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THE DIETS AND DIETARY SEGREGATION OF SEABIRDS AT THE SUBANTARCTIC CROZET ISLANDS

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Part 2

Bathothauma sp.	4	3.8	(3.7-3.8)	3	202	(199-205)	57	(55-59)
Taonius sp. (large)	2	6.4	(3.5-9.3)	2	380	(200-559)	162	(33-290)
T. pavo (small A)	1	4.1		1	238		48	
T. pavo (small B)	1	6.7		1	401		142	
Galiteuthis glacialis	571	4.8±0.4	(3.0-5.7)	200	209	(133-246)	84	(26-123)
Mesonychoteuthis hamiltoni	1	7.9		1	336		265	
Unidentified	1	4.8						
Eroded beaks	8							
SEABIRDS								
Penguin feathers	numerous							

[a] Lower Rostral Length
[b] Dorsal Mantle Length

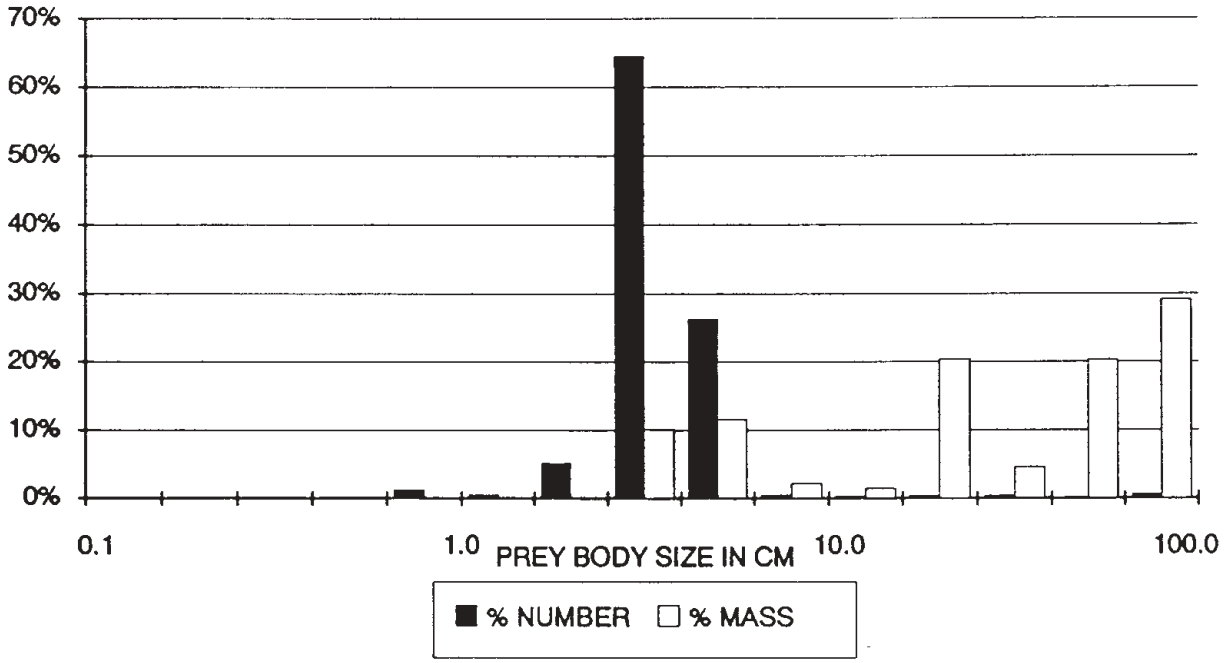

Figure 10

Prey-size distribution in the diet of the Lightmantled Sooty Albatross.

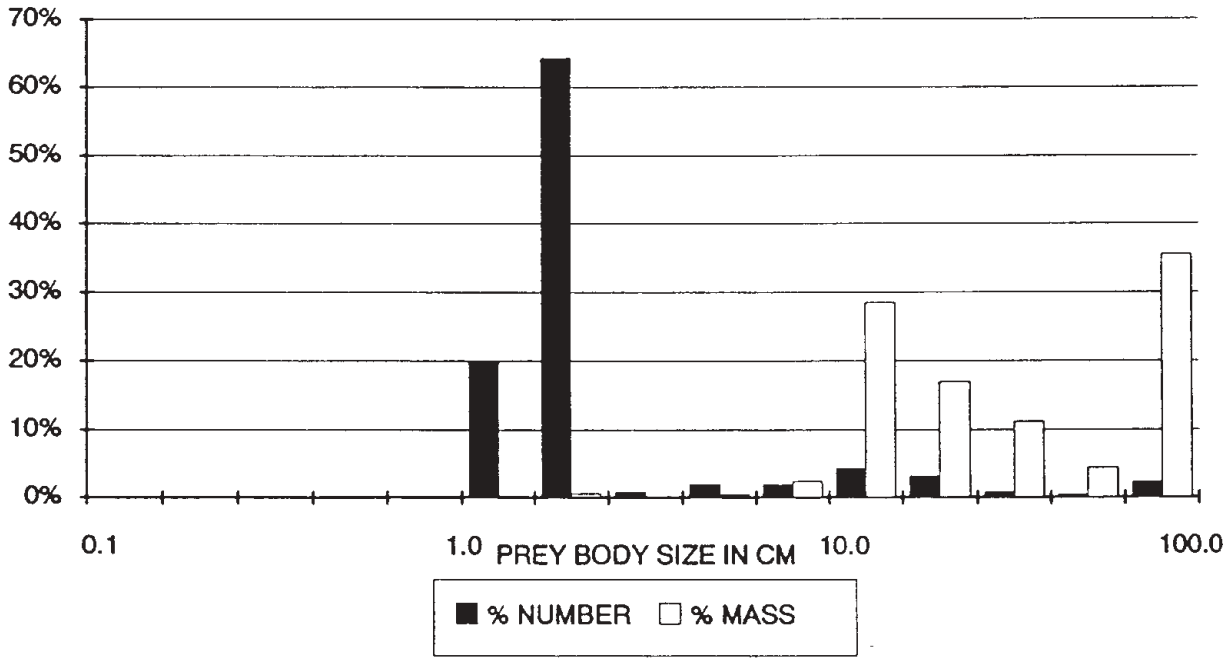

Figure 11

Prey-size distribution in the diet of the Sooty Albatross.

Previous reports on the diet of the Sooty Albatross are mostly qualitative or only deal with the squid part of the diet. Indeed, squid have long been considered as the main dietary item. Other prey types were considered to be minor components of the diet and included fish, crustaceans and scavenged seabirds at the Crozet Islands (Mougin 1970b, Weimerskirch *et al.* 1986), penguins, Common Diving Petrels *Pelecanoides urinatrix*, crustaceans and fish at Tristan da Cunha (Hagen 1952), and penguins, *Velella* cnidarians and fish, among which *Thyrsites atun*, at Saint-Paul and Amsterdam Islands (Segonzac 1972).

The analysis of squid beaks from pellets at Marion Island showed a broad array of 36 species with the family Onychoteuthidae accounting for 70% of the total estimated squid biomass and the families Cranchiidae and Histioteuthidae representing 19% and 8%, respectively (Berruti & Harcus 1978, Imber & Berruti 1981). The order of prevalence was thus the same as in the current study although the onychoteuthids *K. longimana* and *M. knipovitchi* were more dominant by percentage mass at Marion Island than at the Crozets.

Foraging range and behaviour

The Sooty Albatross has a very broad latitudinal distribution in the Southern Ocean, from 37° to 57°S in the Atlantic sector (Bierman & Voous 1950) and from 35° to 50°S with vagrants as far south as 65°S in the Indian sector. The species is more abundant in the northern part of this range (Weimerskirch *et al.* 1986, Stahl 1987). The occurrence of Antarctic Krill on the one hand and of numerous squid species of temperate or tropical affinities (*Cycloteuthis* sp., *Ancistrocheirus lesueuri*, Lycoteuthidae, *Histioteuthis* spp. A, *Octopoteuthis* sp., *Liocranchia* sp. and *Megalocranchia* sp.) on the other confirms that breeding birds have distant feeding grounds as suggested by at-sea sightings.

Feeding methods of Sooty Albatrosses are poorly known since they are rarely seen feeding. However, surface seizing, the most common albatross feeding method, is supposed to be the rule (Harper *et al.* 1985). The occurrence of euphausiids in the present results suggests filter feeding whereas the importance of seabirds and large squids, some of them estimated to reach 6 kg in body mass (Table 25) suggests extensive scavenging. Sooty Albatrosses are reported to be always excluded by larger seabird species competing for food and extensive nocturnal foraging is suspected (Weimerskirch *et al.* 1986). In contrast with the *Diomedea* albatrosses, which readily congregate at the same food source, Sooty Albatrosses are mostly solitary at sea (Weimerskirch *et al.* 1986). Nocturnal feeding, dark plumage, solitary foraging in oceanic regions with relatively low productivity might combine to reduce interactions with the more powerful and aggressive *Diomedea* albatrosses and giant petrels *Macronectes* spp. A similar combination of features is found in the gadfly petrels (see below).

NORTHERN GIANT PETREL *MACRONECTES HALLI* AND SOUTHERN GIANT PETREL *MACRONECTES GIGANTEUS*

Results

Samples

The stomach contents of five Northern Giant Petrels were collected on Ile de l'Est, Crozet Islands, in February 1982 and 25 on Ile de la Possession in January 1983. The samples were obtained by collecting regurgitations of chicks previously observed being fed by an adult. The mean mass of the samples was 522 ± 244 g (70-1005 g) of which 159 ± 150 g (10-530 g) was oil and 211 ± 158 g (10-520 g) was fine unidentifiable liquid mush drained out through the 250 μ-mesh-sized sieve. The quantitative analysis was performed on the identifiable

fragments which amounted to 150 ± 121 g (0-410 g).

The stomach samples of 10 Southern Giant Petrels were collected on Ile de l'Est in February 1982 and 18 additional samples were obtained on Ile de la Possession from January to March 1983 from chicks recently fed by their parents. Mean sample mass was 426 ± 147 g (255-720 g) of which 141 ± 108 g (30-350 g) was oil and 109 ± 93 g (15-375 g) was unidentifiable mush of less than 250 μ. Identifiable remains (170 ± 155 g, 0-450 g) were analysed quantitatively.

