  km, then at a nested scale of  $68 \pm 28$  km (Table 3). The remaining four birds performed area-restricted search directly at small scales, averaging  $29 \pm 6$  km. Interestingly, three of the small-scale

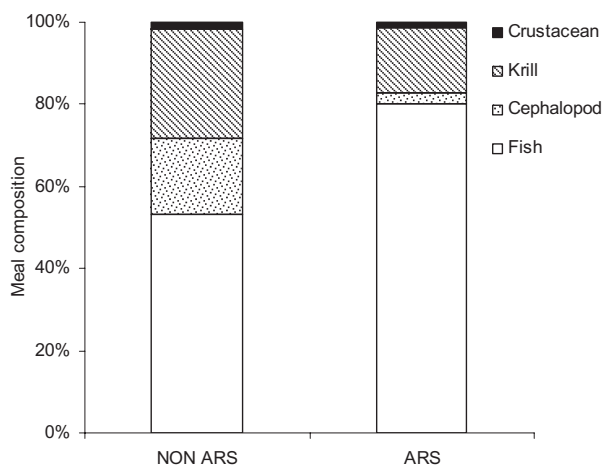
foragers performed long trips over neritic waters at a scale comparable with short trips.

Hierarchical searches were most commonly performed by birds travelling the farthest from the colony. For example, bird 52463 performed a hierarchical search after reaching 6952 km on day 11, and covered a total minimum distance of 15 220 km in the 32-day trip (Fig. 3). The maximum distance reached by small-scale area-restricted search birds and non-area-restricted search birds was significantly lower than hierarchical searchers (Kruskal–Wallis:  $\chi^2 = 5.4$ ,  $P = 0.009$ ,  $n = 9$ , and  $\chi^2 = 4.5$ ,  $P = 0.02$ ,  $n = 10$ , consecutively).

**Table 3.** Area-restricted search (ARS) parameters of different search patterns performed by long trip foragers, derived from first-passage time analysis

| Search pattern             | Mean         |     | Mean                                 |      | Mean        | Median ARS scale |
|----------------------------|--------------|-----|--------------------------------------|------|-------------|------------------|
|                            | Hierarchical | SE  | Small-scale                          | SE   | Non-ARS     |                  |
| Large scale                | 269          | 84  | 29                                   | 6    | None        | 72               |
| Nested ARS                 | 68           | 28  | None                                 | None | None        |                  |
| Number ARS zones           | 4            | 1   | 7                                    | 1    | None        |                  |
| Distance to first ARS zone | 2273         | 539 | 811                                  | 427  | None        |                  |
| Proportion trip in ARS (%) | 37           | 5   | 40                                   | 7    | None        |                  |
| Depth region               | All Oceanic  |     | 3 Neritic/Shelf slope,<br>1× Oceanic |      | All Oceanic |                  |
| <i>n</i>                   | 6            |     | 4                                    |      | 3           |                  |

Spatial scales reflect the linear radius (km) of the spatial area at which ARSs were most detectable. SE, standard error.

**Fig. 4.** Composition of short trip meals returned from area-restricted search area-restricted search and non-area-restricted search foraging trips.

Comparisons of travel speed and distance covered exemplify the different search tactics employed during direct *versus* continuous search strategies. For example, on long trips non-area-restricted search birds performing a continuous search travelled at a significantly faster average speed ( $32 \pm 2 \text{ km h}^{-1}$ ) than hierarchical foragers performing direct searches ( $23 \pm 3 \text{ km h}^{-1}$ ) ( $t = -1.73$ , d.f. = 6,  $P = 0.03$ , Table 2). Despite this, non-area-restricted search birds only covered half the average total distance of hierarchical foragers (Table 2). This indicates that the continuous search strategy involved a more convoluted and contorted flight path, representative of widespread searching.

