

Food and feeding ecology of the sympatric thin-billed *Pachyptila belcheri* and Antarctic *P. desolata* prions at Iles Kerguelen, Southern Indian Ocean

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ABSTRACT: The food and feeding ecology of the 2 closely related species of prions *Pachyptila belcheri* and *P. desolata* was investigated over 3 consecutive chick-rearing periods at Iles Kerguelen, the only place where they nest sympatrically in large numbers. In all years, the 2 prion species fed on crustaceans, with a small proportion of mesopelagic fish and squid. The hyperiid amphipod *Themisto gaudichaudii* was consistently the dominant prey item, accounting for 76 and 70% by number, and 57 and 57% by reconstituted mass of the diet of *P. belcheri* and *P. desolata*, respectively. Prions, however, were segregated by feeding on different euphausiids, *P. belcheri* on *Thysanoessa* sp. (18% by number and 16% by mass) and *P. desolata* on *Euphausia vallentini* (9% by number and 15% by mass). *P. desolata* also caught more small prey such as copepods (9 vs <1% by number) and cypris larvae of *Lepas australis* (8 vs 3% by number) than *P. belcheri*, which can be related to the beak filtering apparatus present only in the former species. Biogeography of the prey and their state of digestion indicate that prions foraged in a wide variety of marine habitats, including the kelp belt, kelp rafts, and coastal, neritic and oceanic waters. Noticeable is the occurrence of *E. superba* in a significant number of food samples (15 and 10% for *P. belcheri* and *P. desolata*, respectively), suggesting feeding in distant foraging grounds in southern Antarctic waters, >1000 km from the breeding colonies, during the chick-rearing period. The stable-carbon and -nitrogen isotopic compositions of chick feathers were identical in both species, indicating no important trophic segregation during the breeding period, when adult birds are central-place foragers. The ratios were, however, different in adult feathers, suggesting moulting in Antarctic waters for *P. belcheri* and in subtropical waters for *P. desolata*, i.e. in distinct foraging areas when birds are not constrained to return to the colonies.

KEY WORDS: *Euphausia superba* · *Pachyptila* · Petrels · Seabirds · Trophic relationships · Stable-carbon isotopes · Stable-nitrogen isotopes · *Themisto gaudichaudii*

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INTRODUCTION

Prions (genus *Pachyptila*) are small seabirds restricted to the Southern Ocean, where they are among the most numerous of the procellariiforms. All prion species closely resemble one another, which makes

them one of the most difficult petrel groups for the taxonomist. Specific separation is mainly based on the size, shape, structure and colour of their bills, which allow the recognition of 6 different species (Warham 1990). In *P. desolata*, *P. salvini* and *P. vittata*, the width of the bill is progressively larger and all species have well-developed, comb-like lamellae inside the upper mandible which are used to filter small particles of

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marine food from seawater. The 3 other species, *P. belcheri*, *P. turtur* and *P. crassirostris*, have the least-modified bills, lack palatal lamellae and hence have no specialised filtering apparatus (Prince & Morgan 1987).

At Iles Kerguelen, southern Indian Ocean, 3 species of prions breed sympatrically. They include a medium-sized population of *Pachyptila turtur* (1000 to 10 000 breeding pairs) and 2 large populations of *P. belcheri* (0.7 to 1.0 million) and *P. desolata* (2 to 3 million) (Weimerskirch et al. 1989). *P. desolata* (Antarctic prion) has a circumpolar range in Antarctic and subantarctic islands, with important populations at South Georgia, Iles Kerguelen and the Auckland Islands, while *P. belcheri* (thin-billed or slender-billed prion) has a more restricted range, being abundant at the Falklands-Tierra del Fuego and at Iles Kerguelen only (Marchant & Higgins 1990). The latter archipelago is thus the only place where the 2 species nest sympatrically in significant numbers. There, they are segregated by breeding in different terrestrial habitats at different times, *P. belcheri* laying on average 40 d before *P. desolata* (Weimerskirch et al. 1989). In the hand, the 2 species can be distinguished by the differences in bill proportions (Bretagnolle et al. 1990), *P. belcheri* having a narrow

bill (10.2 to 12.5 mm) without filtering apparatus, and *P. desolata* having the narrowest bill (12.1 to 14.6 mm) within the group of prions possessing large bills and palatal lamellae. Whether or not this has an implication for their food, feeding ecology and trophic segregation has not been investigated.

Almost nothing is known of the diet of *Pachyptila belcheri*, but that of *P. desolata* has been investigated in detail at 1 locality during the breeding season. At South Georgia, the food of *P. desolata* is dominated by euphausiids, copepods and amphipods (mainly the hyperiid *Themisto gaudichaudii*), with the presence of Antarctic krill *Euphausia superba* being inversely related to that of copepods and amphipods (Prince 1980, Liddle 1994, Reid et al. 1997). Elsewhere, the information available from a few individuals indicates that the species feeds on *E. superba* and myctophid fish at sea (Ainley et al. 1984, 1992, Harper 1987), and on euphausiids and amphipods, including *T. gaudichaudii*, at Iles Kerguelen (Bretagnolle et al. 1990) and Heard Island (Ealey 1954). Preliminary analysis also suggested that *T. gaudichaudii* is a main prey for *P. belcheri*, because this species was consistently found in the diet of birds sampled in the breeding colonies at the Falklands (Strange 1980, Thompson 1989), Iles Kerguelen (Bretagnolle et al. 1990) and at sea (Harper 1972). This leads to the hypothesis that *P. belcheri* is closely linked ecologically to *T. gaudichaudii* throughout its range. However, detailed information from the main breeding grounds is needed for confirmation (Imber 1981).

The main objective of this study was first to detail and second to compare the food and feeding ecology of these 2 closely related species of prions nesting at Iles Kerguelen. Prey species, chick-feeding frequency and food mass were recorded over 3 consecutive chick-rearing periods (1995, 1996 and 1997). We also focused on the foraging ecology during the interbreeding period, for which no other information is available, 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. 2000a, Cherel et al. 2000). In adult prions, like in many seabirds, synthesis of flight feathers takes place after the breeding season, i.e. mainly in March-April for *Pachyptila belcheri* and in April-May for *P. desolata* (Marchant & Higgins 1990, Stahl et al. in press). Thus, a comparison between the stable isotope ratios of feathers from chicks (which moult in their burrows while being fed by their parents) and those from adults can give valuable information on foraging grounds of adult seabirds during chick-rearing and moult, respectively.

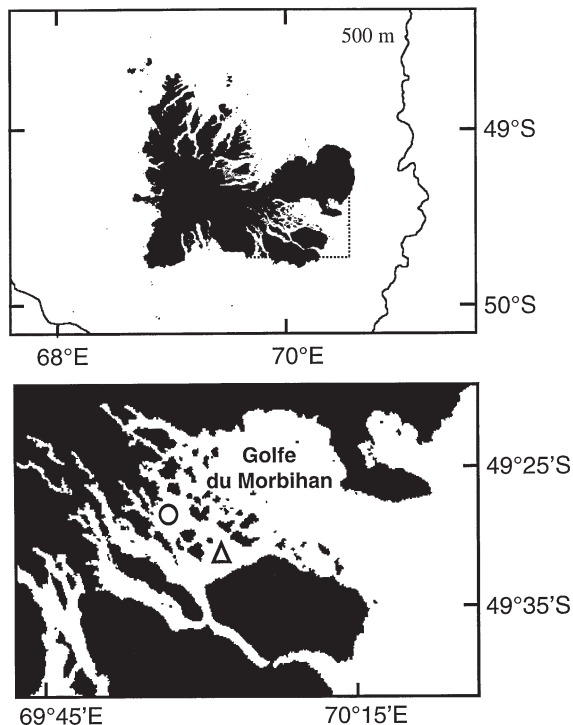


Fig. 1. *Pachyptila* spp. Map of Iles Kerguelen (upper panel) and details of the eastern part of the archipelago (lower panel) showing the location of the study colonies within the Golfe du Morbihan (circle: Ile Mayes; triangle: Ile Verte)

MATERIALS AND METHODS

Study sites, birds and breeding success. Fieldwork was carried out during 3 consecutive summer seasons (1994/1995, 1995/1996 and 1996/1997) in the Golfe du Morbihan, eastern Kerguelen Archipelago. The study colonies were located at 2 adjacent islands where large populations of prions breed: *Pachyptila belcheri* at Ile Mayes (49° 28' S, 69° 57' E) and *P. desolata* at Ile Verte (49° 31' S, 70° 04' E) (Fig. 1). The 2 species nest in different habitats, *P. belcheri* digging their burrows in stony soils where plant cover is generally poor, and *P. desolata* in cinder soils where the main plant is *Acaena adscendens* (Bretagnolle et al. 1990, Genevois & Bufard 1994). At each site, 2 nearby colonies of prions 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 pre-breeding period to estimate the number of visited burrows, and subsequently during the breeding season at laying, hatching and prior to fledging to estimate the hatching, fledging and breeding success. A total of 185 to 223 burrows of *P. belcheri*, and 52 to 60 burrows of *P. desolata* were monitored each year in the demographic colonies. Chicks were weighed and their wings measured at a fixed date (corresponding roughly to a few days before fledging). In the dietary colonies, each species was studied each year during 11 to 19 consecutive days, corresponding to the middle of the chick-rearing period, which lasts about 50 d for these species (Marchant & Higgins 1990). In the Golfe du Morbihan, *P. desolata* breeds later than *P. belcheri* (Bretagnolle et al. 1990); consequently, the 2 species were studied at an interval of 1 mo, *P. belcheri* at the end of January-beginning of February, and *P. desolata* in early March (Table 1).