General composition

The food of both species was constituted mostly of bird carrion complemented by marine organisms which accounted for no more than 10% by mass in the Southern Giant Petrel diet and less than 1.5% for the northern species (Table 26). Owing to the peculiarity of their feeding habits no numerical analysis was performed since food items rarely occurred as discrete individuals. In both species, penguins largely prevailed in the analyses by occurrence and by mass and no significant difference was observed in the occurrence of penguin and procellariiform remains in their diets. The frequency of marine organisms in the diet of the Southern Giant Petrel was significantly higher than in the diet of its congener (Chi square = 4.96; df = 1; $p < 0.05$).

Crustaceans

A single stalked parasitic copepod *Sphyrion lumpi* was the only crustacean item found in the samples from Northern Giant Petrels. Such copepods (about 40 mm long from the hook to the posterior margin) are known to be hosted by several benthic fish families of which two are known in the Southern Ocean: the deep-sea cods Moridae and the grenadiers Macrouridae (Z. Kabata pers. comm.). The lophogastrid mysid *Gnathophausia ingens* and another unidentified taxon were the only crustacean prey items found in the food of the Southern Giant Petrel.

Cephalopods

Three unidentified tentacles were the only fresh squid remains found in the food of the Northern Giant Petrel. However, 43 loose lower beaks accumulated in the stomachs from previous meals were identified as belonging to six taxa, of these *Kondakovia longimana* and *Moroteuthis knipovitchi* were by far the most important squid species either by number or estimated mass (Table 27). Fresh squid remains occurred twice in the samples from Southern Giant Petrels and included fragments (90 mm-long fin, tentacles and gladius) of *Moroteuthis* sp. Additionally, 12 accumulated lower beaks of seven taxa were also found (Table 28).

The cephalopod species found as accumulated items in both species of giant petrels were almost the same as those found loose in King Penguin stomach contents and were substantially different from the species preyed upon by surface squid eaters like the albatrosses (see relevant sections in the present work). Furthermore, with the exception of the larger ones, many of these were eroded in a manner typical to those found in King Penguin samples, suggesting that most of them might have been ingested through scavenging on penguin carcasses rather than directly preyed upon at sea.

Fish

No fish remains occurred in the food of the Northern Giant Petrels whereas fragments of large (about 350 mm) unidentified fish were present in three samples of its congener.

Carrion

Penguin scraps constituted by far the bulk of the food for both Northern and Southern Giant Petrels (Table 26). King Penguins and crested

TABLE 26

THE DIET OF GIANT PETRELS AT THE CROZET ISLANDS

Prey Species	Northern Giant Petrel (N=30)			Southern Giant Petrel (N=28)		
	Occurrence %	Mass (g)	Mass %	Occurrence %	Mass (g)	Mass %
CRUSTACEANS	**3.3**	**3**	**0.1**	**3.6**	+	+
Copepods						
Sphyrion lumpi	3.3	3	0.1			
Mysids						
Gnathophausia ingens				3.6	+	+
Unidentified crustaceans				3.6	+	+
CEPHALOPODS	**3.3**	**55**	**1.4**	**7.5**	**160**	**4.7**
Teuthoidea						
Moroteuthis sp.				3.3	50	1.5
Unidentified	3.3	55	1.4	3.3	110	3.2
FISH	**0.0**	**0**	**0.0**	**10.7**	**200**	**5.9**
Unidentified	0.0	0	0.0	10.7	200	5.9
CARRION	**96.3**	**3830**	**98.5**	**94.6**	**3035**	**89.4**
Penguins						
Aptenodytes patagonicus	10.0	120	3.1	21.4	200	5.9
Eudyptes sp.	30.0	1165	30.0	7.1	235	6.9
Unidentified penguins	40.0	1865	48.0	53.6	2415	71.1
Procellariiformes						
Pachyptila salvini	6.7	160	4.1	3.6	30	0.9
Unidentified prions	6.7	160	4.1	10.7	40	1.2
Halobaena caerulea				3.6	20	0.6
Pelecanoides urinatrix	23.3	360	9.3	7.1	30	0.9
P. georgicus				3.6	20	0.6
Unidentified diving-petrels	17.9	25	0.7			
Unidentified procellariiformes	3.3	+	+	7.1	45	1.3

TABLE 27

SUMMARY OF ACCUMULATED ITEMS IN NORTHERN GIANT PETREL STOMACH CONTENTS (N=30)

Items	Number of items	Measurements (mm)[a]		Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean±S.D. (range)	n	Mean	(range)	Mean	(range)
CEPHALOPODS							
Upper beaks	25						
Lower beaks	43						
Onychoteuthis sp. A	1	5.6	1	211		355	
Moroteuthis ingens	1	10.7	1	743		3371	
M. knipovitchi	8	4.6±0.6 (4.0-5.3)	6	149	(126-179)	186	(110-293)
Kondakovia longimana[c]	18	7.8±3.9 (2.5-12.5)	12	476	(71-943)	2264	(21-5988)
Gonatus antarcticus	1	6.1	1	218		214	
Lycoteuthis sp. B	1	5.1	1	108		60	
Eroded beaks	13						
Gladii							
Kondakovia longimana	1	550	1	550		1743	
Taonine cranchiid	1	400	1	400		395	
Unidentified teuthoidea	1	300	1				

[a] Lower Rostral Length and Gladius Length

[b] Dorsal Mantle Length

[c] *K. longimana* LRL distribution was clearly bimodal with seven small individuals (estimated DML 19.5±12.4 cm, range 7.1-43.2 cm; estimated body mass 330±371 g, range 21-1083 g) and five large individuals (estimated DML 87.0±7.3 cm, range 76.9-94.3 cm; estimated body mass 4972±994g, range 3656-5988 g)

TABLE 28

SUMMARY OF ACCUMULATED ITEMS IN SOUTHERN GIANT PETREL STOMACH CONTENTS (N=33)

Items	Number of items	Measurements (mm)[a]			Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean±S.D.	(range)	n	Mean	(range)	Mean	(range)
CEPHALOPODS								
Upper beaks	5							
Lower beaks	12							
Onychoteuthis sp. A	1							
Moroteuthis ingens	1							
Kondakovia longimana	1	6.1		1	266		405.4	
Psychroteuthis sp.	1	6.1		1			63.6	
Batoteuthis sp.	2	4.2	(4.0-4.4)	2	121	(116-126)	76.6	(67.5-85.7)
Teuthowenia pellucida	1	5.3		1	226		100.3	
Eroded beaks	13							
Gladii								
Taonine cranchiid	1	320		1	320		246.4	

[a] Lower Rostral Length or Gladius Length
[b] Dorsal Mantle Length

penguins were identified. Small Procellariiformes, mainly diving petrels and prions, were the second most important form of carrion. No seal or fur seal carrion was found. No significant interspecific differences were observed in the occurrence and relative proportion by mass of penguin *vs* procellariiform remains. Size distributions for all prey species pooled are nearly identical for both giant petrels (Figs 12 and 13).

Field observations

Additional non-quantitative dietary data came from opportunistic field observations of foraging giant petrels at Ile de la Possession (Table 29). These observations match with the diet determined from the stomach sample analysis but, in addition, provided evidence of seal consumption either from carcasses on the beach, from placentae or through association with feeding Killer Whales *Orcinus orca*. Marine mammal scavenging mostly occurred in spring during the Southern Elephant Seal *Mirounga leonina* breeding season, at a time when stomach contents were not sampled.

Comparison with other studies

Early observers working close to whaling or seal hunting stations or on board whaling vessels mainly reported giant petrels feeding on offal of marine mammal origin (Matthews 1929, Falla 1937, Bierman & Voous 1951) whereas at other localities penguin carcasses were reported as providing the bulk of their diet (Paulian 1953, Mougin 1968, Voisin 1968, Conroy 1972, Johnstone 1977).

Direct predation on seabirds and various marine organisms has also been reported as an important component of the diet. In Adélie Land, Southern Giant Petrels preyed on live Emperor Penguin *Aptenodytes forsteri* chicks, with the aim of eating their viscera and stomach contents (Arnaud 1974). At Kerguelen channichthyid fish were also caught, their viscera being the only part consumed (Arnaud 1972). At Heard Island, procellariiform and cephalopod prey caught at sea were more frequently found in the food of the Southern Giant Petrels than were penguin or seal fragments (Downes *et al.* 1959). In the Ross Sea, two Southern Giant Petrels collected at sea had been feeding on pelagic squid (including *Psychroteuthis glacialis* and *Galiteuthis glacialis*) and Antarctic Krill (Ainley *et al.* 1984). This variety of food resources demonstrates the plasticity of giant petrel feeding behaviour according to local food resources but shows no clear interspecific differences in their diets.

Comparative studies performed at Macquarie Island and South Georgia, two localities where both species breed sympatrically, also failed to exhibit clear-cut interspecific differences. At the former locality, both species rely largely on penguin corpses, generally found at sea. Some degree of segregation only appeared with the secondary food sources, Southern Giant Petrels preyed on marine organisms such as fish and squids and the northern species complemented its diet with pinniped and penguin carcasses found ashore (Johnstone 1977). At South Georgia, the only previous quantitative study indicated also the same kind of slight interspecific differences. Penguins provided the bulk of the food for both species. However, the proportion of Antarctic Fur Seal *Arctocephalus gazella* carrion and of marine organisms varied between the two species of giant petrels (Table 30, Hunter 1983). In addition, annual and seasonal variations and, above all, sexual intraspecific differences were of greater magnitude than were interspecific differences (Hunter 1987).

Dietary results obtained at the Crozet Islands are consistent with previous studies and further emphasize the poor feeding segregation between both species of giant petrels.

