

# Scale-dependent habitat use in a long-ranging central place predator

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## Summary

1. It is predicted that the movements of foraging animals are adjusted to the hierarchical spatial distribution of resources in the environment, and that decisions to modify movement in response to heterogeneous resource distribution are scale-dependent. Thus, controlling for spatial scales of interaction with environment is critical for a better understanding of habitat selection, which is likely to follow scale-dependent processes.
2. Here we study the scales of interactions and habitat selection in a long-ranging marine predator foraging from a central place, the yellow-nosed albatross. We use first-passage time analysis to identify the scales of interaction with environmental variables and compositional analysis to study habitat selection.
3. Of 26 birds, 22 adopted an area restricted search (ARS) at a scale of  $130 \pm 85$  km, and 11 of these 22 birds adopted a second, nested ARS scale at  $34 \pm 20$  km. Habitat use differed according to the spatial scale considered. At the oceanic basin macro-scale, birds foraged in pelagic, subtropical waters. Birds commuted to the ARS zones after a *c.* 1500-km trip to reach predictable turbulence zones from Agulhas return current, where primary productivity was enhanced at large scale. At a smaller, meso-scale, birds increased their search effort according to sea surface height anomalies (SSHa) and chlorophyll-*a* concentrations (Chl-*a*), indicating association with productive cyclonic eddies.
4. Among birds, differences in search pattern were noted: 11 birds concentrated their search effort directly at a small scale of  $77 \pm 22$  km, avoiding anticyclonic eddies. The 11 other birds showed two scales of ARS pattern: (i) first at  $180 \pm 90$  km with a preference for high Chl-*a* concentrations but unrelated to SSHa; and (ii) secondly at a nested scale at  $34 \pm 20$  km related exclusively to SSHa where prey patches were expected to be distributed at this scale. This second group of birds appeared to be less efficient, spending more time at sea for the same mass gain than the first group.
5. Our study is the first to demonstrate scale-dependent adjustments, with interindividual variability, in relation to environmental features for predators with a central-place constraint.

*Key-words:* area-restricted search, compositional analysis, first-passage time, satellite telemetry, yellow-nosed albatross.

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## Introduction

Understanding how organisms exploit their environment is a central topic in ecology. As environment is not spatially uniform, animals should spend more time in areas where resources are more available. When the resources are distributed in patches (*sensu* Fauchald

1999), the search activity of foragers could potentially be concentrated in these high-density areas (e.g. Kareiva & Odell 1987). Thus, movements of animals should follow the structure of the environment, exhibiting, for example, an increase in turning rate and decreased speed where resources are plentiful, in response to increased intake rate. This behaviour is called area-restricted search (ARS). Considering that resources can be distributed in a nested patch hierarchy (Johnson 1980; Kotliar & Wiens 1990), we expect that predators should be able to respond to patches at several spatial scales (Fauchald 1999). To gain a better

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understanding of habitat selection and how organisms exploit their environment, it is thus crucial to identify the scales of interaction with the environment (e.g. Johnson 1980; Levin 1992), particularly in nested scale systems where large-scale patterns tend to mask fine-scale patterns (Fauchald, Erikstad & Skarsfjord 2000). Different methods have been used recently to study scale-dependent movements (e.g. Fauchald *et al.* 2000; Fritz, Saïd & Weimerskirch 2002; Johnson *et al.* 2002; Becker & Beissinger 2003), but there is still a need to link these scale-specific individual responses to environmental features (Johnson *et al.* 2002). Recently, first-passage time analysis (FPT, Fauchald & Tveraa 2003) has allowed assessment of the scales of interaction in a patchy environment when animals adopt an ARS behaviour. FPT analysis is based on the calculation of the time taken for a bird to cross a circle with a given radius, as a scale-dependent measure of search effort. Almost all studies on habitat selection concern terrestrial environment where habitat is often well defined and to date few have considered marine habitats, and more specifically oceanic habitats.

Marine predators represent interesting organisms to study scale-dependent predator-prey interactions because of the wide range of spatial and temporal scales in resource distribution and abundance. The marine environment is a highly variable environment with a heterogeneous, patchy, scale-dependent (hierarchical) resource distribution (Ashmole 1971). Thus, we can expect that marine predators should be able to respond to the hierarchical patch distribution at several spatial scales. In marine environments, interactions between ocean currents, bathymetry and other physical and biological processes promote growth and retention of plankton, leading to higher productivity zones (Haury, McGowan & Wiebe 1978). The distribution of mobile vertebrates is uncoupled from the underlying physical structure at fine scale (10 s km), but there is some evidence that physical processes influence predator distributions at medium (100 s km) and large scales (1000 s km). Several studies have found relationships between large-scale aggregations of seabirds and marine mammals and oceanographic features (e.g. Pakhomov & McQuaid 1996; Tynan 1998; Hunt *et al.* 1999; Becker & Beissinger 2003) or main prey (e.g. Veit, Silverman & Everson 1993). At a medium (meso) scale, aggregation of top-predators is found in predictable regions which have enhanced productivity such as bathymetric gradients, fronts or eddies (see Hunt *et al.* 1999; Becker & Beissinger 2003). For example, eddies can promote life near the surface through vertical mixing from deep nutrient rich waters (review in Rhines 2001). Thus, hierarchical decisions during foraging may be made first to find predictable and productive large-scale features, and then to locate fine-scale habitats, where prey are aggregated (see Fauchald *et al.* 2000). At smaller scales the cues used to locate good foraging zones could depend on either odour (Nevitt, Veit & Kareiva 1995), increased intake (e.g. Weimerskirch, Wilson & Lys 1997)

or the presence of other predators through local enhancement (e.g. Grünbaum & Veit 2003). However, the cues used to find large-scale prey aggregations remains unclear, and the individual experience of the forager could play a major role (see Hunt *et al.* 1999; Bonadonna *et al.* 2001).

Almost all the studies cited here on aggregations of seabirds and marine mammals in relation to oceanographic features are vessel-based and focused at a population level, and thus the origin and reproductive status of individuals are unknown (but see Hyrenbach, Fernandez & Anderson 2002). A substantial proportion of these top predators are long-ranging central-place foragers, at least during the breeding season. Thus, integrating, at the individual level, the constraint of reproduction with the central-place foraging concept is likely to be essential. The constraint of distance to breeding site could play a major role in the evolution of long-range foragers such as seabirds (Warham 1990), based on their ability to reach predictable regions of enhanced productivity within a time constraint. The strong constraint of distance between breeding and foraging grounds, associated with a variable environment, could lead to learning and site fidelity of foraging individuals, where decisions of ARS at larger scales could be determined by past foraging experience (Irons 1998; Hunt *et al.* 1999; Bonadonna *et al.* 2001). Tracking techniques allow us to follow foraging individuals in marine environments (satellite tracking, Jouventin & Weimerskirch 1990), allowing the assessment of habitat selection at various scales. Some studies have shown habitat selection at an individual level (see Bost *et al.* 1997; Waugh *et al.* 1999; Guinet *et al.* 2001; Bradshaw *et al.* 2002; Hyrenbach *et al.* 2002; Waugh & Weimerskirch 2003), but none has assessed and controlled explicitly for the nested spatial scales of interaction with environment.

