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Diet and feeding ecology of blue petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean

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ABSTRACT: The food and feeding ecology of the blue petrel *Halobaena caerulea* was investigated over 4 consecutive chick-rearing periods at Iles Kerguelen. In all years, blue petrels fed on a large diversity of crustaceans and fish, with a small proportion of squid and other organisms. Crustaceans ranked first by number (98%) and second by reconstituted mass (37%). The hyperiid *Themisto gaudichaudii* and the euphausiid *Thysanoessa* sp. were the dominant prey items, accounting each for 42% by number, and for 12 and 4% by mass of the diet, respectively. Other important crustacean prey were the Antarctic krill *Euphausia superba* (2% by number and 10% by mass) and the large shrimp *Pasiphaea scotiae* (<1 and 5%, respectively). Fish were minor items by number (<1%) but, owing to their large size, they dominated the diet by reconstituted mass (57%). Mesopelagic fish of the families Myctophidae (14% by mass) and Melamphaidae (12%) were the main fish prey together with the gempylid *Paradiplospinus gracilis* (19%). Adult blue petrels use a 2-fold foraging strategy, performing short trips (ST, 2 d on average) and long trips (LT, 7 d) during the chick-rearing period. Birds fed more on *T. gaudichaudii* during ST and more on *Thysanoessa* sp. during LT. The subantarctic krill *Euphausia vallentini* were found in ST samples, and Antarctic krill and stomach oil were found in LT samples. Biogeography of the prey shows that blue petrels fed in a wide variety of marine habitats. During ST, they foraged in the kelp belt and over the shelf, but favoured oceanic waters in the vicinity of the archipelago. During LT, the occurrence of Antarctic krill indicates feeding in southern Antarctic waters, >1000 km from the breeding colonies, but blue petrels also foraged on their way back to Iles Kerguelen from these distant foraging grounds to feed their chicks. A comparison of the stable carbon and nitrogen isotopic compositions of chick and adult feathers reveals that adult blue petrels fed at the same trophic level during the chick-rearing and moulting period, and that they renew their flight feathers in Antarctic waters.

KEY WORDS: *Euphausia superba* · Mesopelagic fish · Seabirds · Stable carbon isotopes · Stable nitrogen isotopes · *Themisto gaudichaudii* · *Thysanoessa*

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INTRODUCTION

The blue petrel *Halobaena caerulea* is a small procellariiform species that is taxonomically closely related to the prions (genus *Pachyptila*). It is the sole member of the genus and inhabits the subantarctic and Antarctic zones of the Southern Ocean (Warham 1990). The species is circumpolar and nests colonially in burrows at 6 locations close to the Antarctic polar front. The main population of blue petrels is in the southern Indian Ocean and at Diego Ramirez (Chile) with smaller numbers at Macquarie and South Georgia (Marchant & Higgins 1990). At Iles Kerguelen, the species is numerous (100 000 to 200 000 pairs), and it breeds sympatrically with 3 different prion species: the fairy prion *P. turtur* and 2 large populations of thin-billed prions *P. belcheri* and Antarctic prions *P. desolata* (Weimerskirch et al. 1989). The species is wide-

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spread in subantarctic and Antarctic waters, and observations at sea suggest that breeders forage primarily in Antarctic waters during the chick-rearing period and that they disperse southwards at the end of the reproductive season to moult (Stahl et al. in press).

The diet of blue petrels was previously studied at 3 different localities during the breeding season. The species feed mainly on crustaceans, with fish and squid being of lesser importance in the diet. Depending on their availability in the area, the major crustacean prey are the subantarctic krill *Euphausia vallentini* at Marion Island (Steele & Klages 1986), *E. vallentini* together with *Thysanoessa* sp. and the hyperiid *Themisto gaudichaudii* at Crozet (Ridoux 1994), and Antarctic krill *Euphausia superba* at South Georgia (Prince 1980). However, as Prince (1980) pointed out, mass analysis alone may significantly underestimate the importance of fish, which probably form the bulk of unidentifiable material and thus dominate over crustaceans in the food at South Georgia (Prince & Morgan 1987). At Iles Kerguelen, almost nothing is known about the dietary habits of blue petrels (Marchant & Higgins 1990), but the species showed a particular strategy of food provisioning for a seabird (Chaurand & Weimerskirch 1994). During the chick-rearing period, adult birds regularly alternate short (ST) and long trips (LT), ST enabling them to increase the chick-feeding frequency at the expense of energy reserves built up during LT. Preliminary analysis of food indicated that undetermined amphipods, euphausiids and myctophid fish dominated both ST and LT samples, but some deep-water crustaceans were found in LT samples only. This led to the hypothesis that birds forage over oceanic waters during LT, with ST restricted to the Kerguelen shelf (Chaurand & Weimerskirch 1994).

The main objectives of this work were, first, to study the food and feeding ecology of blue petrels breeding at Iles Kerguelen. An integrative programme (Interactions Oiseaux-Zooplancton [IOZ]) was developed to investigate the community of planktivorous petrels in relation to the marine environment during the breeding cycles 1994/95, 1995/96 and 1996/97. The present paper follows others devoted to the feeding habits of prions (Cherel et al. 2002, in this issue) and diving petrels (genus *Pelecanoides*) (Bocher et al. 2000). Prey species, chick-feeding frequency and food mass were recorded over the 3 chick-rearing periods. A special emphasis was the determination of the fish prey through the examination of otoliths and bones (for details see Cherel et al. 2000b) because fish found in food samples from blue petrels are extensively digested, and only a few individuals have been identified to the species level up to now (Prince 1980, Steele & Klages 1986, Ridoux 1994). Second, we investigated during a fourth year (1998) the prey items collected during trips of known duration in order to determine and compare the marine resources consumed during ST and LT. The biogeography of the prey was thus used to give a first insight into the foraging grounds during both kinds of trips, the small size of blue petrels precluding the use of satellite tags.

We also focused on the foraging ecology during the inter-breeding period through stable isotopic analyses of adult flight feathers. Since keratin is metabolically inert after synthesis (Kelly & Finch 1998), the stable carbon and nitrogen isotopic composition of feathers are markers that have the potential for investigating the birds' trophic relationships and foraging areas during the moulting period (Bocher et al. 2000, Cherel et al. 2000a). In adult blue petrels, as in many seabirds, flight feathers are synthesised after the breeding season, in February and March, before birds transiently return to their burrows in April and May (Fugler et al. 1987, Marchant & Higgins 1990, Stahl et al. in press). Thus, a comparison of the stable isotope ratios of feathers from chicks (which moult in their burrows while being fed by their parents) with those from adults can give valuable information on foraging grounds of adult seabirds during chick rearing and moult, respectively.

MATERIALS AND METHODS

Study sites, birds and breeding success. Fieldwork was carried out during 4 consecutive summer seasons: the 3 years of the IOZ programme (1994/95, 1995/96 and 1996/97) and a fourth year (1997/98) during which the food and feeding ecology during foraging trips of known duration (ST and LT) was investigated. The study colonies were located at Ile Mayes (49° 28′ S, 69° 57′ E) in the Golfe du Morbihan, eastern Kerguelen Archipelago (southern Indian Ocean) (Fig. 1), where a large population of blue petrels breeds.

During the 3 breeding seasons of the IOZ programme, 2 nearby colonies of blue petrels were used, one for investigating their foraging ecology and the other to study their demographic parameters. In the latter colonies, all birds were given individual leg bands, and the burrows were checked several times during a given year: first, during the prebreeding period to estimate the number of visited burrows and subsequently during the breeding season at laying, hatching and before fledging to estimate the hatching, fledging and breeding success. Between 207 and 233 burrows were monitored in the demographic colonies. Chicks were weighed and their wing measured a few days before fledging. In the dietary colonies, birds were studied each year during 10 to 12 consecutive days (Table 1) in mid-January, corre-

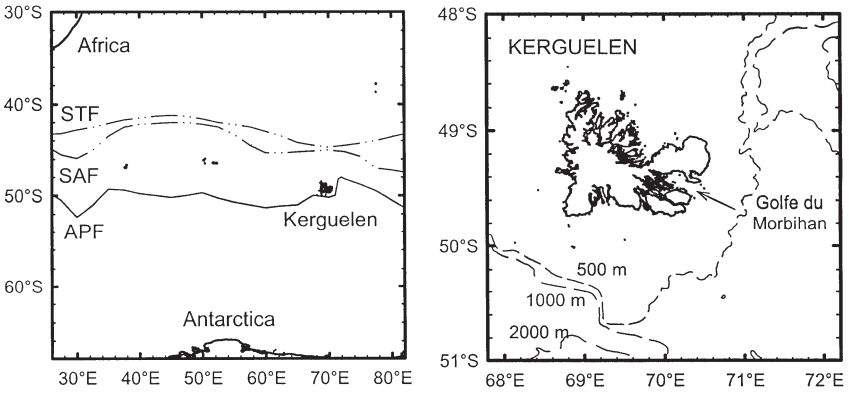

Fig. 1. Map of the Southern Indian Ocean showing the location of Kerguelen Islands. APF: Antarctic polar front; SAF: Subantarctic front; STF: Subtropical front

sponding to the middle of the chick-rearing period, which lasts about 50 d for this species (Marchant & Higgins 1990).