Food mass and feeding frequency. Fourteen to 30 chicks of each species were monitored each year during the study period (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 adult 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 represent 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.

Table 1. *Pachyptila* spp. Chick body mass, chick feeding frequency and food mass delivered by the adults to the chicks at night during 3 consecutive chick-rearing periods. Values are means \pm SD with ranges in parentheses

Study period	No. of chicks (begin-end)	Chick mass (g)		Total no. of nights	Nights with feeding events		Food mass		Samples (n)
		Beginning	End		n	%	Mass (g)	Mass (g)	
<i>Pachyptila belcheri</i>									
26 Jan to 5 Feb 1995	25-21	107 \pm 26 (62-158)	111 \pm 22 (70-148)	251	133	53.0	27.5 \pm 15.5 (2-77)	109	
27 Jan to 7 Feb 1996	30-26	127 \pm 31 (44-177)	124 \pm 22 (85-172)	330	171	51.8	32.6 \pm 15.9 (2-96)	128	
23 Jan to 4 Feb 1997	30-30	142 \pm 28 (84-190)	131 \pm 23 (60-172)	389	176	45.2	37.5 \pm 16.8 (2-102)	168	
Total	85-77	126 \pm 31 (44-190)	123 \pm 23 (60-172)	970	480	49.4	33.3 \pm 16.7 (2-102)	405	
					$\chi^2 = 4.75$, $p = 0.093^a$		$F_{2,402} = 12.92$, $p < 0.0001^a$		
<i>Pachyptila desolata</i>									
1 to 17 Mar 1995	14-9	87 \pm 26 (40-124)	92 \pm 23 (45-120)	215	111	51.6	26.2 \pm 13.2 (2-52)	87	
27 Feb to 17 Mar 1996	27-25	59 \pm 21 (20-114)	121 \pm 24 (76-178)	537	286	53.2	31.1 \pm 14.8 (2-120)	238	
5 to 16 Mar 1997	30-30	102 \pm 26 (50-152)	125 \pm 27 (82-200)	369	208	56.4	29.3 \pm 13.5 (2-86)	169	
Total	71-64	83 \pm 31 (20-152)	119 \pm 28 (45-200)	1121	605	54.0	29.6 \pm 14.2 (2-120)	494	
					$\chi^2 = 1.44$, $p = 0.487^a$		$F_{2,491} = 3.90$, $p = 0.021^a$		
					$\chi^2 = 4.19$, $p = 0.041^b$		$t = 3.49$, $p = 0.001^b$		

^aPearson's chi-squared test and 1-way ANOVA between values of 3 years

^bPearson's chi-squared test and *t*-test between values (all 3 years pooled) of the 2 species

Chick-feeding frequency was calculated as the ratio between the number of nights with feedings (sum for all the chicks) divided by the total number of nights with weighings (sum for all the chicks; Table 1). Note that 15.6 and 18.3% of feeding events occurred after midnight for *Pachyptila belcheri* and *P. desolata*, respectively. No attempt was made to differentiate between single and double meals given by 1 or both parents within the same night, because the sampling protocol could not distinguish single and double feeds (Granadeiro et al. 1999).

Dietary analyses. Outside the study colonies, prions were caught 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 either by spontaneous regurgitation or, in a few cases, by the stomach lavage technique (Bocher et al. 2000b). After food sampling, prions 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.

Total numbers of common and rare prey items were counted in each individual 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 and/or intact eyes) of the main crustacean prey were randomly selected per dietary sample. Total length and eye diameter were determined to nearest 0.01 mm using an ocular scale in a binocular microscope. Total length (TL) of amphipods, euphausiids, and copepods was measured from the front of the eye to the tip of the longest uropods, from the tip of the rostrum to the tip of the uropods, and from the tip of the rostrum to the furca, respectively. For digested specimens, total length was estimated from eye diameter measurements by the use of allometric equations (Ridoux 1994, authors' unpubl. data), as was estimated the length of fish and cephalopods by the use of otolith or dentary length, and lower rostral length (to the nearest 0.01 mm), respectively. In order to estimate the composition by mass of the diet, the body mass of crus-

taceans, fish, cephalopods and other organisms was estimated from body length using published relationships (Clarke 1986, Adams & Klages 1987, Hecht & Hecht 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 then calculated as the percentage it represented in the total reconstituted mass.

Maximum dive depths. In March 1995 and 1996, maximum depths reached by *Pachyptila desolata* were investigated using capillary-tube depth gauges (Burger & Wilson 1988), following Chastel & Bried (1996), who previously worked at Ile Mayes on the diving behaviour of *P. belcheri* and the blue petrel *Halobaena caerulea*. Briefly, a 10 to 12 cm length of plastic tube (Tygon brand; internal diameter, 0.8 mm) was coated inside with icing sugar and sealed at one end. The tube was fitted on the back feathers using a waterproof adhesive tape. Each recorder weighed 0.6 g, <0.5% of the mean body mass. Maximum dive depth was estimated by the equation: $d = 10.08 [(L_s/L_d) - 1]$, where d is the maximum depth (m), L_s is the initial length (mm) of undissolved sugar, and L_d the length (mm) on recovery (accuracy ± 0.5 mm) (Burger & Wilson 1988).

Stable isotope analysis. Feathers were collected from intact wings of adults and fledgling prions killed by subantarctic skuas *Catharacta antarctica lönnerbergi*, or they were taken from the tip of the first few primaries from live birds in their burrows.

Before isotopic analysis, 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. Feathers were cleaned of surface contaminants using a 2:1 chloroform:ether rinse, air-dried, and then cut with stainless steel scissors into small fragments.

Stable-carbon and -nitrogen isotope assays were performed on 1 mg subsamples of homogenised materials by loading into tin cups and combusting 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 (CFIRMS) with every 5 unknowns separated

by 2 laboratory standards. Stable isotope abundances were expressed in δ notation as the deviation from standards in ppt (‰) according to the following equation:

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

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

Statistics. Data were analysed statistically using SYSTAT 9 for WINDOWS (Wilkinson 1999). Values are means \pm SD, significance at 0.05 level.

RESULTS

Pachyptila belcheri

Food mass and feeding frequency

Chicks of *Pachyptila belcheri* were fed at least 1 meal by their parents on 49% of nights during the middle of the nesting period, with no significant differences among the 3 yr. When fed, chicks received on average 33 g of food per night, with significant inter-annual differences (Table 1). Food mass was lighter in summer 1995, medium in 1996 and heavier in 1997 (post hoc Tukey's HSD multiple comparison test, all $p < 0.05$). The decrease in the number of chicks to the end of the study periods was due 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 negative (-7 ± 24 g) in 10 d, with significant

differences among years (1 ± 21 , -17 ± 25 and -4 ± 23 g for the summers of 1995, 1996 and 1997, respectively, 1-way ANOVA, $F_{2,75} = 3.96$, $p = 0.023$). 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 both species of prions (Bretagnolle et al. 1990, authors' unpubl. data).

The mean adult body mass (after food sampling) of *Pachyptila belcheri* was 154 g and did not differ significantly among years ($F_{2,80} = 0.40$, $p = 0.675$). The wet mass of the 85 food samples averaged 20 g, with significant differences among years ($F_{2,82} = 8.36$, $p < 0.0001$). The food samples collected in 1995 were lower in mass than those collected in 1996 and 1997 (post hoc Tukey's HSD multiple comparison test, all $p = 0.002$) (Table 2). The mass of dietary samples was lower than that of the food mass measured by weighing chicks, because spontaneous regurgitation is not very effective in collecting the whole stomach content of prions (Klages & Cooper 1992).

Diet

Pachyptila belcheri fed mainly on crustaceans (91 and 82% by fresh and reconstituted masses of the overall diet, respectively). Fish ranked second (6 and 12% by fresh and reconstituted masses), squids ranked third (3 and 6%) and other organisms (mainly the salp *Salpa thompsoni*) were negligible (<1%; Tables 2 & 3). The proportions of crustaceans, fish and cephalopods were similar for 1995 and 1996, but *P. belcheri* relied less on crustaceans and more on fish and squids in 1997 (Table 2). Crustaceans occurred in all diet samples. They dominated by number and by fresh mass in 100 and 93% ($n = 79$) of the samples, respectively. Stomach oil was found in 49% ($n = 42$) of the samples.