Here, we assess foraging scales, foraging strategy and habitat selection in a long-range top predator with a central-place constraint: the yellow-nosed albatross *Thalassarche carteri* (Rothschild). As marine environment shows a hierarchical and patchy resource distribution, we expect that birds adopt an ARS behaviour at several scales in relation to the environment spatial structure. We compare foraging trips and habitat selection during 2 years to test the following hypotheses: (1) since marine environment shows a hierarchical and patchy resource distribution, birds should adopt an ARS behaviour at different, nested spatial scales as revealed by FPT analysis; (2) this search behaviour should shape the foraging trip structure at a large scale, where birds tend to commute to these intense search areas; and (3) if prey distribution is affected by oceanic features at particular scales, albatrosses should search intensively according to these environmental features as revealed by habitat use. Habitat use should be scale-dependent, probably in relation to the immediate intake rate and bird's past experience. The individual ability to track rapidly this spatially structured system

may affect trip success parameters such as duration at sea or total mass gain.

## Methods

### FIELD PROCEDURES

The study was carried out in 2000 and 2002 at Pointe d'Entrecasteaux (37°51'42" S; 77°31'08" E), Amsterdam Island (Southern Indian Ocean), from early October to early November during the incubation period for yellow-nosed albatrosses. Eggs are laid in late September and chicks hatch in early December (Jouventin *et al.* 1983). During incubation, partners alternate incubating at the colony, typically in shifts lasting from 10 to 20 days while the partner forages at sea. Prey of this species include mainly fish and large crustaceans (review in Chérel & Klages 1997). In the study colony (a part of a big colony with *c.* 60 pairs), nine and 17 adults were fitted in 2000 and 2002 using, respectively, five and nine 32-g satellite transmitters (PTTs; platform terminal transmitters PTT100, Microwave Telemetry, Columbia, MD, USA) and wet/dry activity data loggers (mass 12 g, Francis Scientific Instruments, Caxton, UK) which record immersion period in salt water at a sampling rate of 15 s. The PTTs were fitted onto back feathers with adhesive tape (Weimerskirch, Doncaster & Cuenot-Chaillet 1994) and left on the birds for one foraging trip. The wet-dry loggers were attached to plastic bands using adhesive tape, and the bands were fitted onto the tarsus of the birds. The overall weight of device carried by each bird represented 1.5% of the average body mass of yellow-nosed albatross. During the study period, two people observed the study colony continuously, between dawn and dusk (adults do not return at night). The arrival and departure times of the adults were noted, yielding the duration of the individual foraging trips.

### DATA ANALYSIS

#### *Bird locations*

Argos provides a quality index to each location (Argos 1996). Argos locations were filtered by, first, excluding low quality fixes (Class B, with a average precision of 46–69 km) and secondly, calculating the speed between consecutive fixes and removing all locations that required unrealistic flying speeds exceeding 75 km h<sup>-1</sup> (maximum speed recorded, Alerstam, Gudmundsson & Larsson 1993; calculated, Pennycuik 1982). Mean duration between Argos locations was 2.13 ± 0.187 h (0.02–22.1). We used ARCVIEW version 3.2 GIS (ESRI Inc., Redlands, CA, USA) to overlay bird locations and environmental data over a grid of 20 km cell size, extended from 35°E to 115°E and from 25°S to 47°S (149 × 365 cells). This large zone corresponds also to the known distribution of yellow-nosed albatrosses (Weimerskirch, Jouventin & Stahl 1986). The size of the cell was chosen to be twice the size of the maximum

Argos quality class (calculated from the errors of fixes from PTTs when albatrosses were known to be in the colony: 12.70 km for class 0. The errors were 0.56, 1.25, 2.38 and 4.93 km for classes 3, 2, 1 and A, respectively). Albers equal area conic projection was used to control for distance and area. For each individual, time and distance between successive Argos fixes were used to calculate total time spent over each 20-km square cell. This was then used to calculate time at sea as a function of distance to the colony. In the case of incomplete trips when the PTT stopped at sea (five individuals), the trip was classified as ending at the last known location at sea. The proportion of time spent at sea in relation to the distance to the colony was given by:  $y = 4.23 \cdot 10^{-11} x^3 - 2.89 \cdot 10^{-7} x^2 + 4.83 \cdot 10^{-4} x + 0.02$  ( $R^2 = 0.89$ ,  $F_{3,6} = 8.01$ ,  $P = 0.06$ ). This relationship was used in the habitat selection analysis, in order to weight habitat availability proportions as a function of distance to the colony.

#### *First-passage time analysis*

We followed Fauchald & Tveraa (2003) to perform FPT analysis at a large and at a small nested scale. Analyses were performed using the software R (version 1.8.1, R Development Core Team 2003) distributed under the GNU General Public License (<http://www.r-project.org/index.html>). FPT is defined as time required to cross a circle with a given radius *r* (see Fauchald & Tveraa 2003). For each trip, FPT was calculated for points at 2-km intervals along each individual path, according to the radius *r*. This calculation was performed with *r* varying from 20 to 1000 km. Then, the relative variance *S(r)* in FPT was calculated as a function of radius *r*. This variance is given by  $\text{Var}(\log(t(r)))$ , where *t(r)* is FPT for circle of radius *r*, and is log-transformed to make the variance *S(t)* independent of the magnitude of the mean FPT (see Fauchald & Tveraa 2003). *S(r)* was then plotted in relation to *r* (for *r* from 50 to 1000 km). A peak in relative variance *S(r)* indicates the scale at which an ARS occurred. This value was confirmed by plotting FPT against time since departure and examining FPT variation pattern indicating intensive search (see Fig. 3, right side, in Fauchald & Tveraa 2003). Once the ARS scale was identified, intensive search areas were defined as giving the longest FPT (see Fauchald & Tveraa 2003, Fig. 3, left side). As in nested scale systems, large-scale patterns tend to mask fine-scale patterns (Fauchald *et al.* 2000), a second analysis was performed on the ARS of each foraging trip to identify a nested fine-scale search pattern. This second analysis was performed with *r* from 10 to 340 km and with only birds where the large-scale search pattern was > 50 km (in scales of search pattern between 10 and 50 km, the radius lag was too small to perform the FPT analysis).