Foraging range and behaviour

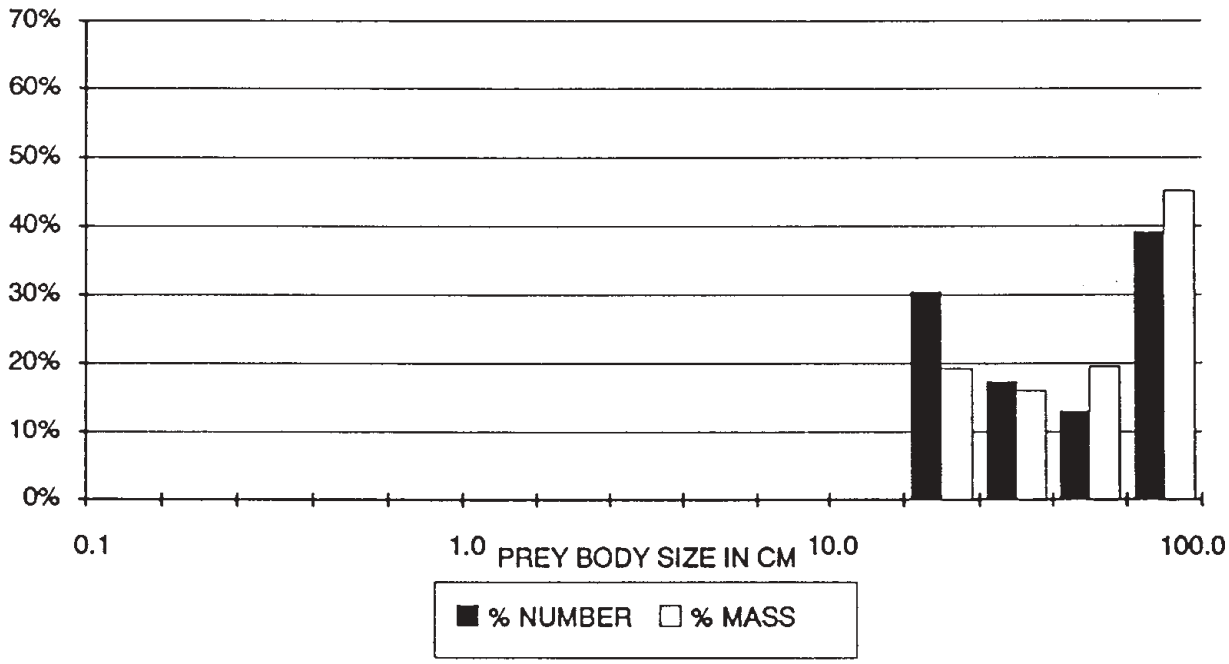

Figure 12
Prey-size distribution in the diet of the Northern Giant Petrel.

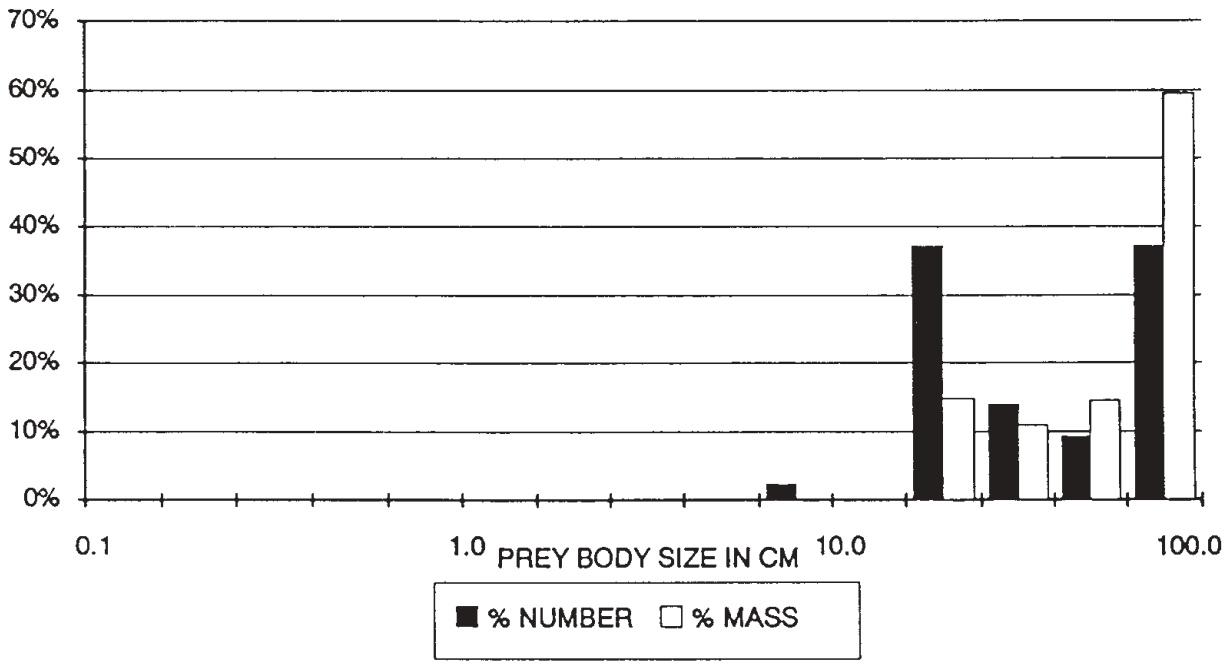

Figure 13
Prey-size distribution in the diet of the Southern Giant Petrel.

TABLE 29

OBSERVATIONS OF GIANT PETRELS FORAGING IN THE LITTORAL ZONE

Dates	Foraging habitats	Food source	Numbers of giant petrels	
			M. halli	*M.giganteus*
18.06.82	sandy beach	King Penguin regurgitations (myctophids)	---------- 10 ----------	
10.08.82	kelp beds	adult King Penguin carcass	4	2
11.08.82	sandy beach	King Penguin chick carcass	7	6
18.09.82	sandy beach	King Penguin chick carcass	1	0
23.09.82	sandy beach	elephant seal placentae	5	0
11.10.82	kelp beds	moribund fish (*c.* 1-m long)	3	0
19.10.82	coastwards of kelp beds	*Eudyptes* sp. carcass	3	0
21.10.82	sandy beach	elephant seal pup carcass	5	1
31.10.82	seawards of kelp beds	unidentified Killer Whale food	---------- 25 ----------	
14.11.82	coastwards of kelp beds	young elephant seal killed by Killer Whales	----------20 to 30 ----------	
30.01.83	coastal rocks	Gentoo Penguin carcass	5	2

TABLE 30

GIANT PETREL DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in brackets)					References
		Carrion		Marine organisms		
	Mammals	penguins	Other birds	crustaceans	Others	
			Northern Giant Petrel *Macronectes halli*			
South Georgia (52S)	14 (1)	53 (2,3)	7 (4,5)	21 (6)	5 (7,8)	Hunter 1983
Crozet Islands (46S)		81 (2,3)	18 (4,5)	+	1 (9)	(this work)
			Southern Giant Petrel *Macronectes giganteus*			
South Georgia (52S)	3 (1)	75 (2,3)	7 (4,5)	11 (6)	3 (7,8)	Hunter 1983
Crozet Islands (42S)		80 (2,4)	10 (4,5)	+	10	(this work)

The main prey species are: (1) *Arctocephalus gazella*, (2) *Aptenodytes patagonicus*, (3) *Eudyptes* spp., (4) *Pachyptila* spp., (5) *Pelecanoides* spp., (6) *Euphausia superba*, (7) nototheniids, (8) *Martialia hyadesi*, (9) onychoteuthids

Within their broad latitudinal distribution at sea (40° to 60°S in the Crozet sector of the Southern Ocean, 0° to 10°C sea-surface temperature, Stahl 1987) giant petrels are most abundant over areas of high marine productivity. These areas include oceanic habitats such as the Antarctic Divergence, the Antarctic Polar Front and the Antarctic Convergence but also neritic areas from the continental slope to the littoral fringe (Stahl 1983). Of all large-sized omnivorous surface feeding seabirds, only giant petrels forage to such an extent in the littoral zone (Jouventin *et al.* 1981) and, unique among Procellariiformes, obtain a significant portion of their food on land at penguin and seal breeding sites. In accordance with their broad dietary overlap, giant petrels hardly segregate in terms of foraging habitats (Jouventin *et al.* 1981, Stahl *et al.* 1985a). Only fine coastal habitat definitions allowed some differences to be noted. The Northern Giant Petrel shows preferences for eudyptid penguin colonies, whereas the Southern Giant Petrel preferred King Penguin and Southern Elephant Seal breeding sites (Jouventin *et al.* 1981). The relative abundance of these penguins in the food of both giant petrels at the Crozet Islands seemed to be consistent with these observations but sample numbers were too small to test the significance of such slight differences.

Beside their land-based scavenging behaviour, giant petrels foraging at sea are mostly diurnal feeders which secure their prey by surface seizing and, less commonly, by shallow plunging and filtration (Harper 1987). Additionally both species readily follow vessels for floating offal and opportunistically congregate around predators such as Leopard Seals *Hydrurga leptonyx*, fur seals and Killer Whales feeding in coastal waters (Downes *et al.* 1959, Bonner & Hunter 1982 and Ridoux 1987, respectively).

WHITECHINNED PETREL *PROCELLARIA AEQUINOCTIALIS*

Results

Samples

Thirty stomach samples from Whitechinned Petrels were collected at the Crozet Islands from spontaneous regurgitations complemented by water flushing recently fed chicks and occasionally from adults returning to the colony. One sample was obtained at Ile de l'Est on 30 September 1981 and four others in February 1982; 25 samples were collected at Ile de la Possession from mid December to late March 1982 and 1983. All but one were collected during the chick-rearing period. The mean mass of the solid fraction was 45 $\pm$ 60 g (0-232 g). Three samples contained accumulated items but no fresh remains; they were excluded from subsequent quantitative analysis.

General composition

Micronektonic crustaceans dominated the diet when analysed on the basis of number of items but ranked only third by mass (Table 31). Conversely fish and, to a lesser extent, squid accounted for high mass percentages but low numbers of items. Tunicates and offal were minor components of the diet. Fish, squid and crustaceans accounted for more than 50% by mass in 10, seven and five samples, respectively.

Crustaceans

The most important crustacean species was Antarctic Krill. This species dominated four of the five largely crustacean samples while the smaller Subantarctic Krill dominated the fifth. Large mesopelagic taxa such as the mysid *Gnathophausia gigas* and the decapod *Pasiphaea longispina* accounted for substantial proportion of the diet in only a few samples.