Table 2. *Pachyptila* spp. Birds' 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 \pm 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
<i>Pachyptila belcheri</i>								
1995	152 \pm 13 (129–183)	28	14.1 \pm 7.2 (3.3–33.8)	28	97.4	1.2	0.9	0.5
1996	154 \pm 14 (132–176)	30	23.3 \pm 10.2 (9.1–51.4)	30	96.7	1.6	1.7	0.0
1997	155 \pm 14 (136–194)	25	23.6 \pm 11.7 (10.3–49.3)	27	81.7	13.0	5.3	0.0
Total	154 \pm 14 (129–194)	83	20.4 \pm 10.7 (3.3–51.4)	85	91.3	5.7	2.9	0.1
<i>Pachyptila desolata</i>								
1995	160 \pm 11 (128–180)	37	16.7 \pm 7.7 (4.6–37.7)	38	93.4	4.8	1.3	0.5
1996	158 \pm 14 (130–188)	40	21.2 \pm 7.6 (5.7–40.2)	40	87.1	6.2	5.5	1.2
1997	161 \pm 11 (146–188)	26	16.3 \pm 9.9 (4.3–40.4)	26	87.2	2.6	0.1	10.1
Total	159 \pm 12 (128–188)	103	18.3 \pm 8.5 (4.3–40.4)	104	88.9	4.9	2.9	3.3

Table 3. *Pachyptila* spp. Frequency of occurrence, number, reconstituted mass and length of prey items recovered from stomach contents of *P. belcheri* during chick-rearing (total for all 85 samples pooled)

Prey species	Occurrence in stomachs		Number		Reconstituted mass		Body length (mm)		n
	n	%	n	%	g	%	Mean	Range	
Crustaceans	85	100.0	60 047	99.7	1191.4	81.9			
Euphausiacea									
<i>Euphausia superba</i>	13	15.3	41	<0.1	51.8	3.6	56.1 ± 6.2	36.9–69.1	23
<i>Euphausia vallentini</i>	14	16.5	129	0.2	8.7	0.6	21.9 ± 2.0	17.8–27.0	79
<i>Euphausia</i> sp.	3	3.5	4	<0.1	0.8	<0.1	27.3 ± 2.7	24.5–31.0	6
<i>Thysanoessa macrura/vicina</i>	46	54.1	10 644	17.7	229.7	15.8	16.4 ± 1.7	11.7–23.7	1052
Decapoda									
<i>Pasiphae scotiae</i>	8	9.4	9	<0.1	24.0	1.7	98.9 ± 9.2	88.5–112.5	6
<i>Halicarcinus planatus</i> (zoeal larvae)	1	1.2	1	<0.1	<0.1	<0.1	2.9		1
Mysida									
<i>Neognathophausia gigas</i>	1	1.2	1	<0.1	8.5	0.6	89.2		1
Amphipoda									
Dexaminidae									
<i>Polycheria kergueleni</i>	18	21.2	1320	2.2	3.1	0.2	5.5 ± 0.9	3.9–9.7	127
Eusiridae s.l.									
<i>Eusirus antarcticus</i>	2	2.4	11	<0.1	0.2	<0.1	11.4 ± 0.4	10.5–11.8	7
<i>Paramoera fissicauda</i> s.l.	4	4.7	39	<0.1	0.6	<0.1	10.8 ± 1.4	7.8–12.2	8
Ischyroceridae									
<i>Jassa</i> sp.	1	1.2	1	<0.1	0.1	<0.1			
Lysianassidae s.l.									
<i>Cicadosa cicadoides</i>	4	4.7	11	<0.1	1.4	<0.1	16.2 ± 4.4	10.5–20.8	10
<i>Eurythenes obesus</i>	1	1.2	1	<0.1	0.1	<0.1	23.5		1
<i>Uristes gigas</i>	10	11.8	149	0.2	11.9	0.8	13.8 ± 3.0	9.7–21.0	59
Vibiliidae									
<i>Cylopus magellanicus</i>	32	37.6	82	0.1	4.9	0.3	15.1 ± 2.8	6.2–20.1	57
<i>Vibilia antarctica</i>	16	18.8	44	<0.1	2.5	0.2	13.6 ± 1.4	10.9–15.8	25
Hyperiididae									
<i>Hyperiella antarctica</i>	11	12.9	24	<0.1	0.4	<0.1	10.6 ± 2.7	7.3–17.1	17
<i>Hyperoche luetkenides</i>	3	3.5	7	<0.1	0.3	<0.1	12.6 ± 0.5	12.1–13.1	4
<i>Themisto gaudichaudii</i>	81	95.3	45 712	75.9	830.0	57.0	11.7 ± 5.8	4.0–33.8	3389
Phrosinidae									
<i>Primno macropa</i>	28	32.9	152	0.3	7.3	0.5	12.9 ± 1.5	9.0–16.3	86
Unidentified amphipods	3	3.5	3	<0.1	0.1	<0.1			
Ostracoda									
<i>Gigantocypris</i> sp.	1	1.2	1	<0.1	1.2	<0.1	17.2		1
Copepoda									
<i>Calanus simillimus</i>	1	1.2	1	<0.1	<0.1	<0.1	3.3		1
<i>Drepanopus pectinatus</i>	1	1.2	1	<0.1	<0.1	<0.1	1.6		1
<i>Paraeuchaeta antarctica</i>	1	1.2	1	<0.1	<0.1	<0.1	6.5		1
Unidentified copepods	1	1.2	5	<0.1	<0.1	<0.1			
Cirripedia									
<i>Lepas australis</i> (cypris larvae)	27	31.8	1650	2.7	4.0	0.3	2.4 ± 0.2	1.9–2.8	174
Unidentified crustaceans	3	3.5	3	<0.1	0.1	<0.1			
Fish	35	41.2	59	0.1	168.2	11.6			
Paralepididae									
<i>Arctozenus risso</i>	1	1.2	1	<0.1	3.8	0.3			
<i>Notolepis coatsi</i>	1	1.2	1	<0.1	3.8	0.3			
Myctophidae									
<i>Electrona antarctica</i>	5	5.9	5	<0.1	73.5	5.0	102.1		1
<i>Electrona carlsbergi</i>	3	3.5	3	<0.1	25.4	1.7	82.6		1
<i>Krefflichthys anderssoni</i>	11	12.9	33	<0.1	43.7	3.0	49.3 ± 4.9	30.8–59.0	7
Unidentified Myctophidae	6	7.1	6	<0.1	8.0	0.5			
Nototheniidae									
Nototheniidae sp.	2	2.4	2	<0.1	2.0	0.1			
Unidentified postlarvae	2	2.4	2	<0.1	0.3	<0.1			
Unidentified fish	6	7.1	6	<0.1	8.0	0.5			

Table 3 (continued)

Prey species	Occurrence in stomachs		Number		Reconstituted mass		Body length (mm)		n
	n	%	n	%	g	%	Mean	Range	
Cephalopods	20	23.5	81	0.1	87.3	6.0			
Onychoteuthidae									
<i>Moroteuthis knipovitchi</i>	1	1.2	1	<0.1	3.2	0.2	49.8		1
Gonatidae									
<i>Gonatus antarcticus</i>	10	11.8	54	<0.1	37.9	2.6	28.1 ± 3.1	23.9–35.0	45
Brachioteuthidae									
<i>Brachioteuthis ?riisei</i>	9	10.6	16	<0.1	27.3	1.9	34.7 ± 8.5	27.2–56.3	13
Oegopsida sp. A	2	2.4	2	<0.1	3.3	0.2			
Unidentified squids	6	7.1	8	<0.1	15.6	1.1			
Others	8	9.4	35	<0.1	8.3	0.6			
Polychaeta									
<i>Platynereis australis</i>	3	3.5	5	<0.1	0.3	<0.1			
Bivalvia									
<i>Gaimardia trapesina</i>	1	1.2	1	<0.1	0.1	<0.1			
Salpidae									
<i>Salpa thompsoni</i>	6	7.1	29	<0.1	7.9	0.5			
Total	85		60 222	100.0	1455.2	100.0			

A total of 60 222 prey items was recovered from 85 samples and included 60 047 crustaceans (99.7%), 59 fish (0.1%), 81 squids (0.1%) and 35 other organisms (polychaetes, bivalves and salps). Overall, 24 species of crustacean, 5 species of fish and 4 species of cephalopod were identified (Table 3). By far, the diet was dominated by the hyperiid amphipod *Themisto gaudichaudii*, which occurred in most of the samples (95%) and accounted for 76% of the total number of prey and 57% of the food by estimated reconstituted mass. The second main prey was the euphausiid *Thysanoessa* sp., which occurred in 54% of the samples and accounted for 18% by number and 16% by reconstituted mass. Other significant crustacean prey were cypris larvae of the cirriped *Lepas australis*, the gammarid *Polycheria kergueleni* (>1% by number), the shrimp *Pasiphaea scotiae* (the dominant species by mass in 2 samples) and Antarctic krill *Euphausia superba* (the dominant species by mass in 4 samples). *E. superba* was the second crustacean prey by mass in 1995, but none was found in 1996, and it accounted for a smaller percentage in 1997 (Fig. 2). Other common but minor crustacean prey were the subantarctic krill *Euphausia vallentini* and the amphipods *Uristes gigas*, *Cylopus magellanicus*, *Vibilia antarctica* and *Primno macropa*.