#### Identifying habitat preferences using a multi-scale approach

Habitat associations were poor for both area-restricted search and non-area-restricted search birds when

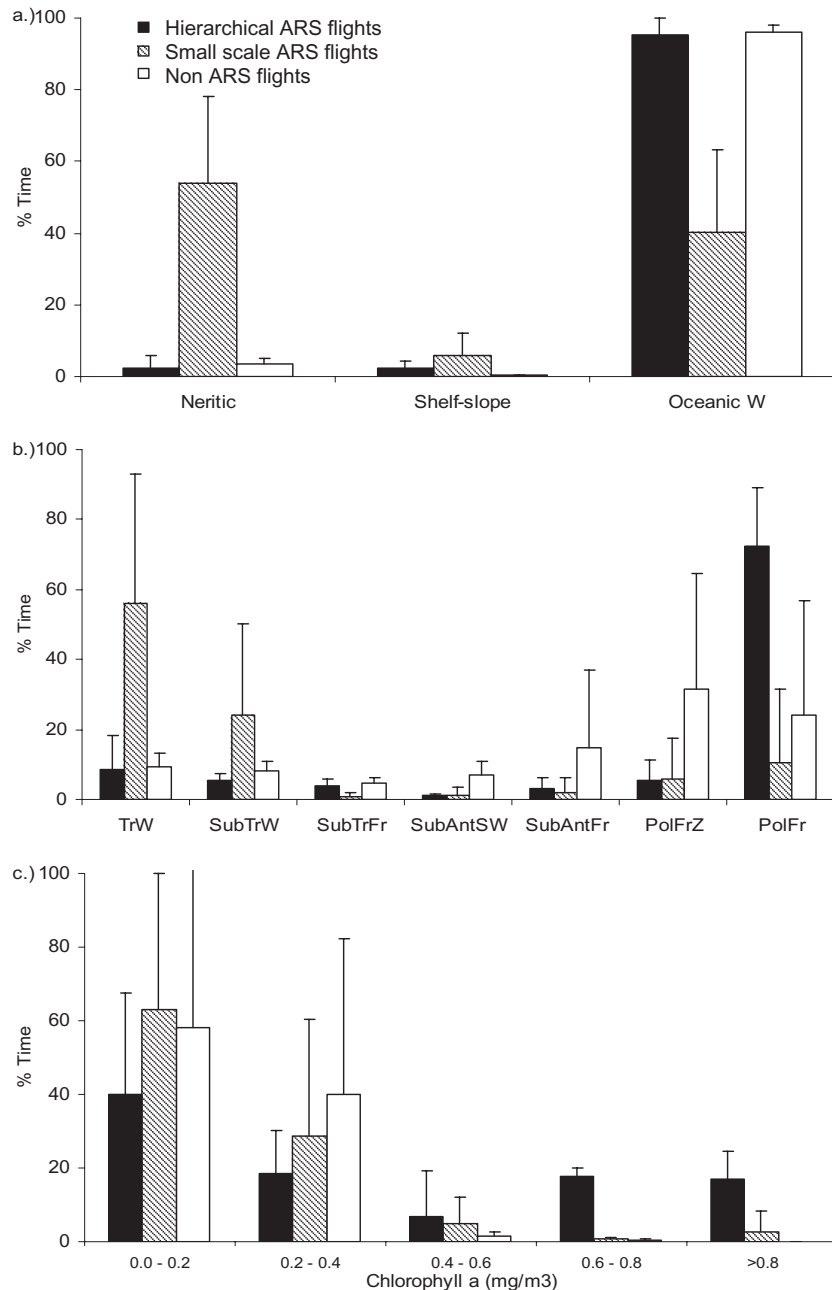
performing short trips, indicating that none of the habitat variables were the major drivers of first-passage time at the scales studied.

For long trip foragers the proportion of time spent in each habitat category differed with the search strategy. Birds performing hierarchical area-restricted searches on long trips spent  $95 \pm 4\%$  of the proportion of the trip recorded in oceanic habitat, and  $72 \pm 16\%$  at the Polar Front (Fig. 5a,b). 18% of their long trip was in waters of medium Chl *a* ( $0.6\text{--}0.8 \text{ mg m}^{-3}$ ), and 17% in high Chl *a* ( $>0.8 \text{ mg m}^{-3}$ ) (Fig. 5c). Similar to hierarchical foragers, non-area-restricted search birds spent most of their time in oceanic waters ( $96 \pm 2\%$ ) (Fig. 5a), but a wider range of sea surface temperature zones were visited (Fig. 5b), and they did not enter waters of high Chl *a* (Fig. 5c).

