

PREY DISTRIBUTION AND PATCHINESS: FACTORS IN FORAGING SUCCESS AND EFFICIENCY OF WANDERING ALBATROSSES

HENRI WEIMERSKIRCH,^{1,3} AGNÈS GAULT,^{1,2} AND YVES CHEREL¹

¹Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360 Villiers en Bois, France

²Laboratoire de Conservation des Espèces, Restauration et Suivi des Populations (CERSP), Muséum National d'Histoire Naturelle, 61 rue Buffon, 75005 Paris, France

Abstract. Seabirds are considered to rely on prey that are patchily distributed and whose abundance differs greatly according to physical processes or water masses. However, very little information is available about the environmental factors and individual factors that affect the foraging success of marine predators. We studied the distribution of prey encounters, foraging success, and efficiency in different water masses and during two stages of the breeding season when energy requirements differed in Wandering Albatrosses (*Diomedea exulans*) of known experience and sex. The birds were simultaneously fitted with satellite transmitters, stomach temperature sensors, and activity recorders. Only 27% of prey were captured in patches (distance between two prey < 1 km); the rest were caught at an average distance of 64 km. Prey in patches were smaller than isolated prey and were caught mainly at night. Diet analysis indicated that albatrosses preyed mainly upon adult squid: squid taken at night were smaller (bioluminescent species), whereas those taken during the day were larger (nonbioluminescent species). Birds spent more time foraging farther from the colony during incubation than during brooding, when their energy requirement was highest, but foraging effort (landings per hour, or kilometers per hour), foraging success (grams of prey per hour), and efficiency (grams of prey per landing per hour) were similar during the two stages. The rate of prey encounter and foraging efficiency did not differ between water masses or between oceanic and shelf-slope waters. We found no differences between the sexes in terms of foraging success and efficiency. Young, inexperienced individuals had foraging success and efficiency similar to those of older, experienced birds but had a different strategy: they foraged more actively and caught more prey at night than did experienced birds. These results suggest strongly that Wandering Albatrosses rely on prey that are highly dispersed, catch few prey within the same patch, and do not adjust foraging effort according to energy requirements. The unpredictability of the location of prey and the type of prey caught by Wandering Albatrosses indicate that the species has a unique foraging strategy compared to most seabirds, which generally concentrate in more predictable foraging areas.

Key words: age- and sex-specific foraging; bioluminescence; central-place foraging; Crozet Islands; *Diomedea exulans*; experience; foraging success; Indian Ocean; prey patchiness; squid; telemetry; Wandering Albatross.

INTRODUCTION

The distribution of animals in the environment is generally aggregated and not random. As a consequence, predators encounter prey over a range of densities and a variety of assemblages. Most ecological systems can be viewed as hierarchical patch systems in which high-density patches at small scales are nested within low-density patches at larger scales (Kotliar and Wiens 1990, Fauchald 1999). Optimal foraging theory (MacArthur and Pianka 1966, Schoener 1971, Stephens and Krebs 1986) predicts that animals in such complex environments should forage so as to maximize net energy gain. Foragers should adjust their search pattern

accordingly (Fauchald 1999) and distribute themselves so as to maximize foraging efficiency (Fretwell and Lucas 1970). In the open ocean, the distribution of prey depends to a large extent on physical processes, and varies in spatial and temporal scales (see Hunt et al. [1999] for a review). Prey distribution is generally considered to be patchy and the predictability of the prey patches in space and time depends on the processes responsible for their formation. For example, large-scale frontal zones at the boundary of water masses can support large concentrations of prey patches whose location is predictable over long periods (Schneider 1993). Conversely, the predictability of prey patches at finer scales is lower than at coarser scales (Hunt and Schneider 1987). Marine predators such as seabirds, which forage over vast surface of ocean, concentrate in these zones of enhanced presence of prey (Schneider 1993), but the way in which they detect prey patches

Manuscript received 9 December 2004; revised 11 March 2005; accepted 24 March 2005. Corresponding Editor: M. Wikelski.

³ E-mail: henriw@cebc.cnrs.fr



PLATE 1. A male Wandering Albatross foraging in the Southern Ocean. This large pelagic seabird covers thousands of kilometers in a single foraging trip to search for prey that are highly dispersed. Photo credit: H. Weimerskirch.

is still poorly known (Nevitt and Veit 1999) and their foraging success is almost unknown. With the recent developments of telemetry, it is now possible to study the rate of prey encounter by marine predators (Weimerskirch and Wilson 1992, Weimerskirch et al. 1994, Bevan et al. 1995, Wilson et al. 1995, Charrassin et al. 2001). It is therefore possible to obtain information on the distribution of prey through the monitoring of the prey encounter by top predators.

When breeding, Wandering Albatrosses are typical central-place foragers that search for prey over extensive surfaces and at long distances from their nest (Weimerskirch et al. 1993, 2000a; see Plate 1). They adjust their movements at various scales from ocean basin (thousands of kilometers) to fine scales (100 m) according to environmental conditions and probably in response to the distribution of prey (Weimerskirch et al. 2000b, Fritz et al. 2003). Adjustment of movements at fine and coarse scales (100 m and hundreds of kilometers) is likely to correspond to optimal use of wind for their dynamic soaring flight and to the use of large-scale weather systems, respectively (Weimerskirch et al. 2000b, Fritz et al. 2003). At intermediate scales, the movement of birds is probably optimized to cope with prey searching (Fritz et al. 2003). Wandering Albatrosses feed mainly on squid and, to a lesser extent, on fish and carrion (Cherel and Klages 1998). Squid generally form shoals and their distribution is considered to be patchy and dispersed (Rodhouse and Nigmatullin 1996). Very little information is available about the distribution of squid taken by albatrosses, but it is likely that the birds adjust their search pattern to cope with

the distribution of their main prey. The location of prey capture and foraging success are therefore useful for providing information on the distribution and patchiness of squid in the marine environment.

However, foraging success depends on foraging effort (energy expended or distance covered per unit of time) and thus should differ according to factors inherent to the predator. First, as for other oceanic seabirds (Ricklefs 1983), energy requirements of foraging Wandering Albatrosses differ extensively according to the stage of the breeding season (Salamolard and Weimerskirch 1993), and are highest during the brooding period, when foraging effort should be highest (Weimerskirch et al. 1997). Second, males and females differ in their involvement in breeding: females provision less than males, even accounting for size differences between sexes (Weimerskirch et al. 2000a). Third, foraging efficiency also is likely to depend on the age, experience, or quality of the forager. Indeed, because foraging efficiency influences foraging and breeding success, and age and experience greatly influence breeding success and individual fitness (Clutton-Brock 1988, Saether 1990), it is very likely that foraging success varies according to the age or experience of animals. Young animals are generally considered to be less efficient than older individuals in prey searching, and learning processes are probably involved in the exploitation of patchily distributed food (Kacelnik and Krebs 1985).

