At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study

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Summary

1. In order to study and predict population distribution, it is crucial to identify and understand factors affecting individual movement decisions at different scales. Movements of foraging animals should be adjusted to the hierarchical spatial distribution of resources in the environment and this scale-dependent response to environmental heterogeneity should differ according to the forager's characteristics and exploited habitats.

2. Using First-Passage Time analysis, we studied scales of search effort and habitat used by individuals of seven sympatric Indian Ocean Procellariiform species fitted with satellite transmitters. We characterized their search effort distribution and examined whether species differ in scale-dependent adjustments of their movements according to the marine environment exploited.

3. All species and almost all individuals (91% of 122 individuals) exhibited an Area-Restricted Search (ARS) during foraging. At a regional scale (1000s km), foraging ranges showed a large spatial overlap between species. At a smaller scale (100s km, at which an increase in search effort occurred), a segregation in environmental characteristics of ARS zones (where search effort is high) was found between species.

4. Spatial scales at which individuals increased their search effort differed between species and also between exploited habitats, indicating a similar movement adjustment for predators foraging in the same habitat. ARS zones of the two populations of wandering albatross *Diomedea exulans* (Crozet and Kerguelen) were similar in their adjustments (i.e. same ARS scale) as well as in their environmental characteristics. These two populations showed a weak spatial overlap in their foraging distribution, with males foraging in more southerly waters than females in both populations.

5. This study demonstrates that predators of several species adjust their foraging behaviour to the heterogeneous environment and these scale-dependent movement adjustments depend on both forager and environment characteristics.

Key-words: albatross, area-restricted search, First-Passage Time, foraging distribution, spatial scale.

Introduction

Understanding the response of organisms to environmental heterogeneity is an important topic in ecology when studying species habitat selection and is at the basis of the growing landscape ecology discipline (Lima & Zollner 1996; Fortin & Agrawal 2005). To achieve this goal, an increasing number of studies have focused on the movements of foraging animals and on the perception of ecological scales by organisms through an adjustment of their movement in response to heterogeneity in the landscape (Johnson *et al*. 2002; Fauchald & Tveraa 2003; Fritz, Saïd & Weimerskirch 2003; Frair *et al*. 2005; Nams 2005; Pinaud & Weimerskirch 2005; Bailey & Thompson 2006). These studies are based on the hypothesis that a foraging animal should increase its search effort in areas where resources are plentiful rather than in areas where resources are scarce. For example, an animal should increase its turning rate and/or reduce its speed as a response to increases in intake rate or prey encounter rate, adopting a so-called Area-Restricted Search (ARS) behaviour (Kareiva & Odell 1987). Then one can study these changes in animal movements as a response to heterogeneity in its

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environment, helping to understand underlying processes acting on population dynamics across habitats (Lima & Zollner 1996). As environmental heterogeneity is present at several temporal and spatial scales, we expect that these adjustments in search effort vary also with scale (Fauchald 1999). In addition, as different species can exploit the same environment (resulting in a spatial overlap at large scale) but with different foraging strategies (e.g. orientated vs. random search in albatrosses; Weimerskirch 1998) or exploiting different resources, we can also expect differences in movement adjustment (i.e. in ARS) between species (Fritz *et al.* 2003). To our knowledge, the hypotheses have never been explored among predator species foraging in a heterogeneous and patchy environment. However, studying how different species of the same guild respond to environmental heterogeneity allows us to understand their coexistence in a spatially varying environment, where segregation at a finer scale (i.e. a foraging niche specialization) is expected to minimize competition (Brown 2000). Here we focus on a comparison of scale-dependent movement adjustment and spatial distribution between foraging seabird species.

Marine predators are good focal organisms to study scale-dependent adjustments in relation to environmental heterogeneity because of the wide range of spatial and temporal scales occurring in their resource distribution and abundance. In the marine environment, interactions between ocean currents, bathymetry and other physical and biological processes promote growth and retention of plankton, leading to higher spatial heterogeneity in organism distribution (Haury, McGowan & Wiebe 1978), which influences the distribution of top predators such as seabirds (see Hunt *et al.* 1999). In such conditions, scale-dependent adjustments of movement are found in some foraging seabirds (Viswanathan *et al.* 1996; Fauchald & Tveraa 2003; Fritz *et al.* 2003; Pinaud & Weimerskirch 2005; see also Johnson *et al.* 2002 for a terrestrial example). One might expect these adjustments to be widely adopted by these predators.

Factors affecting these adjustments could be numerous. Considering that some habitats should be more profitable than others for a predator, Fritz *et al.* (2003) suggested that different species of predator should respond at different scales according to the exploited habitat, because of differences in prey distribution or density in habitats. In fact, Fauchald (1999) described a model where a predator should adjust its search radius according to its prey encounter rate, which is related to the prey density and the size of the patch. In this case, higher encounter rates (meaning small patches with high prey density) led to an adjustment with a smaller search radius. Then similarities in movement adjustment among a predator guild could be expected in relation to prey availability in a particular habitat.

Among predators, differences in movement adjustments could be also expected in relation to targeted prey (difference in prey distribution) and the forager's own strategy. More than 10 species of large Procellariiforms (albatrosses and petrels > 1 kg in mass) inhabit the southern part of the Indian Ocean. They feed on prey (mainly fish, squid and crustacean in different proportion according to species, see review in Cherel & Klages 1998) known to present a heterogeneous, patchy, scale-dependent (hierarchical) resource distribution (Pakhomov & Froneman 2000). The distribution and foraging movements of such long-ranging central-place predators has been studied more frequently since the use of satellite tracking (Jouventin & Weimerskirch 1990). Between species, there is an extensive overlap in foraging distribution at the regional (1000s km) scale (Weimerskirch 1998; BirdLife International 2004; Phillips, Silk & Croxall 2005). Different foraging strategies can be identified (Weimerskirch 1998): some species use a 'loop searching' strategy, whereas others commute quickly to a specific area where foraging effort is high. These strategies can be related to the prey distribution. For example, the wandering albatross *Diomedea exulans* (L.) relies mainly on squid whose distribution is extremely patchy and scattered over extensive areas using a low-cost looping strategy to cover extensive surface (Weimerskirch, Gault & Cherel 2005). Therefore, one might expect intrinsic differences in foraging adjustments between species.