Cephalopods, fish and other organisms

TABLE 31

THE DIET OF THE WHITECHINNED PETREL AT THE CROZET ISLANDS (N=30)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.[a]	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**70.4**	**448**	**88.2**	**221.3**	**16.3**			
Gammarid amphipods								
Eurythenes obesus	3.7	1	0.2	0.2	+	19		1
Unidentified	3.7	1	0.2	+	+			
Hyperiid amphipods								
Themisto gaudichaudii	44.4	140	27.0	13.9	1.0	15 ± 3	(6-19)	102
Unidentified	3.7	1	0.2	+	+			
Euphausiids								
Euphausia superba	37.0	176	33.9	175.0	12.9	51 ± 4	(39-60)	82
E. vallentini	3.7	125	26.0	4.8	0.4	19 ± 3	(13-23)	34
Mysids								
Gnathophausia gigas	7.4	1	0.2	14.0	1.0	118		1
Decapods								
Pasiphaea longispina	18.5	3	0.6	13.4	1.0	84	(82-89)	3
CEPHALOPODS	**51.9**	**(15)**	**3.1**	**335.0**	**24.7**			
Teuthoidea								
Moroteuthis knipovitchi	7.4	(2)	0.4	125.0	9.2			
Oegopsid A	7.4	(5)	1.0	20.0	1.5			
Unidentified fragments	37.0	(8)	1.7	190.0	14.0			
FISH	**66.7**	**(18)**	**3.5**	**742.0**	**54.7**			
Magnisudis sp.	7.4	(2)	0.4	245.0	18.0	230	(200-260)	2
Unidentified myctophids	7.4	2	0.4	5.0	0.4	65	(40-90)	2
Unidentified nototheniids	7.4	(2)	0.4	145.0	10.7	230	(200-260)	2
Unidentified	44.5	(12)	2.3	347.0	25.6	126 ± 47	(70-190)	7
OTHER ORGANISMS	**37.0**	**(27)**	**5.2**	**58.6**	**4.3**			
Unidentified tunicates	33.3	24	4.6	18.6	1.4	40 ± 17	(15-80)	24
Unidentified offal	11.1	(3)	0.6	40.0	2.9			

* numbers in parentheses indicate that the taxon appeared as fragments rather than complete individuals

Cephalopods occurred in 14 stomachs as unidentifiable fragments of mantles or crowns of arms and only seven buccal masses of two taxa were found (Table 31). Sixteen distinct taxa were identified from accumulated beaks, of which *Gonatus antarcticus* and Oegopsid A were the most common (Table 32).

Fish remains were often fragmentary and highly digested. Only three families were recognized from the examination of the caudal skeletons: nototheniids, paralepidids and myctophids. Tunicates and unidentified organic remains accounted for low mass percentages.

Prey sizes

The crustaceans ranged in size from 6-mm *Themisto gaudichaudii* to 118-mm *G. gigas*, with 39 to 60 mm-long Antarctic Krill accounting for 80% of the crustacean mass. Fish standard lengths were from 40 to 260 mm but the larger specimens were likely not to have been ingested whole since skeleton remains were seldom complete. Likewise, squid ranged between 62 and 464-mm DML estimated from LRL measurements of loose and fresh beaks (Tables 31 and 32) but complete squid were not found. Figure 14 indicates the broad range of prey sizes, all species combined, taken by the Whitechinned Petrel.

Comparison with previous studies

A number of studies has reported on the occurrence of cephalopod beaks in the stomachs of Whitechinned Petrels (Matthews 1929 in South Georgia, Paulian 1953 at Kerguelen, Mougin 1970c and Despin *et al.* 1972 at the Crozets), sometimes associated with fish and crustacean remains (Hagen 1952 at Tristan da Cunha). Further examination of such beaks showed that *Histioteuthis* spp., *Taonius pavo* and *Gonatus antarcticus* prevailed at Antipodes and Campbell Islands (Imber 1976) whereas *Taonius* sp. and *Gonatus* sp. were the dominant identified taxa by number in the Benguela Current and at Marion Island, respectively (Lipinski & Jackson 1989). Quantitative studies performed at breeding sites indicate a broader prey array than these studies. At South Georgia, cephalopods accounted for a lower mass percentage than it was previously thought from the abundance of loose beaks reported in earlier studies (Table 33). Results from the Crozet Islands show still lower squid amounts and an accordingly higher fish fraction. Recent investigations at Marion Island are broadly similar to the present results with fish accounting for about 55% of the diet by mass and crustaceans and squids representing 16 to 25% each. Another study performed at sea in the Benguela Current region, an important area for nonbreeding birds, indicated that the Whitechinned Petrel relied heavily on trawler offal for food (Jackson 1988).

Foraging range and behaviour

The Whitechinned Petrel is one of the most widely distributed southern petrels, being observed at sea from 33° to 66°S in summer (Stahl 1987, Woehler *et al.* 1990). In winter, adult birds migrate to waters off southern Africa and the Benguela Current region where birds are present all year (Bierman & Voous 1950, Weimerskirch *et al.* 1985). Around the Crozet Islands, Whitechinned Petrels forage mostly over productive areas, either neritic (continental shelf and slope) excluding inshore waters, Jouventin *et al.* 1982a, Stahl 1983, Stahl *et al.* 1985a) or oceanic (convergence zone at 40°-43°S, Antarctic Divergence at 60°-62°S, various frontal areas). In accordance with such a broad latitudinal and habitat range, its diet at the Crozet Islands includes antarctic (Antarctic Krill) and temperate to subtropical species (*Histioteuthis* spp. A, *Lycoteuthis* sp., *Bathothauma lyroma*) as well as neritic (*Todarodes filippovae*, *Moroteuthis knipovitchi*, nototheniids) to oceanic species (*Eurythenes obesus*, *Gnathophausia gigas*, *Pasiphaea longispina*, most squid, myctophids). This suggests that breeding birds can forage in

TABLE 32

SUMMARY OF ACCUMULATED ITEMS IN WHITECHINNED PETREL STOMACH CONTENTS (N=30)

Items	Number of items	Measurements (mm)[a]		Estimated body length (mm)[b]			Estimated body mass (g)	
		Mean±S.D.	(range)	n	Mean	(range)	Mean	(range)
CEPHALOPODS								
Lower beaks	122							
Teuthoidea								
Todarodes filippovae	2	4.4	(3.50-5.40)	2	173	(134-212)	167	(76-258)
Moroteuthis knipovitchi	1	6.3		1	285		586	
Kondakovia longimana	5	2.3	(2.2-2.4)	3	62	(60-67)	21	(19-25)
Gonatus antarcticus	11	6.9	(6.3-7.7)	3	252	(227-287)	332	(238-465)
Lycoteuthis sp. A	1	3.7		1	81		30	
Histioteuthis spp. A	4							
Histioteuthis spp. B	1	2.1		1	54		26	
Chiroteuthis imperator	1	5.8		1	152		88	
Bathothauma sp.	1	3.6		1	193		52	
Taonius sp. (large)	1	7.8		1	464		195	
Taonius pavo (small A)	1							
Taonius/Megalocranchia	3							
Galiteuthis glacialis	6	3.9±0.7	(3.0-4.8)	5	172	(133-210)	54	(26-83)
Galiteuthis sp.	1							
Oegopsid A	21	2.7±0.6	(1.9-3.5)	15	123	(90-157)	23	(9-40)
Unidentified	1							
Sepioidea								
Unidentified sepiid	1							
Octopoda								
Unidentified octopodid	1							
Eroded beaks	59							

[a] Lower Rostral Length
[b] Dorsal Mantle Length

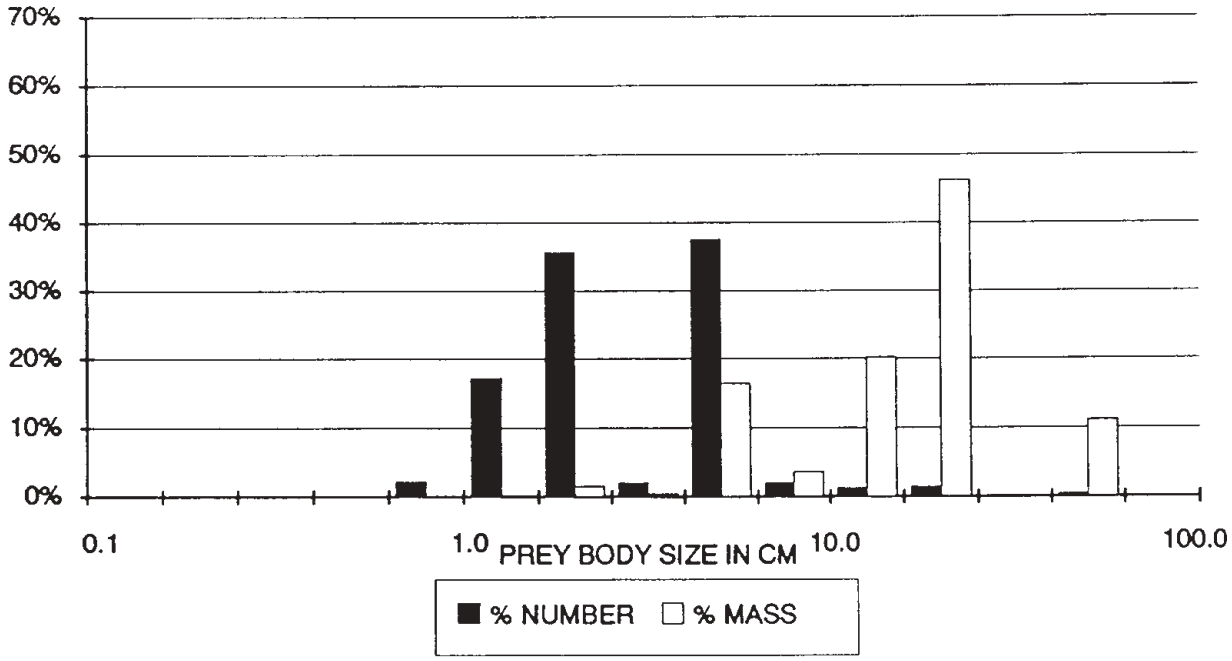

Figure 14
Prey-size distribution in the diet of the Whitechinned Petrel.