Finer-scale assessment of habitat associations provides further evidence of the selection of more productive waters by hierarchical foragers. When modelling habitat associations for hierarchical foragers at each individual area-restricted search scale, there was weak evidence for a correlation between habitat variables and first-passage time (Table 4). Two models containing latitude and Chl *a* had the highest BIC weights and the largest % deviance explained (LAT:  $w\text{BIC} = 0.057$ , %DE = 10.43; Chl *a*:  $w\text{BIC} = 0.049$ , %DE = 4.94) (Table 4). There was evidence for a positive correlation between latitude and first-passage time (Fig. 6a) suggesting that hierarchical foragers concentrate their foraging effort at higher latitudes. A positive relationship with Chl *a* also indicates that these birds increased search effort within regions of elevated productivity (Fig. 6b).

Modelling the habitat associations of hierarchical foragers at a single median scale (72 km, Table 2) did not improve model fit. As for the individual scale model, the same habitat parameters were weakly correlated with first-passage time. Latitude had the highest BIC weights and % deviance explained ( $w\text{BIC} = 0.042$ ; %DE = 3.67) (Table 4), and there





**Fig. 5.** Mean (standard deviation) per cent of time spent in each habitat type in relation to area-restricted search (ARS) spatial scales. Showing: (a) depth; (b) sea surface temperature; and (c) chlorophyll *a* concentration.

was some evidence for a weak effect between Chl *a* gradient and first-passage time ( $wBIC = 0.039$ ; %DE = 4.15) (Table 4).

In contrast to hierarchical foragers, area-restricted search birds that concentrated their search effort directly at a fine scale showed increased evidence of habitat effects, and improved goodness of fit (i.e. proportion of deviance explained (%DE), when examining habitat interactions at the median scale compared with individual scale. Again, model fit was highest for

models containing the single habitat variables latitude ( $wBIC = 0.104$ ; %DE = 45.99) and Chl *a* ( $wBIC = 0.076$ ; %DE = 21.22) (Table 4). Contrary to hierarchical foragers, the relationship between first-passage time and latitude was positive. This indicates that most birds concentrated their search effort in more northerly waters (Fig. 7a). Search effort was also increased within regions of elevated productivity, with a weak positive relationship between first-passage time and Chl *a* (Fig. 7b).

**Table 4.** Comparison of generalized linear mixed models of habitat associations of the short-tailed shearwater for models sets that contained models with some evidence of effects

| Model                    | $wBIC$ | $\Delta BIC$ | $wAICc$ | $\Delta AICc$ | % dev |
|--------------------------|--------|--------------|---------|---------------|-------|
| (a)                      |        |              |         |               |       |
| Null model               | 0.694  | 0.000        | 0.225   | 0.000         | 0.00  |
| IFPT ~ LAT + (Bird ID)   | 0.057  | 4.979        | 0.106   | 1.513         | 10.43 |
| IFPT ~ Chla + (Bird ID)  | 0.049  | 5.309        | 0.089   | 1.843         | 4.94  |
| IFPT ~ SSHg + (Bird ID)  | 0.047  | 5.396        | 0.086   | 1.930         | 3.50  |
| (b)                      |        |              |         |               |       |
| Null model               | 0.750  | 0.000        | 0.235   | 0.000         | 0.00  |
| IFPT ~ Chlag + (Bird ID) | 0.039  | 5.750        | 0.072   | 1.850         | 4.15  |
| IFPT ~ LAT + (Bird ID)   | 0.042  | 5.770        | 0.092   | 1.884         | 3.67  |
| IFPT ~ Chla + (Bird ID)  | 0.040  | 5.860        | 0.088   | 1.974         | 2.10  |
| (c)                      |        |              |         |               |       |
| Null model               | 0.615  | 0.000        | 0.192   | 0.000         | 0.00  |
| IFPT ~ LAT + (Bird ID)   | 0.052  | 4.943        | 0.079   | 1.771         | 4.84  |
| IFPT ~ BATH + (Bird ID)  | 0.051  | 4.977        | 0.077   | 1.806         | 4.34  |
| IFPT ~ SSHg + (Bird ID)  | 0.050  | 4.995        | 0.077   | 1.823         | 4.09  |
| (d)                      |        |              |         |               |       |
| Null model               | 0.374  | 0.000        | 0.232   | 0.000         | 0.00  |
| IFPT ~ LAT + (Bird ID)   | 0.104  | 2.565        | 0.112   | 1.455         | 45.99 |
| IFPT ~ Chla + (Bird ID)  | 0.076  | 3.184        | 0.083   | 2.073         | 21.22 |