In this study, we use a scale-dependent approach to analyse individual foraging trips of six albatross and a large petrel species (1·2–10 kg) in the South Indian Ocean, using satellite-tracking data and First-Passage Time (FPT) analysis (Fauchald & Tveraa 2003). FPT analysis is based on the calculation of time taken for an animal to cross a circle with a given radius. This calculation is done all along the path by moving the circle every *d* distance and for increasing radii. Then, FPT can be used as a scale-dependent measure of search effort. Furthermore, it allows the determination of the spatial scale at which a forager increases its search effort (when adopting an ARS) and adjusts its movements according to environmental heterogeneity. We used this approach to address the following points. First, one might expect movement adjustments (i.e. ARS) in these top predators. Second, by adopting this scale-dependent approach and determining ARS magnitude, we can identify interspecific and intraspecific differences in search effort distribution. We expect that responses in foraging movement of these predators should differ according to species and habitats, as species differ in their characteristics and in their foraging strategy, and also that oceanic habitats differ in prey distribution and availability.

Materials and methods

SATELLITE TRACKING AND ANALYSIS

The field studies were carried out on seven species of large size Procellariiforms equipped with the Argos system (satellite transmitters, Platform Terminal Transmitters, 32g PTT100 and 64g Toyocom 2038C, Microwave Telemetry, Columbia, MD, USA) during the same reproductive period (mid-incubation), from three study sites in South Indian Ocean: Crozet (46°26′S; 51°52′E),

Kerguelen (49°40′S; 70°15′E) and Amsterdam (37°51′S; 77°31′E) Islands in south Indian Ocean. Deployments were carried out on different bird populations, from Crozet on wandering albatross *Diomedea exulans* L. (WAc) in 1998 ($n = 17$ individuals), 1999 ($n = 14$) and 2000 ($n = 9$), sooty albatross *Phoebetria fusca* Hilsenberg (SA) in 1992 ($n = 5$), 1993 ($n = 3$) and 1994 ($n = 5$), light-mantled albatross *P. palpebrata* Forster (LMA) in 1994 ($n = 3$) and white-chinned petrel *Procellaria aequinoctialis* L. (WCP) in 1996 ($n = 6$); from Kerguelen on wandering albatross (WAk) in 2002 ($n = 12$) and black-browed albatross *Thalassarche melanophrys* Temminck (BBA) in 1999 ($n = 7$); from Amsterdam, Amsterdam albatross *D. amsterdamensis* Roux *et al.* (AA) in 1996 ($n = 6$) and 2000 ($n = 9$) and Indian yellow-nosed albatross *T. carteri* Rothschild (YNA) in 2000 ($n = 9$) and 2002 ($n = 17$). Signal emission rate was the same for all PTTs (i.e. 90 s). Details about deployments can be found in Weimerskirch (1998), Weimerskirch *et al.* (1999), Pinaud & Weimerskirch (2002, 2005) and Waugh & Weimerskirch (2003). The satellite transmitter represented 0·5–2% of the mass of birds. In some cases, several trips existed for the same individual, so we used the first one for analysis to avoid pseudoreplication. Gender was determined for WA, AA and YNA only, using morphometric measurements. According to Argos location accuracy class (A, B, 0, 1, 2 and 3, Argos 1996), all class B fixes were removed since their accuracy was low (46 km ± 59, $n = 67$, calculated with PTTs at a fixed position). Locations were then filtered according to maximum speeds (see Weimerskirch *et al.* 1993, 2000; for details) obtained from calculations (Pennycuick 1982) and observations (Alerstam, Gudmundsson & Larsson 1993) for each species. After filtering the Argos locations, accuracy was better than 2 km. Position of the sun was calculated at each location, with the civil twilight considered at 6° below the horizon.

ENVIRONMENTAL DATA

Environmental data, i.e. bathymetry, sea surface temperature (SST) and chlorophyll-*a* concentration (Chl-*a*, as a proxy of biological production), were extracted for the study zone containing all locations, located between 10°E and 115°E and between 25°S and 70°S (see Fig. 1). Bathymetric data were obtained from the ETOPO5 $5 × 5$ min Navy database (http://ingrid.ldeo.columbia.edu/SOURCES/WORLDBATH/). In order to link search zones to an average primary productivity, seasonal (austral spring and summer) SeaWiFS Chl-*a* 1997–2004 climatologies were obtained from Level-3 Standard Mapped Images (http://seawifs.gsfc.nasa.gov/cgi/level3.pl) at a resolution of 9 km. We used monthly Sea Surface Temperature (SST) with a resolution of 9 km from the NOAA/NASA Pathfinder Advanced Very High Resolution Radiometer (AVHRR), distributed by the Physical Oceanography Distributed Active Archive Center at the Jet Propulsion Laboratory (http://poet.jpl.nasa.gov/). SST data were obtained for the

month of tracking for each bird and Chl-*a* data for the corresponding season. Oceanographic habitats were delimited using SST gradients calculated with ArcView 3·2 GIS (ESRI Inc., Redlands, CA, USA) over a grid of a resolution of 9 km. Fronts, as zones of strong SST gradients, appeared clearly by this method, and indicated precisely oceanographic habitat limits rather than by the method using SST values alone. In the study area according to Holliday & Read (1998), we defined from the north to the south the following oceanographic habitats: Benguela Current (BC), Agulhas Front (AF), Agulhas Current Retroflection (ACR), North Subtropical Front (NSTF), Subtropical Waters (north of ARF; STWn), Agulhas Return Front (ARF), Subtropical Waters (south of ARF; STWs), South Subtropical Front (SSTF), Sub-Antarctic Surface Waters (north of SAF; SASWn), Sub-Antarctic Front (SAF), Sub-Antarctic Surface Waters (south of SAF; SASWs), Polar Front (PF), Antarctic Surface Waters (AASW), Southern Boundary of Antarctic Circumpolar Current (SB), Marginal Ice Zone (MIZ).