In January 1998, the duration of foraging trips of individual birds was determined on 26 pairs of blue petrels during 24 consecutive nights (6 to 29 January). Each burrow was fitted with a trap door at the entrance to retain the adults (Weimerskirch et al. 1999). During the night, burrows were regularly inspected, and, if visits were detected, banded adults were caught and identified. The stomach contents of some of them were collected by spontaneous regurgitation at the end of the study period.

Food mass and feeding frequency. Twenty-three to 35 randomly selected chicks were monitored each year during the IOZ programme (Table 1). Burrows were marked with numbered wood stakes; in the case of deep burrows, an opening was dug out over the nesting chamber and covered with rock and earth slabs to facilitate access to the birds. Chicks were weighed (accuracy ±2 g) twice daily, before dusk at 19:00 h (local time), when adults were at sea, and at 00:00 h, when most birds visiting the colony had fed their chick. An increase in body mass of at least 2 g, either between the 2 successive weighings within a given night or between weighings at midnight and the following evening, was considered to result from a feeding event. However, food mass delivered by adults to chicks during a given night was calculated as the difference between a chick's body mass at 19:00 and 00:00 h only. Chick feeding frequency was calculated as the ratio of the number of nights with feedings (sum for all the chicks) to the total number of nights with weighings (sum for all the chicks) (Table 1). Note that 20.1% of feeding events occurred after midnight.

Dietary analyses. Blue petrels were caught either by mist netting at night or in burrows fitted with trap doors at the entrance to retain the adult before the chick was fed. Food samples were collected by spontaneous regurgitation at the time of capture. Since birds often began to regurgitate as soon as they hit the net or were handled, samples were only collected from birds that had not started regurgitating until they were inverted over a funnel (Steele & Klages 1986). After food sampling, birds were weighed, measured and banded. No individual bird was sampled more than once in the study. Diet samples were immediately frozen at –20°C and returned to Chizé, France, for analysis. In the laboratory, each sample was thawed overnight over a sieve so that the liquid fraction was separated from the solid items and collected in a graduated tube. The volumes of the liquid fraction, water and stomach oil, and mass of the solid fraction were measured. The solid fraction was then placed in a large, flat-bottomed tray and fresh remains were divided into broad prey classes (crustaceans, fish, cephalopods and others), which were weighed to estimate their proportions by fresh mass in the diet.

Table 1. *Halobaena caerulea* chick body mass, chick feeding frequency (nights with feeding events) and food mass brought by the adults to the chicks at night during 3 consecutive chick-rearing periods. Values are means ± SD with ranges in parentheses

Study period	No. of chicks (begin–end)	Chick mass (g) Beginning	Chick mass (g) End	Total no. of nights	Nights with feeding events n	Nights with feeding events %	Food mass Mass (g)	Food mass Samples (n)
16–27 Jan 1995	23–19	154 ± 31 (106–238)	159 ± 22 (110–208)	247	112	45.3	45.9 ± 17.8 (2–102)	91
15–26 Jan 1996	32–27	168 ± 31 (106–234)	195 ± 41 (87–267)	361	163	45.1	51.2 ± 13.8 (10–99)	127
11–20 Jan 1997	35–35	163 ± 33 (62–226)	170 ± 35 (74–260)	350	142	40.6	48.5 ± 21.1 (2–136)	115
Total	90–81	162 ± 32 (62–238)	176 ± 37 (74–267)	958	417	43.5	48.8 ± 17.7 (2–136)	333
					$\chi^2_2 = 1.96$, p = 0.375[a]		$F_{2,330} = 2.42$, p = 0.090[a]	

[a]Pearson chi-squared test and 1-way ANOVA between values of 3 years

Total numbers of common and rare prey items were counted in each sample. Prey were identified using keys and descriptions in Bellan-Santini & Ledoyer (1974), Clarke & Holmes (1987), Baker et al. (1990), Williams & McEldowney (1990), Razouls (1994), Vinogradov et al. (1996) and Boltovskoy (1999), and by comparison with material held in our own reference collection. Thirty to 60 items (either intact specimens or intact eyes) of the main crustacean prey were randomly selected per dietary sample. Total length and eye diameter were determined using an ocular scale in a binocular microscope. Total length of amphipods, euphausiids and copepods was measured from the front of the eye to the tip of the uropods, from the tip of the rostrum to the tip of the uropods, and from the tip of the rostrum to the furca, respectively. Total length of amphipods and euphausiids was also estimated from eye diameter measurements by the use of allometric equations (Ridoux 1994, Cherel et al. unpubl.). The length of fish and cephalopods was estimated by the use of otolith or dentary length and lower rostral length, respectively. To estimate the composition by mass of the diet, the body mass of crustaceans, fish, cephalopods and other organisms was estimated from body length using published relationships (Adams & Klages 1987, Hindell 1988, Mizdalski 1988, Huntley et al. 1989, Williams & McEldowney 1990, Ridoux 1994) and our own equations. Where equations for certain species were not available, estimates were made from equations for closely related species or for species with a similar morphology. The reconstructed mass of each taxon for each sample was calculated from the average wet body mass for the species in the sample. The value was then multiplied by the number of individuals in the sample, and the resulting value was pooled with those calculated for the same taxon in the other samples. The calculated masses for all the different taxa were consequently pooled, and the reconstituted proportion by mass of each taxon was then calculated as its percentage of the total reconstituted mass.

Stable isotope analysis. Feathers were collected from intact wings of adults and fledglings killed by subantarctic skuas *Catharacta antarctica lönnbergi* at the beginning and the end of the breeding season, respectively. Before isotopic analysis, feathers were cleaned of surface contaminants using a 2:1 chloroform:ether rinse, air dried and cut with stainless steel scissors into small fragments. Food samples were freeze dried or dried in an oven at +60°C and ground to a fine powder in an analytical mill. Lipids were then removed using a Soxhlet apparatus with chloroform solvent for 4 to 6 h.

Stable carbon and nitrogen isotopes were assayed on 1 mg subsamples of homogenised materials by loading them into tin cups and combusting them at 1800°C in a Robo-Prep elemental analyser. Resultant CO_2 and N_2 gases were then analysed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer with every 5 unknowns separated by 2 laboratory standards. Stable isotope abundances were expressed in δ notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio, $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The $R_{standard}$ values were based on the PeeDee Belemnite standard for ^{13}C and atmospheric N_2 (air) for ^{15}N. Replicate measurements of internal laboratory standards (albumen) indicate measurement errors of ±0.1 and ±0.3‰ for stable carbon and nitrogen isotope measurements, respectively.

Statistical analysis. Data were analysed statistically using SYSTAT 9 for WINDOWS (SPSS Inc., Chicago, Illinois, USA). Values are means ± SD, with significance set at the 0.05 level.

RESULTS

Food mass and feeding frequency

Chicks of blue petrels were fed at least 1 meal by their parents on 44% of nights during the middle of the nesting period, with no significant differences between the 3 years. When fed, chicks received on average 49 g of food night^{-1}, with again no significant inter-annual differences (Table 1). The decrease in the number of chicks to the end of the study periods in January 1995 and 1996 was due mainly to predation by subantarctic skuas on chicks located in shallow burrows. When taking into account the chicks followed during the whole study period only, the overall mass gain of chicks was positive (15 ± 35 g) in 10 d, with significant differences between years (–3 ± 28, 33 ± 37 and 11 ± 30 g for summers 1995, 1996 and 1997, respectively, 1-way ANOVA, $F_{2,76} = 7.62$, p = 0.001). The large range in mass of the chicks was due to the 2 wk delay in the timing of the breeding cycle between early and late pairs of blue petrels (Fugler et al. 1987, Weimerskirch et al. 1989, Y.C. et al. unpubl.).