TABLE 33

WHITECHINNED PETREL DIETS AT VARIOUS LOCALITIES

Localities[a]	Diets (% by mass, main prey species in brackets)				References
	Crustaceans	Fish	Cephalopods	Other food types	
Southern Benguela (33S) (s)	13.2 (1)	21.2	11.4 (4)	51.2 (11)	Jackson 1988[b]
Marion Island (46S) (c)	23.6 (2)	56.3	17.0 (5)	4.1	Cooper *et al.* 1993
Crozet (46S) (c)	16.3 (3)	54.7	24.7 (6,7)	4.3 (12,13)	(this work)
South Georgia (52S) (c)	29 (3)	24	47 (8,9,10)		Croxall & Prince 1980, Prince unpubl. cited in Prince & Morgan 1987

The main prey species are: (1) *Squilla armata*, (2) *Euphausia vallentini*, (3) *E. superba*, (4) Sepiidae, (5) *Martialia hyadesi*, (6) *Gonatus antarcticus*, (7) Oegopsid A, (8) *Teuthowenia* sp., (9) *Todarodes* sp., (10) *Kondakovia longimana*, (11) fish offal from trawlers, (12) tunicates, (13) unidentified offal

[a] sampling details : collected at sea (s) or at the colony (c)

[b] percent dry mass

shelf and oceanic areas from *c.* 55°-60°S to north of 40°S, i.e. up to *c.* 1200 km from their nests.

Foraging techniques used by Whitechinned Petrels are also quite diversified. Harper (1987) observed feeding by day and by night using surface seizing (85%) or deep plunge (15%) and noticed their aggressiveness towards other, even larger, competitors such as albatrosses and giant petrels (also quoted by Stahl 1983). Their association with ships awaiting offal discharge has long been reported (Bierman & Voous 1950) and is a very substantial food resource on their wintering grounds of the Benguela Current area (Jackson 1988). Similarly, the species was also shown to associate with Killer Whales, feeding off floating detritus from kills. Under these circumstances Whitechinned Petrels follow the whales in coastal areas where they normally do not forage (Ridoux 1987). Whitechinned Petrels have been reported more frequently associating with cetaceans than has any other Southern Ocean seabird (Griffiths 1982, Enticott 1986).

GREY PETREL *PROCELLARIA CINEREA*

Results

Samples

Thirty stomach contents were collected by water flushing recently fed chicks at Ile de la Possession, Crozet Islands, from 15 June to 20 September 1982. Due to the low breeding population of Grey Petrels at Ile de la Possession and the very scattered distribution of the nests, most samples come from a single chick located very close to the permanent base which therefore was easily monitored. From late July to mid September any daily mass increase was interpreted as indicating a nocturnal meal and the stomach was flushed. At the laboratory the liquid fraction was immediately measured and any solid items removed for further analysis. The chick was then re-fed with the liquid material complemented with mashed fish and squid equivalent to the total mass of solid material removed. Despite this continuous disturbance the chick displayed growth parameters similar to published values and fledged at an age consistent with the species fledging season. The mean mass of the samples was 126 $\pm$ 70 g (30-250 g) with the solid fraction (*i.e.* excluding the oil and less than 250 μ fine mush fractions) amounting to 36 $\pm$ 21 g (4-80 g).

General composition

The food of the Grey Petrel consisted mainly of squid remains which constituted 70.5% by mass of the solid fraction, and fish remains which amounted to 27.8% by mass. All other prey groups formed a negligible portion of the diet (Table 34).

Crustaceans

The crustacean part of the diet was limited to one mysid *Gnathophausia gigas* and one parasitic copepod *Sphyrion lumpi*. This latter food item is known to be hosted by only a few fish families among which two, the deep-sea cods Moridae and the grenadiers Macrouridae, belong to the Southern Ocean fish fauna (Z. Kabata pers. comm.). The specimen found in this collection was associated with bones and flesh remains of the morid *Halargyreus johnsoni* and was therefore very likely to have been ingested with the fish.

Cephalopods

Cephalopods were the predominant prey group either by occurrence or mass. They occurred mainly as pieces of mantle, fins, arms and tentacles rather than as whole individuals and were therefore rarely identifiable to species. However, four beaks found in buccal masses and seven others present as accumulated items allowed five taxa to be identified (Tables 34 and 35).

TABLE 34

THE DIET OF THE GREY PETREL AT THE CROZET ISLANDS (N=30)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length[b] (mm)		
	%	No.[a]	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**6.7**	**2**	**4.4**	**4.4**	**0.4**			
Copepods								
Sphyrion lumpi	3.3	1	2.2	1.1	0.1	30		1
Mysids								
Gnathophausia gigas	3.3	1	2.2	3.3	0.3	61		1
CEPHALOPODS	**86.7**	**(28)**	**62.2**	**780.0**	**70.4**			
Teuthoidea								
Moroteuthis ingens	3.3	(1)	2.2	43.0	3.9	511		1
Gonatus antarcticus	3.3	(1)	2.2	45.0	4.1	216		1
Brachioteuthis sp. A	3.3	(1)	2.2	14.0	1.3	106		1
Histioteuthis eltaninae	3.3	(2)	4.4	20.0	1.8	72	(69-76)	2
Unidentified fragments	76.7	(23)	51.1	658.0	59.4			
FISH	**46.7**	**(14)**	**31.1**	**307.5**	**27.8**			
Gadiformes								
Halargyreus johnsoni	3.3	(1)	2.1	55.0	5.0	240		1
Unidentified	43.3	(13)	28.9	252.5	22.8	170 ± 76	(50-250)	5
OTHER ORGANISMS	**3.3**	**(1)**	**2.2**	**15.5**	**1.4**			
Unidentified offal	3.3	(1)	2.2	15.5	1.4			

[a] numbers in prentheses indicate that the taxon appeared as fragments rather than complete individuals (see text under data processing)

[b] Dorsal Mantle Length for squid, total body length for the other prey taxa

TABLE 35

SUMMARY OF ACCUMULATED ITEMS IN GREY PETREL STOMACH CONTENTS (N=30)

Items	Number of items	Measurements (mm)[a]			Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean±S.D.	(range)	n	Mean	(range)	Mean	(range)
CEPHALOPODS								
Lower beaks	7							
Teuthoidea								
Moroteuthis ingens	1	6.3		1	290		602.8	
Gonatus antarcticus	1	6.1		1	218		214.1	
Histioteuthis eltaninae	2	2.7	(2.5-2.8)	2	68	(64-72)	42.1	(37.4-46.9)
Chiroteuthis sp. (large)	1	6.1		1	161		103.7	
Eroded beaks	2							
FISH								
Otoliths	1							
Halargyreus johnsoni	1	9.7		1	240			

[a] Lower Rostral Length in squid, Otolith Length in fish
[b] Dorsal Mantle Length in squid, Standard Length in fish

Fish

Fish ranked second by occurrence and mass and, as observed for squid, were ingested in pieces. Consequently, very few remains could be identified. Only one species, the morid fish *Halargyreus johnsoni*, was positively recognized (Tables 34 and 35).

Prey sizes

In accordance with the very fragmentary nature of the food items only few length data could be recorded. Fish length averaged 172 $\pm$ 74 mm standard length (50-250 mm; n=7) and squid DML 190 $\pm$ 144 mm (67-511 mm; n=9). However, as indicated above these prey may not have been ingested whole. For all species combined, prey size distribution is narrower and modal prey size is higher in the Grey Petrel (Fig. 15) than in its summer-breeding congener the Whitechinned Petrel (see Fig. 14). This difference is consistent with the almost total absence of crustaceans in the food of the winter-breeding Grey Petrel.

Comparison with previous studies

No quantitative dietary studies have previously been published on the Grey Petrel. However, various qualitative records on the food of the species are broadly consistent with the present findings. At the Kerguelen Islands, squid beaks were found in five out of six stomachs and fish remains in two. These fish were estimated to be 100-120 mm-long (Falla 1937, Paulian 1953, Milon unpubl. cited in Mougin 1975). At Gough Island a single stomach sample contained remains of nine squid belonging to the families Histioteuthidae and Cranchiidae (Williams & Imber 1982).

Foraging range and behaviour

The Grey Petrel is generally considered as an indicator of Subantarctic waters (Harper 1987, Woehler *et al.* 1990). In the Crozet sector where the Subtropical and Antarctic Convergences are close together (Gamberoni *et al.* 1982) the subantarctic water zone is very narrow and Grey Petrel distribution (45° to 55°S) is widely spread over the antarctic modified waters as far south as the Antarctic Polar Front (Stahl 1987). Breeding birds forage in oceanic areas between 200 and 600 km from the islands and somewhat nearer in areas of narrow continental shelf (Stahl 1983). Accordingly the prey species found are oceanic squid and slope dwelling deep-sea fish. Also noteworthy is the occurrence of a single species of the family Histioteuthidae *Histioteuthis eltaninae*. By comparison, the Greatwinged Petrel *Pterodroma macroptera*, another medium-sized winter breeder, was found to consume as many as five distinct *Histioteuthis* taxa (see below). Such a difference in species diversity within this family is consistent with its biogeographical affinities (more diversified in temperate and tropical waters, *H. eltaninae* the only antarctic species, Nesis 1987) and the at-sea distributions of the two petrels (Greatwinged Petrel north of the convergence zone and Grey Petrel south of it). Indications from birds caught on longlines suggest that breeding birds can forage as far as 1100 to 1460 km from their colony and that females forage to the north of their breeding sites, whereas males remain at high latitudes (Bartle 1990).

The foraging methods of the Grey Petrel are poorly known. In the African sector of the Southern Ocean it has been considered as a squid-eating and/or a scavenging bird feeding by surface seizing (Griffiths *et al.* 1982), which compares well with the present dietary results and prey size range. On the other hand, Harper (1987) only reported on a single observation of 13 Grey Petrels feeding in association with Killer Whales by shallow plunging from *c.* 3 m above the surface. This observation is not typical of the species since the same author mostly observed Grey Petrels foraging solitarily or in very small groups. Nocturnal feeding was not observed but

cannot be totally ruled out since data remain scarce.