FIRST-PASSAGE TIME ANALYSIS

We followed Fauchald & Tveraa's (2003) method to calculate First-Passage Time (FPT) along each trip. Analyses were written and performed using the Software R (Version 2·0·0, R Development Core Team 2005). FPT is defined as the time required to cross a circle with a given radius r (see Fauchald & Tveraa 2003). Values of FPT were calculated every second kilometre travelled, for spatial scales r from 5 to 1000 km. The relative variance $S(r)$ in FPT was calculated as a function of radius r. This variance is given by $\mathrm{Var}(\log(t(r)))$, where $t(r)$ is FPT for circle of radius r, and is log-transformed to make the variance $S(r)$ independent of the magnitude of the mean FPT (see Fauchald & Tveraa 2003). $S(r)$ was then plotted in relation to r (for r from 5 to 1000 km). According to Fauchald & Tveraa (2003), a peak in relative variance $S(r)$ reveals presence of ARS behaviour and indicates the ARS scale r at which a bird increased its search effort. By inspecting the plot of FPT values at the correct spatial scale (where a peak of variance occurred) as a function of time elapsed since departure (see Fauchald & Tveraa 2003 in their fig. 3), we were able to locate where the bird increased its search effort implying more intense foraging behaviour (Weimerskirch, Wilson & Lys 1997). Following this FPT/travelling time plot, we selected the spatial locations of high search effort (i.e. high FPT values) called hereafter 'ARS zones'. To do so, a FPT value threshold was determined according to its multimodal distribution: ARS zones corresponded to the mode of higher FPT values (see Fig. S1 in Supplementary materials for an example). Environmental variables were extracted according to the location of ARS zones. These zones were generally close in time together (mainly less than 6 h) and in the same oceanographic habitat for the same individual. For each individual trip, we calculated
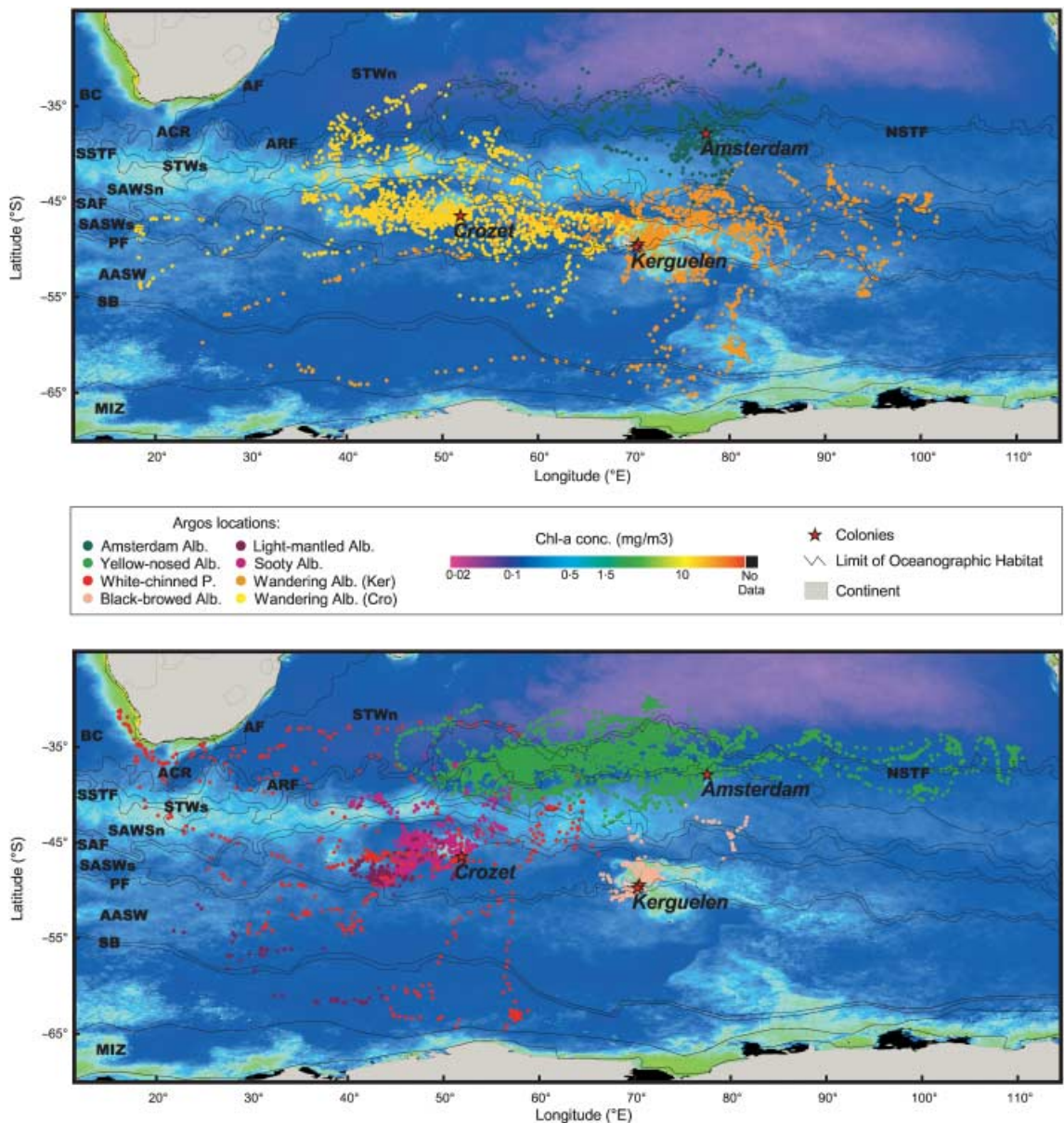
Fig. 1. Argos satellite tracking locations for the seven Procellariiform species in south Indian Ocean (one colour per species/population). Chl-*a* concentration (mg m⁻³) austral summer climatology for the period 1997–2003 is represented in the background. Lines indicate oceanographic habitat limits in January 1999 as revealed by SST gradients (see text for details). Red stars indicate study colonies and continents are in grey. (upper panel) Amsterdam and wandering albatrosses; (lower panel) black-browed, yellow-nosed, light-mantled and sooty albatrosses and white-chinned petrel.