Frequent diurnal landing behaviour can be associated with foraging behaviour (see Weimerskirch *et al.* 1997). Wet/dry logger data were used as a measure of foraging intensity and to examine whether birds tend to land more frequently where they adopt an intensive

search behaviour. Birds can sit on water while resting/sleeping, but in these cases they sit on water for several hours and landing frequency is low. For complete trips, rates of diurnal landings (number of landings divided by duration of trip segment), mean duration of diurnal landings and proportion of time spent on water were compared for different trip segments: time from departure to arrival on the intensive search zone (outbound), time on the intensive search zone (ARS) and time since departure from this zone to arrival to the colony (inbound).

#### MARINE ENVIRONMENT

Marine habitats were characterized in October of each year using four environmental variables: bathymetry (*BATHY*), sea surface temperature (*SST*), sea surface height anomalies (*SSHa*) and chlorophyll-*a* concentrations (*Chl-a*). Monthly data sets were used: there was no significant change between weeks during the period considered. Data for bathymetry ( $0.083^\circ \times 0.083^\circ$ ) and *SST* ( $1^\circ \times 1^\circ$ , Reynolds & Smith 1994) were obtained from the IRI/LDEO Climate Data Library (<http://ingrid.ldeo.columbia.edu/SOURCES/>). *SSHa* data derived from observations by ERS and TOPEX/POSEIDON satellites and were compiled by the Colorado Center for Astroynamics Research (<http://www.ccar.colourado.edu/~leben/research.html>). *Chl-a* data correspond to observations from Terra MODIS satellite (<http://daac.gsfc.nasa.gov/MODIS/>), with a global coverage at a resolution of 4 km. Chlor\_a\_2 (parameter number 26) was used, corresponding to the chlorophyll-*a* concentration in  $\text{mg m}^{-3}$  (SeaWiFS analogue – OC3M). For each habitat variable, values were interpolated over the  $20 \times 20$ -km cell size grid, using ARCVIEW version 3.2.

#### HABITAT SELECTION ANALYSIS

We used compositional analysis (Aebischer, Robertson & Kenward 1993) to examine whether albatross distribution at sea is significantly different from random in relation to the distribution of each environmental variable. This method uses individuals as sampling units, is unaffected by the unit-sum constraint and permits tests for differential habitat use among categorical or continuous variables (e.g. age or year). As cells are not uniformly accessible (or 'available') for a long-range central place forager such as albatrosses, it is necessary to weight availability as a function of the distance to the colony. Availability was weighted by the proportion of time spent in a cell in relation to distance to the colony (see Bird locations). To perform compositional analysis, continuous variables must be classified into classes. *SSHa*, a centred distribution variable, was categorized into extreme values (0–20%: --- and 80–100%: + + +), intermediate (20–40%: - and 60–80%: +) and around median (40–60%: 0). *Chl-a*, a gradient distribution variable, was grouped into classes of low to high values (A–E, by 20%). Bathymetry classes were defined following Hyrenbach *et al.* (2002): pelagic ( $< -3000$  m, *Pel*);

continental slope ( $-3000$  m to  $-1000$  m, *C.Slope*); continental shelf ( $-1000$  m to  $-200$  m, *C.Shelf*); Coastal waters ( $> -200$  m, *CW*). *SST* classes were defined according to Park *et al.* (2002): tropical waters ( $> 18^\circ\text{C}$ , *TrW*), Agulhas current return front ( $16$ – $18^\circ\text{C}$ , *ACRFr*), subtropical waters ( $14$ – $16^\circ\text{C}$ , *SubTrW*), subtropical front ( $12$ – $14^\circ\text{C}$ , *SubTrFr*), subAntarctic surface waters ( $11$ – $12^\circ\text{C}$ , *SubASW*), subAntarctic front ( $9$ – $11^\circ\text{C}$ , *SubAFr*), polar frontal zone ( $6$ – $9^\circ\text{C}$ , *PFRZ*) and polar front ( $< 6^\circ\text{C}$ , *PFR*). Due to the constraints of data resolution, *BATHY* and *SST* variables were treated as large-scale variables only. The *SSHa* and *Chl-a* variables had a higher resolution, allowing their spatial structure to be studied from large to fine scales. To analyse the spatial structure of ocean according to *SSHa* and *Chl-a*, a spatial semivariogram (plot of variance between pairs of fixes as a function of distance between fixes) was calculated for each year using the *Sgeostat* R package. A spatial Spearman cross-correlation was performed between *SSHa* and *Chl-a* to examine how these two fine-scale variables covaried.

Habitat selection analysis was performed at two scales according to the results from the FPT analysis, which gives the zones in which birds concentrated their search effort. For large-scale analysis, we compared habitat availability proportions (weighted by distance), to the proportions in ARS zones where birds concentrated their search effort. For small, nested-scale analysis, proportions of habitat in large ARS zones defined the availability of habitat, and proportions in nested fine-scale ARS areas defined utilization. This fine-scale analysis was performed using only the high-resolution variables, *SSHa* and *Chl-a*. The habitat selection analysis at both scales was performed by two steps. First, we tested whether habitat use was random and, if not, habitats were ranked in preference order. Secondly, where possible we tested the hypothesis of differential habitat selection between the 2 years. Assessment of significance levels of the *t*-values (Aebischer *et al.* 1993) used randomization (1000 iterations), because distributions of log-ratios did not follow a normal distribution. Significance level was considered at  $P < 0.05$ . In cases where the proportion of used habitat was 0%, the zero values were replaced with values representing the lowest 10% of the observed proportions (in most cases, these proportions were replaced by 0.01%). In cases where some habitat types were not available (available habitat = 0%), we followed Aebischer *et al.* (1993) in their Appendix 2, and calculated a mean-weighted  $\lambda$ . Habitat types which were unused by all birds (used proportion was 0% for all birds) were removed from the analysis.