The mean adult body mass (after regurgitation) of blue petrels was 198 g and did not differ significantly between years ($F_{2,100} = 1.20$, p = 0.306). The wet mass of the 105 food samples averaged 24 g, with significant differences between years ($F_{2,102} = 3.85$, p = 0.024), the food samples collected in 1995 being heavier than those collected in 1997 (post hoc Tukey's HSD multiple comparison test, p = 0.019) (Table 2). The mass of dietary samples was lower than that of the food mass

Table 2. *Halobaena caerulea* body mass (after regurgitation), mass of food samples and broad prey class composition of the diet during 3 consecutive chick-rearing periods. Values are means ± SD with ranges in parentheses

Study period	Birds		Food sample mass		Prey class (% by fresh mass)			
	Mass (g)	Ind. (n)	Mass (g)	Samples (n)	Crustaceans	Fish	Cephalopods	Others
1995	196 ± 14 (174–223)	30	28.5 ± 11.0 (11.3–49.8)	30	66.5	28.9	4.0	0.6
1996	196 ± 15 (168–220)	39	23.9 ± 10.0 (7.0–48.3)	39	52.0	44.6	3.2	0.2
1997	204 ± 27 (154–268)	34	21.3 ± 11.0 (5.4–40.9)	36	67.7	32.0	0.2	0.1
Total	198 ± 20 (154–268)	103	24.3 ± 10.9 (5.4–49.8)	105	61.4	35.8	2.5	0.3

measured by weighing chicks because spontaneous regurgitation is not a very effective way to collect the whole stomach content of petrels (Klages & Cooper 1992, Cherel et al. 2002).

Diet

Blue petrels fed mainly on crustaceans (61 and 37% by fresh and reconstituted masses of the overall diet, respectively) and on fish (36 and 57%), while squids (3 and 2%) and other organisms (mainly the salp *Salpa thompsoni*) (<1 and 4%) were minor items (Tables 2 & 3). The proportions by fresh mass of crustaceans and fish were similar for 1995 and 1997, but blue petrels relied less on crustaceans and more on fish in 1996 (Table 2). Crustaceans occurred in all samples. They dominated by number and by fresh mass in 100 and 60% (n = 63) of the samples, respectively. Fish were found in 81% of the samples and they dominated by fresh mass in 39% (n = 41) of them. Finally, cephalopods were the major prey by mass in 1 sample. Note, however, that the most important squid taxon, Oegopsid A (Table 3), consists only of eye lenses of the same large diameter, suggesting that, as in South Georgia (Prince 1980), birds scavenged on squids too large to be swallowed whole. Stomach oil was found in 66% (n = 69) of the regurgitations.

A total of 17 325 prey items was recovered from 105 samples collected in 1995, 1996 and 1997. There were 17 021 crustaceans (98.2%), 163 fish (0.9%), 17 squids (0.1%) and 124 other organisms (polychaetes and salps) (0.7%). Overall, 25 species of crustaceans, 15 of fish, 1 of squid, 2 of polychaetes and 1 of salp were identified (Table 3). By number, the diet was dominated by the hyperiid amphipod *Themisto gaudichaudii* and the euphausiid *Thysanoessa* sp., which occurred in most of the samples (94 and 65%, respectively) and each accounted for 42% of the total number of prey. Owing to their small size, however, their importance by reconstituted mass was lower (12 and 4%, respectively). Two large crustacean species were also significant items by reconstituted mass: the Antarctic krill *Euphausia superba* (2% by number and 10% by mass) and the shrimp *Pasiphaea scotiae* (<1 and 5%). Other common crustacean prey (>1% by number) were *Euphausia vallentini*, the gammarid *Polycheria kergueleni*, and the hyperiids *Cyllopus magellanicus* and *Vibilia antarctica* (Table 3).

Themisto gaudichaudii prevailed by number and by mass in 45% (n = 47) and 19% (n = 20) of the samples, respectively. It was the dominant crustacean prey in 1996 (41% by reconstituted mass of the crustacean diet) and 1997 (37%), and the second item (19%) in 1995 (Fig. 2). Overall, 2 size classes of *T. gaudichaudii* were eaten by blue petrels: small individuals (3 to 14 mm total length), which were the dominant size class (63% of the total number of *T. gaudichaudii*) with a mode at 9 to 10 mm, and larger individuals (15 to 34 mm) with a mode at 18 to 19 mm (Fig. 3). Large variations in the size of *T. gaudichaudii* were observed between the 3 years (10.5 ± 4.9, 15.6 ± 5.5 and 15.5 ± 6.8 mm, n = 821, 830 and 574 for 1995, 1996 and 1997, respectively, 1-way ANOVA, $F_{2,2222} = 209.40$, $p < 0.0001$), amphipods being smaller in 1995 than in 1996 and 1997 (post hoc Tukey's HSD multiple comparison test, all $p < 0.0001$), with no differences between 1996 and 1997 ($p = 0.907$). Accordingly, length-frequency distributions were significantly different between years (Kolmogorov-Smirnov, all $p < 0.0001$). The small size class accounted for 93, 44 and 40% of the total number of *T. gaudichaudii* in 1995, 1996 and 1997, respectively, with a concomitant increase in the number of larger individuals during the study period (Fig. 3). Length-frequency distributions of small individuals were identical in 1995 and 1996 (Kolmogorov-Smirnov, $p = 0.085$) but differed in 1997 (both $p < 0.0001$), amphipods being slightly smaller in 1997 (data not shown).

The second main crustacean prey, *Thysanoessa* sp., prevailed by number and by mass in 40% (n = 42) and 8% (n = 8) of the samples, respectively. Its importance in the diet of blue petrels was relatively constant throughout the 3 years, accounting for 9, 14 and 12% by mass of the crustacean diet in 1995, 1996 and 1997, respectively (Fig. 2). Only 1 size class of *Thysanoessa*

Table 3. *Halobaena caerulea*. Frequency of occurrence, number, reconstituted mass and length of prey items recovered from stomach contents during chick-rearing (total for all 105 samples pooled)

Prey species	Occurrence in stomachs		Number		Reconstituted mass		Body length (mm)		
	n	%	n	%	n	%	Mean	Range	n
Crustaceans	**105**	**100.0**	**17021**	**98.2**	**860.9**	**37.4**			
Euphausiacea									
Euphausia superba	37	35.2	361	2.1	236.7	10.3	46.8 ± 9.7	26.1–63.7	224
Euphausia vallentini	9	8.6	290	1.7	18.1	0.8	22.7 ± 3.5	14.8–28.5	101
Euphausia triacantha	1	1.0	1	<0.1	<0.1	<0.1	26.7 ± 5.1	19.6–40.4	38
Euphausia sp.	15	14.3	65	0.4	9.4	0.4	19.3		1
Thysanoessa macrura/vicina	68	64.8	7293	42.1	103.0	4.5	14.6 ± 1.6	9.8–21.1	1380
Decapoda									
Pasiphae scotiae	34	32.4	42	0.2	111.4	4.8	98.3 ± 11.3	73.6–119.3	39
Mysida									
Unidentified mysid	1	1.0	1	<0.1	2.5	0.1	64.6		1
Isopoda									
Unidentified isopods	4	3.8	4	<0.1	<0.1	<0.1	7.2		1
Amphipoda									
Polycheria kergueleni	8	7.6	429	2.5	1.4	0.1	6.3 ± 0.8	4.5–7.9	89
Cyphocaris richardi	8	7.6	9	<0.1	2.1	0.1	28.7 ± 1.8	27.5–31.3	3
Eurythenes gryllus	3	2.9	3	<0.1	15.0	0.7			
Eurythenes obesus	9	8.6	9	<0.1	3.3	0.1	36.0 ± 4.2	30.8–43.1	7
Eurythenes sp.	2	1.9	2	<0.1	0.8	<0.1			
Uristes gigas	1	1.0	1	<0.1	<0.1	<0.1	11.4		1
Parandania boecki	1	1.0	1	<0.1	<0.1	<0.1			
Cyllopus lucasii	6	5.7	7	<0.1	0.4	<0.1	15.8 ± 1.4	14.5–17.7	4
Cyllopus magellanicus	70	66.7	429	2.5	24.1	1.0	14.0 ± 3.1	3.8–17.7	255
Vibilia antarctica	60	57.1	610	3.5	18.0	0.8	12.1 ± 1.5	6.8–15.8	245
Hyperiella antarctica	22	21.0	73	0.4	0.7	<0.1	8.1 ± 1.4	5.4–11.4	45
Hyperoche luetkenides	13	12.4	36	0.2	1.5	0.1	12.7 ± 1.5	10.7–17.3	20
Themisto gaudichaudii	99	94.3	7309	42.2	286.8	12.5	13.3 ± 6.4	2.8–37.7	2225
Primno macropa	7	6.7	15	<0.1	1.1	<0.1	14.3 ± 3.3	7.5–19.7	11
Unidentified amphipods	8	7.6	10	<0.1	0.6	<0.1			
Copepoda									
Calanus simillimus	1	1.0	1	<0.1	<0.1	<0.1	3.4		1
Rhincalanus gigas	1	1.0	1	<0.1	<0.1	<0.1	5.8		1
Drepanopus pectinatus	1	1.0	1	<0.1	<0.1	<0.1	2.1		1
Paraeuchaeta antarctica	1	1.0	2	<0.1	<0.1	<0.1	8.7		1
Heterorhabdus austrinus	1	1.0	1	<0.1	<0.1	<0.1			
Candacia maxima	1	1.0	1	<0.1	<0.1	<0.1			
Cirripedia									
Lepas australis (cypris larva)	1	1.0	1	<0.1	<0.1	<0.1	2.5		1
Crustacea sp. A	2	1.9	2	<0.1	2.6	0.1			
Unidentified crustaceans	11	10.5	11	<0.1	21.2	0.9			
Fish	**85**	**81.0**	**163**	**0.9**	**1307.3**	**56.8**			
Microstomatidae									
?*Nansenia antarctica*	1	1.0	1	<0.1	52.5	2.3			
Bathylagidae									
Bathylagus tenuis	1	1.0	1	<0.1	20.9	0.9			
Paralepididae									
Arctozenus risso	3	2.9	3	<0.1	80.4	3.5	274.0		1
Unidentified Paralepididae	1	1.0	1	<0.1	26.8	1.2			
Myctophidae									
Electrona antarctica	12	11.4	14	<0.1	65.0	2.8	85.3 ± 5.2	75.9–90.6	7
Electrona carlsbergi	13	12.4	14	0.1	121.6	5.3	65.8 ± 8.1	55.4–77.6	6
Electrona subaspera	1	1.0	1	<0.1	12.2	0.5	87.4		1
Gymnoscopelus microlampas	2	1.9	2	<0.1	26.1	1.1	98.2		1
Gymnoscopelus sp.	2	1.9	2	<0.1	14.1	0.6			