The aim of this study was first to examine whether prey encounter in Wandering Albatrosses is clustered and whether foraging success varies according to the

water masses visited. We used information based on the squid diet of Wandering Albatrosses and on the biology of squid to examine whether the measurements of prey size and prey patchiness obtained from albatrosses correspond to what is known about the biology of squid. Second, we examined whether birds adjust foraging effort according to different energetic constraints, i.e., between incubation and brooding periods. Finally, we tested whether individuals differ in their foraging success, and, in particular, whether the sex and experience of individuals influence prey encounter and foraging success. To do so, we simultaneously fitted Wandering Albatrosses of known sex, age, and status with a stomach temperature sensor, an activity recorder, and a satellite transmitter. Satellite transmitters allowed us to study the movements of birds, activity recorders provided the exact location and timing of landings, and stomach temperature loggers recorded the timing and location of prey capture, as well as prey mass (Wilson et al. 1995). The number of landings is a good proxy for estimating energy expenditure (Weimerskirch et al. 2000b, Shaffer et al. 2001).

METHODS

The study was carried out on Possession Island (46° S, 51° E) in the Crozet Islands, southwestern Indian Ocean, during the incubation and brooding periods in 1998, 1999, 2000, and 2001. The age, sex, and previous experience of individuals were known from our long-term database for the Possession Island Wandering Albatross population (Weimerskirch and Jouventin 1987). Birds were identified as inexperienced (no previous record of breeding) or experienced (with at least one previous breeding event). Inexperienced birds were young individuals (6–11 years old); experienced birds were 12–30 years old or older.

In total, 46 breeding individuals of both sexes were fitted simultaneously with an Argos satellite transmitter (Platform Terminal Transmitter, PTT), a stomach temperature transmitter and associated receiver-recorder, and an activity recorder before they departed for a foraging trip at sea. The PTTs (Microwave Telemetry, Columbia, Maryland, USA; 30 g) were taped on the back feathers. Temperature recorders were used to estimate the timing of prey ingestion and the mass of prey swallowed (see Wilson et al. [1995] for estimation of mass of prey). The birds were induced to swallow a 20-g Stomach Temperature Pill that transmits the temperature of the stomach to the recorder (Wildlife Computer, Redmond, Washington, USA; 25 g), which receives and stores every 15 seconds the information sent by the pill. The recorder was taped to the back feathers. Activity patterns (sitting on water or in flight) were measured with an activity recorder (Francis Instrument, Cambridge, UK, 15 g) that recorded every 15 seconds whether it was submerged in seawater or in the air. This activity recorder was fitted on the tarsus to a plastic leg band. When in flight, albatrosses tuck their legs

within their plumage (dry; when on water, their legs are submerged). Not all loggers worked properly simultaneously, but we were able to obtain complete records from 23 individuals. We also used similar data obtained in 1992 (Weimerskirch et al. 1994) on seven individuals (only with PTTs and stomach temperature recorder, but without activity recorder), making a total of 30 individuals for some parameters.

Birds were caught by hand after they had been relieved from incubation or brooding duties by their partner, when they were about to leave the colony for a foraging trip. After being equipped, they were released and generally took off within minutes. The loggers were attached with white TESA tape, a procedure used for 12 years on albatrosses (Weimerskirch et al. 1994) that allowed us to attach the device quickly to minimize handling stress. It also allowed us to recover the logger without damaging the feathers (Wilson et al. 1997). Birds were recaptured after they returned to their nest, and equipment was removed from the bird incubating or brooding the chick. Upon recovery, tape strips were completely removed. We had neither egg loss nor chick desertion during the attachment and removal of loggers, nor any longer term effect on the bird. The total mass of the equipment was 100 g, or 0.8–1.2% of the bird mass, well below the 5% threshold beyond which behavioral disruptions are likely to occur in flying birds (Croll et al. 1992).

To avoid the stress of stomach lavaging, the stomach temperature pills were not recovered from the bird. The presence of the pill was checked with a metal detector just after placement and at the return to the nest. Wandering Albatrosses regularly regurgitate pellets made of hard parts of prey such as squid beaks; through this process, birds regularly regurgitate pills. Of the pills we placed, 66% were no longer present in the stomach of the birds when they returned to the nest, and we expect that all loggers were regurgitated within a month after placement (H. Weimerskirch, *unpublished data*). To assess the possible impact of the loggers on the birds' performance, we compared foraging trip durations of the birds fitted with transmitters with those of birds without equipment during other studies on Crozet. Foraging trip duration is a good proxy for foraging effort in Wandering Albatrosses (Weimerskirch 1995). The durations of trips were similar ($P > 0.2$) to those of birds without equipment studied in other years (Weimerskirch 1995, Weimerskirch et al. 2000a).

We used all location types (except class B) provided by the Argos system, and the locations were filtered using the method of Weimerskirch et al. (1993), with a maximum flight speed of 95 km/h. We also discarded locations too closely separated in time (by <10 minutes), discarding the less accurate one following the classification provided by Argos, because the distance that a bird could travel during this short time is that of the inherent error of the locations. The stomach temperature data were analyzed using Software MT (Jen-

sen Software, Loehe, Germany), which detects feeding events and estimates the mass of prey (see Wilson et al. 1995). Locational data, activity data, and feeding events were then merged with environmental data (i.e., bathymetry, sea-surface temperature) using a custom software package "Diomedea" (Filippi [1999]; see Weimerskirch et al. [2000b] for details and other examples of its use). This software integrates all behavioral and environmental data and estimates geographic positions every minute, based on activity and positioning by the Argos system, as well as flight speed. The calculation takes into account the time spent on water and in flight by birds equipped with activity loggers, so that the real mean speed of travel between successive satellite locations can be estimated. Birds may regurgitate the stomach pill before they return to the colony (but the recorded information is still retained on the receiver-recorder on the back), so some temperature recordings were incomplete. For these tracks, the analysis was performed only on the part of the track during which the bird was carrying the pill.

Two prey were considered as being caught in a same patch when they were caught at the same location (no takeoff between two prey captures) or within a distance of <1 km. The rationale for this is derived from two factors. (1) Squid are likely to be aggregated in swarms not >1 km in a similar way that Antarctic krill individuals are congregated for hours in swarms with a diameter of 1–100 m (Murphy et al. 1988). (2) The precision of the Argos system is not better than 1 km (Brothers et al. 1997). The bathymetric domains were separated into three classes: shelf (depth < -200 m), slope (depth -200 to -2000 m), and oceanic waters (depths > -2000 m). The southern Indian Ocean water mass was split into four zones of sea-surface temperature (SST) following Park et al. (1993, 2002) for the Crozet basin: the Subtropical Zone (SST > 13°C), Subantarctic Zone (10° < SST < 13°C), Polar Frontal Zone (5° < SST < 9°C), and Antarctic Zone (SST < 4°C).

We collected 64 stomach contents in 1992 and 1994 by induced regurgitation of chicks. Because Wandering Albatrosses fed mainly on squid (75% by mass) at the Crozet Islands (Cherel and Weimerskirch 1999), we only considered in the present study the main squid prey (>5% by number) identified from accumulated lower beaks of squid. Lower beaks were identified by reference to features given by Clarke (1986) and by comparison with material held in our own reference collection. Lower rostral length (LRL) of squid beaks was measured to 0.1 mm with vernier calipers. Allometric equations given by Clarke (1986), Adams and Klages (1987), Lu and Williams (1994), and Jackson (1995) were used to estimate whole wet mass from LRL. Wandering Albatrosses consistently preyed upon the same range of squid species of the same size from year to year, but percentages of the main species consumed differed (Cherel and Weimerskirch 1999). We are thus confident that the main prey identified in stom-

ach contents collected in 1992 and 1994 are representative of the diet in 1998–2001.