the distance from the main (i.e. highest duration in ARS) ARS zone to the colony. As these birds can move and search at night (Weimerskirch & Guionnet 2002), FPT was calculated all along the path, including locations during the night. But, in some cases (11 birds, independently of species) when inspecting the FPT/travelling time plot, high FPT values corresponded strictly to night-time periods for the whole path (see Fig. S2 in Supplementary materials for an example), particularly when the peak of variance occurred at very small spatial scales (10–20 km). In this case, we suspected that birds were sitting on water at night for a long period. This artefact (mix-up between searching at small scale and resting at night) can be caused by the accuracy inherent in the Argos system, which does not

allow the discrimination of small-scale movements within a 1 km radius from the absence of movement (Weimerskirch, Salamolard & Jouventin 1992). Previous FPT analysis on paths including locations on the nest (motionless incubating birds equipped with PTT) showed that search at very small scale (< 10 km) cannot be separated from resting periods. High FPT values occurring every night could therefore reflect sitting on the water (sleeping or foraging at night waiting for prey (Weimerskirch *et al.* 1997) rather than in-flight searching behaviour. As we were interested in searching movements rather than resting, these periods with high FPT values at night were removed for these birds. To do so, all the locations corresponding to the ARS zone were deleted and time and positions in the path were

recalculated accordingly. Then FPT analysis was done in order to detect changes in movements at a larger scale. After this removal, the influence of suspected resting periods at night was considered again in this second calculation by inspecting the FPT/travelling time plot and if this effect was still suspected (high FPT values at night), the bird was not considered for further analysis.

We explained ARS scales (log-transformed) as a function of species, oceanographic habitats and Chl-*a* concentrations. To do so, Type I linear models (i.e. considering each term in addition) were compared and selected using Akaike's Information Criterion (AIC, Burnham & Anderson 1998). Individual search effort in a habitat was defined as the sum of FPT in this habitat (as an index of search effort at the spatial scale at which effort was increased) divided by the total distance moved in this habitat according to Argos tracking. Distribution of search effort was compared with the general distribution at sea used by the considered population. This was achieved by calculating the utilization distribution (UD) kernel estimation (Worton 1989) of all Argos locations by population, as an assessment of general distribution at sea. UD was estimated using

'adehabitat' package on R software (Calange & Basille 2004). We set the smoothing factor *h* constant for each population at 2·59 decimal degrees (mean of the *h* calculated on each population using Least-Squares Cross-Validation, Silverman 1986), in order to allow comparison as *h* could vary between each population. To study interspecific and intraspecific differences in search effort distribution according to environmental characteristics (bathymetry, SST and Chl-*a*), we performed a normalized linear discriminant analysis on ARS zones under SYSTAT 9 and R package 'ade4' (Thioulouse, Dufour & Chessel 2004). This allows the discrimination (as a measure of nonoverlapping) of the environmental characteristics for each ARS zone according to species (or populations). Each ARS zone was characterized by median (to minimize influence of extreme values and effect of difference in ARS scales) SST, bathymetry and Chl-*a* concentration (log-transformed), and its position in oceanographic habitat. Data were transformed to satisfy normality, and statistics used the R and SYSTAT 9 software.

Results

Large petrels and albatrosses breeding at Crozet, Kerguelen and Amsterdam Islands foraged over a wide geographical range, from Antarctica close to the ice edge to subtropical regions and South Africa (Fig. 1). All oceanographic habitats were crossed during movements at sea, but the majority of Argos locations were concentrated in the sub-Antarctic and subtropical waters around colonies.

AREA-RESTRICTED SEARCH AND SCALE OF SEARCH EFFORT

According to FPT analysis, 110 individuals (for a total of 122) showed a peak of variance, varying from 30 to 120 km (Table 1 and see Fig. 2A for some examples), indicating the presence of ARS behaviour during foraging trips for all species (71–100% of individuals according to species/populations). Examples of individual foraging trips showing an ARS behaviour (peak of variance) are represented in Fig. 2. Among these 110 individuals, seven birds (four YNA, two WA and one AA) presented a high search effort associated strictly with the night, suspecting that birds were resting on water for a long time rather than moving (see Fig. S2 in Supplementary materials). As we were not able to identify clearly changes in search effort in these birds, they were not considered from further analysis. As revealed by the pattern of variation (FPT values in function of time since departure, see an example in Fig. S1, Supplementary materials), birds used from one to six ARS zones per trip, generally grouped in time, indicating that birds generally concentrated their search effort in one habitat. Averaged parameters for each species are presented in Table 1. With species sampled at different years, no significant differences were observed between years.
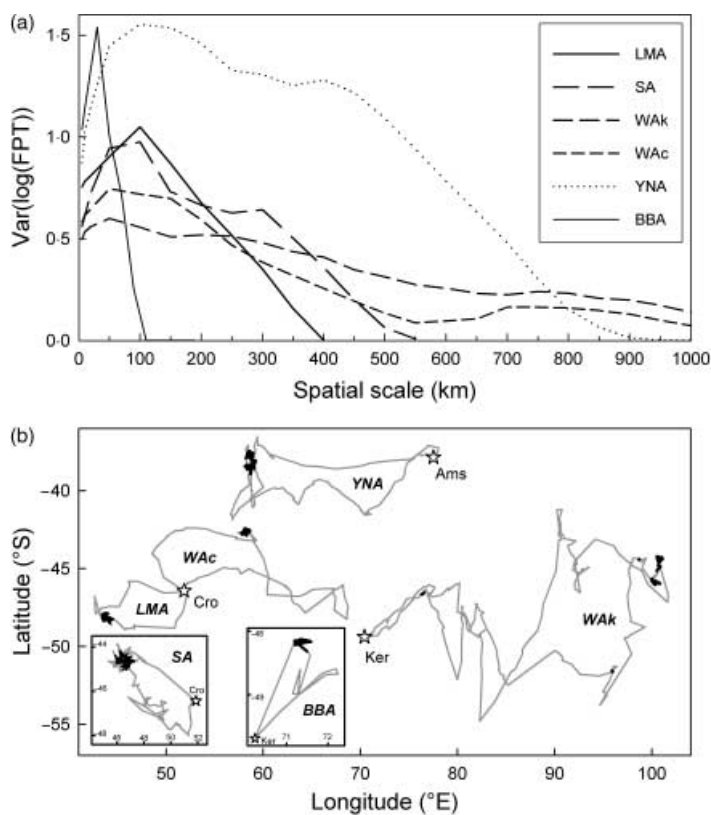
Fig. 2. Results given by FPT analysis for representative individual trips of a given species for large Procellariiforms in the South Indian Ocean during the incubation period. (a) Variance in log(FPT) in function of spatial scale. A peak of variance reveals an increase in search effort at the corresponding scale. (b) The foraging trips (grey, thin lines) and ARS zones (where individuals increased their search effort, in black, large lines) of the same individuals as revealed by FPT analysis. Colonies are indicated by white stars. LMA, light-mantled albatross; SA, sooty albatross; WAc, wandering albatross from Crozet and WAk from Kerguelen; YNA, Indian yellow-nosed albatross; BBA, black-browed albatross.