Table 3 (continued)

Prey species	Occurrence in stomachs n	%	Number n	%	Reconstituted mass n	%	Body length (mm) Mean	Range	n
Myctophidae (continued)									
Krefftichthys anderssoni	19	18.1	23	0.1	27.0	1.2	49.8 ± 4.4	42.1–55.3	7
Protomyctophum andriashevi	1	1.0	1	<0.1	1.6	<0.1			
Protomyctophum bolini	19	18.1	27	0.2	24.8	1.1	40.9 ± 3.1	34.7–44.4	9
Protomyctophum choriodon	1	1.0	1	<0.1	1.0	<0.1			
Protomyctophum sp.	2	1.9	2	<0.1	2.0	<0.1			
Unidentified Myctophidae	17	16.2	21	0.1	22.6	1.0			
Muraenolepididae		0.0							
Muraenolepis marmoratus	3	2.9	3	<0.1	62.6	2.7	204.4	203.9–204.8	2
Melamphaidae									
Poromitra crassiceps	1	1.0	1	<0.1	19.8	0.9			
Sio nordenskjöldii	5	4.8	5	<0.1	99.0	4.3			
Melamphaidae sp. A	4	3.8	4	<0.1	125.7	5.5			
Melamphaidae sp. B	1	1.0	1	<0.1	31.3	1.4			
Nototheniidae									
Unidentified Nototheniidae	1	1.0	1	<0.1	1.0	<0.1			
Gempylidae									
Paradiplospinus gracilis	19	18.1	19	<0.1	447.5	19.5	283.1		1
Unidentified fish	15	14.3	15	<0.1	21.9	1.0			
Cephalopods	**15**	**14.3**	**17**	**0.1**	**48.1**	**2.1**			
Onychoteuthidae									
Kondakovia longimana	1	1.0	1	<0.1	7.2	0.3	55.3		1
Oegopsida sp. A	6	5.7	7	<0.1	25.8	1.1			
Unidentified squids	9	8.6	9	<0.1	15.1	0.7			
Others	**30**	**28.6**	**124**	**0.7**	**84.0**	**3.7**			
Polychaeta									
Platynereis australis	1	1.0	1	<0.1	<0.1	<0.1			
Tomopteris sp.	1	1.0	1	<0.1	<0.1	<0.1			
Salpidae									
Salpa thompsoni	29	27.6	122	0.7	83.9	3.6	16.0 ± 4.3	9.4–25.2	45
Total	**105**		**17325**	**100.0**	**2300.4**	**100.0**			

sp. was found, with a mode at 13 to 14 mm (Fig. 4). The size of the euphausiid varied little but significantly over years (14.6 ± 2.1, 14.5 ± 1.4 and 14.8 ± 1.4 mm, n = 255, 607 and 518 for 1995, 1996 and 1997, respectively, 1-way ANOVA, $F_{2,1377}$ = 4.90, p = 0.008), as did its length-frequency distributions (Kolmogorov-Smirnov, all p < 0.008).

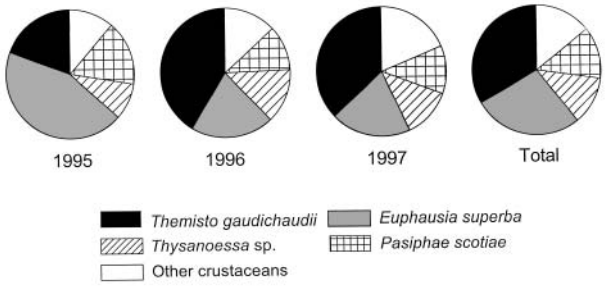

Fig. 2. *Halobaena caerulea*. Composition by reconstituted mass of the crustacean diet during 3 consecutive chick-rearing periods

Antarctic krill *Euphausia superba* prevailed by number and by mass in 6% (n = 6) and 17% (n = 18) of the samples, respectively. It was the main crustacean prey in 1995 (44% by reconstituted mass of the crustacean diet) and the second item in 1996 (21%) and 1997 (20%) (Fig. 2). The size of Antarctic krill varied significantly over years (53.2 ± 4.4, 42.4 ± 11.0 and 43.2 ± 8.7 mm, n = 86, 67 and 71 for 1995, 1996 and 1997, respectively, 1-way ANOVA, $F_{2,221}$ = 42.32, p < 0.0001), *E. superba* being larger in 1995 than in 1996 and 1997 (post hoc Tukey's HSD multiple comparison test, all p < 0.0001). Length-frequency distributions were significantly different between years (Kolmogorov-Smirnov, all p < 0.0001). Blue petrels fed on only 1 large size class (mode at 50 to 52 mm) in 1995, and on 2 distinct size classes in 1996 (mode at 26 to 28 and

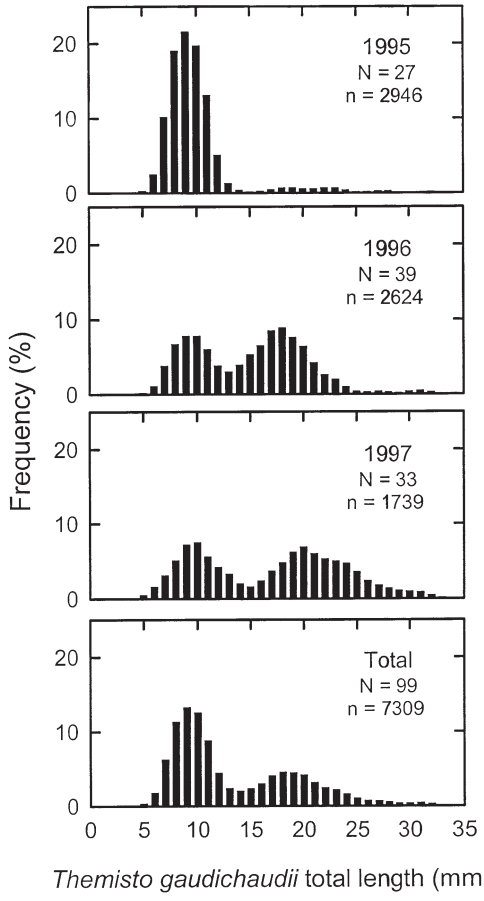

Fig. 3. Length-frequency distribution of the hyperiid *Themisto gaudichaudii* in the diet of *Halobaena caerulea* during 3 consecutive chick-rearing periods. N: number of food samples; n: number of individuals

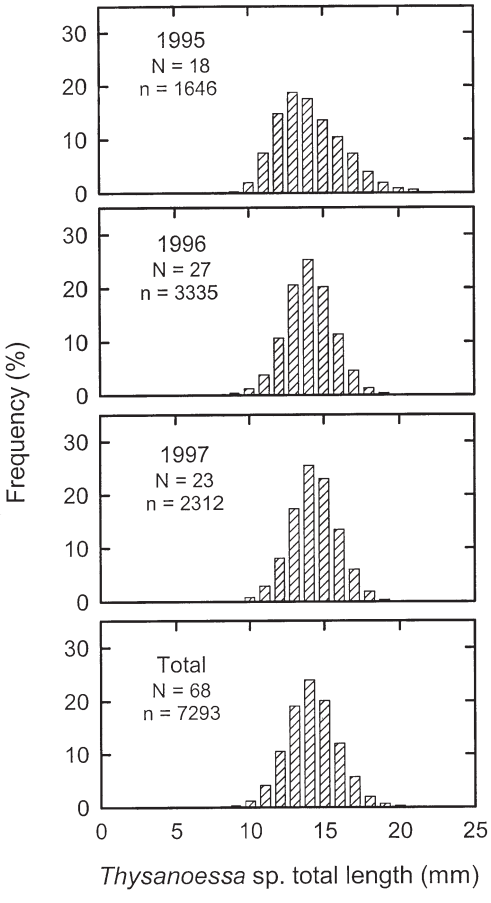

Fig. 4. Length-frequency distribution of the euphausiid *Thysanoessa* sp. in the diet of *Halobaena caerulea* during 3 consecutive chick-rearing periods. N: number of food samples; n: number of individuals

48 to 50 mm) and 1997 (mode at 34 to 36 and 50 to 52 mm) (Fig. 5). Note that the smaller size class was found in only 1 food sample in 1996 and in 4 samples in 1997. Excluding the smaller individuals, the body length of large *E. superba* (>42 mm) was different between years ($F_{2,154}$ = 5.00, p = 0.008), krill being larger in 1995 than in 1996 (post hoc Tukey's HSD multiple comparison test, p = 0.004).