To analyze the effects of various factors (including sex, year, and period) on dependent variables such as prey mass or distance between prey, we first checked for normality. If the distribution was significantly different from normality, we log-transformed the data and checked again for normality. Because there are several prey captures for each individual during a foraging trip, data for prey mass and time between prey capture were analyzed in mixed-model ANOVAs. Mass of prey, distance, foraging success, and the similar data were the dependent variables; the individual bird was a random factor; and sex, year, period (incubation or brooding), and classes of marine habitats were fixed factors. Interactions between individuals and dependent variables were examined, and are noted in the text only if significant. All statistical tests were performed with Statistica 6.0 (Statsoft 2001) and SYSTAT 10.0 (Systat 2000).

RESULTS

Values are given as mean \pm 1 SD unless otherwise noted. Durations of foraging trips were longer during incubation than during the brooding period (12.7 ± 5.8 and 3.6 ± 1.5 d, respectively; ANOVA $F_{1,29} = 23.4$, $P < 0.0001$). When foraging at sea, Wandering Albatrosses spent only 2% of their time over the shelf, 30% over slope waters, and 68% over oceanic waters. There was no difference between incubation and brooding in the proportion of time spent in the three domains (ANOVA $F_{2,21} = 0.348$, $P = 0.562$). Albatrosses caught prey throughout their foraging trip (Fig. 1). During the study period, the prey captured were distributed over a large surface of ocean around the Crozet Islands, with high numbers over the Crozet slope waters and over oceanic waters to the west of Crozet (Fig. 2). There was no difference between years in the various parameters examined, so years were combined.

Distance between prey

The median distance between prey was 16.6 km. The distribution of distances between prey is best described by a power-law distribution with a long tail (Fig. 3a). There was no influence of water masses on distance between prey captured ($P > 0.2$). The distance between prey varied significantly according to prey mass categories, large prey being encountered at longer intervals (every 114 km) than medium (every 61 km) or small prey (every 57 km) (mixed-model ANOVA $F_{3,29} = 3.4$, $P = 0.0351$). A significant number of prey were caught at the same location at a distance <1 km (Fig. 3b), i.e., in the same patch (see *Methods*). Over the shelf, 70.3% ($n = 37$ prey) were in patches, whereas over oceanic and slope waters only 22.8% (225 prey) and 25.5% (196 prey) of prey were in patches ($\chi^2 = 36.7$, $P < 0.001$). Distance between patches was 64.3 ± 93.0 km. The distance between prey patches was not

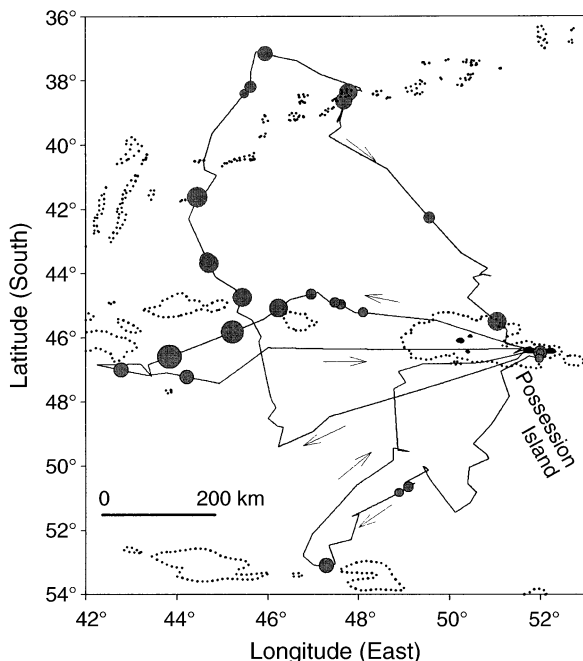


FIG. 1. Three foraging trips of Wandering Albatrosses around the Crozet Islands, southern Indian Ocean, during the incubation period. Dots indicate prey captures. The size of the dots is proportional to the mass of prey caught (range 10–3130 g). The dotted lines represent –2000 m isobaths.

different between sexes, between stages of the breeding season, or between night and day ($P > 0.8$), but it differed between classes of bathymetry, being much shorter over the shelf and over slopes than over oceanic waters (mixed-model ANOVA $F_{3,29} = 14.2$, $P < 0.001$; Fig. 3c).

Prey mass and squid captured

The range of prey masses estimated from stomach sensors (324 ± 518 g, $n = 479$) varied from 10 g to 3130 g (Fig. 4a). There was no effect of sex or year on the mass of prey ($P > 0.3$), but prey appear to be significantly heavier during the brooding period than during incubation (758 g vs. 361 g, on average; mixed-model ANOVA $F_{1,29} = 7.6$, $P = 0.0169$), and when caught during daytime than at night (mixed-model ANOVA $F_{1,29} = 13.9$, $P = 0.0061$; Fig. 4a). Prey caught in patches were smaller than isolated prey (mixed-model ANOVA $F_{3,29} = 16.1$, $P = 0.007$; 180 ± 218 g vs. 382 ± 594 g). The mass of prey in patches did not differ between the two periods ($F_{1,19} = 1.2$, $P = 0.315$) or between day and night ($F_{1,19} = 1.7$, $P = 0.241$), whereas isolated prey differed significantly between stages and period of the day, being larger during the brooding period ($F_{1,28} = 7.6$, $P = 0.021$) and during the day ($F_{1,28} = 13.1$, $P = 0.018$).

The mass of prey caught during daytime or at night did not differ between oceanic, slope, or shelf habitats (mixed-model ANOVA $F_{2,29} = 2.34$, $P = 0.130$ for

daytime; $F_{2,29} = 0.61$, $P = 0.554$ at night; Fig. 4). Over oceanic waters, the mass of prey caught during the day was similar between water masses (mixed-model ANOVA $F_{3,28} = 1.4$, $P = 0.328$), as for those caught at night (mixed-model ANOVA $F_{3,24} = 1.3$, $P = 0.317$), but there was a significant interaction ($F = 3.0$, $P = 0.0364$), indicating that prey masses differed between night and day in cold waters (Fig. 4c).

Diet samples indicate that Wandering Albatrosses preyed mainly on squid (71% by mass), the remainder being fish (22%) and carrion (7%). Five squid species together accounted for 77% of the total number of identified accumulated lower squid beaks ($n = 2318$). There were two large species of onychoteuthids, *Moroteuthis ingens* and *Kondakovia longimana*, with mean body mass of 1.0 kg and 2.7 kg, respectively (Table 1). The other three species were much smaller and included one cranchiid, *Galiteuthis glacialis* (0.10 kg) and two histioteuthids, *Histioteuthis eltaninae* (0.08 kg) and the larger *H. atlantica* (0.22 kg). Most of the lower beaks had darkened (wholly chitinized) wings, indicating that Wandering Albatrosses preyed mainly upon adults of the five squid species.