Table 1. Scale of search effort, distance between the colony and main ARS zone, and averaged values for environmental parameters on intensive search areas for foraging trips showing an ARS behaviour of seven Procellariiform species ('a' for Amsterdam, 'c' for Crozet and 'k' for Kerguelen Is.). Body mass information comes from the publications cited in the Materials and Methods section. Values are indicated with ± SD

Species (island)	Mean body mass (kg)	Birds with ARS (n/total)	Birds with ARS (% total)	ARS scale (km)	Distance ARS zone to colony (km)	Median SST (°C)	Median Bathymetry (m)	Median Chl-a conc. (mg m⁻³)
AA (a)	6·5	10/14	71·4	72 ± 119	915 ± 825	19·4 ± 1·2	−3581 ± 1188	0·138 ± 0·065
BBA (k)	3·7	7/7	100	29 ± 15	187 ± 68	2·1 ± 0·7	−1006 ± 824	0·531 ± 0·232
LMA (c)	3·1	3/3	100	73 ± 46	1089 ± 645	3·7 ± 3·1	−4052 ± 799	0·232 ± 0·059
SA (c)	2·6	10/13	76·9	78 ± 50	543 ± 277	4·4 ± 5·5	−2888 ± 668	0·244 ± 0·430
WA (c)	9·6	34/40	85·0	63 ± 64	845 ± 486	8·4 ± 5·2	−2386 ± 1409	0·244 ± 0·139
WA (k)	9·5	11/12	91·7	39 ± 27	782 ± 620	7·4 ± 4·5	−3161 ± 1220	0·240 ± 0·140
WCP (c)	1·2	6/6	100	97 ± 73	1935 ± 952	17·2 ± 8·4	−3297 ± 2311	0·341 ± 0·125
YNA (a)	2·4	22/26	84·6	121 ± 78	1513 ± 522	15·5 ± 1·1	−4446 ± 535	0·240 ± 0·063

### DISTRIBUTION OF SEARCH EFFORT ACCORDING TO HABITAT

FPT analysis allowed us to study the search effort distribution of each species (Fig. 3). YNA and AA concentrated their search effort mainly in the subtropical habitats, while SA, LMA and BBA foraged mainly in the sub-Antarctic habitat. A last group of species (WA, WCP) was able to spread their search effort from sub-Antarctic to subtropical habitats, from Antarctica to South Africa coasts.