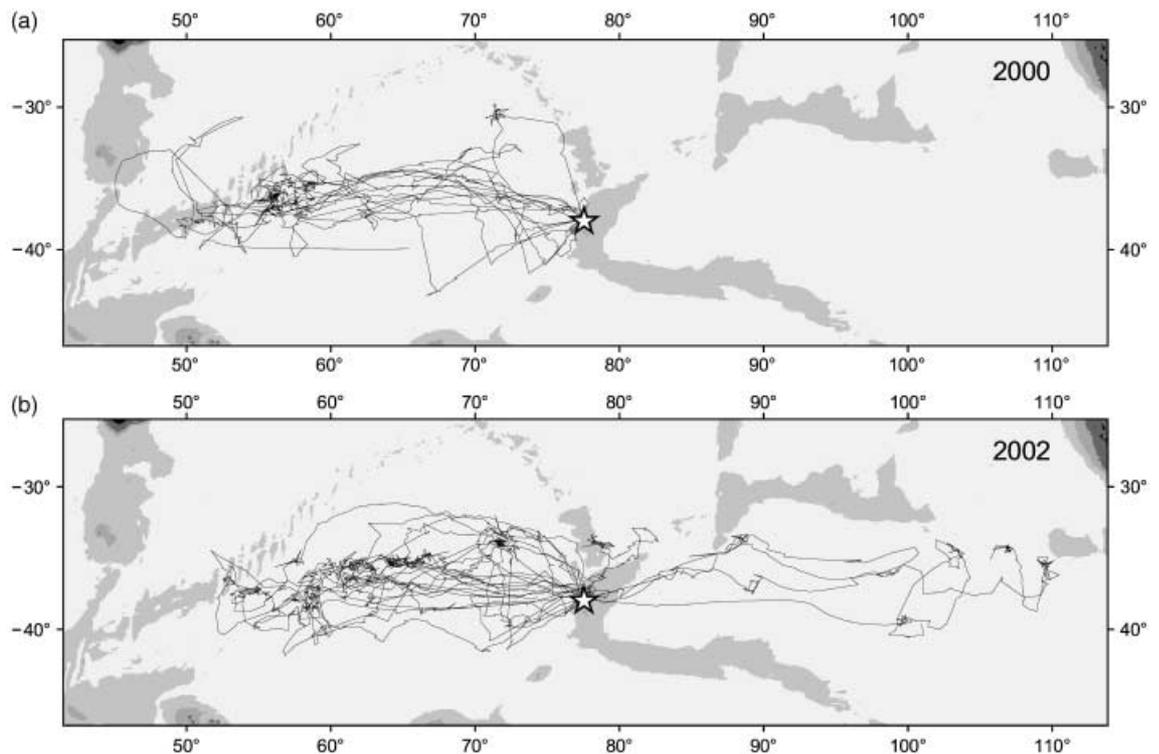
## Results

#### DISTRIBUTION AT SEA AND ARS BEHAVIOUR

In 2000 and 2002, yellow-nosed albatrosses foraged for trips lasting on average 17 days, at an average maximum range of 1800 km from the colony (Table 1). In 2000,

**Table 1.** Description of yellow-nosed albatross trips performed during the study, with an indication of the large and fine spatial scales at which the animal concentrated its search effort. To define fine ARS scale, individuals with a searching behaviour at a first large scale of 50 km were not tested (see text for details). Presence (SC2) or absence (SC1) of a second, nested ARS scale is indicated in the last column

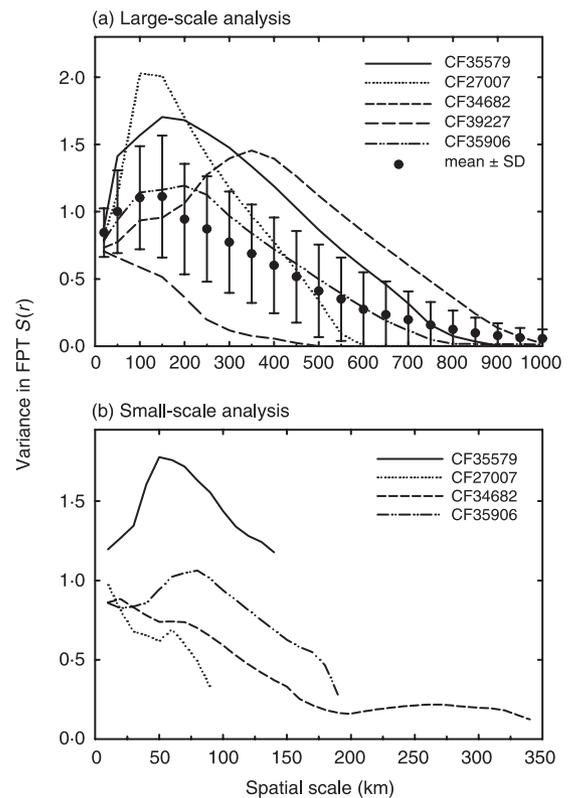
Individual	Sex	Year	Departure (UT + 5)	Trip length (d)	Mass gain (g)	Total distance travelled (km)	Max. distance to colony (km)	Large scale (km)	Max. FPT1 (d)	Distance to colony (km)	Fine scale (km)	Max FPT2 (d)	Distance to colony (km)	ARS pattern group
CF20088	?	2000	06/10/2000, 10 : 30	22.13	425	10517	2923	50	1.84	2145	–	–	–	SC1
CF24533C	?	2000	06/10/2000, 10 : 55	12.1	672	5758	1845	350	5.9	1567	20	0.64	1611	SC2
CF27007	?	2000	03/10/2000, 16 : 30	8.8	380	3751	1065	100	5.96	966	None	–	–	SC1
CF27225	?	2000	22/10/2000, 12 : 10	18	466	7605	2315	150	8.62	1965	None	–	–	SC1
CF27250	?	2000	24/10/2000, 16 : 20	18.66	–	7544	1987	150	8.52	1876	40	2.26	1920	SC2
CF34191	?	2000	07/10/2000, 11 : 05	18.09	278	8452	2286	100	4.35	1714	20	1.01	1721	SC2
CF34330	?	2000	05/10/2000, 16 : 45	16.93	174	10321	2619	None	–	–	–	–	–	–
CF34682	?	2000	07/10/2000, 10 : 00	20.25	247	8202	2603	350	15.32	1749	20	1.17	1936	SC2
CF34683	?	2000	22/10/2000, 15 : 50	20.7	–	8231	1804	None	–	–	–	–	–	–
CF18245	F	2002	04/10/2002, 07 : 20	8.26	250	2940	794	50	2.33	661	–	–	–	SC1
CF35578	M	2002	23/10/2002, 09 : 45	25.07	350	8057	2388	100	2.13	1987	20	0.51	1941	SC2
CF35579	F	2002	04/10/2002, 12 : 00	18.9	450	7540	1514	150	11.14	1330	50	4.15	1431	SC2
CF35621	M	2002	26/10/2002, 11 : 30	21.9	450	10205	2929	100	4.62	2855	20	0.79	2874	SC2
CF35626	F	2002	11/10/2002, 08 : 20	22.92	450	10022	2151	200	10.58	1973	30	1.31	1939	SC2
CF35841	F	2002	09/10/2002, 10 : 30	16.06	150	5838	1612	50	4.91	1014	–	–	–	SC1
CF35847	F	2002	09/10/2002, 16 : 30	16.77	175	6349	857	150	9.51	675	50	2.94	682	SC2
CF35906	M	2002	05/10/2002, 16 : 30	12.85	250	5587	1519	200	6.99	1320	80	4.15	1420	SC2
CF39126	M	2002	01/10/2002, 18 : 00	18.85	275	7711	1820	100	3.77	1721	None	–	–	SC1
CF39206	F	2002	11/10/2002, 08 : 20	23.11	700	10282	2231	150	4.26	1058	20	1.13	1505	SC2
CF39207	F	2002	11/10/2002, 09 : 20	13.25	275	7545	2109	100	3/11	1059	None	–	–	SC1
CF39208	M	2002	12/10/2002, 15 : 30	9.81	450	4174	1234	50	3.1	1151	–	–	–	SC1
CF39225	M	2002	19/10/2002, 13 : 50	16.91	300	7833	2346	50	1.99	1458	–	–	–	SC1
CF39226	F	2002	20/10/2002, 15 : 00	17.85	550	5587	1314	50	4.96	1218	–	–	–	SC1
CF39227	F	2002	22/10/2002, 12 : 00	12.27	300	4076	677	None	–	–	–	–	–	–
CF39228	M	2002	24/10/2002, 15 : 45	15.01	450	5190	1326	–	–	–	–	–	–	–
CF39230	M	2002	25/10/2002, 17 : 35	19.68	250	7584	1830	100	8.43	1652	None	–	–	SC1
Mean				17.12	359.4	7185	1829	129.5	6.02	1526	33.64	1.82	1725	
SD				4.51	148.9	2152	617	85.4	3.52	517	19.63	1.35	532	