Themisto gaudichaudii prevailed by number and by mass in 68% (n = 58) and 60% (n = 51) of the samples, respectively. It was the dominant prey every season, accounting for 31 to 68% by mass of the whole diet and for 48 to 76% by mass of the crustacean diet (Fig. 2). Two prey size-classes of *T. gaudichaudii* were eaten by *Pachyptila belcheri*, small individuals (4 to 14 mm TL), which were the dominant prey size class with a mode

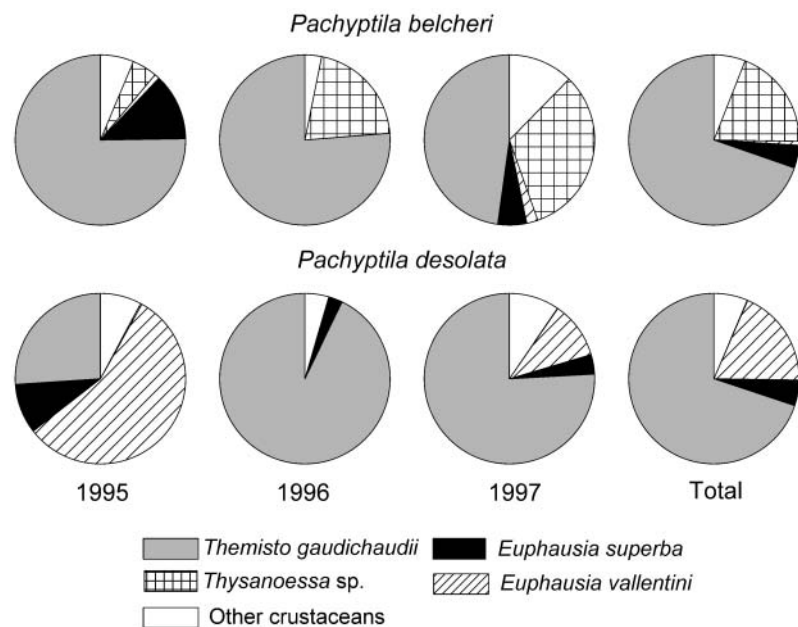


Fig. 2. *Pachyptila* spp. Composition by reconstituted mass of the crustacean diet during 3 consecutive chick-rearing periods

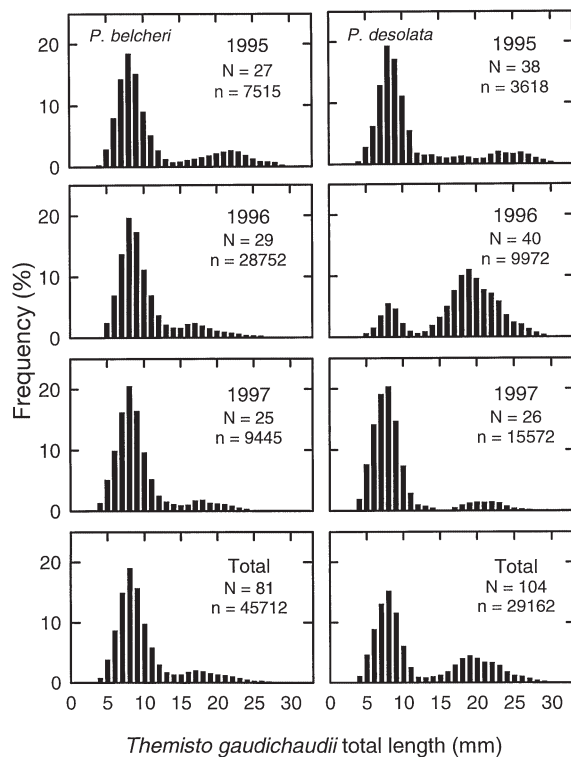


Fig. 3. *Pachyptila* spp. Length-frequency distribution of the hyperiid *Themisto gaudichaudii* in the diet of *P. belcheri* and *P. desolata* during 3 consecutive chick-rearing periods. N: number of food samples; n: number of individuals

at 8 mm, and larger individuals (15 to 34 mm), with no clear mode (Fig. 3). Length-frequency distributions of *T. gaudichaudii* were significantly different among years (Kolmogorov-Smirnov, all $p < 0.0001$). The small prey size class accounted for 78, 87 and 90% of the total number of *T. gaudichaudii* in 1995, 1996 and 1997, respectively, with a concomitant decrease in the number of larger individuals during the study period (Fig. 3). Overall, individuals of the small prey size class (<15 mm) had about the same length over the 3 years.

The second main prey, *Thysanoessa* sp., prevailed by number and by mass in 32% ($n = 27$) and 18% ($n = 15$) of the samples, respectively. Its importance in the diet of *Pachyptila belcheri* increased over the 3 years, accounting for 5, 20 and 32% by mass of the crustacean diet in 1995, 1996 and 1997, respectively (Fig. 2). Only 1 prey size class (11 to 24 mm) of *Thysanoessa* sp. was found with a mode at 16 to 17 mm (Fig. 4). Length-frequency distributions of *Thysanoessa* sp. were similar in 1996 and 1997 (Kolmogorov-Smirnov, $p = 0.424$), but they were different from the distribution found in 1995 (both $p < 0.0001$). The digested condition of the specimens of *Thysanoessa* precluded their identification to the species level. The fact that *P. belcheri* fed upon

1 well-defined size class of *Thysanoessa* sp., however, suggests that specimens belonged to 1 species only (either *T. macrura* or *T. vicina*).

Most fish eaten were myctophids ($n = 47$), which, owing to their larger size than crustaceans, accounted for a significant percentage by reconstituted mass of the food (10%). The commonest species was *Krefflichthys anderssoni*, which prevailed by mass in 3 samples, while the 2 other species, *Electrona carlsbergi* and *E. antarctica*, dominated by reconstituted mass in 1 and 4 samples, respectively. Two squid species were regularly found: *Gonatus antarcticus* and *Brachio-teuthis ?riisei*, which prevailed by mass in 2 samples each (Table 3).

Stable isotopes

A brief examination showed the occurrence of *Themisto gaudichaudii* in the 10 dietary samples collected for isotopic analyses. Only 1 sample contained a significant amount of stomach oil. Food of *Pachyptila belcheri* and feathers from chicks and adults were segregated by their stable isotope values (MANOVA, Wilk's Lambda, $F_{4,52} = 14.71$, $p < 0.0001$) (Table 4). Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were overall different ($F_{2,27} = 8.48$ and 35.01 , $p = 0.001$ and $p < 0.0001$, respectively). Carbon stable-isotope ratios of chick food were lower than the ratio in chick feathers (post hoc Tukey's HSD multiple comparison test: $p = 0.001$), and $\delta^{15}\text{N}$ of chick food was lower than the values in chick and adult feathers (all $p < 0.0001$; Table 4).

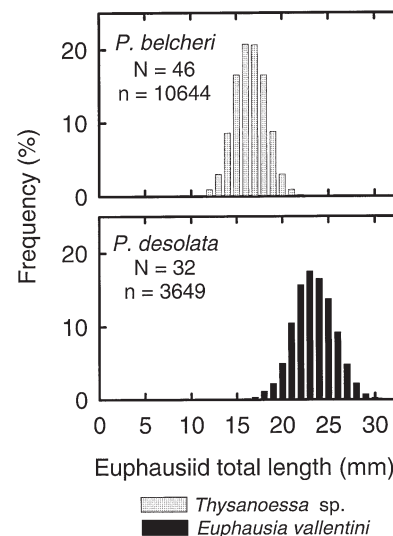


Fig. 4. *Pachyptila* spp. Length-frequency distribution of the euphausiids *Thysanoessa* sp. and *Euphausia vallentini* in the diet of *P. belcheri* and *P. desolata*, respectively. N: number of food samples; n: number of individuals

Breeding success

Hatching and fledging successes of *Pachyptila belcheri* averaged 61 and 83 %, respectively, and they did not vary significantly among the 3 study years (hatching success: $\chi^2_2 = 0.21$, $p = 0.902$; fledging success: $\chi^2_2 = 0.57$, $p = 0.753$). Consequently, breeding success averaged 50 % with no interannual variations (Table 5). However, at the end of the rearing period, chicks were lighter in 1995 than in 1996 (post hoc Tukey's HSD multiple comparison test, $p = 0.005$), with no differences between 1997 and either 1995 or 1996 ($p = 0.225$ and $p = 0.164$, respectively). Wing length of chicks measured at the same date each year were significantly different, ranging from 111 mm (1995) to 153 mm (1997) (Table 5).

Pachyptila desolata

Food mass and feeding frequency

Chicks of *Pachyptila desolata* were fed by the adults on 54 % of nights during the middle of the nesting period, with no significant differences among the 3 seasons (Table 1). When fed, chicks received on average of 30 g of food per night, with significant interannual differences, food mass being on average lower in summer 1995 than in 1996 (post hoc Tukey's HSD multiple comparison test, $p = 0.015$). The overall mass gain

Table 4. *Pachyptila* spp. Stable-carbon and -nitrogen isotope concentrations (mean \pm 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's HSD multiple comparison test $p < 0.05$)

Sampling group	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Pachyptila belcheri</i>			
Food	10	-25.5 ± 2.5^a	4.5 ± 2.1^a
Chick feathers	10	$-22.7 \pm 0.7^{b,c}$	8.9 ± 0.5^b
Adult feathers	10	$-24.3 \pm 0.6^{a,b}$	8.5 ± 0.7^b
<i>Pachyptila desolata</i>			
Food	10	$-22.9 \pm 2.9^{b,c}$	3.6 ± 1.2^a
Chick feathers	8	-21.5 ± 0.6^c	8.5 ± 0.5^b
Adult feathers	10	-17.0 ± 1.0^d	10.5 ± 1.7^c
ANOVA		$F_{5,52} = 29.61$ $p < 0.0001$	$F_{5,52} = 45.19$ $p < 0.0001$

of chicks was 27 ± 25 g in 10 d, with significant differences among years (1 ± 16 , 41 ± 22 and 23 ± 23 g for 1995, 1996 and 1997, respectively, $F_{2,62} = 12.78$, $p < 0.0001$).

The mean adult body mass (after food sampling) of *Pachyptila desolata* was 159 g and did not differ significantly among seasons ($F_{2,100} = 0.43$, $p = 0.653$). The wet mass of the 104 food samples averaged 18 g, with no significant differences between years ($F_{2,101} = 2.25$, $p = 0.111$; Table 2).