From the discriminant analysis, Axis 1 and 2 (eigenvalues of 1·82 and 0·16, respectively) explained 94·9% of the cumulative proportion of total variance. The dis-tribution of ARS zone characteristics between populations was not random (Wilks' $\lambda = 0\cdot273$, $P < 0\cdot001$), meaning significant specific differences in environmental characteristics on ARS zones, even for different species breeding on the same island (for example YNA and AA for Amsterdam Island, Fig. 4). Segregation in ARS zones between populations occurred mainly according to a gradient of surface temperature (highest F-value, indicating that SST had the highest contribution in discrimination), and secondarily according to the Chl-a concentration and bathymetry. SST and Chl-a concentration were negatively correlated. Thus, despite a wide spatial overlap in at-sea occurrence observed at a large scale (see Figs 1 and 3), populations intensified
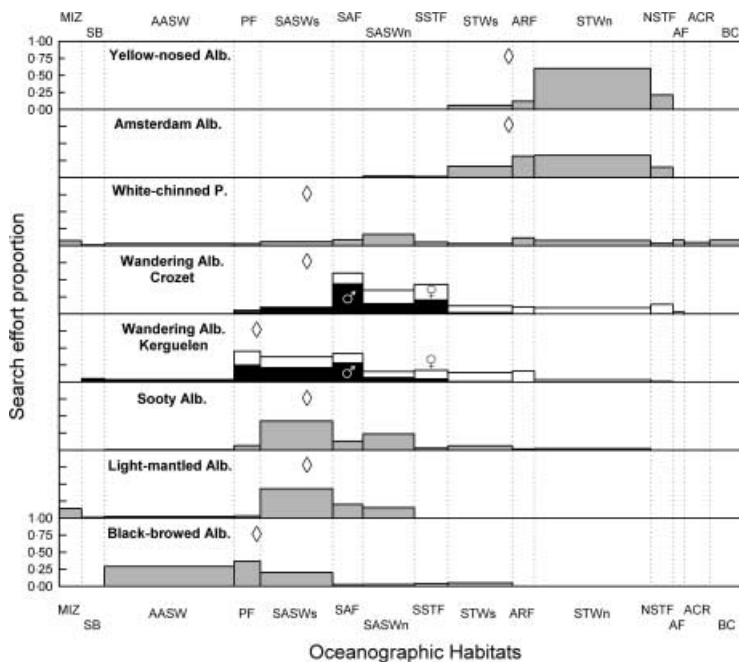
Fig. 3. Search effort for seven Procellariiform species, with intensity of search effort as defined by FPT analysis given for each population in each oceanographic habitat (from left to right: habitats from south to north). Bar width is proportional to surface habitat availability. Diamonds indicate colony position in oceanographic habitats. For WA from Crozet and Kerguelen, black bars represent males and white bars represent females. See Materials and methods for acronyms.
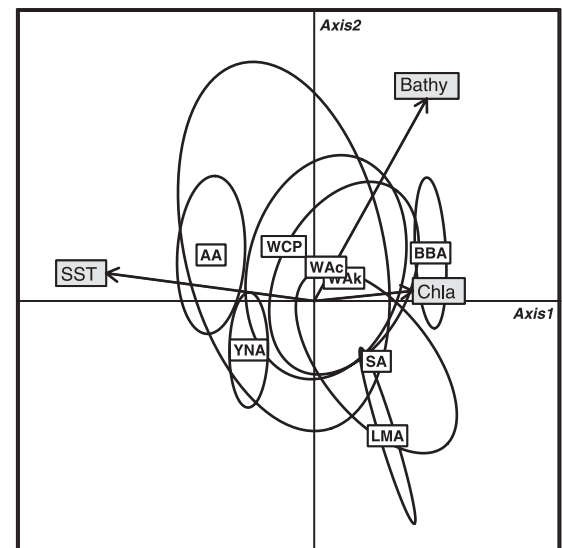
Fig. 4. Results of the discriminant analysis (factors 1 and 2 are represented by axis 1 and 2, respectively) on ARS zones according to populations, as a function of Bathymetry, SST and Chl-a concentration on these ARS zones. Ellipses represent the dispersion of ARS zones with a 95% interval. AA, Amsterdam albatross; LMA, light-mantled albatross; SA, sooty albatross; WAc, wandering albatross from Crozet and WAk, from Kerguelen; WCP, white-chinned petrel; YNA, Indian yellow-nosed albatross; BBA, black-browed albatross.
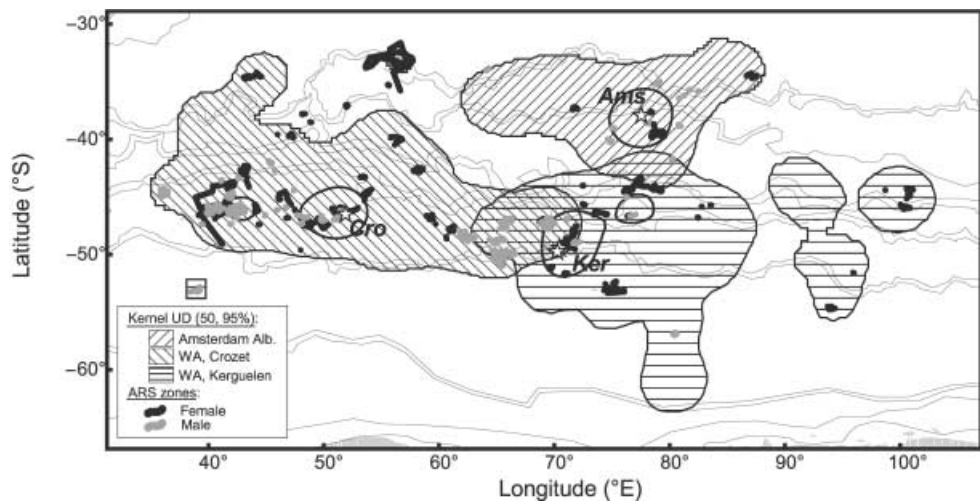
Fig. 5. Distribution of ARS zones of wandering albatross (WA) from Crozet and Kerguelen, and Amsterdam Albatross. Lines indicate 95 and 50% contour of Utilization Distribution (UD) from Kernel analysis on all Argos locations. Fixes represent individual ARS zones, with darker grey for females, paler for males.

Table 2. Deviance, r^2 and AIC comparison for type I linear models explaining ARS scales in function of species, oceanographic habitat and Chl-*a* concentration. The complete model is Log(ARS scale) = S + H + C + S × H + S × C + H × C + S × H × C with *log(ARS scale)*, logarithm of ARS scale; *S*, species; *H*, oceanographic habitat on main ARS area; *C*, log-transformed Chl-*a* concentration on main ARS area. The model retained is the additive one (S + H)

| Models	Adjusted r^2	Deviance	No. of parameters	AIC	ΔAIC
Constant	–	283·16	2	287·16	11·55
S	0·143	260·94	8	276·94	1·33
S + H	0·235	235·60	20	275·61	0
S + H + S × H	0·226	222·29	31	284·29	8·68
S + C	0·136	260·75	9	278·76	3·15
S + C + S × C	0·097	258·53	15	288·53	12·92
S + H + C	0·226	235·53	21	277·53	1·92
Complete	0·260	190·32	48	286·32	10·71

their search effort on areas with different environmental characteristics with relatively little overlap at this fine scale. The apparent overlap in environmental characteristics in ARS zones of WCP, WAc and WAk is due to their wide at-sea distribution, reflecting a large inter-individual difference in ARS characteristics, which was not present in the other species (AA, YNA, LMA, BBA and SA). It is interesting to note that, despite breeding 1200 km away and thus experiencing different water masses, the two WA populations from Crozet and Kerguelen present ARS zones with similar environmental characteristics (the smallest between group $F_{3,483} = 4·286$, see Fig. 3, and also Supplementary materials S3 for detailed values), indicating that they exploit habitats with the same environmental characteristics.