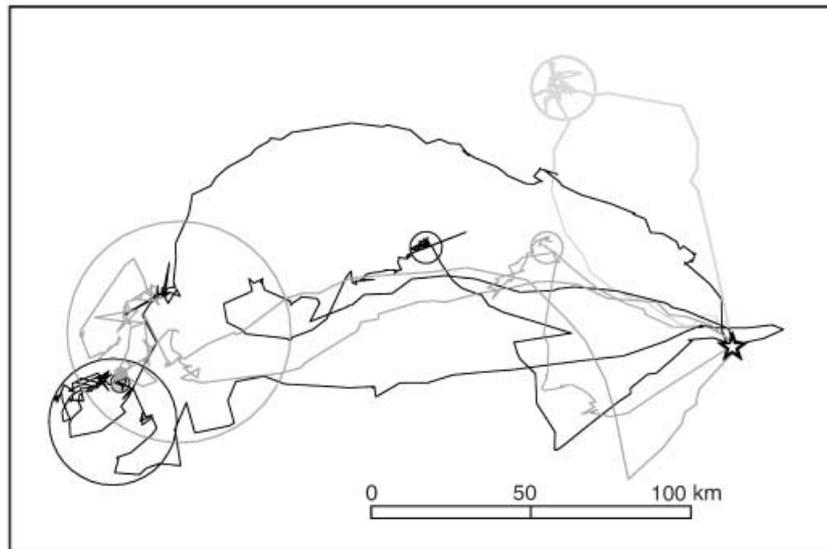
**Fig. 1.** Map showing the study area around Amsterdam Island (white star) in the south Indian Ocean, with all albatross trips in 2000 ( $n = 9$  individuals) and 2002 ( $n = 17$ ). Bathymetric classes (see text for details) are, from dark to light, *CW*, *C.Shelf*, *C.Slope* and *Pel*. Continents are in black.

all birds ( $n = 9$ ) foraged to the west of Amsterdam Island: the main foraging zone was located at an average distance of 1800 km. In 2002, the pattern was the same, with the majority of the birds (14 of 17) moving 1500 km west from the colony. Three birds foraged east, near western Australia (Fig. 1). No statistical difference was detected between years for trip length, mass at departure, mass gain, maximum distance reached or total distance travelled (Mann–Whitney tests, all  $P > 0.1$ ).

In both years, a majority of birds adopted an ARS pattern. This occurred at both large (22 of 26) and small (11 of 16) spatial scales, as revealed by peaks of  $S(r)$  plotted in function of radius  $r$  (Fig. 2). In 2000, seven of nine birds adopted this behaviour at large scale, and four of six at small scale. For 2002, the ratios were 15 of 17 and seven of 10, respectively. On average, the spatial scale at which an ARS pattern was adopted was  $130 \pm 85$  km (see Table 1). These zones of intense search effort were located far from the colony (*c.* 1500 km). During both years, nested small scales were observed, indicating that birds concentrated their search effort at fine-scale within the intensively searched large-scale area (see Figs 2 and 3). No statistical difference was detected between years for spatial scale  $r$  (Mann–Whitney  $U$ -test statistic = 70.5,  $P = 0.19$ ) or distance between these zones and the colony (ANOVA,  $F_{1,20} = 1.35$ ,  $P = 0.26$ ). For the 14 complete trips with activity data, birds spent on average 30%, 40% and 30% of their time during outbound, ARS and inbound parts of the trip, respectively. Diurnal landings were significantly more frequent in intensive search areas ( $2.20 \pm 0.70$  landings  $h^{-1}$ ) and



**Fig. 2.** Example of variance in FPT analysis,  $S(r)$ , as a function of radius  $r$ , for five individuals. (a) Analysis of the total trips: peaks in variance indicate large-scale ARS behaviour. Bird CF39227 shows no evidence of ARS. Mean and SD are given for all individuals which showed a pattern of ARS (black dots). (b) Nested fine-scale analysis, indicating ARS within the first large scale area.

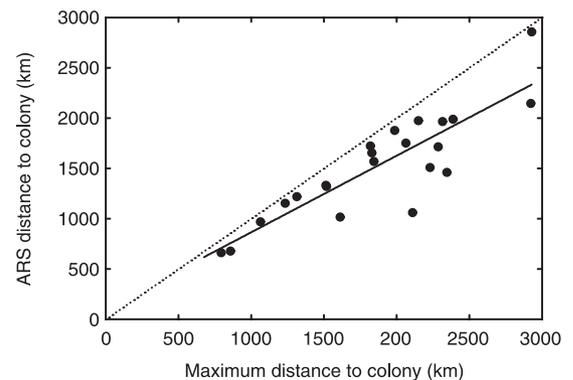


**Fig. 3.** Example of five individual foraging trips with an ARS behaviour. Each circle shows the area where the bird adopted an ARS behaviour. A second analysis was performed on these areas to define a second, nested scale of searching. In this example, areas where birds adopted an ARS behaviour at a nested fine scale are shown by the small, dark circles.

longer ( $0.19 \pm 0.18$  h) compared to either the outbound parts of the trip ( $1.72 \pm 0.71$ , Wilcoxon's rank test,  $Z = -2.6$ ,  $P = 0.009$ ;  $0.09 \pm 0.07$  h,  $Z = 2.92$ ,  $P = 0.004$ ) or the inbound part ( $1.52 \pm 0.79$ ,  $Z = -2.7$ ,  $P = 0.008$ ; but no significant difference was noted for duration:  $0.16 \pm 0.12$  h,  $Z = 1.53$ ,  $P = 0.13$ ). Proportion of time on the water during ARS ( $44.4 \pm 12.2\%$ ) was significantly different from the outbound part ( $20.0 \pm 11.4\%$ ,  $Z = 3.29$ ,  $P = 0.001$ ), but not from the inbound part ( $34.0 \pm 18.2\%$ ,  $Z = -1.41$ ,  $P = 0.10$ ).