Blue petrels fed on a large diversity of fish. No species was a significant prey by number but, owing to their large sizes, 11 fish species each accounted for more than 1% of the diet by reconstituted mass (Table 3). At the species level, the commonest prey was the gempylid *Paradiplospinus gracilis* (12 and 34% of the fish diet by number and reconstituted mass, respectively), but, at the family level, myctophids (66 and 24%) and melamphaids (7 and 21%) were also important items (Fig. 6). Four myctophids were commonly encountered: *Protomyctophum bolini* (17% of the fish prey), *Krefftichthys anderssoni* (14%), *Electrona antarctica* (9%) and *E. carlsbergi* (9%). The fish diet was similar in 1996 and 1997, but no *P. gracilis* was found in 1995, a year during which melamphaids were the main fish prey (54% by mass) (Fig. 6).

Since blue petrels returned to their burrows outside the breeding season (after moult, in April and May), we tried to collect food samples at that time in 1995. Most of the birds had empty stomachs. Among 10 samples, only 4 contained a significant amount of food (6.7 to 26.0 g). Interestingly, *Euphausia vallentini* occurred in the contents of all 4 stomachs and the species formed, by far, the bulk of the diet (n = 737, 95% by number).

ST and LT

In January 1998, the distribution of durations of adult foraging trips was bimodal (modes at 2 and 6 to 8 d) (Fig. 7). We separated trips into ST (1 to 3 d) and LT (>3 d) because food analysis (see below) clearly indi-

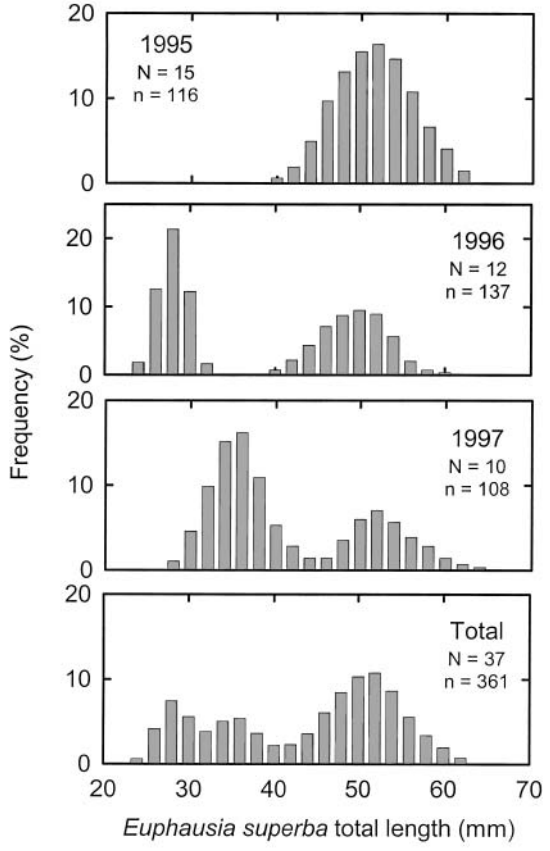

Fig. 5. Length-frequency distribution of the Antarctic krill *Euphausia superba* in the diet of *Halobaena caerulea* during 3 consecutive chick-rearing periods. N: number of food samples; n: number of individuals

cated that the uncommon foraging trips of 4 d were LT. On average, the duration of ST and LT was 2.0 ± 0.6 d (n = 57) and 6.9 ± 1.5 d (n = 46), respectively. Twenty-six food samples were collected after trips of known duration: 12 after ST and 14 after LT (from 4 to >10 d). All the LT samples contained stomach oil (from traces to 4 ml) with generally an orange colour (sometimes yellowish), while only 1 ST sample was oily (1 ml), with the oil being an unusual brown colour.

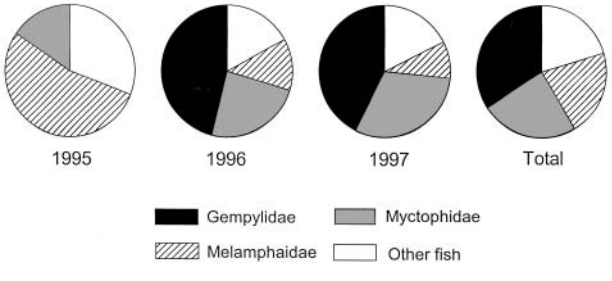

Fig. 6. *Halobaena caerula*. Composition by reconstituted mass of the fish diet during 3 consecutive chick-rearing periods

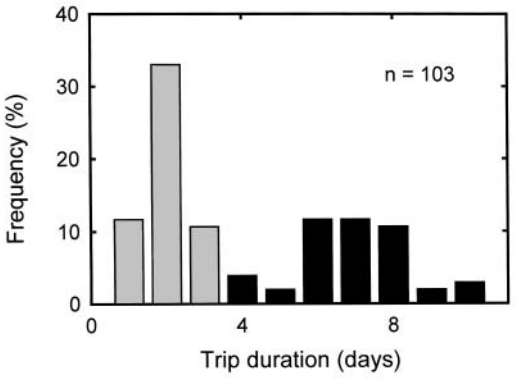

Fig. 7. *Halobaena caerulea.* Frequency distribution of the duration of adult foraging trips during chick-rearing in January 1998

In 1998, as in the previous years, the diet was dominated by crustaceans (98% of the total number of prey). The 2 main prey were, again, *Thysanoessa* sp. and *Themisto gaudichaudii*, but, compared with the other years, *Thysanoessa* sp. was much more abundant than *T. gaudichaudii* in 1998 (74 vs 11% by number). *Thysanoessa* sp. occurred more frequently (79 vs 33%; Pearson $\chi^2 = 5.42$, $p = 0.020$) and was more numerous (86 vs 35%; $\chi^2 = 1382$, $p < 0.0001$) in LT than in ST samples, and the reverse was true for *T. gaudichaudii* (frequency of occurrence: 50 vs 92%; $\chi^2 = 5.27$, $p = 0.022$; percentage by number: 1 vs 39%; $\chi^2 = 1589$, $p < 0.0001$). Blue petrels also fed more on *Cyllopus magellanicus* and *Vibilia antarctica* during ST ($\chi^2 = 49$ and 151, respectively; $p < 0.0001$). Two of the prey occurred exclusively in one kind of foraging trip. The subantarctic krill *Euphausia vallentini* was found only in ST samples (frequency of occurrence: 42%), and the Antarctic krill *Euphausia superba* in LT samples (71%) (Table 4). Two stomach contents were collected after a 4 d trip; both contained orange-coloured oil, and *E. superba* occurred in 1 sample, thus indicating that 4 d trips were LT.

Since *Euphausia superba* indicates LT and stomach oil is much more prominent after LT than ST in the 1998 samples, food samples previously collected during the IOZ programme were divided into 2 groups according to the presence (presumably LT) or absence (presumably ST) of oil or *E. superba*. The comparison indicates that blue petrels fed more on the amphipods *Polycheria kergueleni*, *Cyllopus magellanicus*, *Vibilia antarctica* and *Themisto gaudichaudii* and the salp *Salpa thompsoni* during ST, and more on *Thysanoessa* sp., the shrimp *Pasiphaea scotiae* and gammarids of the genus *Eurythenes* during LT. Noticeably, the amphipods *Cyphocaris richardi* and *Cyllopus lucasii* were present during LT only. There was also a tendency for birds to prey more on fish, including myctophids, during LT.