KERGUELEN PETREL *PTERODROMA BREVIROSTRIS*

Results

Samples

The stomach contents of 31 Kerguelen Petrels were collected from 18 October 1981 to 2 February 1982 at Ile de l'Est, Crozet Islands. Three of them were obtained during incubation, seven during the hatching period and 21 during chick rearing. All the samples were obtained by collecting spontaneous regurgitations of adults mist-netted by night as they returned to the colonies. The mean mass of the identifiable fraction was 10 ± 11 g (1-56 g, n=30). One sample exclusively consisting of accumulated items and liquid material was discarded. Liquid and oil fractions were not quantified as they were partly lost during sampling operations.

General composition

Crustaceans dominated the diet of the Kerguelen Petrel either by number of items or by mass. Unidentified offal, most of which was probably gelatinous plankton (tunicates), was second by mass. Fish and squid were minor food sources (Table 36).

Crustaceans

The most important crustacean taxa were a variety of bathypelagic large-sized and brighly-coloured forms which included the gammarid amphipods *Eurythenes* spp., the pasiphaeid shrimp *Pasiphaea longispina* and the lophogastrid mysid *Gnathophausia gigas*. Epipelagic forms such as hyperiid amphipods and euphausiids also occurred regularly but, owing to their smaller size, did not account for a substantial proportion by mass (Table 36).

Cephalopods

Cephalopod prey were scarce in the fresh material. Forty lower beaks found as accumulated items were identified as belonging to nine distinct taxa, of which *Kondakovia longimana*, *Batoteuthis* sp. and *Teuthowenia* sp. were the most important by number and calculated mass (Table 37).

Fish

Only occurring as traces in the fresh fractions, fish were represented in the accumulated fraction by numerous unidentified eye lenses, one paralepidid lower jaw and a pair of myctophid otoliths (Table 37).

Prey sizes

The crustaceans ranged from 5 to 110 mm total length but the bulk of the food consisted of large crustaceans 50 to 100 mm long which provided 1-15 g of food per individual caught. The very fragmentary data obtained from the fish and squid fractions suggest similar size ranges (Table 36, size distribution for all prey species pooled in Fig. 16). However, the largest squid beaks were estimated to come from individuals as large as 430-mm DML. This most probably indicates scavenging feeding habits and fragmentary ingestion.

Comparison with previous studies

Most qualitative studies on the diet of the Kerguelen Petrel highlighted the prevalence of squid in its food. This conclusion was based on the observation of numerous loose beaks, eye lenses and gladii in the stomach of birds collected at the colonies and otherwise empty of any fresh remains (Paulian 1953, Mougin 1969, Despin *et al.* 1972). Beaks of *Histioteuthis eltaninae*, *Sepia*

TABLE 36

THE DIET OF THE KERGUELEN PETREL AT THE CROZET ISLANDS (N = 30)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.[a]	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**100.0**	**92**	**82.1**	**222.7**	**72.5**			
Ostracods								
Gigantocypris muelleri	3.3	3	2.7	1.3	0.4	16		1
Gammarid amphipods								
Eurythenes obesus	23.3	8	7.1	6.9	2.2	23 ± 4	(15-27)	6
E. gryllus	20.0	4	3.6	40.4	13.2	79 ± 8	(68-83)	4
Paracallisoma alberti	6.7	3	2.7	1.5	0.5	25	(24-27)	3
Cyphocaris richardi	20.7	9	8.0	4.0	1.3	25 ± 3	(21-30)	5
Unidentified	6.7	1	0.9	0.1	+			
Hyperiid amphipods								
Themisto gaudichaudii	6.7	4	3.6	0.1	+	8	(6-10)	3
Hyperiella antarctica	3.3	5	4.5	0.1	+	7 ± 2	(5-9)	4
Cyllopus lucasii	6.7	3	2.7	0.2	0.1	15	(11-20)	3
Lanceola sp.	3.3	1	0.9	0.6	0.2	27		1
Euphausiids								
Euphausia superba	3.3	6	5.3	4.0	1.3	43 ± 9	(29-51)	5
Unidentified	10.0	1	0.9	+	+			
Mysids								
Gnathophausia gigas	20.0	6	5.3	46.4	15.1	85 ± 21	(49-110)	6
Decapods								
Pasiphaea longispina	63.3	38	33.9	117.1	38.1	77 ± 10	(46-90)	31
Unidentified	3.3	+	+	+	+			
CEPHALOPODS	**16.7**	**(5)**	**4.5**	**18.3**	**6.0**			
Teuthoidea								
Unidentified	16.7	(5)	4.5	18.3	6.0			
FISH	**10.3**	**(3)**	**2.7**	**1.0**	**0.3**			

Unidentified	10.3	(3)	2.7	1.0	0.3
OTHER ORGANISMS	**40.0**	**(12)**	**10.7**	**65.0**	**21.2**
Insects					
Unidentified	6.7	2	1.8	+	
Unidentified offal	33.3	(10)	8.9	65.0	21.2

[a] numbers in parentheses indicate that the taxon appeared as fragments rather than complete individuals (see text under data processing)

TABLE 37

SUMMARY OF ACCUMULATED ITEMS IN KERGUELEN PETREL STOMACH CONTENTS (N=30)

Items	Number of items	Measurements (mm)[a]		Estimated body length (mm)[b]			Estimated body mass (g)	
		Mean±S.D. (range)	n	Mean	(range)		Mean	(range)
CEPHALOPODS								
Upper beaks	60							
Lower beaks	40							
Kondakovia longimana	3	7.6 (5.4-9.9)	2	334	(234-433)		994	(281-1707)
Brachioteuthis sp. B	1	2.5	1	66			6.2	
Histioteuthis sp. A	1							
Histioteuthis eltaninae	1	3.4	1	87			69	
Bathyteuthis abyssicola	2	0.9 (0.8-1.0)	2	48	(46-51)		12	(10-14)
Batoteuthis sp.	3	4.3 (4.1-4.4)	3	122	(116-128)		78	(67-88)
Taonius sp.	2							
Teuthowenia sp.	4	3.8 (3.4-4.0)	3	167	(151-175)		47	(36-53)
Unidentified	1	1.1	1					
Eroded beaks	22							
Gladii								
Unidentified	3	190	1					
FISH								
Jaws	1							
Paralepididae	1	17.5	1	140			3.0	
Otoliths	2							
Electrona sp.	2	2.8	1	61			3.2	

[a] Lower Rostral Length and Gladius Length in squid, Otolith and Jaw Length in fish
[b] Dorsal Mantle Length in squid, Standard Length in fish

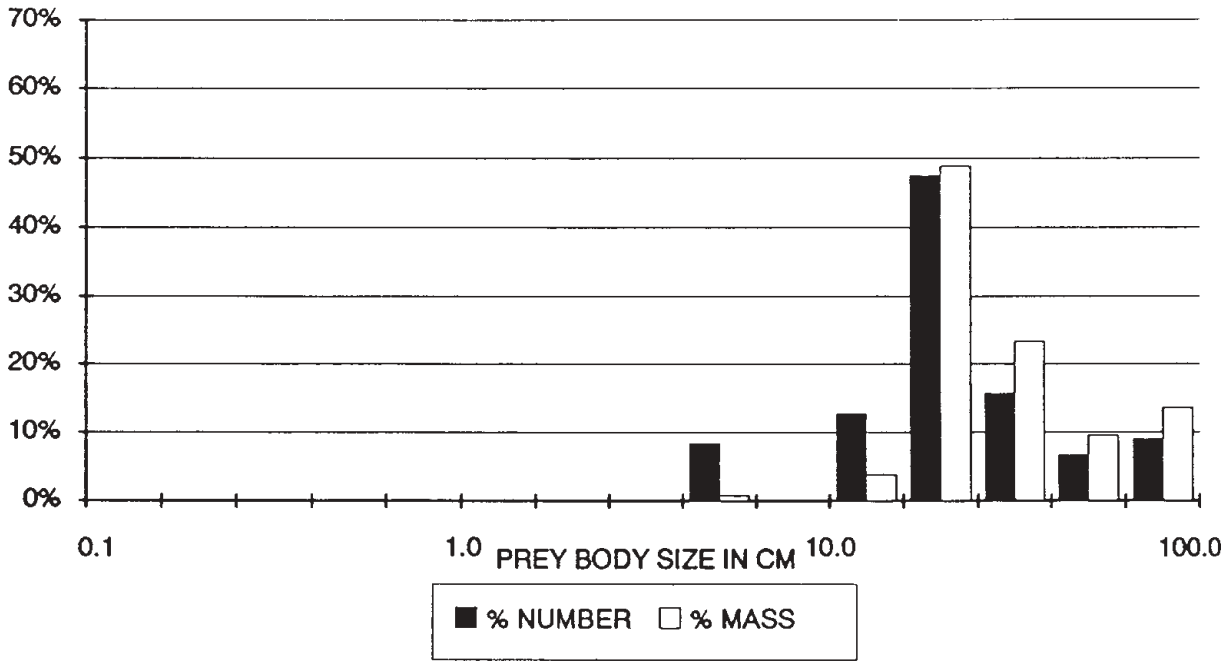

Figure 15
Prey-size distribution in the diet of the Grey Petrel.