#### STRUCTURE OF FORAGING TRIPS AND MAXIMUM DISTANCE FROM THE COLONY

Maximum distance from the colony was strongly related to the total distance travelled ( $y = 3.08x + 1559$ ,  $F_{1,25} = 84.18$ ,  $R^2 = 0.77$ ,  $P < 0.0001$ ). To determine whether the observed maximum distances from the colony are reached randomly or correspond to a defined structure of the foraging paths, we simulated random trips derived from observed paths. For each trip, all segments (a segment is considered as the linear path between two consecutive Argos locations) were sampled randomly without replacement, to construct a random path. For each trip, 1000 iterations were performed. The observed maximum distances of actual foraging trips were greater than maximum distances estimated from simulated trips (1820 km vs. 1330 km, respectively, two-sided paired Wilcoxon's rank test,  $Z = -3.83$ ,  $P < 0.001$ ), indicating that observed orders of segments are not random and birds tended to commute to foraging areas far from the colony. This result was confirmed by the relationship between maximum distance reached and the distance from the colony at which birds increased their search effort (Fig. 4,  $F_{1,21} = 60.88$ ,  $R^2 = 0.74$ ,  $P < 0.0001$ ). The ARS zones were far

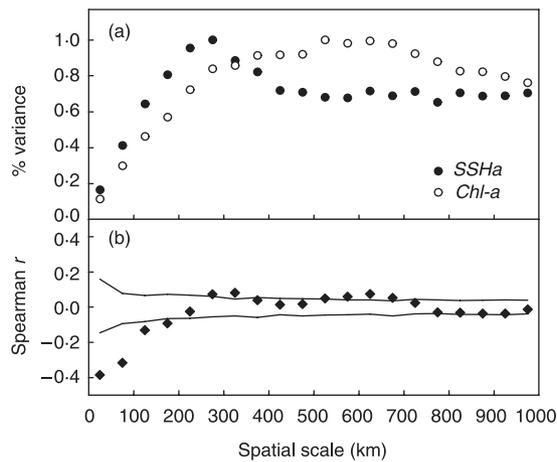


**Fig. 4.** Maximum distance reached by yellow-nosed albatrosses from Amsterdam Island in relation to distance of ARS zones from the colony ( $y = 0.76x + 102.1$ ,  $R^2 = 0.74$ ,  $P < 0.0001$ ). Locations along the dotted line ( $y = x$ ) would indicate an ARS zone situated at the maximum distance to the colony.

from the colony, indicating that birds tended to adopt a large-scale commuting strategy.

#### ENVIRONMENTAL VARIABLES AND HABITAT SELECTION

*SSHa* and *Chl-a* showed meso-scale variations as indicated by variograms (Fig. 5a). *Chl-a* showed large-scale variations in association with oceanic domains: tropical waters were less productive than southern waters, and an east–west gradient was apparent in subtropical areas, where high productive zones were influenced by the Agulhas return current. A peak in semivariance at a scale of *c.* 300 km revealed the alternation of negative (cyclonic eddies) and positive (anticyclonic eddies) rings (Rhines 2001), which are very active in this part of Indian Ocean due to the Agulhas return current (Lutjeharms 2001; Park



**Fig. 5.** (a) Spatial structure of *SSHa* (black dots) and *Chl-a* (open dots) for 2002, showing variance (% of maximum variance) between pairs of fixes as a function of distance between fixes. *Chl-a* is spatially structured at a larger scale than *SSHa*. The peak in variance in *SSHa* at a scale of *c.* 250 km can be related to the important meso-scale activity in the study area. (b) Spearman's spatial cross-correlation between *SSHa* and *Chl-a* with 99.9% interval (1000 iterations, solid lines), showing significance negative correlation at fine scale (< 100 km).

*et al.* 2002). Meso-scale variations in *Chl-a* could be related to high meso-scale activity in this area, with a significant negative correlation between *Chl-a* and *SSHa* at a fine scale (< 100 km, see Fig. 5b). These patterns were observed in both 2000 and 2002.

At a large scale, yellow-nosed albatrosses used marine habitat non-randomly in relation to environmental variables. In relation to bathymetry (Fig. 6a), albatrosses preferred pelagic habitats ( $\lambda = 0.205$ ,  $P < 0.001$ ). No significant difference was observed between years ( $\lambda = 0.859$ ,  $P = 0.093$ ). In terms of SST, albatrosses concentrated their search effort in subtropical waters ( $\lambda = 0.05$ ,  $P < 0.001$ , Fig. 6b). Waters with SST less than 9 °C were entirely avoided. Habitat selection was significantly different between years ( $\lambda = 0.355$ ,  $P = 0.004$ ), with a concentration of search effort in subtropical waters and the Agulhas return current front in 2000 ( $\lambda = -1.10 \times 10^{-14}$ ,  $P = 0.03$ ) but only in subtropical waters in 2002.

Within a meso-scale environmental structure as defined by *SSHa* birds increased their search effort by avoiding extreme positive *SSHa* ( $\lambda = 0.643$ ,  $P = 0.048$ ), which can be associated with anticyclonic eddies (Rhines 2001). No significant difference was observed between years ( $\lambda = 0.928$ ,  $P = 0.863$ ). Yellow-nosed albatrosses concentrated their search effort in areas with higher *Chl-a* concentrations ( $\lambda = 0.199$ ,  $P < 0.001$ ). No significant difference was observed between years ( $\lambda = 0.659$ ,  $P = 0.106$ ).