Search effort, foraging success, and efficiency

The distance covered (search effort) per hour was not influenced by sex or breeding period. On average, birds caught a prey item every 3.6 ± 4.5 h of foraging. The rate of prey encounter was similar between day and night (Wilcoxon test for paired samples, $Z = 0.52$, $P = 0.599$). Foraging success (mass of prey caught per hour) was 76 ± 47 g/h, and it was higher during daytime than at night (86 ± 42 and 63 ± 124 g/h, respectively, $Z = 2.64$, $P = 0.008$). The number of landings per hour is positively related to energy expenditure (Shaffer et al. 2001); therefore, we used this parameter as a proxy for measuring foraging costs. The number of landings per hour did not differ significantly between periods and between sexes ($P > 0.310$); it was, on average, 0.52 landing per hour ± 0.32 (range 0.19–1.57, $n = 23$). The number of landings per hour was similar at night and during daytime (Wilcoxon paired test, $Z = 1.1$, $P = 0.263$). There was no effect of sex or period when considering the number of landings per hour over the shelf, over the slope, and over oceanic waters. The number of landings per hour was similar over the slope and oceanic waters (Wilcoxon paired test, $Z = 0.46$, $P = 0.46$). The number of landings per hour was lower over the shelf than over oceanic and slope waters ($Z = 2.1$, $P = 0.038$, and $Z = 2.04$, $P = 0.042$; 0.16 ± 0.31 landing/h compared to 0.51 ± 0.36 and 0.65 ± 0.87 landing/h, respectively).

The mass gain at the return to the nest was positively related to the catch rate at sea ($y = 0.0195x + 0.0556$, $R^2 = 0.2294$, $P = 0.033$). The rate of prey encounter (number of prey caught per hour), foraging success, and efficiency (mass of prey per landing per hour) did

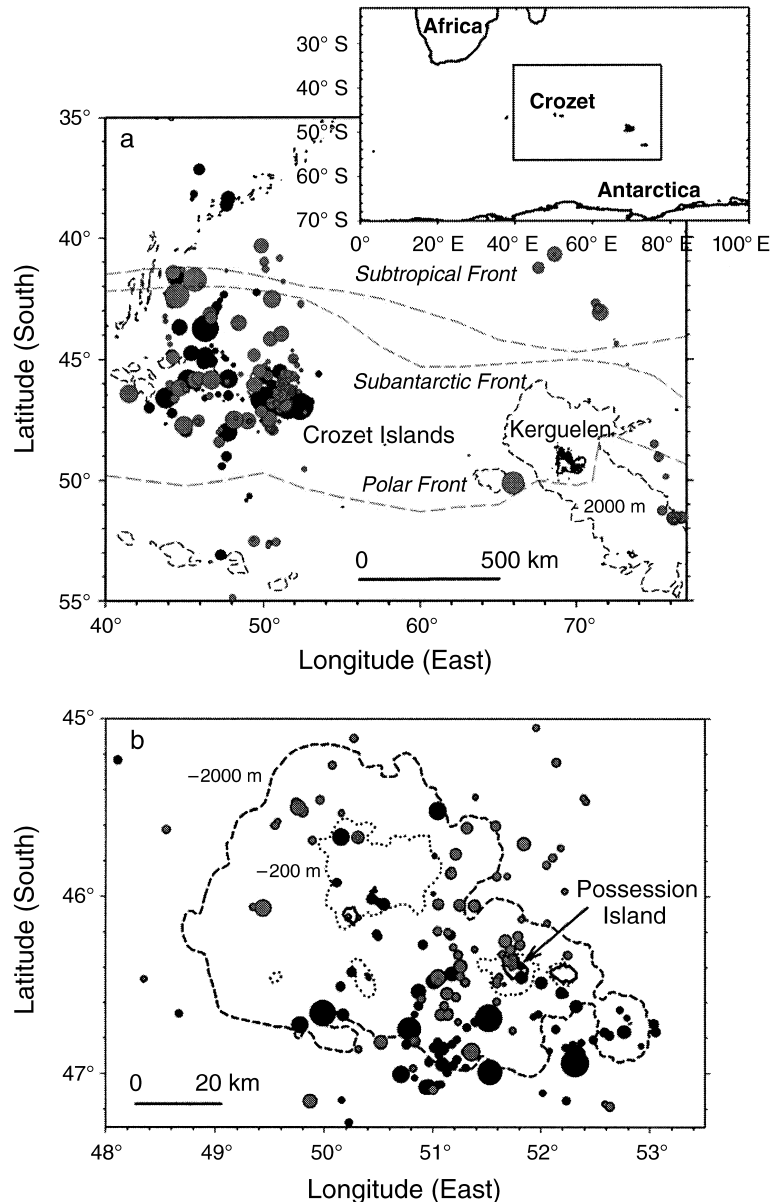


FIG. 2. (a) Distribution in the southern Indian Ocean of prey caught by Wandering Albatrosses breeding on Possession Island in the Crozet Islands. (b) Enlargement of the Crozet Islands sector. Gray dots represent prey caught during incubation; black dots represent prey caught during brooding. The size of the dots is proportional to the mass of the prey.

not differ between the sexes or between the periods ($P > 0.1$) in all depth habitats combined, or in oceanic or slope areas. Only over shelf areas did foraging success tend to be higher during the brooding period than during incubation ($P = 0.054$) (Fig. 5).

Influence of age and experience

Experienced and inexperienced birds caught prey of similar mass and at similar distance between prey ($P > 0.5$). They had similar foraging effort, foraging success, and efficiency. However, inexperienced and experienced birds differed in their foraging behavior. In-

experienced individuals took a larger amount of prey at night than did experienced birds: $77.0\% \pm 17.1\%$ of the total mass was caught by experienced birds during the day, compared to $53.7\% \pm 34.5\%$ for inexperienced birds ($F_{1,26} = 5.8722$, $P = 0.0226$). Efficiency during the day was higher than at night for experienced birds (0.46 ± 0.17 and 0.30 ± 0.26 landing/h; $Z = 2.0$, $P = 0.040$), but not for inexperienced birds (0.56 ± 0.11 and 0.66 ± 0.49 landing/h; $Z = 0.1$, $P = 0.901$). The mass of prey caught per hour was higher during daytime than at night for experienced birds (85 ± 40 g/h vs. 33 ± 31 g/h; $Z = 3.0$, $P = 0.004$), whereas