Table 5. *Pachyptila* spp. Breeding success and fledging mass during 3 consecutive breeding seasons. Values are means \pm SD with ranges in parentheses

Study period	Monitored burrows n	Occupied burrows n	Hatching success %	Fledging success %	Breeding success %	Chicks' body mass g	Chicks' wing length mm	No. of chicks
<i>Pachyptila belcheri</i>								
1995	223	163	73.1	59.4	88.3	133 ± 23 (70–195)	111 ± 16 (70–151)	50
1996	185	138	74.6	58.5	80.0	148 ± 23 (92–200)	128 ± 18 (82–160)	43
1997	219	183	83.9	61.3	83.2	140 ± 22 (72–198)	153 ± 18 (91–181)	76
Total	627	484	77.3	60.5	82.9	140 ± 23 (70–200)	134 ± 25 (70–181)	169
						$F_{2,166} = 4.84$, $p = 0.009^a$		
						$\chi^2_2 = 0.60$, $p = 0.741^a$	$F_{2,166} = 85.92$, $p < 0.0001^a$	
<i>Pachyptila desolata</i>								
1995	52	32	65.4	62.5	75.0	149 ± 31 (101–192)	106 ± 29 (33–148)	15
1996	60	29	58.3	55.2	81.2	166 ± 41 (98–236)	103 ± 27 (53–156)	13
1997	58	29	56.9	58.6	85.0	135 ± 25 (94–176)	99 ± 27 (48–137)	17
Total	170	90	60.0	62.2	80.3	149 ± 34 (94–236)	102 ± 27 (33–156)	45
						$F_{2,42} = 3.25$, $p = 0.049^a$		
						$t = 1.54$, $p = 0.129^b$		
						$\chi^2_2 = 1.30$, $p = 0.523^a$	$F_{2,42} = 0.24$, $p = 0.785^a$	
						$\chi^2 = 0.001$, $p = 0.981^b$	$t = 7.10$, $p < 0.0001^b$	
^a Pearson's chi-squared test and 1-way ANOVA between values of 3 years								
^b Pearson's chi-squared test and <i>t</i> -test between values (all 3 years pooled) of the 2 species								

Table 6. *Pachyptila* spp. Frequency of occurrence, number, reconstituted mass and length of prey items recovered from stomach contents of *P. desolata* during chick-rearing (total for all 104 samples pooled)

Prey species	Occurrence in stomachs		Number		Reconstituted mass		Body length (mm)		n
	n	%	n	%	g	%	Mean	Range	
Crustaceans	104	100.0	41197	98.6	1499.8	82.2			
Euphausiacea									
<i>Euphausia superba</i>	10	9.6	67	0.2	73.2	4.0	54.5 ± 6.1	43.4–69.1	50
<i>Euphausia vallentini</i>	32	30.8	3649	8.7	280.7	15.4	23.2 ± 2.1	16.2–30.8	707
<i>Euphausia</i> sp.	11	10.6	19	<0.1	1.4	<0.1	23.8 ± 9.5	11.0–42.6	33
<i>Thysanoessa macrura/vicina</i>	7	6.7	117	0.3	1.5	<0.1	9.9 ± 4.2	5.0–25.6	38
Decapoda									
<i>Pasiphae scotiae</i>	6	5.8	7	<0.1	14.9	0.8	90.8 ± 9.8	78.4–105.8	6
Mysida									
<i>Neognathophausia gigas</i>	2	1.9	2	<0.1	17.0	0.9			
Isopoda									
Unidentified Gnathiidae	1	1.0	4	<0.1	0.3	<0.1			
Amphipoda									
Dexaminidae									
<i>Polycheria kergueleni</i>	12	11.5	91	0.2	0.2	<0.1	6.0 ± 1.9	3.9–10.6	20
Eusiridae s.l.									
<i>Eusirus antarcticus</i>	1	1.0	1	<0.1	<0.1	<0.1	11.3		1
<i>Paramoera fissicauda</i> s.l.	18	17.3	491	1.2	9.5	0.5	12.0 ± 1.1	9.4–14.4	90
Lysianassidae s.l.									
<i>Cicadosa cicadoides</i>	2	1.9	2	<0.1	0.2	<0.1	14.1	11.2–16.9	2
<i>Cyphocaris richardi</i>	2	1.9	2	<0.1	0.5	<0.1			
<i>Eurythenes gryllus</i>	1	1.0	1	<0.1	5.0	0.3			
<i>Eurythenes obesus</i>	2	1.9	2	<0.1	0.3	<0.1	18.4		1
<i>Uristes gigas</i>	18	17.3	223	0.5	19.0	1.0	13.7 ± 3.4	7.1–21.6	92
Vibiliidae									
<i>Cylopus magellanicus</i>	27	26.0	161	0.4	9.8	0.5	16.0 ± 2.9	11.4–27.1	69
<i>Vibilia antarctica</i>	18	17.3	61	0.1	2.9	0.2	13.5 ± 1.9	9.1–16.9	36
Hyperiididae									
<i>Hyperia gaudichaudii</i>	2	1.9	2	<0.1	0.3	<0.1	22.6	20.8–24.4	2
<i>Hyperiella antarctica</i>	12	11.5	18	<0.1	0.2	<0.1	8.0 ± 1.6	5.9–10.8	12
<i>Hyperoche luetkenides</i>	1	1.0	1	<0.1	0.1	<0.1	14.8		1
<i>Themisto gaudichaudii</i>	104	100.0	29162	69.8	1048.0	57.4	14.1 ± 6.9	3.1–32.8	3477
Phrosinidae									
<i>Primno macropa</i>	9	8.7	16	<0.1	0.1	<0.1	13.0 ± 3.4	4.7–16.5	15
Unidentified amphipods	5	4.8	11	<0.1	0.7	<0.1			
Ostracoda									
<i>Gigantocypris</i> sp.	1	1.0	1	<0.1	1.2	<0.1	17.2		1
Copepoda									
<i>Calanus simillimus</i>	6	5.8	3253	7.8	2.5	0.1	2.7 ± 0.3	1.8–3.6	135
<i>Calanoides acutus</i>	3	2.9	8	<0.1	<0.1	<0.1	4.4 ± 0.4	3.9–5.1	8
<i>Rhincalanus gigas</i>	1	1.0	186	0.4	2.6	0.1	7.5 ± 1.1	4.3–9.2	55
<i>Paraeuchaeta antarctica</i>	4	3.8	132	0.3	1.8	0.1	7.9 ± 1.5	6.5–8.7	130
Unidentified copepods	2	1.9	2	<0.1	<0.1	<0.1			
Cirripedia									
<i>Lepas australis</i> (cypris larvae)	46	44.2	3501	8.4	5.6	0.3	2.5 ± 0.2	2.0–3.0	304
Unidentified crustaceans	4	3.8	4	<0.1	0.3	<0.1			
Fish	33	31.7	41	<0.1	235.8	12.9			
Microstomatidae									
? <i>Nansenia antarctica</i>	1	1.0	1	<0.1	52.5	2.9			
Myctophidae									
<i>Electrona antarctica</i>	2	1.9	2	<0.1	29.4	1.6			
<i>Gymnoscopelus microlampas</i>	1	1.0	1	<0.1	21.4	1.2			
<i>Krefflichthys anderssoni</i>	1	1.0	1	<0.1	1.3	<0.1			
<i>Protomyctophum bolini</i>	1	1.0	1	<0.1	1.9	0.1			
Unidentified Myctophidae	6	5.8	6	<0.1	28.0	1.5			
Melamphaidae									
<i>Sio nordenskjöldii</i>	1	1.0	1	<0.1	19.8	1.1			
Melamphaidae sp. A	1	1.0	1	<0.1	31.3	1.7			
Harpagiferidae									
<i>Harpagifer spinosus</i>	1	1.0	1	<0.1	1.7	<0.1	40.6		1

Table 6 (continued)

Prey species	Occurrence in stomachs		Number		Reconstituted mass		Body length (mm)		n
	n	%	n	%	g	%	Mean	Range	
Gempylidae									
<i>Paradiplospinus gracilis</i>	2	1.9	2	<0.1	34.3	1.9	259.6		1
Unidentified postlarvae	5	4.8	8	<0.1	1.1	<0.1			
Unidentified fish	16	15.4	16	<0.1	13.2	0.7			
Cephalopods	16	15.4	26	<0.1	52.3	2.9			
Brachioteuthidae									
<i>Brachioteuthis ?riisei</i>	7	6.7	7	<0.1	11.6	0.6	33.7 ± 8.7	25.6–47.8	5
Oegopsida sp. A	11	10.6	14	<0.1	36.9	2.0			
Unidentified squids	5	4.8	5	<0.1	3.8	0.2			
Others	28	26.9	519	1.2	37.4	2.0			
Polychaeta									
<i>Platynereis australis</i>	22	21.2	495	1.2	27.3	1.5	20.2 ± 4.3	15.0–26.8	7
Bivalvia									
<i>Gaimardia trapesina</i>	4	3.8	6	<0.1	0.6	<0.1			
Salpidae									
<i>Salpa thompsoni</i>	6	5.8	18	<0.1	9.5	0.5			
Total	104		41 783	100.0	1825.3	100.0			

Diet

Pachyptila desolata fed mainly on crustaceans (89 and 82% by fresh and reconstituted masses of the overall diet, respectively). Crustaceans occurred in all of the food samples and dominated by fresh mass in 90% (n = 94) of them. Fish ranked second (5 and 13% by fresh and reconstituted masses), squids and other organisms being less important (Tables 2 & 6). No large interannual variations in the proportion by fresh mass of the broad prey classes were found, but prions fed more on other organisms (mainly the polychaete *Platynereis australis*) and less on cephalopods in 1997 (Table 2). Stomach oil was found in 35% (n = 36) of the samples.