#### INDIVIDUAL DIFFERENCES AND FORAGING SUCCESS

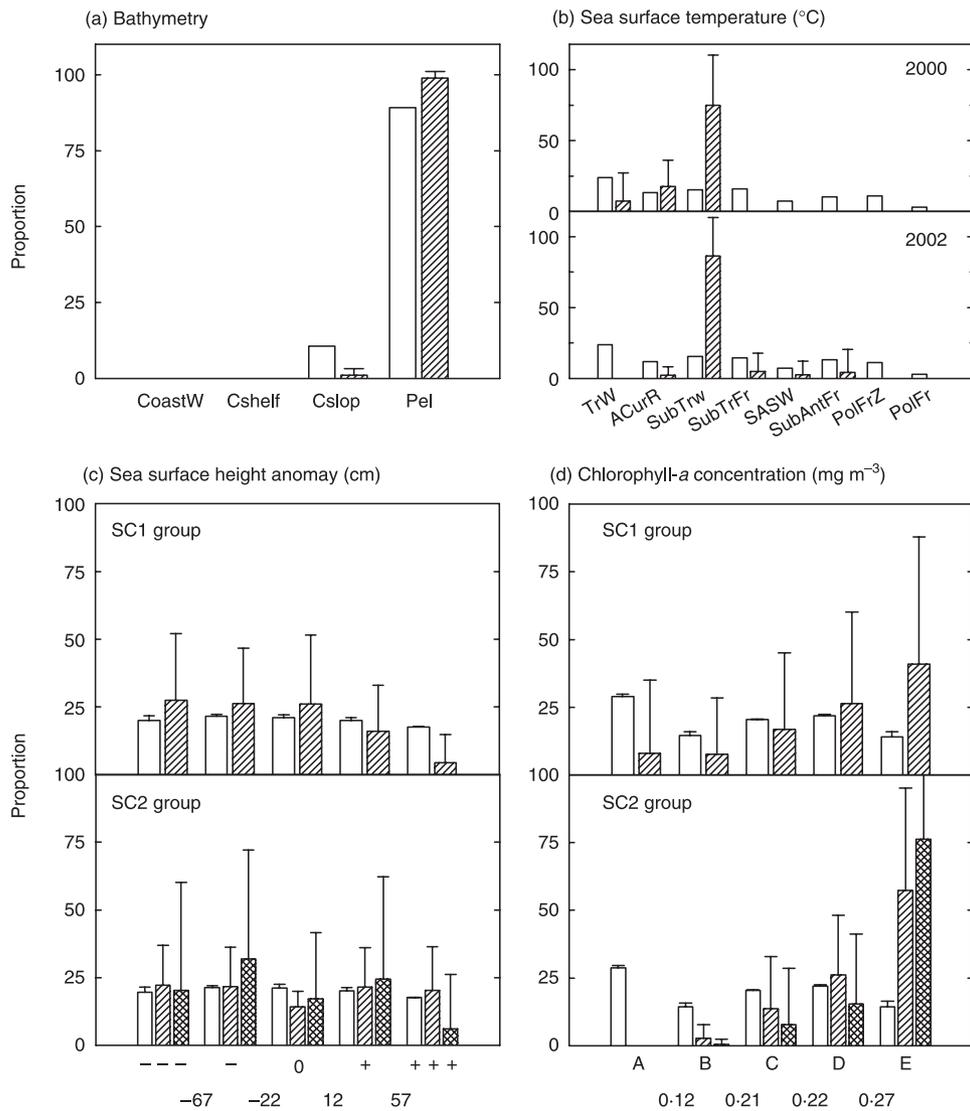
A difference in movement pattern was observed among individuals (in terms of the presence/absence of a

second, nested, small-scale ARS). As this difference could be related to the acquisition of information (prey encountered, Fauchald 1999), we tested whether habitat use differed according to hierarchical scale patterns. Prey distribution in marine environments is very difficult to assess but can be related to environmental features, depending on the corresponding scale. Differences in habitat use were expected, under the hypothesis that spatial links observed between ARS and habitat should reflect prey detection by the predator rather than the ability of birds to detect habitat characteristics such as SST or *SSHa*. Thus, habitat selection was performed according to the ARS pattern: group SC1 ( $n = 11$ ) with a single, fine ARS scale ( $77 \pm 22$  km); and group SC2 ( $n = 11$ ) with two ARS scales (a larger one at  $180 \pm 90$  km and a smaller, nested one at  $34 \pm 20$  km). The SC2 group corresponds to birds searching at fine scale after searching at a large scale, suggesting that they were searching for prey patches at fine scale, whereas the SC1 group corresponds to birds finding directly a prey patch. Habitat use by these groups was different in relation to *SSHa* (Fig. 6c,  $\lambda = 0.62$ ,  $P = 0.05$ ) and *Chl-a* (Fig. 6d,  $\lambda = 0.598$ ,  $P = 0.042$ ). Individuals that foraged directly at smaller scales (the SC1 group) avoided areas with positive *SSHa* ( $\lambda = 0.257$ ,  $P = 0.02$ ), while individuals that foraged at two scales (the SC2 group) did not exhibit detectable habitat selection at the large scale ( $\lambda = 0.473$ ,  $P = 0.165$ ), but had significant selection at the nested fine scale ( $\lambda = 0.165$ ,  $P = 0.017$ ), avoiding areas with positive *SSHa*. In terms of *Chl-a*, individuals that increased their search effort directly at smaller scale (the SC1 group) selected areas with higher concentrations ( $\lambda = 0.387$ ,  $P = 0.03$ ). The SC2 group had a significant preference for high chlorophyll concentrations at large scales ( $\lambda = 0.003$ ,  $P < 0.001$ ), but not at smaller nested scales ( $\lambda = 0.382$ ,  $P = 0.112$ ).

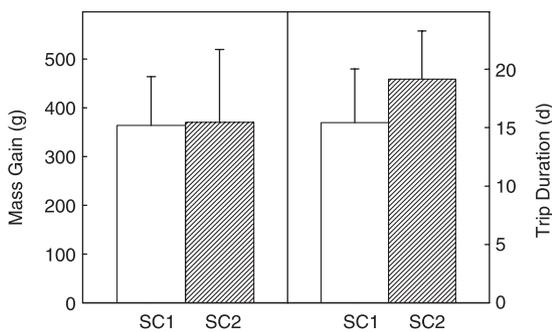
We tested whether these different foraging patterns could be related to foraging success parameters such as total mass gain or trip duration (Fig. 7, ANOVA,  $F_{1,18} = 0.09$ ,  $P = 0.92$ ;  $F_{1,20} = 3.90$ ,  $P = 0.06$ , respectively). Individuals from the SC2 group seemed to spend more time at sea for the same mass gain compared to the SC1 group. We were not able to detect significant differences in movement pattern and foraging parameters between sexes (see Table 1).

#### Discussion

Scale-dependent hierarchical adjustments of animal movements are expected to be related to resource distribution (Fauchald 1999) but few studies have documented this (see Fritz *et al.* 2002; Johnson *et al.* 2002; Fauchald & Tveraa 2003). Only Johnson *et al.* (2002) demonstrated that changes in movements of woodland caribou could be related to environmental factors, but their study was based on only five animals. Here, we applied powerful statistical habitat selection analysis on 22 individual trips by taking into account



**Fig. 6.** Use of habitat types in relation to ARS spatial scales. Availability on study area is indicated by white bars, used proportions at ARS (large) scales by hatched bars and used proportions at ARS nested (fine) scales (for SC2 group only) by doubled hatched bars. (a) Bathymetry. Compositional analysis indicates a preference for pelagic habitat. (b) Sea surface temperature. There was significant difference between years. (c) Sea surface height anomalies. Compositional analysis indicates a significant avoidance by the SC1 group for extreme positive values. This avoidance is only found at nested, fine scale for the SC2 group. (d) Chl-*a* concentrations. Compositional analysis indicates a significant preference for higher Chl-*a* concentrations at large scale for both SC1 and SC2 groups, but this preference disappears at fine, nested scale for the SC2 group. Limits between classes are indicated for *SSHa* and *Chl-a*.