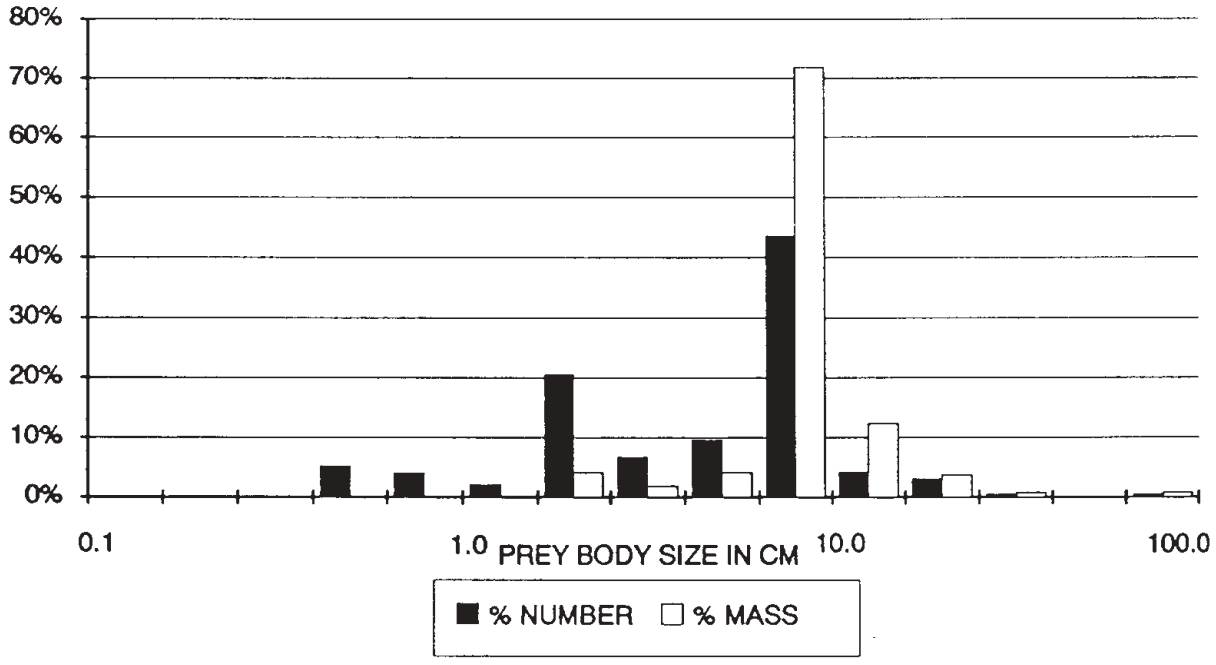

Figure 16
Prey-size distribution in the diet of the Kerguelen Petrel.

sp. and *Onychoteuthis* sp. were found accumulated in the stomachs of Kerguelen Petrels sampled at sea in the Benguela Current area (Lipinski & Jackson 1989). Antarctic Krill was also reported as a possible prey species from nocturnal observations at sea (Harper 1987).

The only previous quantitative study, performed at Marion Island (Schramm 1986), indicated a mixed diet with squid accounting for 70% by mass and crustaceans and fish for 24 and 6% by mass, respectively (Table 38). The most important crustacean taxa fit well the species list found in the current study and consist mainly of bathypelagic species. In contrast, the squid species differed between localities. *Discoteuthis* sp., *Gonatus antarcticus* and *Chiroteuthis* spp. accounted together for as much as 74% by mass of the squid diet at Marion Island but were absent at the Crozet Islands. Conversely, *Kondakovia longimana*, *Brachioteuthis* sp., *Bathyteuthis abyssicola* and *Batoteuthis* sp. which amounted to 80% by mass of the cephalopod fraction in the present study were absent in the Marion Island diet. The differences in diet between these two localities warrant comment. Kerguelen Petrels as well as Softplumaged Petrels *Pterodroma mollis* were mostly reported as squid eaters at Marion Island and crustacean eaters at the Crozet Islands (Table 38). Schramm (1986) found 10 times as many accumulated squid beaks in samples of Greatwinged Petrels as in Kerguelen and Softplumaged Petrels. Such a finding agrees with the results obtained at the Crozet Islands since an average of 11.3 lower beaks per sample were found in the Greatwinged Petrel but only 1.3 and 0.6 in Kerguelen and Softplumaged Petrels, respectively. This indicates that, at both localities, the former species preyed on squid at a significantly higher frequency than the other two species. Although frequency of occurrence and percent by mass are not directly linked due to differences in individual body mass, we might expect that such an important interspecific difference as the one observed between the three gadfly petrels should have some consequences for the analyses by mass. Unlike the results obtained at the Crozet Islands (see relevant sections for the other species of gadfly petrels) no clear-cut interspecific difference was observed at Marion Island (Table 38). Methodological differences in processing the accumulated items may explain most of this inter-locality discrepancy.

Foraging range and behaviour

In the Crozet sector of the Southern Ocean, the Kerguelen Petrel is reported from 45° to 65°S (Stahl 1987). The species forages over oceanic areas deeper than 750 m and avoids the vicinity of the islands except where the continental shelf is very narrow and sea bottom reaches great depths within a few kilometres from the coast, *i.e.* mostly in the eastern part of the archipelago (Stahl 1983, Stahl *et al.* 1985a). In February, soon after the fledging period all breeding populations move southwards to antarctic waters (0° to 2°C, Bierman & Voous 1950, Stahl *et al.* 1985a). The presence of numerous oceanic deep-dwelling species in its diet agrees well with this off-shore distribution (but see also the Softplumaged Petrel account for discussion on the occurrence of these reportedly non-migratory bathypelagic forms in the food of surface-feeding birds and its significance). Furthermore, the presence of Antarctic Krill indicates that breeding birds can also forage far to the south since they are very unlikely to find this species north of 55°S. This corresponds to *c.* 2000-km foraging trips.

Kerguelen Petrels generally forage solitarily or in very small (< five) groups (Bierman & Voous 1950). Feeding techniques include surface seizing, only briefly sitting on the water, and some aerial methods such as dipping and shallow plunges (Bierman & Voous 1950, Griffiths 1982, Griffiths *et al.* 1982, Harper 1987). Harper (1987) only reported them feeding nocturnally but the other studies did not specify this point and it seems likely that they also feed during daylight hours, particularly when they are foraging in the

TABLE 38

THE DIETS OF THE GADFLY PETRELS IN THE SOUTHERN OCEAN

Localities	Diets (% by mass, main prey species in brackets)					References
	Deep-sea crustaceans	Other crustaceans	Fish	Cephalopods	Other food types	
			Kerguelen Petrel *Pterodroma brevirostris*			
Marion Island (46S)	22 (1,2,3)	2	6 (5)	70 (7,9)		Schramm 1986
Crozet Islands (46S)	70.9 (1,2,3)	1.6 (4)	0.3	6.0	21.2 (11)	(this work)
			Softplumaged Petrel *Pterodroma mollis*			
Marion Island (46S)	9 (1)	1	1 (5)	89 (9,10)		Schramm 1986
Crozet Islands (46S)	61.1 (1,2,3)	16.7 (4)	+	15.7	6.5	(this work)
			Greatwinged Petrel *Pterodroma macroptera macroptera*			
Marion Island (46S)	6 (1,2)		4 (5)	90 (7,8,9)		Schramm 1986
Crozet Islands (46S)	31.7 (1,2,3)	0.3	4.2	63.9 (7,8,9)		(this work)
			Greyfaced Petrel *Pterodroma macroptera gouldi*			
New Zealand (38S)	6 (2,3)	6	28 (5,6)	58 (8,9)	3 (12)	Imber 1973

The main prey species are: (1) *Eurythenes* spp. (2) *Gnathophausia gigas*, (3) Pasiphaeidae, (4) *Euphausia suberba*, (5) Myctophidae, (6) Gonostomatidae, (7) *Gonatus antarcticus*, (8) *Histioteuthis* spp., (9) Cranchiidae, (10) Chiroteuthidae, (11) offal and gelatinous plankton, (12) Tunicata

vicinity of the Antarctic Divergence in February. Scavenging was not reported for this species but the presence of rather large *Kondakovia longimana* (280-1710-g individual body mass) in the food of this medium-sized petrel (331-g mean body mass) strongly suggests some degree of necrophagy or at least association with more powerful predators. On the other hand the prevalence of large brightly-coloured (*Eurythenes* spp., *P. longispina*, *G. gigas*) and photophore-bearing species (Antarctic Krill, numerous squid, *Electrona* sp.) are consistent with aerial feeding methods and some nocturnal foraging, respectively. Indeed the foraging strategy of the Kerguelen Petrel (and the other two gadfly petrels) seems to reduce competition for food with other more powerful seabirds (*e.g.* Whitechinned Petrel) by avoiding the most productive zones of the ocean (Stahl *et al.* 1985a). They compensate for the low prey density by searching over large areas of ocean foraging on items that provide a good compromise between food intake per individual caught and seizability. The most important crustacean species in the Kerguelen Petrel diet fit this compromise. Their size (and colour) makes them readily spotted by flying birds but does not preclude quick seizure and ingestion. This is crucial if birds wish to avoid attracting neighbouring competitors. Such a feeding strategy applies to all three gadfly petrels in the current study.

SOFTPLUMAGED PETREL *PTERODROMA MOLLIS*

Results

Samples

The stomach contents of 12 Softplumaged Petrels were obtained at Ile de l'Est, Crozet Islands, from 21 September 1981 to 2 March 1982 from regurgitations of adults caught by night as they returned from the sea. The single sample in September was collected during the prelaying period whereas the others obtained in February and March all corresponded to the chick-rearing period. As with samples from Kerguelen Petrels the oil and other liquid material were not quantified. The identifiable fraction weighed 5 $\pm$ 6 g (1-20 g, n=12).

General composition

Crustaceans dominated the diet by number of prey individuals and by mass. Squid ranked second by mass whereas fish was only found as traces (Table 39).

Crustaceans

The crustacean diet of the Softplumaged Petrel showed a strong prevalence of bathypelagic forms including the gammarid amphipod *Eurythenes obesus*, the pasiphaeid shrimp *Pasiphaea longispina* and the lophogastrid mysid *Gnathophausia gigas*. Epipelagic forms were rare.

Cephalopods

Fresh fragments of cephalopods consisted of shapeless mantle or tentacle remains and were not identifiable. However, seven accumulated lower beaks were identified as belonging to at least five taxa (Table 40).

Fish

Besides the unidentifiable remains which constituted the fish fraction in every sample, only one loose otolith pair (*Melamphaes* sp.) was found.