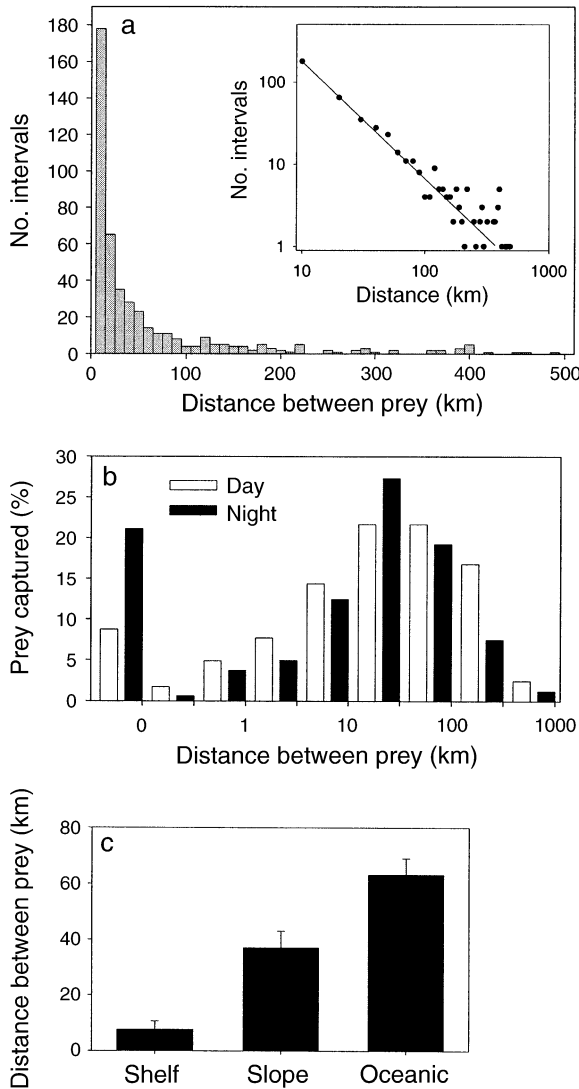


FIG. 3. (a) Distribution of number of intervals during which Wandering Albatrosses traveled a distance of 0–500 km. The inset shows the log–log plot of the same data. A power-law relationship fits the data with $r^2 = 0.865$, $P < 0.001$. The estimated value of the exponent is -1.256 . (b) Distribution of distance between prey caught during the day and at night, and (c) influence of the bathymetry on the average distance between prey (mean \pm SE).

there was no difference for inexperienced birds (73 ± 55 g/h vs. 150 ± 240 g/h; $Z = 0.68$, $P = 0.489$).

DISCUSSION

Prey patchiness, prey distribution, and foraging strategy

Whereas it is generally considered that oceanic seabirds feed on prey with a patchy distribution (Ashmole 1971, Logerwell and Hargraves 1996), our results indicate that only a small percentage (27.5%) of prey is encountered at the same location or at distances >1 km. These prey in patches are of small size compared

to those caught isolated, and primarily are caught at night. The distribution of the distances between prey (Fig. 3b) indicates that distances of 1–10 km are rare, and prey are mostly found at distances between 10 and 100 km. Although it cannot be ruled out that prey caught isolated are in a patch, our results indicate that Wandering Albatrosses are not catching a large percentage of prey within patches, but rather are moving

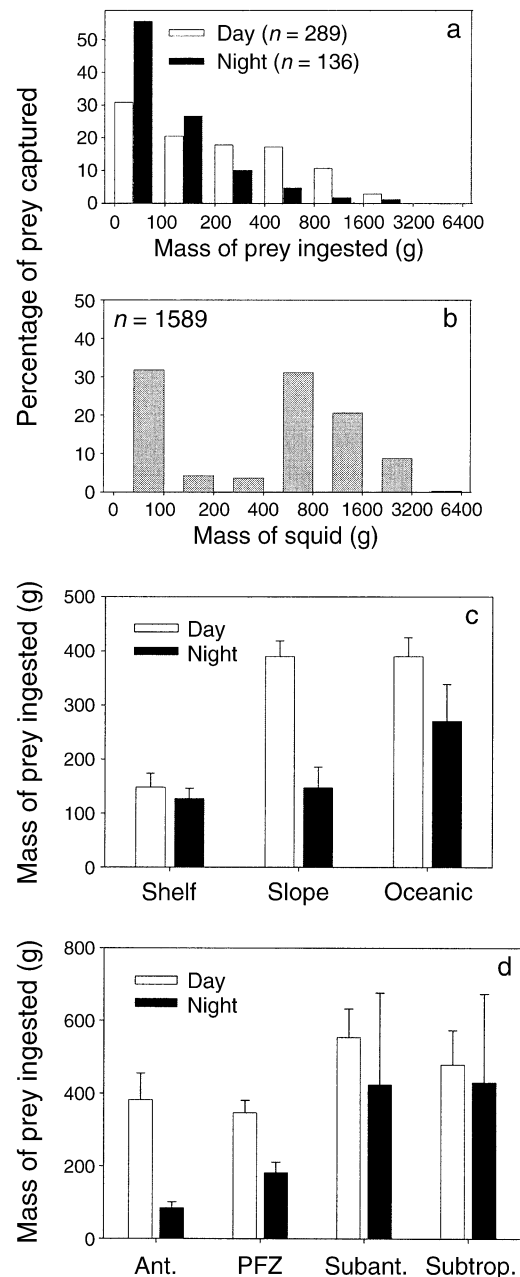


FIG. 4. Distribution of (a) the mass of prey ingested at night and during the day, and of (b) the estimated mass of squid found in the diet of Wandering Albatrosses. Mass of prey ingested (mean \pm SE) in relation to (c) bathymetry and (d) water masses.

TABLE 1. Percentages by number, size, and biological characteristics of the main squid prey (>5% by number) of Wandering Albatrosses at Crozet Islands.

Species	Number		<i>n</i>	Size	
	<i>n</i>	%		LRL (mm)	Mass (g)
Onychoteuthidae					
<i>Moroteuthis ingens</i>	575	24.8	505	8.1 ± 0.7 (5.5–10.7)	1016 ± 219 (352–2150)
<i>Kondakovia longimana</i>	617	26.6	515	13.5 ± 1.7 (6.8–19.0)	2719 ± 1112 (299–7676)
Histioteuthidae					
<i>Histioteuthis eltaninae</i>	231	10.0	230	3.4 ± 0.3 (2.5–3.9)	84 ± 16 (40–116)
<i>Histioteuthis atlantica</i>	124	5.3	119	5.0 ± 0.9 (2.7–6.9)	216 ± 83 (51–429)
Cranchiidae					
<i>Galiteuthis glacialis</i>	233	10.1	220	5.3 ± 0.4 (4.1–6.2)	102 ± 15 (59–146)

Notes: Values are means ± SD (with range below in parentheses). LRL is lower rostral length, Biolum. is bioluminescence, and PFZ is Polar Frontal Zone. Zone abbreviations are: Ant., Antarctic; Subant., Subantarctic; Subtrop., Subtropical.

† From Nesis (1987, 1995), Kubodera et al. (1998), Nesis et al. (1998), Voss et al. (1998), Cherel et al. (2004).

between distant patches or isolated prey. Wandering Albatrosses also are known to attend fishing boats to feed on discards. However, in the Crozet sector at the time of the study, only long-liners for toothfish occur occasionally: they operate only over shelf slopes and around Crozet, and they concentrate mainly on the western part of the slope where very few prey ingestions were measured in our study, suggesting that most, if not all prey ingestions occurred naturally.