**Fig. 7.** Mass gain (left) and trip duration (right) for the 22 foraging trips according to the search pattern group: SC1 group (unique fine-scale ARS) and SC2 group (two, nested scales ARS). According to the two groups, difference in total mass gain is not significant ( $F_{1,18} = 0.09$ ,  $P = 0.92$ ). Difference in trip duration is nearly significant ( $F_{1,20} = 3.90$ ,  $P = 0.06$ ).

scale-dependent patterns, and have shown explicitly for the first time (to our knowledge) the use by a central-place predator of scale-dependent adjustments with interindividual variability, in relation to environmental features.

The presence of an ARS behaviour in yellow-nosed albatrosses is consistent with studies on other albatrosses (Veit & Prince 1997; Weimerskirch *et al.* 1997). Veit & Prince (1997) showed that black-browed albatrosses increased their turning rate at fine scale in response to the presence of krill swarms. Here, yellow-nosed albatrosses adopted a hierarchical searching strategy in relation to meso-scale oceanic features. In order to reach productive areas at large scales, albatrosses conducted intensive searches at a scale of 130 km after a 1500 km trip. Only four birds did not show any evidence

for ARS; this could be due to the absence of a clear ARS behaviour during the trip at the observed range of scales.

At the oceanic basin macro-scale, birds foraged in pelagic, subtropical waters, reaching turbulence zones from the Agulhas return current, where primary productivity is enhanced. They adopted a long commuting strategy as revealed by the trip structure. This pattern was observed during the 2 years, with a tendency for birds in 2000 to forage in warmer waters than in 2002. This difference could be explained by the shift in Agulhas return current circulation, which slightly changed the position of water masses between years (Lutjeharms 2001). This part of the subtropical domain shows a large west–east Chl-*a* gradient, in relation to the high meso-scale activity from the Agulhas current (Lutjeharms 2001; Park *et al.* 2002). This high primary productivity seems to be predictable at the basin (large) scale and could explain the commuting strategy of yellow-nosed albatrosses from Amsterdam Island. This strategy with exploitation of predictable large-scale structures is observed widely in other central place marine predators. For example, grey-headed and black-browed albatrosses breeding on Campbell Island reach the productive polar front *c.* 2000 km from the colonies (Waugh *et al.* 1999). Others species exploit predictable, productive structures (e.g. white-chinned petrel, Catard & Weimerskirch 1999; Catard, Weimerskirch & Cherel 2000; king penguin, Bost *et al.* 1997). Thus, past experience and orientation seem to play a major role in large-scale habitat selection in marine predators (Hunt *et al.* 1999).

Once in these high productive areas, our results show that yellow-nosed albatrosses searched intensively in relation to the meso-scale structure of environment, which is dominated by presence of eddies with a diameter of  $280 \pm 50$  km (Lutjeharms 2001). Biological production can be linked to these meso-scale features: cyclonic eddies (as revealed by extreme negative SSHa) promote life near the surface through vertical mixing from deep nutrient rich waters (review in Rhines 2001), while warm (anticyclonic) eddies may exhibit elevated primary productivity at the edges (Froneman, McQuaid & Laubscher 1999). These relationships were visible in this zone by the significant negative correlation at fine scale (less than 100 km) between SSHa and Chl-*a* (Fig. 5b). As eddies may persist for several months (Lutjeharms 2001), they can support the development of a predictable food web and thus provide attractive feeding grounds for predators (Sugimoto & Tameishi 1992; Rodhouse *et al.* 1996). Prey aggregation is expected to occur within the eddy system at a spatial scale smaller than the eddy size (280 km), and could explain the ARS scale of albatross. As meso-scale activity is an important determinant of biological production in this part of the ocean (Quartly & Srokosz 2003), the exploitation associated with such features by a species of albatross has been suggested previously (Rodhouse *et al.* 1996; Nel *et al.* 2001). However, primary productivity and organism aggregation in relation to physical

mechanisms of such mesoscale structures are still poorly understood and need to be studied in this complex ecosystem.

Another important result of this individual approach is the existence of different scale-dependent foraging patterns among individuals, which can be due to stochastic variation in prey encounter rate or bird's characteristics. Some individuals (SC1 group) concentrated their search effort directly at a fine scale and showed avoidance for anticyclonic eddies. The other group (SC2) showed two scales of ARS, first at 180 km with a preference of higher productivity zones but not related to SSHa, and a second one at 34 km, in relation to SSHa but not Chl-*a* concentrations. Because of spatio-temporal lags due to water movement and biological transfers within the food web, the foraging pattern of marine predators at small scales is expected to have a better match to prey distribution, compared to primary production (see review in Hunt *et al.* 1999). Birds that foraged directly at small scales seemed to increase their search effort at the scale that had a better match to meso-scale features, where prey patches are expected to be distributed. Individuals which increased the search effort at a scale of *c.* 180 km and then at smaller scales (*c.* 35 km) seemed to detect prey patches in relation to eddies after a time lag. In fact, Fauchald (1999) explored the tracking efficiency of a hypothetical forager in a hierarchical prey system, where the only information conveyed by the system to the forager was through encounter with prey. When he related the search radius to the prior foraging success, he showed that the predator, in a hierarchical patchy system, is expected to have a large search radius when prior success has been low and a short search radius when the prior success has been high. Then, difference in scale-dependent foraging patterns among individuals could be interpreted as difference in efficiency or ability to find a prey patch. At the large scale, the SC2 group did not have a relationship between ARS and SSHa, as might be expected if prey were encountered in a fine-scale patch system in relation to eddies. This idea is reinforced by our results, which show that this group of birds tended to spend more time at sea, while no statistical difference was detected for the total mass gain between the two groups. As albatrosses maximize mass gain (the energetic storage necessary to prepare for the next incubating shift, Weimerskirch 1999) for a foraging trip during incubation (Pinaud & Weimerskirch 2002; Shaffer, Costa & Weimerskirch 2003), inter-individual variability in trip duration is expected to be higher than total mass gain, and thus could be a better indicator of foraging success than total mass gain.

We have shown in this study that a top predator such as the yellow-nosed albatross increased its search effort at different, hierarchical spatial scales in relation to environmental structure, probably according to its own past foraging experience. Perception of environment and foraging decisions are thus scale-dependent, and could lead to difference in individuals (Rettie & Messier

2000; Johnson *et al.* 2002), with a repercussion on individual fitness. The differences in trip duration observed between individuals according to their search pattern suggest that foraging efficiency in a hierarchical system could be linked to the forager's ability to track the system. This emphasizes the importance of such scale-dependent individual approaches to understand habitat selection and its consequences for population processes.

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