A total of 41 783 prey items was recovered from 104 samples and included 41 197 crustaceans (99%), together with 41 fish (<0.1%), 26 cephalopods (<0.1%) and 519 other organisms (1.2%). Overall, 27 species of crustacean, 9 species of fish and 2 species of squid were identified (Table 6). By far, the diet was dominated by *Themisto gaudichaudii*, which occurred in all samples and accounted for 70% of the total number of prey and 57% of the food by reconstituted mass. The subantarctic krill *Euphausia vallentini* ranked second (9% by number and 15% by mass). Other significant crustacean prey were cypris larvae of *Lepas australis*, the copepod *Calanus simillimus* and the gammarid *Paramoera fissicauda* s.l. (sensu lato) (>1% by number) and the Antarctic krill *Euphausia superba* (the dominant species by mass in 6 samples) and the gammarid *Uristes gigas* (the dominant species by mass in 1 sample). Other common but minor crustacean prey

were *Thysanoessa* sp., *Polycheria kergueleni*, *Cylopus magellanicus* and *Vibilia antarctica*. The copepods *Rhincalanus gigas* and *Paraeuchaeta antarctica* formed each the bulk of the food in 1 food sample.

Themisto gaudichaudii prevailed by number and by reconstituted mass in 72% (n = 75) and 59% (n = 61) of the samples, respectively. It was the dominant crustacean item in 1996 (93% by mass of the crustacean diet) and 1997 (76%) and ranked second after *Euphausia vallentini* in 1995 (26%) (Fig. 2). Two prey size-classes of *T. gaudichaudii* were eaten by *Pachyptila desolata*, small individuals (3 to 14 mm TL), with a mode at 8 mm, and larger individuals (15 to 33 mm TL) (Fig. 3). The small prey size-class prevailed in 1995 and 1997, where they accounted for 80 and 90% of the total number of *T. gaudichaudii*, respectively. In 1996, small amphipods amounted to 25% only, and the large prey size-class dominated by number with a mode at 19 mm TL. Length-frequency distributions of *T. gaudichaudii* were significantly different among the 3 years (Kolmogorov-Smirnov, all p < 0.0001), as were the frequency distributions of the small prey size-class only (Kolmogorov-Smirnov, all p < 0.01).

The second main prey, *Euphausia vallentini*, predominated numerically and by mass in 14% (n = 15) and 20% (n = 21) of the samples, respectively, but was subject to large interannual variations. *E. vallentini* was the main prey by mass in the crustacean diet in 1995 (56%), but none was found in 1996, and it ranked second after *Themisto gaudichaudii* in 1997 (11%) (Fig. 2). *E. vallentini* caught by *Pachyptila desolata* belonged to a single prey size-class (16 to 31 mm) with

a mode at 23 mm (Fig. 4), and its length-frequency distributions were different in 1995 and 1997 (Kolmogorov-Smirnov, $p = 0.009$).

No species of fish was abundant in the diet of *Pachyptila desolata*. However, 6 different fish species prevailed each in 1 sample. Overall, the fish diet was dominated by mesopelagic fish (12% by reconstituted mass), including 4 species of myctophids and 2 species of melamphoids (Table 6). *Brachioteuthis ?riisei* was the only cephalopod identified to species level. It dominated by mass in 3 samples. Among other organisms, the polychaete *Platynereis australis* was a common prey, occurring in 21% of the samples and accounting for 1% of the diet by number and by mass. It was the dominant item by mass in 4 samples.

Maximum dive depths

Of 99 recorders that were attached in 1995 and 1996, 78 (79%) were recovered and 67 (68%) gave reliable measurements. Birds were recaptured after 1 foraging trip only. Forty-five recorders were recovered after 1 to 3 d (short trips), and 22 after 4 to 12 d (long trips). The maximum dive depths attained by *Pachyptila desolata* ranged from 0.8 to 7.1 m, and averaged 4.0 ± 1.4 m (Fig. 5). Prions dived deeper in 1995 than in 1996 (4.6 ± 1.2 and 3.6 ± 1.4 m, $n = 27$ and 40, respectively; Mann-Whitney, $U = 769.00$, $p = 0.003$), and they reached shallower depths during short trips than during long trips (3.2 ± 1.0 and 5.5 ± 0.8 m, $n = 45$ and 22, respectively; $U = 949.50$, $p < 0.0001$).

Stable isotopes

A brief examination showed the occurrence of *Euphausia vallentini* in 8 dietary samples (all were collected in 1995) and of *Themisto gaudichaudii* in 2 samples collected for isotopic analyses. Only 1 sample contained *Euphausia superba* together with a significant amount of stomach oil. Food of *Pachyptila desolata* and

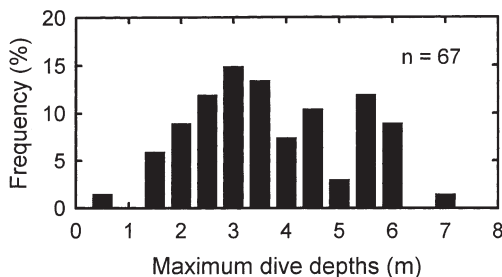


Fig. 5. *Pachyptila* spp. Frequency distribution of maximum dive depths of *P. desolata* during the chick-rearing period

feathers from chicks and adults were segregated by their stable isotope values (MANOVA, Wilk's Lambda, $F_{4,48} = 29.19$, $p < 0.0001$; Table 4). Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were overall different ($F_{2,25} = 26.21$ and 79.61, respectively, both $p < 0.0001$). Stable-carbon-isotope ratios of chick food and feathers were lower than the ratio in adult feathers (post hoc Tukey's HSD multiple comparison test: both $p < 0.0001$), and $\delta^{15}\text{N}$ values were different in chick food, chick feathers and adult feathers (all $p < 0.01$) (Table 4).

Breeding success

Hatching and fledging successes of *Pachyptila desolata* averaged 62 and 80%, respectively, and they did not vary significantly among the 3 years (hatching success: $\chi^2_2 = 1.18$, $p = 0.556$; fledging success: $\chi^2_2 = 0.65$, $p = 0.724$). Consequently, breeding success averaged 50% with no interannual variations (Table 5). At the end of the rearing period, chicks were slightly heavier in 1996 than in 1997 (post hoc Tukey's HSD multiple comparison test, $p = 0.038$), with no differences between 1995 and either 1996 or 1997 ($p = 0.373$ and $p = 0.459$, respectively). No differences in wing length of fledglings were found among the 3 years.

DISCUSSION

The 2 sympatric and related species of prions *Pachyptila belcheri* and *P. desolata* prey mainly on the amphipod *Themisto gaudichaudii* during the chick-rearing period. *P. belcheri* and *P. desolata*, however, are segregated by feeding on different euphausiids, *Thysanoessa* sp. and *Euphausia vallentini*, respectively. The occurrence of Antarctic krill *Euphausia superba* in food samples suggests that the 2 prions performed some trips far away from their breeding grounds, in southern Antarctic waters. The stable-carbon and -nitrogen isotopic compositions of chick feathers were identical in both species, suggesting no important trophic segregation during the breeding period. The ratios were, however, different in adult feathers, indicating distinct moulting foraging areas when birds are not constrained to return to the colonies.

Pachyptila belcheri

This study is the first to detail the dietary habits of *Pachyptila belcheri*. At Iles Kerguelen, the species is mainly a macrozooplankton and micronekton feeder, with crustaceans forming the bulk of the food, and fish and squids accounting for a smaller proportion by mass

of the diet. The 2 more important prey items were *Themisto gaudichaudii*, which dominated both by number and by mass, and the euphausiid *Thysanoessa* sp. This is in agreement with preliminary results showing the predominance of undetermined hyperiid amphipods in its diet, but our results are not in accordance with *Euphausia vallentini* as the main euphausiid prey (Bretagnolle et al. 1990). At the Falkland Islands (southern Atlantic Ocean), where the only other important population of *P. belcheri* breeds (Woods & Woods 1997), the species feeds mainly on crustaceans, the main item being again *T. gaudichaudii*, together with euphausiids (Strange 1980, Thompson 1989). At sea in the subantarctic Pacific, the species also prey upon *T. gaudichaudii* (Harper 1972). Taken together, the results reinforce the hypothesis that *P. belcheri* is ecologically linked to *T. gaudichaudii* by its food throughout its range (Imber 1981), even if the species is able to feed upon a fairly large number of different items (Table 3).

Themisto gaudichaudii is one of the main macrozooplankton species in the Southern Ocean (Kane 1966), including Iles Kerguelen (Bocher et al. 2001). There, *Pachyptila belcheri* consistently caught 2 size classes of the amphipod, smaller individuals outnumbering larger ones during the 3 breeding seasons. A recent detailed comparison of the size structure of *T. gaudichaudii* between *P. belcheri* food samples and concomitant net hauls indicated that birds caught most juveniles and almost all adult amphipods in offshore waters (Bocher et al. 2001). This is also supported by the abundance of *Thysanoessa* sp. in its diet, a species which does not occur in the Golfe du Morbihan (Bost et al. 1994, Bocher et al. 2001).