Showing: (a) Hierarchical long trip foragers using a multi-scale individual approach ( $n = 7$ ); (b) Hierarchical long trip foragers using a median population scale (72 km) ( $n = 7$ ); (c) Small-scale long trip foragers using a multi-scale individual approach, and excluding the individual long trips that foraged in oceanic waters, that is, neritic birds only ( $n = 3$ ); (d) Small-scale long trip foragers using a median population scale (72 km). Explanatory variables are: LAT, latitude; BATH, bathymetry/depth; Chl *a*, chlorophyll *a* concentration; Chl *ag*, chlorophyll *a* gradient; and SSHg, sea surface height gradient. First-passage time (FPT) was the response variable, and individuals were included as a random effects.  $wBIC$  and  $wAICc$  are the relative model weights, which denote the strength of evidence for each model relative to the entire model set.

No habitat associations were apparent within the nested scale of search effort for hierarchical foragers. There was also no evidence of a relationship between habitat variables and first-passage time for non-area-restricted search birds.

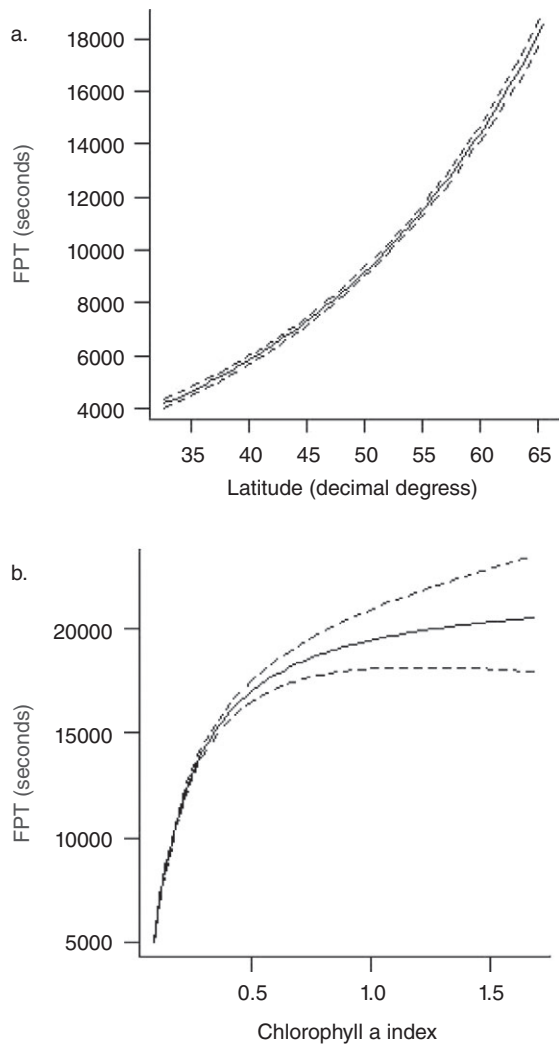
## DISCUSSION

### Identifying primary foraging areas, and the spatial scale of search effort

We have confirmed that the long-ranging flights identified in previous studies on short-tailed shearwaters (Nicholls *et al.* 1998; Klomp & Schultz 2000) are regularly employed in the breeding season, with many individuals travelling in excess of 10 000 km and foraging in Antarctic waters. We also reveal that neritic waters of south-eastern Australia are the site of long trip foraging. This reveals that chick-rearing adults are not programmed to forage in the Southern Ocean, but instead make decisions about the broad-scale regions where they will forage at the outset of each foraging trip. It remains unclear whether staying in neritic waters is a strategy used by some individuals for an entire breeding season, or if an individual mixes long trips to neritic and oceanic waters.

Our first hypothesis, that that the scale of searches will differ between habitats as a reflection of the varied scale of prey aggregations, was supported by the finer-scale searches employed over neritic waters (both long and short trips). Finer area-restricted search scales have been identified in other procellariiforms when exploiting neritic waters around sub-Antarctic islands (e.g. black-browed albatross *Thalassarche melanophrys*  $29 \pm 11$  km – Pinaud & Weimerskirch 2007). Modifying search behaviour due to habitat is considered a response to the smaller spatial scales of upwelling features that aggregate prey in shelf-edge and neritic habitats (Cairns & Schneider 1990; Catard & Weimerskirch 1999; Waugh *et al.* 1999).