Using GPS systems (Weimerskirch et al. 2002) and based on a fractal analysis, Fritz et al. (2003) have shown that Wandering Albatrosses adjust the tortuosity of their movements to different environmental and behavioral constraints. At a fine scale (hundreds of meters), their zigzag movements probably correspond to the adjustment of flight to local wind conditions. A specific pattern in tortuosity at the medium scale (1–10 km) exists and could be consistent with food-searching behavior (Fritz et al. 2003). This medium-sized spatial scale could correspond to the scale of an area-restricted search (Weimerskirch et al. 1997) adopted to search in a small-sized sector such as slopes or frontal zones, where prey availability is considered to be enhanced (Hunt and Schneider 1987). It is during such active search that prey in patches are caught. However, Wandering Albatrosses encounter patches at an average of every 64 km, indicating that their strategy is to move rapidly between distant patches where few prey are caught. The distribution of distances between prey is best described by a distribution with a power-law tail. Such a distribution of flight lengths has been recorded in a series of animals, including Wandering Albatrosses, and conforms to a Lévy distribution (Viswanathan et al. 1996, 1999). Lévy flight motion is predicted to increase the probability of encountering new patches compared to random search. Prey encounter in Wandering Albatrosses appears to conform to Lévy flight

motion and may be an optimal solution for a predator searching for prey that are widely dispersed. However, the value of the exponent, 1.256, is not close to 2, the value predicted by theory for an optimal flight search pattern. Here we are considering not search pattern, but prey encounters, so the value suggests that prey encounter may not be optimal, underlying the difficulty that Wandering Albatrosses have in finding prey.

Energy requirements and foraging in relation to environment

The energy requirement per unit of time for birds is higher when they are brooding chicks compared to the incubation period (Salamolard and Weimerskirch 1993). Surprisingly, foraging effort (either measured from the distance covered per hour, or by the number of landings per hour), prey encounter, foraging success, and efficiency did not differ between the two stages, suggesting that birds do not extensively modify their foraging effort to cover the increased energy requirements, and that prey availability probably does not differ between the two periods. Prey were larger during the brooding period, but were caught in smaller numbers. Birds only modify the range of foraging by doing shorter trips during the brooding period (Weimerskirch et al. 1993), to allow increased provisioning to the young chick. Because birds are unable, or unwilling, to increase foraging effort and the foraging success of trip is not higher when energy requirements are higher, the consequence is that birds lose mass during the brooding period (Weimerskirch and Lys 2000), i.e., they use their energy stores to compensate for their decreased energy balance.

Central-place foragers in a patchy environment are expected to exploit a patch until the harvest rate is lower than the average harvest rate of the next patch where they have to move (Charnov 1976). Wandering

TABLE 1. Extended.

Biological characteristics†			
Age	Buoyancy	Biolum.	Biogeography
mostly adults	float?	no	neritic, slope (oceanic)
mostly adults	float	no	PFZ, Subant. (Ant.) slope, oceanic Ant., PFZ
mostly adults	float	yes	oceanic (slope)
mostly adults	float	yes	PFZ (Ant., Subant.) oceanic (slope) Subant., Subtrop. (PFZ)
mostly adults	float	yes	oceanic (slope) Ant., PFZ

Albatrosses do not spend long periods in a restricted area, or in a patch, but rather move continuously and rapidly to encounter isolated patches of prey. This strategy is made possible by low traveling costs over long distances for Wandering Albatrosses, and the high cost of active foraging through series of landings and take-offs (Weimerskirch et al. 2000b). Although one would expect that shelf areas, and especially slope areas, are zones of enhanced prey availability (Hunt and Schneider 1987), there were few differences between the mass of prey, distance between prey patches, foraging success, and foraging efficiency between the areas prospected (water masses or bathymetric categories). Only

the shelf area, where birds spent a very limited time, appears to be different, with smaller, more aggregated prey than in the slopes or oceanic waters; this was not associated with a higher foraging success. These unexpected results for a marine predator may be related, in part, to the prey caught by Wandering Albatrosses

Foraging strategy and prey characteristics

Wandering Albatrosses from Crozet Islands prey mainly upon adults of five squid species. A common feature of these squid is that they are known to rise to the surface after spawning and die, being thus available to seabirds (Nesis 1995, Nesis et al. 1998). The five species can be split into two groups with different biological characteristics (Table 1): onychoteuthids are large to very large and have no photophores, whereas histioteuthids and *Galiteuthis glacialis* are much smaller and bioluminescent (Table 1). Those characteristics have direct implications on how albatrosses can locate and catch squid. Because Wandering Albatrosses are visual predators, they can easily locate onychoteuthids during the day, but not at night. On the other hand, bioluminescent species are likely to be easier to locate at night. This is probably the main explanation why prey caught during the day were larger (onychoteuthids) than those taken at night (histioteuthids and *G. glacialis*).

Noticeable also is the fact that most onychoteuthids are much heavier than the mean estimated mass of prey ingested by albatrosses. This clearly indicates that onychoteuthids were probably torn into pieces before being ingested, whereas histioteuthids and *G. glacialis* were probably ingested whole. A comparison between the frequency distribution of the mass of prey ingested and that of the squid (Fig. 4) shows that albatrosses swallowed more prey in the 100–400 g range than indicated by the squid mass. Two explanations can account for this discrepancy, the first being that birds preyed on fish of that size. The only available infor-

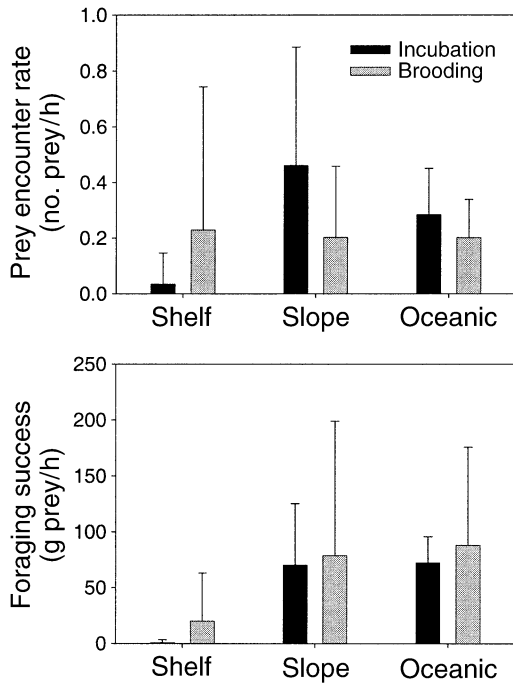


FIG. 5. Efficiency of foraging trips and foraging success in different classes of bathymetry (mean + SD).

mation, however, indicates that Wandering Albatrosses feed upon large to very large fish, including Patagonian toothfish, *Dissostichus eleginoides* (Weimerskirch et al. 1997). The second, and more likely, explanation is that masses of 100–400 g of food mainly correspond to pieces of large squid, fish, and carrion ingested by the birds, i.e., they only take a part of a prey because it is too large to be swallowed whole or because several albatrosses are feeding on the same food item.

Biogeography of the squid also adds new information related to the behavior of the birds. Adult onychoteuthids are abundant in slope waters surrounding the Crozet Islands (Cherel and Weimerskirch 1999, Cherel et al. 2004), and *Kondakovia longimana* also occurs in cold oceanic waters. This is in agreement with albatrosses feeding diurnally on large prey in slope and oceanic waters, especially over the lower slope, and in the Antarctic, Polar Frontal, and Subantarctic Zones (Fig. 4). Finally, biogeography suggests that the small squid caught at night were mainly *Galiteuthis glacialis* in Antarctic waters, *Histioteuthis eltaninae* in the Polar Frontal Zone, and the larger *H. atlantica* in subantarctic waters (Table 1). Unfortunately, we lack detailed information about the shoaling behavior of those squid, but histioteuthids are known to be numerous in some areas (Nesis 1987), and the number of remains in the stomachs of individual sperm whales suggests that they form shoals (Clarke 1980). Such an aggregative behavior is in agreement with albatrosses feeding on small prey in patches mainly at night.