Surprisingly, benthic organisms were common prey of *Pachyptila belcheri*. They include the gammarids *Polycheria kergueleni*, *Paramoera fissicauda* s.l., *Jassa* sp., *Cicadosa cicadoides* and *Uristes gigas* (a benthopelagic species), the polychaete *Platynereis australis* and the bivalve *Gaimardia trapesina*. The species occur in the coastal waters of Iles Kerguelen (Arnaud 1974, Bellan-Santini & Ledoyer 1974, Duchêne 1984), where some of them are known to be associated with fronds of the giant kelp *Macrocystis pyrifera* (Arnaud 1974). This, together with visual observations of prions feeding in inshore waters (Ridoux 1994, Reid et al. 1997), shows that *P. belcheri* regularly foraged close to the coastline in the kelp belt area surrounding the archipelago. Drifting *Macrocystis* and *Durvillea* kelp transport vagile amphipods and sessile benthic invertebrates (*G. trapesina*) and also the barnacle *Lepas australis*, which attaches itself to floating objects (Arnaud 1973, Helmuth et al. 1994). Since prions have been observed foraging on floating kelps in offshore waters (Harper 1987), it is likely that unsettled cypris

larvae of barnacles were caught in association with kelp rafts, as seen with grey-backed storm petrels *Garrodia nereis* (Jouventin et al. 1988). Finally, the occurrence of *Euphausia superba*, *Pasiphae scotiae* and myctophid fish in food samples indicates feeding in more distant oceanic waters (Lomakina 1966, Clarke & Holmes 1987, Duhamel 1998). During the chick-rearing period, *P. belcheri* thus forage in a wide variety of habitats, where they feed on different marine organisms.

Isotopic signatures of chick feathers of *Pachyptila belcheri* show an enrichment relative to food of 2.8‰ for $\delta^{13}\text{C}$ and 4.4‰ for $\delta^{15}\text{N}$ (Table 4). These values are within the range of those (-0.4 to 4.4‰ for $\delta^{13}\text{C}$ and 1.1 to 5.6‰ for $\delta^{15}\text{N}$) obtained from feathers of various species of birds (Mizutani et al. 1990, 1992, Hobson & Clark 1992a,b, Thompson & Furness 1995, Bocher et al. 2000a, Cherel et al. 2000). Feathers from chicks and adults had similar isotopic signatures, an effect most pronounced for $\delta^{15}\text{N}$ values. Similar values in $\delta^{15}\text{N}$ suggest no major changes in the trophic position of the birds between the moulting period of the chicks (breeding period) and the moulting period of adults (inter-breeding period). This is consistent with adults from Iles Kerguelen feeding at the same trophic level year long, assuming that isotopic signatures of major prey items in a given area do not change seasonally.

Pachyptila desolata

The only other detailed dietary investigations of *Pachyptila desolata* were conducted at Bird Island, South Georgia (Prince 1980, Reid et al. 1997). At both localities, the bulk of the food is formed by crustaceans, with fish accounting for most of the remainder. At Iles Kerguelen, which are located in the immediate vicinity of the Polar Front (Park et al. 1993), birds preyed mainly upon *Themisto gaudichaudii* and the subantarctic krill *Euphausia vallentini*, and, to a lesser extent, on *Calanus simillimus* and *Lepas australis*. At South Georgia, located south of the Polar Front (Peterson & Whitworth 1989), the main dietary items include Antarctic krill *Euphausia superba* and the copepods *Calanoides acutus*, *Rhincalanus gigas* and *Drepanopus* sp. (Prince 1980, Reid et al. 1997). Large interannual variations in the dietary importance of *E. vallentini* was found at Iles Kerguelen and birds from South Georgia shift between Antarctic krill to copepods and *T. gaudichaudii* in years of low krill availability (Liddle 1994, Reid et al. 1997). Taken together, these data suggest that *P. desolata* is an opportunist feeder that preys upon the most available swarming pelagic crustaceans. Like *P. belcheri*, the occurrence of benthic

Table 7. *Pachyptila* spp. Broad prey classes and proportions by number (%N) and by mass (%M) of the main prey species ($\geq 10\%$) in the diet of prions breeding at different localities

Species	<i>P. turtur</i>		<i>P. belcheri</i>		<i>P. desolata</i>		<i>P. salvini</i>		<i>P. vittata</i>			
	Crozet (Ridoux 1994) (n = 6) %N %M	South Georgia (Prince & Copestake 1990) (n = 40) %N %M	Kerguelen (present study) (n = 85) %N %M	Kerguelen (present study) (n = 104) %N %M	South Georgia (Prince 1980) (n = 90) %N %M	South Georgia (Reid et al. 1997) (n = 33 & 60) %N %M	Marion (Gartshore et al. 1988) (n = 39) %N %M	Crozet (Ridoux 1994) (n = 33) %N %M	Chatham (Imber 1981) (n = 57) %N %M			
Crustaceans	100	95	100	82	100	98	100	44	100	88	97	
Euphausiacea	<1	2	18	20	18	20	11 ^a	10 ^a	25 ^a	<1	13	6
<i>Euphausia superba</i>	—	38 ^a	<1	4	<1	4	10 ^a	—	—	—	—	—
<i>Euphausia vallentini</i>	<1	—	<1	<1	<1	9	15	5 ^a	25 ^a	<1	6	—
<i>Thysanoessa</i> sp.	<1	—	18	16	<1	<1	<1	—	—	<1	6	—
Amphipoda	7	63	79	59	72	60	6 ^a	—	—	3	59	20
<i>Hyperitella</i> sp./antarctica	<1	—	<1	<1	5 ^a	2 ^a	—	89 ^a	74 ^a	<1	<1	—
<i>Themisto gaudichaudii</i>	3	45	76	57	3 ^a	5 ^a	8–16 ^a	68 ^a	6 ^a	3	41	<1
<i>Primno macropa</i>	3	14	<1	<1	<1	<1	<1	21 ^a	67 ^a	3	10	—
<i>Platyscelus ovoides</i>	—	—	—	—	—	—	—	—	—	—	11	—
Copepoda	—	—	<1	<1	9	<1	78 ^a	32 ^a	—	95	15	70
<i>Neocalanus tonsus</i>	—	—	—	—	—	—	—	—	—	—	—	68
<i>Rhincalanus gigas</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Calanoides acutus</i>	—	37 ^a	—	—	<1	<1	17–78 ^a	7–75 ^a	—	<1	<1	—
<i>Drepanopus</i> sp./pectinatus	—	—	<1	<1	—	—	13–80 ^a	<1–2 ^a	—	85	9	—
Unidentified copepods	—	—	<1	<1	<1	<1	—	—	—	11	4	—
Cirripedia	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lepas australis</i>	93	31	3	<1	8	<1	—	—	—	<1	<1	<1
Fish	<1	<1	<1	12	<1	13	<1	<1	2	<1	2	2
Cephalopods	<1	5	<1	6	<1	3	<1	<1	<1	<1	4	<1
Others	<1	<1	<1	<1	<1	2	<1	<1	—	<1	7	<1

^a% of the crustacean diet

organisms and of *E. superba* and mesopelagic fish in its diet (Table 6), together with observations at sea (Harper 1972, 1987, Prince 1980, Marchant & Higgins 1990, Goss et al. 1997, Reid et al. 1997, Stahl et al. in press), show that *P. desolata* forage in different habitats during the chick-rearing period at Iles Kerguelen.

Prions, including *Pachyptila desolata*, sometimes dive for food, propelled by their wings, and have been reported to dive down to about 3 m (Downes et al. 1959, Harper 1987, Warham 1990, Goss et al. 1997). At Iles Kerguelen, maximum depth gauges indicated that *P. desolata* foraged in the top 7 m of the water column with a mean at 4 m. Such depths are in agreement with the few depth gauges recorded from *P. belcheri* and blue petrels *Halobaena caerulea* showing that the 2 species exploit a water column 5 to 7 m deep (Chastel & Bried 1996). Prions and blue petrels are poorly suited for diving, and accordingly, their diving performance is much lower than that of true diving birds such as diving petrels *Pelecanoides* spp. and small alcid (see review in Bocher et al. 2000b). Consequently, they are epipelagic foragers, obtaining most of their food at or near the surface (Warham 1990).

Stable-carbon and -nitrogen isotope concentrations were higher in adult feathers than in chick feathers of *Pachyptila desolata* (Table 4). Since there is little enrichment in $\delta^{13}\text{C}$ with an increase in trophic level, $\delta^{13}\text{C}$ provides information about the source of carbon at the base of the food chain (Wada et al. 1987, Hobson 1993). In marine habitats, $\delta^{13}\text{C}$ has been used to discriminate between inshore/benthic feeding and pelagic feeding in seabirds (Hobson 1993) and to distinguish between breeding and wintering areas, using latitudinal variations of $\delta^{13}\text{C}$ in phytoplankton (Best & Schell 1996). Higher $\delta^{13}\text{C}$ values in adult feathers could theoretically indicate more inshore feeding habits during moult, but *P. desolata* was not observed on the Kerguelen shelf and in any other neritic areas at that time (Stahl et al. in press). On the other hand, the $\delta^{13}\text{C}$ value of adult feathers are close to those reported for black-browed

albatrosses *Diomedea melanophrys* from Iles Kerguelen, which are known to moult in subtropical waters (Cherel et al. 2000). This suggests a latitudinal migration of adult *P. desolata* during moult, birds foraging north of 40 to 45° S, a belt known as the Subtropical Front, marked by a strong, gradient of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary production in marine surface waters (François et al. 1993, Altabet & François 1994). Higher $\delta^{15}\text{N}$ values in adult feathers than in chick feathers of *P. desolata* are also probably a consequence of this increase in $\delta^{15}\text{N}$ of particulate organic matter, rather than different trophic levels of adult birds between the chick-rearing and moulting periods. The enrichment of adult feathers in both ^{13}C and ^{15}N is thus consistent with adult foraging in different water masses during breeding and wintering, i.e. south and north of 40 to 45° S, respectively. This is in agreement with observations at sea showing birds in the Polar Frontal Zone and Antarctic in summer, and a dispersion towards warmer waters in winter (Stahl et al. in press). Using isotopic analysis of baleen, similar ecological information was obtained previously on the southern right whale *Eubalaena australis*, which migrates annually across the Subtropical Front (Best & Schell 1996).