The broad range of scales recorded on long trips is comparable with that of other wide-ranging procellariiforms derived using first-passage time methods (e.g.  $130 \pm 85$  km – yellow-nosed albatross *Thalassarche carteri* – Pinaud & Weimerskirch 2005). Past studies also commonly record hierarchical foraging in oceanic habitat (e.g. Fauchald *et al.* 2000; Pinaud & Weimerskirch 2005; Suryan *et al.* 2006), enabling birds to concentrate foraging effort at finer scales in areas where prey density is highest (Kotliar & Weins 1990; Fauchald 1999; Fritz *et al.* 2003). Further nested scales of area-restricted search are expected as short-tailed shearwaters intensify their search effort

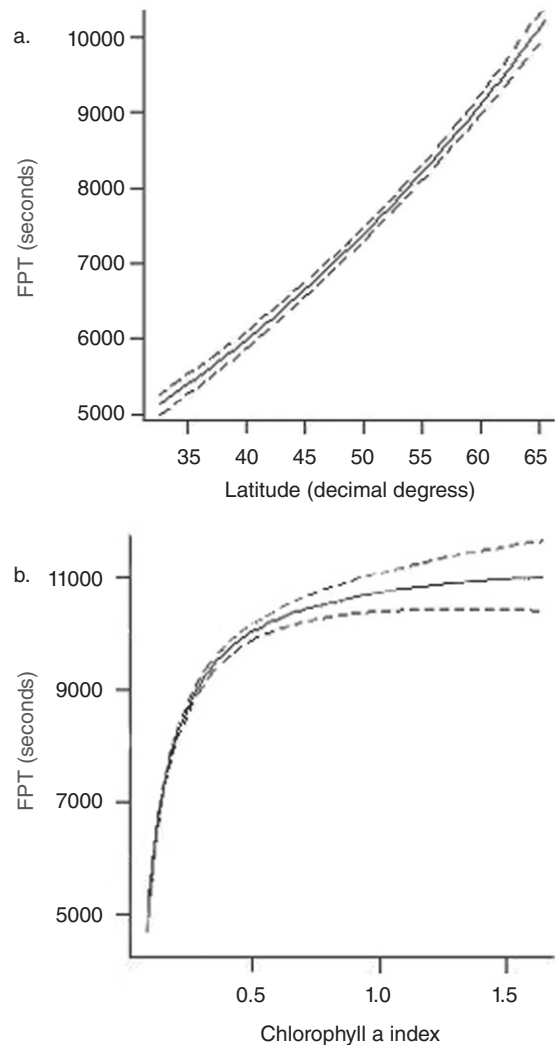


**Fig. 6.** Regression of Generalised Linear Mixed Models (GLMM) models showing the residuals of the predicted relationship between first-passage time and oceanic variables for hierarchical long trip foragers when analysed at the individual scale, showing: (a) positive relationship between first-passage time (FPT) and latitude (LAT); and (b) positive relationship between first-passage time and Chl *a* index.

towards prey aggregations and single prey patches (10–100 m). However, identifying these nested scales requires the use of higher resolution equipment such as global positioning system trackers (e.g. Grémillet *et al.* 2004).

#### Interpreting foraging conditions from foraging behaviour – predictability in neritic and oceanic waters

The higher frequency of direct searching during long trips compared with short trips supports our second hypothesis, that prey distribution and availability is



**Fig. 7.** Regression of Generalised Linear Mixed Models (GLMM) models showing the residuals of the predicted relationship between first-passage time and oceanic variables for long trip foragers who employed search effort directly at small scales (i.e. no nested scale of search effort detected), showing: (a) a positive relationship between first-passage time (FPT) and latitude (LAT); and (b) a positive relationship between first-passage time and Chl *a* index.

more stable in oceanic compared with neritic habitats. Where foragers have to make foraging decisions with little, if any, knowledge of the current distribution and availability of their prey, revisiting areas of past foraging success is a useful search strategy. However, this strategy is only of value where there is a degree of stability in the location of profitable prey aggregations. For short-tailed shearwaters, the direct foraging strategy is beneficial as the commuting phase enables the rapidly travel across areas not used for feeding, thereby maximizing the time spent in more profitable foraging areas. This commuting behaviour is common among wide-ranging seabirds (e.g. grey-headed albatross

*Thalassarche chrysostoma* and black-browed albatross – Waugh *et al.* 1999; white-chinned petrels *Procellaria aequinoctialis* – Catard *et al.* 2000; yellow-nosed albatross – Pinaud & Weimerskirch 2005), and suggests that birds have some prior knowledge about the location of productive areas (Waugh *et al.* 1999; Catard *et al.* 2000; Bradshaw *et al.* 2004).