Table 4. *Halobaena caerulea*. Frequency of occurrence and number of prey items recovered in stomach contents collected from adults after short (ST; n = 12) and long trips (LT; n = 14) during chick-rearing in 1998

Prey species	Occurrence in stomachs				Number			
	ST		LT		ST		LT	
	n	%	n	%	n	%	n	%
Crustaceans	**12**	**100.0**	**14**	**100.0**	**1330**	**97.6**	**4212**	**98.3**
Euphausiacea								
Euphausia superba	0	0.0	10	71.4	0	0.0	50	1.2
Euphausia vallentini	5	41.7	0	0.0	77	5.7	0	0
Euphausia sp.	1	8.3	2	14.3	2	0.1	33	0.8
Thysanoessa macrura/vicina	4	33.3	11	78.6	474	34.8	3677	85.8
Decapoda								
Pasiphae scotiae	4	33.3	5	35.7	4	0.3	6	0.1
Amphipoda								
Eurythenes gryllus/obesus	2	16.7	5	35.7	2	0.1	5	0.1
Uristes gigas	1	8.3	1	7.1	2	0.1	2	<0.1
Cyllopus magellanicus	10	83.3	10	71.4	113	8.3	156	3.6
Vibilia antarctica	11	91.7	4	28.6	102	7.5	53	1.2
Hyperiella antarctica	5	41.7	4	28.6	12	0.9	168	3.9
Hyperoche luetkenides	2	16.7	1	7.1	2	0.1	1	<0.1
Themisto gaudichaudii	11	91.7	7	50.0	537	39.4	58	1.4
Unidentified crustaceans	2	16.7	3	21.4	3	0.2	3	<0.1
Fish	**7**	**58.3**	**8**	**57.1**	**16**	**1.2**	**13**	**0.3**
Myctophidae								
Electrona antarctica	3	25.0	0	0.0	3	0.2	0	0
Electrona carlsbergi	3	25.0	1	7.1	3	0.2	1	<0.1
Gymnoscopelus microlampas	1	8.3	0	0.0	1	<0.1	0	0
Krefftichthys anderssoni	0	0.0	2	14.3	0	0.0	3	<0.1
Protomyctophum bolini	0	0.0	1	7.1	0	0.0	1	<0.1
Protomyctophum choriodon	0	0.0	1	7.1	0	0.0	1	<0.1
Unidentified Myctophidae	5	41.7	2	14.3	5	0.4	2	<0.1
Melamphaidae								
Sio nordenskjöldii	1	8.3	1	7.1	1	<0.1	1	<0.1
Nototheniidae								
Gobionotothen acuta	0	0.0	1	7.1	0	0.0	1	<0.1
Unidentified fish	2	16.7	2	14.3	3	0.2	3	<0.1
Cephalopods	**6**	**50.0**	**2**	**14.3**	**7**	**0.5**	**2**	**<0.1**
Onychoteuthidae								
Unidentified Onychoteuthidae	0	0.0	1	7.1	0	0.0	1	<0.1
Oegopsida sp. A	4	33.3	1	7.1	5	0.4	1	<0.1
Unidentified squids	2	16.7	0	0.0	2	0.1	0	0
Others	**5**	**41.7**	**4**	**28.6**	**9**	**0.7**	**57**	**1.3**
Polychaeta								
Platynereis australis	0	0.0	1	7.1	0	0.0	50	1.2
Salpidae								
Salpa thompsoni	4	33.3	2	14.3	8	0.6	2	<0.1
Unidentified organism	1	8.3	1	7.1	1	<0.1	5	0.1
Total	**12**		**14**		**1362**	**100.0**	**4284**	**100**

Stable isotopes

A brief examination showed the occurrence of crustaceans in all 9 food samples and of fish (mainly myctophids) in 6 samples. Food of blue petrels and feathers from chicks and adults were segregated by their stable isotope values (multivariate analysis of variance, Wilk's lambda, $F_{4, 50} = 18.07$, $p < 0.0001$) (Table 5). Both $\delta^{13}C$ and $\delta^{15}N$ values were different overall. The carbon stable isotope ratio of chick feathers was higher than the ratio in adult feathers (post hoc Tukey's HSD multiple comparison test: $p = 0.027$), and nitrogen stable

Table 5. *Halobaena caerulea*. Stable carbon and nitrogen isotope concentrations (mean ± SD ‰) in dietary samples and in feathers of breeding adults and chicks at Iles Kerguelen, and results of 1-way ANOVA for differences among groups for each isotope. Values in the same column not sharing a common superscript letter are significantly different (post hoc Tukey HSD multiple comparison test, $p < 0.05$)

Sampling group	n	$\delta^{13}C$	$\delta^{15}N$
Food	9	$-23.7 \pm 2.5^{a,b}$	5.5 ± 1.5^{a}
Chick feathers	10	-22.2 ± 0.6^{a}	9.7 ± 0.8^{b}
Adult feathers	10	-24.2 ± 1.3^{b}	9.1 ± 0.6^{b}
ANOVA		$F_{2,26} = 4.18$ $p = 0.027$	$F_{2,26} = 47.79$ $p < 0.0001$

isotope ratio of chick food was lower than the ratios in chick and adult feathers (all $p < 0.0001$) (Table 5).

Breeding success

Hatching and fledging successes of blue petrels averaged 55 and 79%, respectively, and they did not vary significantly between the 3 study years (hatching success: $\chi^2_2 = 0.99$, $p = 0.610$; fledging success: $\chi^2_2 = 0.49$, $p = 0.781$). Consequently, breeding success averaged 43%, with no inter-annual variations (Table 6). However, chick body masses measured at the same date each year were different during the 3 fledging periods (post hoc Tukey's HSD multiple comparison test, all $p < 0.001$). Wing length were also overall different, being larger in 1997 than in 1995 (post hoc Tukey's HSD multiple comparison test, $p = 0.001$) (Table 6).

DISCUSSION

At Iles Kerguelen, blue petrels rearing chicks prey mainly on mesopelagic fish and 2 crustacean items, the hyperiid amphipod *Themisto gaudichaudii* and the euphausiid *Thysanoessa* sp. Birds feed more on *T. gaudichaudii* during ST and more on *Thysanoessa* sp. during LT. The occurrence of *Euphausia vallentini* and *E. superba* in ST and LT samples, respectively, indicates foraging in subantarctic waters during ST and in distant southern Antarctic waters during LT. The stable carbon and nitrogen isotopic compositions of chick and adult feathers suggest that adult birds renew their flight feathers in Antarctic waters, and that they feed at the same trophic level during the chick-rearing and moulting periods.

No inter-annual variations in chick-feeding frequency and in food mass were observed during the 3 years of the IOZ programme. Chicks' growth differed between years, but hatching, fledging and breeding successes were identical between the 3 reproductive seasons. When comparing with breeding success over a longer period (1986/87 to 1994/95, range 26 to 62%), 1994/95, 1995/96 and 1996/97 were normal years (42 to 46%), but 1997/98 was a bad breeding season (28%), as previously observed in 1987/88 (28%) and 1991/92 (26%) (Guinet et al. 1998). The Kerguelen region was marked by a short-term climatic change in the late 1990s, as indicated by an abrupt increase in sea level, which peaked at the end of 1997 to the beginning of 1998, a period coinciding with the strongest El Niño southern oscillation of the last century (Park 2001). Such dramatic changes probably affected the pelagic ecosystem surrounding the archipelago and probably explain the unusual high and low importance of *Thysanoessa* sp. (74% by number) and *Themisto gaudichaudii* (11%), respectively, in the diet of blue petrels in 1998.

Diet

At Iles Kerguelen, the blue petrel is a macrozooplankton and micronekton feeder, with crustaceans and fish forming the bulk of its food (Table 3). A large

Table 6. *Halobaena caerulea*. Breeding success and fledging mass during 3 consecutive breeding seasons. Values are means ± SD with ranges in parentheses

Study period	Monitored burrows (n)	Occupied burrows (n)	Occupied burrows (%)	Hatching success (%)	Fledging success (%)	Breeding success (%)	Chicks' body mass (g)	Chicks' wing length (mm)	Number of chicks
1995	231	141	61.0	51.5	81.1	41.7	156 ± 30 (92–212)	138 ± 21 (76–172)	43
1996	233	138	59.2	57.4	80.6	46.2	216 ± 39 (146–327)	144 ± 24 (97–180)	25
1997	207	160	77.9	58.9	75.8	44.6	186 ± 30 (118–236)	154 ± 20 (109–199)	50
Total	**671**	**439**	**65.4**	**55.3**	**78.7**	**43.5**	**182 ± 39 (92–327)**	**146 ± 22 (76–199)**	**118**
						$\chi^2_2 = 0.34$ $p = 0.842^{a}$	$F_{2,115} = 28.08$ $p < 0.0001^{a}$	$F_{2,115} = 7.31$ $p = 0.001^{a}$	