Sexual differences were observed in the characteristic of main ARS zones for the two WA populations (see Figs 3 and 5). Males of both populations ($n = 17$ for Crozet and 5 for Kerguelen) increased their search effort in colder waters compared with females ($F_{1,41} = 15·92$, $P < 0·001$), with no effect of the breeding population site alone ($F_{1,41} = 2·02$, $P = 0·14$) nor of the interaction population × sex ($F_{1,41} = 0·36$, $P = 0·58$). Otherwise, no

significant difference occurred in SST on ARS zones between males and females in YNA ($F_{1,13} = 1·28$, $P = 0·28$).

VARIATIONS IN AREA-RESTRICTED SEARCH SCALE IN RELATION TO SPECIES AND ENVIRONMENT

No significant difference was found in ARS scale between WA from Crozet and Kerguelen (log-transformation, $F_{1,43} = 0·931$, $P = 0·34$), so these two populations were grouped in Linear Model analysis. Two models presented close AIC, the model with *Species* and the model with the additive terms *Species* and *Habitat* (Table 2). This last model was selected because, despite an important increase in the number of parameters, its AIC was lower than the first one and also because of a larger amount of variance explained ($r^2 = 0·24$ against $r^2 = 0·14$ for the model with *Species* alone, see Table 2). According to this model, the difference in ARS scale was first explained by differences between species (with minimum value of ARS scale for BBA, and maximum scale for YNA), but also by use of different oceanographic habitats, with particularly small ARS scale values for the south
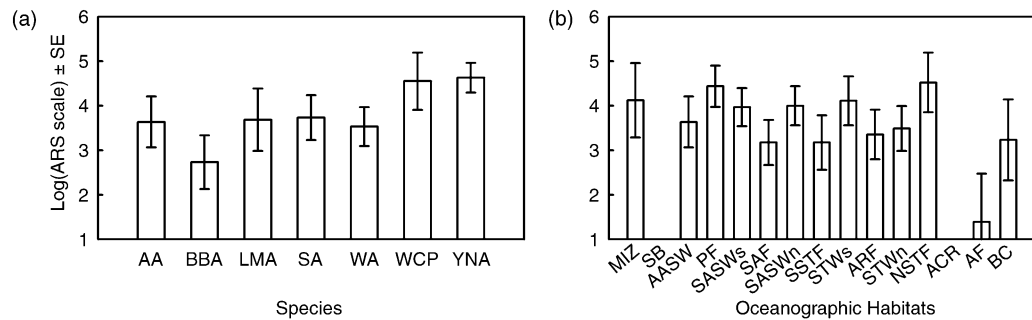
Fig. 6. Estimates (± standard error) of the selected type I linear model (see Table 2). *log(ARS scale)* = SP + HAB, as revealed by FPT analysis for 103 foraging trips of seven Procellariiform species. AA, Amsterdam albatross; LMA, light-mantled albatross; SA, sooty albatross; WA, wandering albatross; WCP, white-chinned petrel; YNA, Indian yellow-nosed albatross; BBA, black-browed albatross. See Materials and methods for habitat acronyms.

subtropical front and the sub-Antarctic front (Fig. 6). According to our results, this indicates that predators of different species foraging in the same habitat tend to adopt the same scale-dependent movement adjustment.

Discussion

Our FPT analysis has demonstrated that the large majority of individuals of all albatross and petrels studied adopted ARS at spatial scales varying from 30 to 120 km, these values depend on both forager species and environment characteristics. Using this approach, one can identify and understand foraging adjustments of these predators at different scales.

Resources in the marine environment present a heterogeneous and hierarchical distribution (Fauchald 1999). Such patchy resource distribution can lead to a scale-dependent pattern of foraging movement adjustment observed in marine predators such as wandering albatross (Viswanathan *et al.* 1996; Fritz *et al.* 2003), Antarctic petrel (Fauchald & Tveraa 2003), yellow-nosed albatross (Pinaud & Weimerskirch 2005) or bottle-nosed dolphin (Bailey & Thompson 2006). According to our results, ARS seems to be widely represented in marine top predators such as seabirds, as a behavioural adaptation to forage in a patchy environment (Benhamou 1992). Although at-sea distribution or trip length can change between years due to interannual environmental variability (Pinaud, Cherel & Weimerskirch 2005), we detected no significant interannual difference in ARS scale according to our data set. Therefore, the observed variations in foraging movement adjustments should be mainly related to species or habitat use.

SPATIAL DISTRIBUTION AND SEGREGATION OF SEARCH EFFORT

By describing foraging distribution at the spatial scale at which the individuals increased their search effort, we can assess interspecific and intraspecific differences, not only in at-sea distribution of these sympatric predators, but also in search effort distribution at a smaller scale. The overall foraging distribution studied by satellite

telemetry of these seven species during breeding is well-known at a regional scale (1000s km) in the Indian Ocean (see review in Weimerskirch 1998; also Weimerskirch 1998; Weimerskirch *et al.* 1999; Pinaud & Weimerskirch 2002, 2005; Waugh & Weimerskirch 2003) and suggests a large spatial overlap. Our study revealed that, although a spatial overlap exists at a regional scale, a reduced overlap occurred in habitat characteristics at a finer scale (where search effort is increased). In fact, to reach a distant foraging zone, these long-range foragers need to cross several habitats, resulting in an overlap in at-sea distribution when movement behaviour is not taken into account (Brown 2000). The apparent overlap in environmental characteristics in ARS zones of WCP, WAc and WAk is due to their wide at-sea distribution that built a large confidence interval (ellipse) in Fig. 4, reflecting rather a large interindividual difference in ARS characteristics. This very long-range foraging strategy is not present in the other species (AA, YNA, LMA, BBA and SA) where we found little overlap at a fine scale. This could be related to a specialization in foraging niche when exploiting the marine habitat. In fact, this specialization is expected at a fine scale, allowing a coexistence by reducing competition (see review in Brown 2000). Another strategy for these seabirds seems to be exploiting habitats far from the breeding islands (such as WCP and WA), where the inter- and intraspecific competition is expected to be less intense (Ashmole 1971).