Influence of experience

Like many animals (Clutton-Brock 1988, Sæther 1990), inexperienced Wandering Albatrosses have a lower breeding success than experienced birds (Weimerskirch 1992). The lower breeding success of young birds is generally attributed, at least in part, to a lower foraging efficiency of inexperienced birds, but very little actual information is available on the foraging success and efficiency of inexperienced and experienced animals (Forslund and Pärt 1995). Surprisingly, in Wandering Albatrosses the overall foraging success and efficiency of both groups are similar. This result is in accordance with results showing that breeding success is lower for inexperienced bird as a result of desertion during incubation (Weimerskirch 1992), not related to differences in mass gain or time spent foraging (Weimerskirch 1995). Thus, as supposed by earlier studies showing an increase in body condition of immature Wandering Albatrosses prior to breeding (Weimerskirch 1992), it is likely that birds only start breeding when they have attained body condition and foraging success similar to those of adults. Hunt et al. (1999) suggested that seabirds might delay their year of first breeding to allow acquisition of knowledge of profitable foraging areas before starting breeding investment.

Interestingly, our study shows that inexperienced birds are foraging to a larger extent at night compared to older experienced birds, suggesting that they might have different foraging strategies, or are forced to forage at night. There are important differences between daytime and night in the mass of prey and the distance between prey, suggesting that the type of prey or the method of prey capture might differ between daytime and nighttime foraging. Furthermore, immature Wandering Albatrosses are known to be less competitive than adults when feeding on the same prey patch (Bretagnolle 1993). It is possible that, during the first year of breeding, young adults still avoid competition with adults by foraging at night.

Conclusion

Wandering Albatrosses appear to rely mainly on adult squid whose distribution is extremely patchy and scattered over extensive areas. The strategy of the species is therefore to cover extensive surface at low cost (Weimerskirch et al. 2000b). The striking result of this study is that the foraging success of trips and the effort of birds do not differ between marine habitats or between the stages of breeding. This result is unexpected, because marine habitats are supposed to have different productivity for seabirds (Hunt et al. 1999), and birds are expected to increase their foraging effort when energy requirements increase. Wandering Albatrosses may be unable or unwilling to increase foraging effort when their energy requirement is highest, possibly because of the unpredictability of foraging success. Although slope areas provide foraging success similar to that of more distant oceanic waters, Wandering Albatrosses still favor oceanic waters, probably because foraging costs and intraspecific competition are lower there. The foraging strategy of this large species is much different from that expected for a seabird (Hunt et al. 1999). This may be due to the large size and particular foraging strategy, based on energy saving by the use of wind (Weimerskirch et al. 2000b). Increasing foraging effort in specific areas may be too costly for the flight type of Wandering Albatrosses, compared to all other species of albatrosses and petrels of smaller size, which tend to have a different strategy. These smaller species have a directed commuting movement to zones of predictable prey concentration, such as fronts or shelf edge (Hunt et al. 1999), where they spend most of their foraging time (see Weimerskirch [1998] for a review). In addition to their particular foraging strategy based on extensive movements at low costs, Wandering Albatrosses have a completely different diet than all other seabirds (Cherel and Klages 1998), underlying the uniqueness of the niche that they occupy in the marine environment. However, results equivalent to those obtained for Wandering Albatrosses are necessary for other species to examine the foraging strategy and related efficiency of birds searching for more predictable and concentrated prey patches.

ACKNOWLEDGMENTS

The study was financed by IPEV (Institut Polaire—Paul Emile Victor, program number 109), and the Ethic Committee of IPEV approved the field procedure. We thank Tatiana Guionnet, Julien Martin, and Géraldine Mabilie for the deployment of equipment in the field, C. A. Bost, James Mandel, and an anonymous reviewer for helpful comments on the manuscript.

LITERATURE CITED

- Adams, N. J., and N. T. Klages. 1987. Seasonal variation in the diet of the king penguin (*Aptenodytes patagonicus*) at sub-Antarctic Marion Island. *Journal of Zoology London* **212**:303–324.
- Ashmole, N. P. 1971. Seabird ecology and the marine environment. Pages 223–286 in D. S. Farner and J. R. King, editors. *Avian biology*. Volume 1. Academic Press, New York, New York, USA.
- Bevan, R. M., P. J. Butler, A. J. Woakes, and P. A. Prince. 1995. The energy expenditure of free-ranging black-browed albatrosses. *Philosophical Transactions of the Royal Society of London* **350**:119–131.
- Bretagnolle, V. 1993. Adaptive significance of seabird coloration: the case of procellariiforms. *American Naturalist* **142**:141–173.
- Brothers, N., R. Gales, A. Hedd, and G. Robertson. 1997. Foraging movements of the Shy Albatross *Diomedea cauta* breeding in Australia; implications for interactions with longline fisheries. *Ibis* **140**:446–457.
- Charrassin, J. B., A. Kato, Y. Handrich, K. Sato, Y. Naito, A. Ancel, C. A. Bost, M. Gauthier-Clerc, Y. Ropert-Coudert, and Y. Le Maho. 2001. Feeding behaviour of free-ranging penguins determined by oesophageal temperature. *Proceedings of the Royal Society of London B* **268**:151–157.
- Cherel, Y., G. Duhamel, and N. Gasco. 2004. Cephalopod fauna of subantarctic islands: new information from predators. *Marine Ecology Progress Series* **266**:143–156.
- Cherel, Y., and N. Klages. 1998. A review of the food of albatrosses. Pages 113–136 in G. Robertson and R. Gales, editors. *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, Australia.
- Cherel, Y., and H. Weimerskirch. 1999. Spawning cycle of onychoteuthid squids in the southern Indian Ocean: new information from seabird predators. *Marine Ecology Progress Series* **188**:93–104.
- Clarke, M. R. 1980. Cephalopoda in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology. *Discovery Report* **37**:1–324.
- Clarke, M. R. 1986. A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford, UK.
- Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Illinois, USA.
- Croll, D. A., A. J. Gaston, A. E. Burger, and D. Konof. 1992. Foraging behavior and physiological adaptations for diving in Thick-billed Murres. *Ecology* **73**:344–356.
- Fauchald, P. 1999. Foraging in a hierarchical patch system. *American Naturalist* **153**:603–613.
- Filippi, D. 1999. *Diomedea* software. CEBC CNRS, Villiers en Bois, France.
- Forslund, P., and T. Pärt. 1995. Age and reproduction in birds—hypothesis and tests. *Trends in Ecology and Evolution* **10**:374–378.
- Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**:16–36.
- Fritz, H., S. Said, and H. Weimerskirch. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long range foraging seabird. *Proceedings of the Royal Society of London B* **270**:1143–1148.
- Hunt, G. L., F. Mehlum, R. W. Russell, D. Irons, M. B. Decker, and P. H. Becker. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. Pages 2040–2056 in N. J. Adams and R. H. Slotow, editors. *Proceedings of the 22nd International Ornithological Congress*, Durban, South Africa. BirdLife South Africa, Johannesburg, South Africa.
- Hunt, G. L., and D. C. Schneider. 1987. Scale-dependent processes in the physical and biological environment of marine birds. Pages 7–41 in J. P. Croxall, editor. *Seabirds: feeding biology and role in marine ecosystems*. Cambridge University Press, Cambridge, UK.
- Jackson, G. D. 1995. The use of beaks as tools for biomass estimation in the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae) in New Zealand waters. *Polar Biology* **15**:9–14.
- Kacelnik, A., and J. R. Krebs. 1985. Learning to exploit patchily distributed food. Pages 189–205 in R. M. Sibley and R. H. Smith, editors. *Behavioural ecology*. Blackwell, Oxford, UK.
- Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* **59**:253–260.
- Kubodera, T., U. Piatkowski, T. Okutani, and M. R. Clarke. 1998. Taxonomy and zoogeography of the Family Onychoteuthidae (Cephalopoda: Oegopsida). *Smithsonian Contributions in Zoology* **586**:277–291.
- Logerwell, E. A., and N. B. Hargraves. 1996. The distribution of seabirds relative to their fish prey off Vancouver Island: opposing results at large and small scales. *Fisheries Oceanography* **5**:163–175.
- Lu, C. C., and R. Williams. 1994. Contribution to the biology of squid in the Prydz Bay region, Antarctica. *Antarctic Science* **6**:223–229.
- McArthur, R. H., and E. R. Pianka. 1966. On the optimal use of a patchy environment. *American Naturalist* **100**:603–610.
- Murphy, E. J., D. J. Morris, J. L. Watkins, and J. Priddle. 1988. Scales of interactions between Antarctic krill and the environment. Pages 120–130 in D. Sahrage, editor. *Antarctic ocean and resources variability*. Springer-Verlag, Berlin, Germany.
- Nesis, K. N. 1987. *Cephalopods of the world. Squids, cuttlefishes, octopuses and allies*. TFH Publications, Neptune City, New Jersey, USA.
- Nesis, K. N. 1995. Mating, spawning, and death in oceanic cephalopods: a review. *Ruthenica* **6**:23–64.
- Nesis, K. N., C. M. Nigmatullin, and I. V. Nikitina. 1998. Spent female of deepwater squid *Galiteuthis glacialis* under the ice at the surface of the Weddell Sea (Antarctic). *Journal of Zoology London* **244**:185–200.
- Nevitt, G., and R. R. Veit. 1999. Mechanisms of prey-patch detection by foraging seabirds. Pages 2072–2082 in N. J. Adams and R. H. Slotow, editors. *Proceedings of the 22nd International Ornithological Congress*, Durban, South Africa. BirdLife South Africa, Johannesburg, South Africa.
- Park, Y.-H., L. Gambéroni, and E. Charriaud. 1993. Frontal structure, water masses and circulation in the Crozet Basin. *Journal of Geophysical Research* **98**:12361–12385.
- Park, Y.-H., R. T. Pollard, J. F. Read, and V. Lebourcher. 2002. A quasi-synoptic view of the frontal circulation in the Crozet Basin during the Antares-4 cruise. *Deep Sea Research II* **49**:1823–1842.
- Ricklefs, R. E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. *Studies in Avian Biology* **8**:84–94.
- Rodhouse, P. G., and C. M. Nigmatullin. 1996. Role as consumers. *Philosophical Transactions of the Royal Society of London B* **351**:1003–1022.