[a]Pearson chi-squared test and 1-way ANOVA between values of the 3 years

majority of fish (71%) were identified to species level, thus allowing the first precise qualitative and quantitative assessment of the fish diet of blue petrels. The amazing diversity of prey items includes a lot of fish that are known to live primarily in the mesopelagic, including myctophids and melamphaids, together with the gempylid *Paradiplospinus gracilis* (Gon & Heemstra 1990). All the determined myctophid species, except *Gymnoscopelus microlampas*, are abundant in the polar frontal zone and in Antarctic waters (Hulley 1981, 1990, Duhamel 1998). The few fish specimens identified in the food of blue petrels nesting at Marion Island (Steele & Klages 1986) and Iles Crozet (Ridoux 1994) belonged mostly to that family, as did the main prey of birds collected at sea in Antarctic waters (Ainley et al. 1992). Myctophids were also previously supposed to be major items of blue petrels at South Georgia (Prince 1980). The data thus emphasise the importance of these small shoaling oceanic fish in the nutrition of seabirds from the Southern Ocean (Ainley et al. 1992, Sabourenkov 1992, Guinet et al. 1996). On the other hand, the present work is, to our knowledge, the first to describe melamphaids and *P. gracilis* as important items for an avian predator. Melamphaids are rare meso- and bathypelagic fish (Gon 1990), and they were accordingly found very occasionally in the diet of seabirds, including the blue petrel (Cherel & Klages 1998, Ridoux 1994, Lorentsen et al. 1998, Catard et al. 2000). Little is known about the biology of *P. gracilis*, but the species lives mainly in the vicinity of land masses, including Iles Kerguelen (Nakamura 1990, Duhamel 1998). It was previously identified as a significant prey of penguins in a few studies (Klages et al. 1990, Cherel & Ridoux 1992) and only as a minor item in the diet of procellariiforms (Ridoux 1994, Cherel & Klages 1998). How these deep-sea fish become available to surface-feeding seabirds remains, however, to be determined, as does their time of capture (daytime versus nighttime) and the extent of their daily vertical migration in the water column.

At Iles Kerguelen, which is near the Antarctic polar front (Park et al. 1993), the 2 main crustacean prey of blue petrels are *Themisto gaudichaudii* and *Thysanoessa* sp. Further north, at Crozet and Marion islands, they feed on the same 2 species plus the subantarctic krill *Euphausia vallentini* and further south, at South Georgia, on the Antarctic krill *Euphausia superba* (Table 7). Taken together, these data suggest that the blue petrel is an opportunist feeder that preys on the most available swarming pelagic crustaceans found in its foraging grounds during the breeding season. *T. gaudichaudii* is one of the main macrozooplankton species in the Southern Ocean (Kane 1966), including the Iles Kerguelen (Bocher et al. 2001). There, blue petrels consistently caught 2 size classes of the amphipod, with large inter-annual variations in their relative importance (Fig. 3). The size structure of *T. gaudichaudii* in food samples was different from that observed in the vicinity of the breeding colony (Bocher et al. 2001), indicating that amphipods were caught in more offshore waters. This is also supported by the abundance of *Thysanoessa* sp. in the blue petrel diet because this euphausiid does not occur in the Golfe du Morbihan (Bost et al. 1994, Bocher et al. 2001). Two species of the genus *Thysanoessa*, *T. vicina* and *T. macrura*, live in the vicinity of the Antarctic polar front and in Antarctic waters, including the Kerguelen region (Lomakina 1966, Pakhomov 1993). The digested condition of the specimens in food samples precluded their identification to the species level, but the occurrence of 1 well-defined size class suggests they belonged to 1 species only (Fig. 4).

The occurrence in significant numbers of *Polycheria kergueleni* in the diet of blue petrels is surprising because this gammarid amphipod is primarily benthic. It occurs commonly at the bottom in coastal waters of Iles Kerguelen (Arnaud 1974, Bellan-Santini & Ledoyer 1974) and is also found associated with the giant kelp *Macrocystis pyrifera* (Arnaud 1974). This, together with observations of blue petrels feeding in inshore waters (Falla 1937), shows that some blue petrels forage close to the coastline in the kelp belt area surrounding the archipelago, probably when they commute between colonies and offshore feeding grounds. On the other hand, the occurrence in food samples of the gammarids *Cyphocaris richardi*, *Eurythenes* spp. and *Parandania boecki* indicate feeding in more distant areas, because these species are strictly pelagic or benthopelagic organisms living in oceanic waters (Barnard 1961, Vinogradov 1999). During the chick-rearing period, blue petrels thus forage in a wide variety of habitats where they feed on different marine organisms.

Isotopic signatures of chick feathers of blue petrels show an enrichment relative to food amounting to 1.5‰ for $\delta^{13}C$ and 4.2‰ for $\delta^{15}N$ (Table 5). These values are within the range of those (–0.4 to 4.4‰ for $\delta^{13}C$ and 1.1 to 5.6‰ for $\delta^{15}N$) obtained from feathers of various species of birds (Mizutani et al. 1990, 1992, Hobson & Clark 1992a,b, Thompson & Furness 1995), including procellariiforms from Iles Kerguelen (Bocher et al. 2000, Cherel et al. 2000a, 2002). Stable nitrogen isotope ratios are similar in chick and adult feathers of blue petrels, indicating that during moult adults fed at the same trophic level as during the breeding period. $\delta^{13}C$ values of adult feathers, however, differ from those in chick feathers. Taking into account latitudinal variations in $\delta^{13}C$ (François et al. 1993), the low value of adult feathers suggests birds moulted in southern Antarctic waters, an hypothesis reinforced by the fact

Table 7. *Halobaena caerulea*. Broad prey classes and proportions by number (%N) and by reconstituted mass (%M) of the main prey species (≥ 10%) in the diet of blue petrels breeding at different localities

	Marion (Steele & Klages 1986) (n = 49)		Crozet (Ridoux 1994) (n = 33)		Kerguelen (Present study) (n = 105)		South Georgia (Prince 1980) (n = 156)	
	%N	%M	%N	%M	%N	%M	%N	%M
Crustaceans	**92**	**59**	**99**	**61**	**98**	**37**	**94**	**91**
Euphausia superba	–	–	<1	4	2	10	24[a]	82[a]
Euphausia vallentini	64	34	13	14	2	<1	–	–
Thysanoessa sp.	–	–	28	14	42	4	29[a]	4[a]
Hyperoche sp.	–	–	<1	<1	<1	<1	11[a]	2[a]
Themisto gaudichaudii	4	3	50	12	42	12	4[a]	<1[a]
Rhincalanus gigas / *Calanoides acutus*	–	–	<1	<1	<1	<1	13[a]	1[a]
Fish	**3**	**21**	**<1**	**11**	**<1**	**57**	**6**	**8**
Myctophidae	Present	Present	<1	5	<1	14	Present	Present
Melamphaidae	–	–	–	–	<1	12	–	–
Paradiplospinus gracilis	–	–	<1	1	<1	19	–	–
Cephalopods	**2**	**16**	**<1**	**27**	**<1**	**2**	**<1**	**<1**
Others	**3**	**4**	**<1**	**2**	**<1**	**4**	**–**	**–**

[a]% of the crustacean diet

that truly Antarctic animals, including fulmarine petrels, have similar low $\delta^{13}C$ values (Hodum & Hobson 2000). Accordingly, observations at sea of moulting blue petrels were confined to south of Iles Kerguelen, in Antarctic waters between 60° S and Prydz Bay (Stahl et al. in press).

ST, LT and foraging areas

As previously described (Chaurand & Weimerskirch 1994), adult blue petrels foraged on ST and LT to feed their chicks in January 1998 (Fig. 7). The main inter-annual difference was that no trips of 4 d were recorded in January 1989 (Chaurand & Weimerskirch 1994). In 1998, the 4 d trips are clearly LT, as indicated by the presence of stomach oil and of *Euphausia superba* in food samples. Data from the 2 years thus show that blue petrels consistently make ST with a mode at 2 d and LT with a mode at 6 to 8 d during the chick-rearing period at Kerguelen. This 2-fold strategy, first described in the blue petrel, has now been generalised to many procellariiform seabirds, including albatrosses, prions, shearwaters and petrels (Weimerskirch et al. 1994, 2001, Granadeiro et al. 1998). Satellite tracking of the largest species show that birds forage in different areas during ST and LT (Weimerskirch et al. 1997, Catard et al. 2000, Waugh et al. 2000). Smaller size, however, precludes the use of electronic devices, but biogeography of the prey identified in food samples has the potential to give a first insight into the foraging grounds during ST and LT (Weimerskirch & Cherel 1998, Weimerskirch et al. 1999).