The value of a direct strategy on long trips is evident from the increased time spent in waters of elevated Chl *a*, and the correlation between first-passage time and Chl *a*. Broad-scale oceanic features are commonly exploited by wide-ranging seabirds after a commuting phase to areas of higher Chl *a* (e.g. yellow-nosed albatross – Pinaud & Weimerskirch 2005; short-tailed albatross *Phoebastria albatrus* – Suryan *et al.* 2006). This essentially enables individuals to maximize the time they spend in habitat more productive than the temperate waters around their colony. Foraging in areas of anticipated higher productivity also enables the offset of costs incurred during broad-scale movement.

When productivity is more variable, prey patches are likely to move, disperse or get depleted. In these conditions direct search strategies are less useful as seabirds forage with less certainty, and direct flight paths may bypass suitable prey patches. Continuous searches, involving slower and more convoluted flight paths, increase the chances of encountering prey. This strategy may also be particularly useful when exploiting sparsely distributed low-density prey (e.g. Weimerskirch *et al.* 2005). While likely to incur greater energy costs, continuous searches have been shown to enable wide-ranging seabirds to maintain a suitable and predictable yield (e.g. Weimerskirch *et al.* 2005).

Despite the reduced prevalence of direct search strategies on short trips compared with long trips, their occurrence was higher than expected. Roughly half of short trip foragers did travel directly to their primary foraging site, suggesting that they either had prior knowledge of the location of a suitable prey patch, or were following a bird who did. Short-tailed shearwaters embarking on short trips should have prior knowledge of the location of profitable feeding areas, as neritic habitat is exploited when birds return from long trips the previous day (i.e. within 24 h of the tracked short trip). This is evidenced by the return of fresh neritic prey in long trip meals (Weimerskirch *et al.* 1993; Weimerskirch & Cherel 1998). The prevalence of direct flights to foraging areas on short trips is contrary to the day-to-day variability in the location of suitable prey patches that was expected in neritic waters. Primary production in neritic waters of the study area fluctuates on a weekly basis through the summer months due to the influence of a wind-driven upwelling system (Kampf *et al.* 2004; Ward *et al.* 2006; Middleton & Bye 2007), so pelagic fish abundance is likely to be highly variable (Dimmlich *et al.* 2004; Ward *et al.* 2006). The relative consistency in the direc-

tion of area-restricted searches on short trips from the colony suggests that this feature creates a broad region where short-tailed shearwaters direct their search effort. Thus, despite their irregularity, local upwelling systems in neritic waters can provide a degree of predictability in the distribution of resources for seabirds across a 20–200 km spatial scale. Targeting neritic waters on long trips provides further evidence that this region contains areas of predictable prey returns for short-tailed shearwaters. Long trips are particularly informative of suitable feeding conditions in neritic waters, as they are performed to accumulate an energy rich meal for the chick, and to replenish the adults own energy stores (Weimerskirch & Cherel 1998).

### The foraging efficiency of different search strategies

We provide evidence of comparable foraging success among short-tailed shearwaters performing varied search strategies. Specifically, continuous searches on short trips returned a comparable-sized meal to direct searches, indicating that a widespread searching tactic offers an effective foraging strategy for this species (as in wandering albatross Weimerskirch *et al.* 1993; Weimerskirch *et al.* 1997). While the contents of the stomach returned to the colony may only represent the final stages of a day-long foraging bout, consideration of changes in adult body mass should account for prey that has already passed through the digestive tract of the adult. The foraging success achieved on continuous searches is evidence that the neritic waters exploited contained enough widely dispersed prey to provide adequate prey returns for chick-rearing short-tailed shearwaters.

The return of a more variable range of prey on short trips also implies that continuous searches are a more opportunistic mode of foraging as individuals consume whatever prey they can find. In contrast, the return of a single prey type suggests individuals are exploiting larger more stable prey aggregations (Weimerskirch 2007). We were unable to identify the foraging success achieved by birds on long trips as they avoided recapture upon their return to the colony. Further studies comparing the quantity of oil returned from different search strategies on long trips would be of value to determine whether short-tailed shearwaters adopting a continuous search strategy are able to attain comparable foraging success to area-restricted search foragers.