Intraspecific and intersite comparison of the two populations of WA shows that difference in foraging distribution appears mainly at a regional scale (1000s km), where the Kerguelen individuals foraged at higher latitudes compared with Crozet population (Fig. 5). In addition, males in both populations increased their foraging effort southward compared with females (Figs 3 and 5; Prince *et al.* 1992; Weimerskirch *et al.* 1993). At the scale where search effort increased (*c.* 100 km), ARS zones of these two populations cannot be separated according to environmental characteristics. Birds appeared to concentrate their search effort on similar patch characteristics, despite the difference in location observed at a regional scale between the two populations. This

distribution at a large scale could be the result of competition for the same resources or more intense interference between the two colonies.

MOVEMENT ADJUSTMENTS IN RELATION TO SPECIES AND ENVIRONMENT

Based on the demonstration of the existence of scale-dependent hierarchical adjustments of wandering albatross movement patterns, Fritz *et al.* (2003) predicted differences in scale response for different groups of predators, according to differences in their prey distribution and environmental constraints. In our study, the majority of individuals for the seven species adopted an ARS behaviour, with variations explained due to species and also habitat, with no interaction between the two factors. Effect of species can be explained by differences in prey targeted (see Cherel & Klages 1998 for a review for these species) or foraging strategies ('searching loop' vs. 'commuting'; Weimerskirch 1998 Weimerskirch *et al.* 2005). For example, the WA searches mainly on adult squid whose distribution is scattered over extensive areas using a low cost strategy ('loops') to cover extensive surface (Weimerskirch *et al.* 2005). In the other side, YNA, as well as breeding grey-headed albatrosses *Thalassarche chrysostoma* (Foster) from Marion Island, were found to adopt a 'commuting' strategy to reach spatially predicted mesoscale eddies where a higher prey density is expected (Nel *et al.* 2001; Pinaud & Weimerskirch 2005). Therefore, one might expect that this affects the decision to increase search effort and the tendency to leave a patch. In addition, morphometrics and wing loads influence flying abilities and energy expenditure in albatrosses (Shaffer, Costa & Weimerskirch 2001) and might therefore affect their searching decisions.

The additive effect of oceanographic habitats on ARS scale variations (independent of species) could be interpreted as a convergence in foraging movement adjustments for these predators according to the structure and prey availability of a particular habitat, rather than responding to a physical parameter. In fact, the ARS radius of the predator could be linked to the prey encounter rate (Kareiva & Odell 1987; Fauchald 1999). In oceans, prey distributions over such large distances are difficult to assess but some studies showed that prey distribution could be linked to heterogeneity in physical and biological characteristics of oceanographic habitats (i.e. Froneman & Pakhomov 2000; Read, Pollard & Bathmann 2002). This can result in higher prey densities in some habitats. For example, YNA from Amsterdam Island exploit the turbulent zone under the influence of the Agulhas Return Current, with the presence of gyres (mean diameter of 250 km) which influence the spatial distribution of primary productivity (Froneman & Pakhomov 2000). In relation to this predictable environmental structure, this predator adopts a 'commuting' strategy and adjusts its searching behaviour inside this system at an average scale of 130 km, in

accordance to the expected prey distribution (Pinaud & Weimerskirch 2005). Alternatively, black-browed albatrosses are known to commute mainly over neritic waters, exploiting the peri-insular slopes on the Kerguelen plateau where their preferred prey are more available (Cherel, Weimerskirch & Trouvé 2000) and distributed in small patches of higher density (see Weimerskirch *et al.* 2005). This could explain the smaller ARS scales observed for this species compared with the others. Our results indicate also that the south subtropical and the sub-Antarctic fronts are exploited with a lower search radius, which is consistent with the higher biological production and prey availability found in these frontal regions (see Hunt *et al.* 1999). It suggests also that, when searching in these productive regions, these predators encounter relatively more prey and behave in the same way in movement adjustments with a smaller search radius. Therefore, the scale-dependent response of an animal to environmental heterogeneity is a complex phenomena, depending on the forager's characteristics as well as on habitat features.

Environmental heterogeneity is considered to affect animal movements at a large range of scales, in terrestrial (Bergman, Schaefer & Luttich 2000; Johnson *et al.* 2002) as well as in marine ecosystems (Fritz *et al.* 2003; Pinaud & Weimerskirch 2005). Our results suggest that, as habitats differ in structure and prey availability at various spatial scales, long-ranging predators such as albatrosses could respond to this environmental heterogeneity from the individual to the population level, by adjusting their searching movements through different habitats. In these adjustments, observed differences are species specific but these predators seem to perceive common ecological characteristics, leading to a similar behaviour in similar habitats. We can speculate that, in this case, immediate prey encounter rate plays a major role for these predators when adjusting their searching movements at small spatial scales, whereas past experience and orientation are expected to act mainly in large-scale movements at a scale where prey distribution is more predictable (Hunt *et al.* 1999; Pinaud & Weimerskirch 2005). Studying movements at a smaller scale in relation to resource distribution is therefore crucial to better understand scale-dependent adjustments and finally foraging distribution of animals.

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constructive comments. The authors declare that the experiments comply with the current laws of the country in which they were performed.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://www.blackwell-synergy.com

Fig. S1. Example plot of FPT values as a function of time since departure (*upper*) and plot of FPT values distribution (*lower*), for the Yellow-nosed Albatross CF27250 with an ARS scale of 150 km. The dashed lines indicate the threshold at FPT = 6 d, to characterize ARS zones for this individual.

Fig. S2. An example of FPT variation pattern of a Black-browed Albatross with a FPT peak of variance at $r = 10$ km. This bird was fitted with an activity recorder (wet/dry logger, see Pinaud & Weimerskirch 2002) showing when it sat on the water. In this case, 85% of night time was spent sitting on the water.

Fig. S3. Results (between groups F-matrix for d.f. = 3, 483) from the discriminant analysis on ARS zones according to populations, in function of Bathymetry, SST and Chl-*a* concentration on these ARS zones.