- Sæther, B. E. 1990. Age specific variation in the reproductive performance of birds. Pages 251–283 in D. M. Power, editor. *Current ornithology*. Volume 7. Plenum Press, New York, New York, USA.
- Salamolard, M., and H. Weimerskirch. 1993. Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. *Functional Ecology* **7**:643–652.
- Schneider, D. C. 1993. Scale-dependent spatial dynamics: marine birds in the Bering Sea. *Biological Review* **68**:579–598.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**:369–404.
- Shaffer, S., D. Costa, and H. Weimerskirch. 2001. Behavioural factors affecting foraging effort of breeding wandering albatrosses. *Journal of Animal Ecology* **70**:864–874.
- Statsoft. 2001. *Statistica*, version 6.0. Statsoft, Tulsa, Oklahoma, USA.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.
- SYSTAT. 2000. *SYSTAT* version 10.0. Systat Software, Point Richmond, California, USA.
- Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley. 1996. Lévy flight search patterns of wandering albatrosses. *Nature* **381**:413–415.
- Viswanathan, G. M., S. V. Buldyrev, S. Havlin, M. G. E. da Luz, E. P. Raposo, and H. E. Stanley. 1999. Optimizing the success of random searches. *Nature* **401**:911–914.
- Voss, N. A., K. N. Nesis, and P. G. Rodhouse. 1998. The cephalopod Family Histoteuthidae (Oegopsida): systematics, biology, and biogeography. *Smithsonian Contributions in Zoology* **586**:293–372.
- Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos* **64**:464–473.
- Weimerskirch, H. 1995. Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia* **102**:37–43.
- Weimerskirch, H. 1998. Foraging strategies of southern albatrosses and their relationship with fisheries. Pages 168–179 in G. Robertson and R. Gales, editors. *Albatross biology and conservation*. Surrey Beatty, Sydney, Australia.
- Weimerskirch, H., C. Barbraud, and P. Lys. 2000a. Sex differences in parental investment and chick growth in Wandering Albatross: fitness consequences. *Ecology* **81**:309–318.
- Weimerskirch, H., F. Bonadonna, F. Bailleul, G. Mabile, G. Dell’Omo, and H. P. Lipp. 2002. GPS tracking of foraging albatrosses. *Science* **295**:1259.
- Weimerskirch, H., Y. Cherel, F. Cuenot-Chaillet, and V. Ridoux. 1997. Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. *Ecology* **78**:2051–2063.
- Weimerskirch, H., P. Doncaster, and F. Cuenot Chaillet. 1994. Pelagic seabirds and the marine environment: foraging of wandering albatrosses in relation to the availability and distribution of their prey. *Proceedings of the Royal Society of London* **B255**:91–97.
- Weimerskirch, H., T. Guionnet, J. Martin, S. A. Shaffer, and D. P. Costa. 2000b. Fast and fuel-efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London* **267**:1869–1874.
- Weimerskirch, H., and P. Jouventin. 1987. Population dynamics of the wandering albatross of the Crozet islands: consequences of the population decline. *Oikos* **49**:315–322.
- Weimerskirch, H., and P. Lys. 2000. Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. *Polar Biology* **23**:733–744.
- Weimerskirch, H., M. Salamolard, F. Sarrazin, and P. Jouventin. 1993. Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk* **110**:325–342.
- Weimerskirch, H., and R. P. Wilson. 1992. When do wandering albatrosses *Diomedea exulans* forage? *Marine Ecology Progress Series* **86**:297–300.
- Weimerskirch, H., R. Wilson, and P. Lys. 1997. Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. *Marine Ecology Progress Series* **151**:245–254.
- Wilson, R. P., K. Pütz, D. Grémillet, B. Culik, M. Kierspel, J. Regel, C. A. Bost, J. Lage, and J. Cooper. 1995. Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *Journal of Experimental Biology* **198**:1115–1135.
- Wilson, R. P., K. Pütz, G. Peters, B. Culik, B. Scolaro, J. B. Charassin, and Y. Ropert-Coudert. 1997. Long term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin* **25**:101–106.