The absence of habitat associations on continuous searches is further evidence that individuals adopting this strategy are searching more opportunistically to sample a wider range of habitats than area-restricted search foragers. Studies of other procellariiforms also found that search effort during continuous searches

is poorly correlated with oceanographic features (Weimerskirch *et al.* 1997).

### Identifying an optimal scale for assessing habitat associations

Many have recognized the limitation of modelling movement at a single, arbitrarily defined scale (e.g. Bergman *et al.* 2000; Johnson *et al.* 2002; Mårell *et al.* 2002; Fauchald & Tveraa 2003). A comparative approach assessing model performance at a range of scales is more effective for identifying the best spatial scale at which to assess and quantify habitat associations (e.g. Suryan *et al.* 2006). We modified this comparative approach further by extracting habitat features at the scale individuals foraged, as well as at a single median scale representative of the population. However, habitat associations did not strengthen when considering search effort at the scale of each individual. Poor performance of individual scale models is likely due to the extent of variation in the scale of initial searches performed (range 22–540 km). This variation is a reflection of the vast array of search tactics employed by seabirds, which are likely a combination of current conditions, and past experience. Studies on wandering albatross have revealed that younger birds perform hierarchical patterns of area-restricted searches at a wide range of scales, whereas older birds tend to perform area-restricted searches directly at finer scales (Weimerskirch *et al.* 2007). This could be due to ontogenetic development in the foragers capacity (Field *et al.* 2005), or may reflect that individuals gain knowledge of where resources can be located predictably as they age (Greig *et al.* 1983). Despite its poor performance, the individual multi-scale approach may be an effective means of identifying seabird habitat preferences. Further attempts to assess habitat associations for wide-ranging species would benefit by segregating hierarchical foragers from those who employ searches directly at small scales.

The weak performance of habitat association models is no surprise as the distribution of prey, and resultant movement of birds is likely to be influenced by a wide range of unmeasurable factors additional to the habitat variables selected in this study. Many other factors can adversely affect the relationship between seabirds and their prey, for example, exogenous factors (response lags, weather conditions, cycles in prey availability); and endogenous factors (individual variation in search patterns and search strategies) (Ryan & Cooper 1989). The limited temporal and spatial resolution of data available from remote sensing satellite equipment may also confound any relationships. For example, we used 8-day averages of Chl *a* and sea surface temperature,

and monthly averages of sea surface height, whereas seabirds are sampling their environment daily.

The absence of any associations between foraging and habitat descriptors at small scales (nested area-restricted search, small-scale area-restricted search and short trip foraging) suggests that the indirect measures of prey distribution that were used have less influence over finer scales of search effort. This may be influenced by the greater mismatch between physical features and prey aggregations that occurs at fine scales (Bradshaw *et al.* 2002). This is no surprise, given that other seabird studies using direct measures of prey distribution (prey aggregations) have also identified a greater mismatch between search effort and prey at fine scales (e.g. common murre *Uria aalge* – Fauchald *et al.* 2000).

### Conclusions

We have provided evidence in support of Klomp and Schultz's (2000) findings that chick-rearing short-tailed shearwaters exploit distant foraging areas in the Southern Ocean (Weimerskirch & Chérel 1998). Neritic waters are the primary site for short trip foraging, and are also exploited during long trips. We propose that the prevalence of certain search strategies in a seabird population may provide a useful tool for assessing predictability in the location of profitable foraging areas in marine habitats. Using this method we have inferred a degree of predictability in the location of prey in neritic waters, likely associated with a regional coastal upwelling. Foraging tactics involving continuous searches indicate that it is not necessary to direct search efforts towards highly productive patches; instead, an array of strategies reveals the degree of flexibility that exists in seabird foraging. This work demonstrates how tracking studies of top predators can provide a potentially valuable means of identifying the biological value and spatial predictability of physical processes. Such an approach has wide-ranging applications to marine and fisheries management, especially at a time when the needs of top predators are being incorporated into ecosystem based management plans in many marine regions around the world.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Long trip flight parameters of 13 satellite tracked short-tailed shearwaters *Puffinus tenuirostris*.