Dietary segregation among prions

This study shows broad similarities in the diet of the sympatric *Pachyptila belcheri* and *P. desolata* during the chick-rearing period at Iles Kerguelen. The 2 species fed mainly on the same macrozooplanktonic species and mesopelagic fish, and their major food item was *Themisto gaudichaudii*, which is an important prey for other species of prions as well (Table 7). However, *P. belcheri* and *P. desolata* segregated by catching different euphausiids, *Thysanoessa* sp. and *Euphausia vallentini*, respectively. A detailed comparison also shows that the food of *P. desolata* included more very small prey (<4 mm), i.e. it fed on more copepods (8.6 vs <0.1% by number) and larvae of *Lepas australis* (8.4 vs 2.7%) than *P. belcheri*. It is nevertheless difficult to assess whether dietary differences result from deliberate prey selection or from changes in abundance and availability of prey items, because *P. belcheri* breeds on average 40 d earlier than *P. desolata* (Bretagnolle et al. 1990), thus reducing the overlap in the chick-rearing periods and hence potential competition for food at that time.

Like most procellariiforms (Prince & Morgan 1987), the main feeding method of prions is surface seizing (Harper 1987). However, unlike *Pachyptila belcheri*, *P. desolata* also forage by hydroplaning and surface filtering (Prince 1980, Harper 1987, Warham 1990, Goss et al. 1997). This behaviour is characteristic of the larger prion species, which have deep broad bills and lamel-

lae fringing the inside of the upper mandible, allowing them to collect minute organisms at the sea surface by filtering (Prince & Morgan 1987). Most of the prey items which occurred in the diet of both *P. belcheri* and *P. desolata* were probably caught individually, but the filtering or hydroplaning technique is likely to be the main explanation of *P. desolata* feeding more on copepods than *P. belcheri* at Iles Kerguelen. A review of the available information on prions shows that the larger the development of palatal lamellae, generally the higher the importance of copepods in their food (Table 7). Copepods are minor items in the diet of *P. belcheri*, *P. turtur* and *P. crassirostris*, which lack a filtering apparatus (Imber 1981, Prince & Copstake 1990, Ridoux 1994, this study), and their importance, together with that of bill width and development of lamellae, increases in the diet of *P. desolata* (Prince 1980, Reid et al. 1997, this study), *P. salvini* (Ridoux 1994) and *P. vittata* (Imber 1981, Klages & Cooper 1992). A puzzling exception is *P. salvini* at Marion Island (Gartshore et al. 1988). The lack of *Drepanopus pectinatus* (a neritic copepod which is the main prey of the species at the nearby Crozet archipelago; Ridoux 1994) in Marion waters (Hulsemann 1985) cannot explain by itself the total absence of copepods in its diet. The situation is more likely to result either from temporal variability in prey availability or from the inability to find small, easily overlooked prey, in digested food samples.

Stable-carbon and -nitrogen isotope concentrations are similar in chick feathers of *Pachyptila belcheri* and *P. desolata*, thus emphasizing that both species fed at the same trophic level in the same broad foraging areas during the chick-rearing period. $\delta^{13}\text{C}$ values of adult *P. desolata*, however, are much higher than in adult *P. belcheri* (Table 4). As discussed above, high $\delta^{13}\text{C}$ values suggest that adult *P. desolata* moulted north of the Subtropical Front. Conversely, the low value of *P. belcheri* feathers suggests birds moulted in Antarctic waters, because Antarctic animals, including fulmarine petrels, have similar low $\delta^{13}\text{C}$ values (Hodum & Hobson 2000). Accordingly, the few observations at sea of moulting *P. belcheri* were confined south of Iles Kerguelen, in Antarctic waters between 57 and 64° S (Stahl et al. in press). The stable isotopic composition of adult feathers thus shows a complete trophic segregation between the 2 species of prions during the inter-breeding periods, birds foraging in different water masses located north and south of the Iles Kerguelen when they moult.

Feeding frequency was slightly higher, but food mass slightly lower, for *Pachyptila desolata* than for *P. belcheri*, resulting in a similar average amount of food given to the chicks (16 g d⁻¹). Also, hatching, fledging and breeding successes were identical, with no large

interannual variations for each of the 2 species (Table 5). When comparing with breeding success over years in *P. belcheri* (Chastel et al. 1995), the years 1995, 1996 and 1997 were normal ones, including no good or bad breeding seasons, even if we observed some variations in food mass and chick's growth between the 3 years (but see also Weimerskirch et al. 1999).

Short trips, long trips and foraging areas

Recent investigations have demonstrated that several procellariiforms use a 2-fold foraging strategy during the chick-rearing period, adults alternating between short (ST) and long trips (LT) (Weimerskirch et al. 1994). Satellite tracking and biogeography of prey show that birds forage in different areas during ST and LT (Weimerskirch et al. 1997, Weimerskirch & Cherel 1998, Catard et al. 2000). Both *Pachyptila belcheri* and *P. desolata* use this strategy, ST lasting 1 to 3 d (most 1 d trips) and LT lasting 4 to 11 d in both species (Weimerskirch et al. 1999, Duriez et al. 2000). The small size of prions currently precludes the use of electronic devices, but food analysis can give an initial insight into their foraging grounds during LT and ST. At first glance, it is obvious that some prey were barely digested (*Euphausia vallentini*, *Polycheria kergueleni*, *Paramoera fissicauda* s.l., *Uristes gigas* and *Lepas australis*) while others were always well digested (*Euphausia superba*), suggesting that the former were taken near the colonies and the latter during LT. The best species indicator of LT is *E. superba*, because the northern limit of Antarctic krill south of Iles Kerguelen is 59° S, with the highest densities always recorded further south (Hosie et al. 1988, Miquel 1991, Pakhomov 2000). Thus, like the larger white-chinned petrel *Procellaria aequinoctialis* (Catard et al. 2000), both *P. belcheri* and *P. desolata* are able to forage on adult *E. superba* (55 mm BL) in southern Antarctic waters >1000 km from the breeding grounds.

Since *Euphausia superba* indicates LT and stomach oil is much more prominent after LT than ST (Weimerskirch & Cherel 1998, Weimerskirch et al. 1999), food samples were divided into 2 groups according to the presence (presumably LT) or absence (presumably ST) of oil and/or *E. superba*. The comparison indicates *Pachyptila belcheri* and *P. desolata* fed more on fish (21 and 22% by reconstituted mass, respectively) and squid (14 and 7%) during LT, and more on crustaceans (95 and 90%), including *Themisto gaudichaudii*, *Polycheria kergueleni*, *Paramoera fissicauda* s.l., *Euphausia vallentini* and *Calanus simillimus* during ST. Overall, the results agree well with the level of digestion of the prey and their known biogeography. *E. vallentini* and *C. simillimus* are mainly found in the Polar Frontal

Zone, occurring commonly in Kerguelen waters (Lomakina 1966, Pakhomov 1993, Semelkina 1993, Atkinson & Sinclair 2000), and *P. kergueleni* and *P. fissicauda* s.l. are species associated with the kelp bed (see above). Some prey items obviously taken in Kerguelen waters also occur in significant amounts in LT samples, indicating that prions collected food for their chicks on their way back from the distant Antarctic foraging grounds to the colonies. For example, much more *T. gaudichaudii* were taken during ST than during LT, but the frequency distributions of amphipod length were identical between ST and LT samples (data not shown), suggesting that *T. gaudichaudii* in LT samples were also taken in Kerguelen waters. Accordingly, the density of *T. gaudichaudii* is known to increase in the vicinity of the archipelago (Pakhomov 1993, Bocher et al. 2001).

Observations at sea during summer (Veit & Hunt 1991, Stahl et al. in press) are in agreement with our data, because high densities of *Pachyptila desolata/salvini* were identified foraging on the Kerguelen shelf and slope (the feeding areas during ST, and presumably at the end of some LT), but also over southern banks and in oceanic Antarctic waters between 61 and 65° S (the feeding area during LT). Fewer *P. belcheri* were identified at sea, but, again, highest densities were recorded either in the Kerguelen area or in oceanic Antarctic waters (Stahl et al. in press). Prions in Antarctic waters are therefore not only non-breeders or failed breeders, but at least some are breeding birds.

When congeneric species are in sympatric conditions, some segregation in nest sites and/or food can be expected. At Iles Kerguelen, 2 pairs of closely related planktivorous species have been studied, the prions *Pachyptila belcheri* and *P. desolata*, and the diving petrels *Pelecanoides georgicus* and *P. urinatrix*. Within each pair, an almost complete segregation was observed in the nesting habitats, together with a partial segregation in the timing of breeding (Weimerskirch et al. 1989, Bretagnolle et al. 1990). The differences are less marked, however, when looking at the feeding ecology. There is a broad overlap in the prey and presumably the foraging areas of prions (this study), while a complete trophic segregation was found in the 2 diving petrels during chick-rearing (Bocher et al. 2000a). Conversely, the stable isotopic composition of feathers indicates a complete trophic segregation between prions, but no segregation between diving petrels (Bocher et al. 2000a), during the post-breeding moulting periods. More information is needed on the birds' foraging areas all year round and on the abundance and availability of marine resources within the areas to further investigate the extent of ecological segregation among sympatric and taxonomically related species of seabirds.

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