After LT, but not ST, food samples of blue petrels consistently contained stomach oil, as recently found in short-tailed shearwaters *Puffinus tenuirostris* and Antarctic prions *Pachyptila desolata* (Weimerskirch & Cherel 1998, Weimerskirch et al. 1999). This is in agreement with the idea that the primarily function of stomach oil is to act as a rich energy reserve by concentrating lipids from the prey, being thus an easy and cheap way to bring and transport energy to the chicks from distant foraging areas (Warham 1977). Together with stomach oil, the best indicator of LT was the Antarctic krill *Euphausia superba* because it was found in LT samples only (Table 4). Blue petrels feed on both juvenile and adult Antarctic krill with large inter-annual differences, as indicated by their length-frequency distribution (Fig. 5). Since the northern limit of *E. superba* south of Iles Kerguelen is 59° S, with the highest densities always recorded further south (Hosie et al. 1988, Miquel 1991, Pakhomov 2000), its occurrence in food samples indicate foraging far away, in southern Antarctic waters located more than 1000 km from the breeding grounds (49° S) (Fig. 1). Observations at sea are in agreement with our data because foraging and feeding blue petrels were recorded in summer over Antarctic waters between 62 and 64° S south of Iles Kerguelen, and in Prydz Bay (Ryan & Cooper 1989, Stahl et al. in press). In the latter area, blue petrels are among the commonest seabirds recorded north of the Antarctic divergence (64° S), where

the species was found to be positively correlated with the abundance of *E. superba* (Ryan & Cooper 1989). Feeding in southern Antarctic waters is also indicated by the occurrence of *Cyllopus lucasii* in a few food samples (Table 3) because the 2 *Cyllopus* species have different patterns of distribution, *C. lucasii* being much more frequent to the south, *C. magellanicus* to the north (Weigmann-Haass 1983).

The presence of *Euphausia superba* in the diet at Crozet (46° S) (Ridoux 1994) suggests that blue petrels also make LT at that breeding locality. The lack of *E. superba* in the food of blue petrels from Marion Island (47° S) (Steele & Klages 1986), which is also located in the Western Indian Ocean, is more puzzling and may result either from the inability to identify very digested remains of *E. superba* that can be easily overlooked in food samples or from a different foraging strategy. However, the occurrence of oil in 58% of the samples (Steele & Klages 1986) clearly suggests that birds also use a 2-fold strategy there. Antarctic krill is very abundant in the immediate vicinity of South Georgia (55° S), and, consequently, it is the main food item of blue petrels (Prince 1980). Whether this leads to a different feeding strategy clearly merits further studies to investigate the foraging plasticity of the species in relation to the marine environment.

Unlike in January 1998, deep-water crustaceans (*Eurythenes* spp. and *Pasiphaea longispina* [= *P. scotiae*]) were found exclusively in LT samples in January 1989 (Chaurand & Weimerskirch 1994). They were also clearly associated with oil or *Euphausia superba*, i.e. presumably LT samples, in stomach contents collected during the IOZ programme. Such differences may result from inter-annual variations because, as previously detailed above, the beginning of 1998 was marked by oceanographic anomalies (Park 2001) and thus probably changes in the pelagic ecosystem. During LT, blue petrels fed more on *Thysanoessa macrura/vicina* than during ST, and the reverse was true for *Themisto gaudichaudii*. The 2 taxons have a broad circumpolar distribution in the Southern Ocean (Kane 1966, Lomakina 1966), and they thus cannot give valuable information on foraging grounds. It is, however, noticeable that the density of *T. gaudichaudii* increases in the vicinity of Iles Kerguelen (Pakhomov 1993, Bocher et al. 2001). The subantarctic krill *Euphausia vallentini* was clearly associated with ST, as were the amphipods *Polycheria kergueleni*, *Cyllopus magellanicus* and *Vibilia antarctica* and the salp *Salpa thompsoni*. *P. kergueleni* is associated with the kelp belt (see above), *E. vallentini* occurs in coastal, neritic and subantarctic oceanic waters (Pakhomov 1993, Bost et al. 1994), and *C. magellanicus* and *V. antarctica* are known to live in association with *S. thompsoni* (Perissinotto & Pakhomov 1997), all being common in oceanic waters surrounding the archipelago (Pakhomov 1993, Cherel et al. unpubl.). Together with the occurrence of mesopelagic fish and deep-water crustaceans, the data suggest foraging mainly, but not exclusively, in oceanic waters during ST. Observations at sea indicate that blue petrels are common between Iles Kerguelen and Heard Island in January and February (Stahl et al. in press), the area being thus presumably one of the foraging grounds during ST. Being located south of Iles Kerguelen, it may also explain the occurrence of the same prey species in ST and LT samples, adult blue petrels collecting food for their chicks on their way back from the distant Antarctic foraging grounds to the colonies, as previously found for other procellariiforms (Weimerskirch & Cherel 1998, Weimerskirch et al. 1999).

In summary, prey biogeography indicates foraging in the relative vicinity of Iles Kerguelen during ST and to southern Antarctic waters during LT, a conclusion that fits well with the time windows available for travelling and foraging during the 2 kinds of trips, i.e. about 2 and 6 to 8 d for ST and LT, respectively.

Blue petrels and prions

When closely related species are in sympatric conditions, some segregation in nest sites or food can be expected. At Iles Kerguelen, we studied during 3 consecutive breeding seasons the food and feeding ecology of 2 species of the genus *Pachyptila*, the thin-billed and Antarctic prions (Cherel et al. 2002), together with that of blue petrels (present study). An almost complete segregation was previously observed in the nesting habitats, together with a partial segregation in the timing of breeding, blue petrels being slightly in advance of thin-billed prions, and Antarctic prions reproducing 40 d later than their congenerics (Weimerskirch et al. 1989, Bretagnolle et al. 1990, Genevois & Buffard 1994). Dietary analysis showed a broad overlap in the prey species and presumably the foraging areas of prions and blue petrels (Cherel et al. 2002, present study). Blue petrels, however, fed more on fish (mainly mesopelagic species) than prions (57 vs 12–13% by reconstituted mass), and, conversely, prions fed more on crustaceans (82 vs 37%). During the only previous study comparing the diet of blue petrels and Antarctic prions, Prince (1980) also found that the 2 species are segregated by the amount of fish in their food. At Iles Kerguelen, the main crustacean prey was *Themisto gaudichaudii* for the 3 bird species, thus emphasising its importance in the local pelagic trophic web (Bocher et al. 2001). Birds segregated by feeding on different euphausiids: *Thysanoessa* sp. for blue petrels and thin-billed prions, and *Euphausia vallentini* for Antarctic

prions. Interestingly, *E. vallentini* was also the main prey for blue petrels during the post-nuptial visit to their burrows, suggesting that this euphausiid species is more available for surface-feeding seabirds in March to May than earlier in the season.

The stable isotopic composition of chick feathers also indicated an overlap in the foraging ecology of the species during the chick-rearing period. $\delta^{13}C$ was similar in feathers of the 3 groups of chicks, but, in agreement with more fish in its diet, $\delta^{15}N$ was higher for the blue petrel. Outside the breeding season, during moult, birds segregated by their foraging areas. Stable carbon isotope concentrations of adult feathers indicated that blue petrels and thin-billed prions renewed their flight feathers in Antarctica, and Antarctic prions in subtropical waters (Cherel et al. 2002, present study).

Like blue petrels, both thin-billed and Antarctic prions made ST and LT during the chick-rearing period at Iles Kerguelen (Weimerskirch et al. 1999, Duriez et al. 2000). ST are, however, shorter in prions (mode at 1 d) than in blue petrels (2 d). Together with the higher occurrence of oceanic prey in blue petrel food samples, it is therefore suggested that prions forage more in neritic waters and blue petrels more in oceanic waters in the vicinity of the archipelago during ST. Another difference is that blue petrels alternate one ST with one LT (Chaurand & Weimerskirch 1994, Weimerskirch et al. unpubl.), while prions alternate several successive ST with one LT (Weimerskirch et al. 1999, Duriez et al. 2000). Consequently, blue petrels make more LT than prions. This difference is the more likely explanation for the higher frequency of occurrence of *Euphausia superba* (35 vs 10–15%) and its higher importance by reconstituted mass (10 vs 4%) in the diet of blue petrels than in that of prions. Note, however, that the 3 species reach southern Antarctic waters during LT (Cherel et al. 2002, present study).

Ecologically, blue petrels and thin-billed and Antarctic prions belong to a group of small and medium-sized procellariiform seabirds that make LT to Antarctic waters during the chick-rearing period. In addition to these 3 species, this feeding strategy has been described for the white-chinned petrel *Procellaria aequinoctialis* (Catard et al. 2000) and the short-tailed shearwater (Weimerskirch & Cherel 1998, Klomp & Schultz 2000), and it is suspected to occur in the white-headed petrels *Pterodroma lessoni* and mottled petrels *P. inexpectata*, because the 2 species are numerous in Antarctic waters in January and February (Veit & Hunt 1991). Adult petrels observed at high latitudes in summer are therefore not only non-breeders or failed breeders, as is generally assumed, but at least some are breeding birds that forage far from their breeding grounds to build up energy reserves and collect food for their chicks.

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