Prey sizes

All crustaceans were within the same size range as already reported for the Kerguelen Petrel (*i.e.* 20 to 100 mm long). Among the accumulated material one loose ommastrephid beak was

TABLE 39

THE DIET OF THE SOFTPLUMAGED PETREL AT THE CROZET ISLANDS (N = 12)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.[a]	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**83.3**	**20**	**74.1**	**29.8**	**77.8**			
Gammarid amphipods								
Eurythenes obesus	50.0	6	22.2	8.8	23.0	36 ± 6	(25-40)	6
Unidentified	16.7	2	7.4	1.3	3.2	21	(20-22)	2
Hyperiid amphipods								
Themisto gaudichaudii	16.7	3	11.1	0.3	0.8	16		1
Unidentified	8.3	1	3.7	1.5	3.9	45		1
Mysids								
Gnathophausia gigas	41.7	2	7.4	0.9	2.3	30	(25-37)	3
Decapods								
Pasiphaea longispina	25.0	3	11.1	12.4	32.4	88	(81-92)	3
Unidentified	8.3	1	3.7	2.6	6.8	76		1
Unidentified	8.3	2	7.4	2.0	5.2			
CEPHALOPODS	**8.3**	**(1)**	**3.7**	**6.0**	**15.7**			
Teuthoidea								
Unidentified	8.3	(1)	3.7	6.0	15.7			
FISH	**16.7**	**(2)**	**7.4**	+	+			
Unidentified	16.7	(2)	7.4	+	+			
OTHER ORGANISMS	**33.3**	**(4)**	**14.8**	**2.5**	**6.5**			
Unidentified offal	33.3	(4)	14.8	2.5	6.5			

[a] numbers in parentheses indicate that the taxon appeared as fragments rather than complete individuals (see text under data processing).

TABLE 40

SUMMARY OF ACCUMULATED ITEMS IN SOFTPLUMAGED PETREL STOMACH CONTENTS (N = 12)

Items	Number of items	Measurements (mm)[a]		Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean ± S.D. (range)	n	Mean	(range)	Mean	(range)
CEPHALOPODS							
Lower beaks	7						
Teuthoidea							
Ommastrephidae	1	4.1	1			905	
Lycoteuthis sp. A	1	3.8	1	82		31	
Histioteuthis eltaninae	1	2.9	1	73		48	
Batyteuthis abyssicola	1	1.0	1	53		17	
Taonius pavo (small A)	1	4.2	1	246		50	
Eroded beaks	2						
FISH							
Otoliths							
Melamphaes sp.	2	6.1	1	100		12	

[a] Lower Rostral Length in squid, Otolith Length in fish
[b] Dorsal Mantle Length in squid, Standard Length in fish

estimated to come from a 905-g individual, which clearly implies scavenging and partial ingestion by this 300-g gadfly petrel. The body size distribution for all prey taxa combined is given in Fig. 17.

Comparison with previous studies

Most previous data on the food of the Softplumaged Petrel are very fragmentary. At Tristan da Cunha, the stomachs of two birds collected at the colony contained loose squid beaks and fish vertebrae (Hagen 1952). Accumulated cephalopod beaks were the only food items reported from six stomach contents collected at Ile de l'Est, Crozet Islands (Despin *et al.* 1972) and two stomachs from Gough Island (Williams & Imber 1982). At this latter locality the squid were identified as belonging to three distinct families: Mastigoteuthidae, Histioteuthidae and Cranchiidae.

The only quantitative study of the food of the Softplumaged Petrel was performed at Marion Island and dealt with nine chick stomach contents (Schramm 1986). The general composition emphasized again the role of squid, with crustaceans being only a distant second in importance by mass. This contrasts strongly with results obtained at the Crozet Islands (Table 38). The crustacean species involved were mostly the same as those found in the current study but none of the squid species identified from loose beaks was common to both localities. It is possible that the high squid diversity known from these latitudes and the low number of beaks examined at each study site at least partly account for this taxonomic discrepancy. However, the clear-cut difference in the general diet composition between Marion and Crozet Islands is rather surprising. It is unclear whether actual differences in prey availability, small sample sizes or differences in methods of quantitative analysis (on this point see discussion in the Kerguelen Petrel section) accounts for the different diets recorded at the two localities.

Foraging range and behaviour

Within its summer latitudinal range (35°-58°S in the Atlantic, Bierman & Voous 1950, 35°-52°S in the Indian Ocean, Stahl 1987), the Softplumaged Petrel forages mainly over oceanic habitats beyond the limits of the continental shelf. In the Crozet sector the species occurs as part of several species groupings observed between 100 and 500 km from the islands over waters deeper than 500 m (Stahl 1983). Around the eastern Crozet Islands, where the continental shelf in narrower, birds can be observed closer to the coasts (Stahl *et al.* 1985a). In the oceanic zones, the abundance of the Softplumaged Petrel is negatively correlated with that of the Whitechinned Petrel, a powerful omnivorous surface feeder. Consequently Softplumaged Petrels avoid the productive convergence and frontal zones where this latter species abounds. Similarly, its absence from the shelf area is interpreted as a response to the abundance of numerous large omnivorous surface feeders such as albatrosses, giant petrels and Whitechinned Petrels (Stahl 1983, Stahl *et al.* 1985a). Most of these considerations apply to the other gadfly petrels as well (again see discussion on feeding strategy under Kerguelen Petrel above). In accordance with this highly oceanic distribution most of the prey species identified in the food of the Softplumaged Petrel were oceanic forms.

The Softplumaged Petrel forages solitarily (Bierman & Voous 1950) and its feeding techniques are barely known. However surface seizing appears important (Harper *et al.* 1985) and scavenging has also been reported (Griffiths *et al.* 1982). Based on observations of the other gadfly petrels, dipping and shallow plunges should be expected. The occurrence in the present samples of large individual prey such as a 905-g ommastrephid is consistent with some degree of necrophagy.

The ostracod *Gigantocypris muelleri*, the amphipods *Eurythenes gryllus* and *E. obesus*, the mysids *Gnathophausia* spp. and *Petalophthalmus armiger*, the decapod *Pasiphaea longispina*, the melamphaid fishes *Melamphaes* sp. and *Sio nordenskioldii* (the latter in Blue Petrel diet only), the family Moridae (otoliths in Grey Petrel, but the family-specific parasitic copepod *Sphyrion lumpi* was found in Greatwinged Petrel among others) and the squid *Bathyteuthis abyssicola* are all deep-sea taxa, seldom, if at all, caught by nets in waters shallower than a few hundred metres (e.g. Fage 1941, Roper & Young 1975, Mauchline 1980, Kirkwood 1984, Clarke & Holmes 1987) and therefore considered to be unavailable to surface-feeding birds. Nonetheless, they accounted together for as much as *c.* 70, 58 and 32% by mass of the diets of the Kerguelen, Softplumaged and Greatwinged Petrels, respectively and still significant fractions in the food of several other volant species (Blue, Grey and Whitechinned Petrels, several albatrosses; see relevant sections in this study). Such deep-sea organisms have also been found in seabird diets at other localities (*e.g.* Tristan da Cunha, Hagen 1952; Hawaii, Harrison *et al.* 1983; Scotland, Furness & Todd 1984; Ross and Weddell Seas, Ainley *et al.* 1984, 1986) but their collective contribution to the diet was not quantified. At the Crozet Islands the three gadfly petrels, whose breeding populations amount to several tens of thousands of pairs each (Jouventin *et al.* 1984), consume substantial amounts of these reportedly deep-sea prey groups and, thus, indicate that, in contrast to the vertical distribution suggested by experimental catches performed to date, these organisms do occur in large numbers at the sea surface. The circumstances in which these organisms reach the surface are still unclear. They might have an upward motion in upwelling areas as already suggested for *Gnathophausia gigas* (Mauchline 1980). However, gadfly petrels are known to avoid such productive zones (see above). In the southern Atlantic Ocean, these bathy- to mesopelagic crustaceans were not collected during trawls at less than 310 m deep either by day or by night in ice-free waters north of 58°S. However, these deep-dwelling species (including most of the taxa reported here from seabird diets) were found at the surface in the area of pack-ice as well as being closely associated with drifting and decaying bergs (Ainley *et al.* 1986). If this indicated foraging in floating ice areas, this would fit the southern distribution limit of the Kerguelen Petrel but not the known oceanic distributions of the other two species of gadfly petrels. Through association with cetaceans, some seabirds have been reported to feed on deep and otherwise unavailable species regurgitated by or included in faeces of surfacing whales (Clarke *et al.* 1981, Clarke & Prince 1981, review in Evans 1982). Nevertheless, although these taxa were found in cetacean stomachs (*G. gigas* in balaenopterid whales, Kawamura 1980; melamphaids in toothed whales, N.T.W. Klages pers. comm.), they are not known to be anything more than minor components of their diet. Furthermore, gadfly petrels have not been reported to associate with cetaceans to any significant extent. The lack of any diel vertical migration allowing this deep nektonic community to reach the surface may have been over-emphasized in the past due to difficulties in sampling such fast-swimming forms. Recently, the large scavenging amphipod *E. gryllus* was found to migrate vertically and reach the upper 100 m water layer by night (Thurston 1988). Finally, these deep-sea organisms might also become buoyant when moribund or dead due to differential degradation rates of lipids and proteins. Most of these crustaceans control their buoyancy with lipids and *Bathyteuthis abyssicola* is one of the rare squid whose density is controlled by lipids too, due to its modified liver.

To conclude, more data on the vertical distribution and migration of these reportedly deep-dwelling prey species and the foraging behaviour of gadfly petrels are clearly needed to elucidate the circumstances under which these prey are available at the sea surface. However, in

terms of oceanic food web, these observations indicate that beside the downward flow of particles from the surface layer to the sea bottom an upward flux of food material could also occur.

GREATWINGED PETREL *PTERODROMA MACROPTERA*

Results

Samples

The stomach contents of 27 Greatwinged Petrels were sampled by collecting regurgitations from adults caught at night as they returned to their nests at Ile de l'Est, Crozet Islands. Additionally partial regurgitations of several birds were pooled. This latter material was not dealt with in the analysis by frequency of occurrence but was included in the analyses by number of items and mass. Sampling took place from 17 September to 12 November 1981 during the chick-rearing period. The mass of the identifiable part of the samples was 3 $\pm$ 4 g (1-16 g). Oil and other liquid fractions were not quantified.

General composition

The diet of the Greatwinged Petrel was a mixture of crustaceans, dominant by number, and squids, the bulk of the food by mass. Fish was not important either by number or by mass (Table 41).

Crustaceans

As for Kerguelen and Softplumaged Petrels the crustacean prey species were almost exclusively bathy- to mesopelagic taxa with the pasiphaeid shrimp *Pasiphaea longispina* and the lophogastrid mysids *Gnathophausia gigas* being prevalent. Epipelagic species were scarce and owing to their smaller size were negligible in the analysis by mass.

Cephalopods

Cephalopod fragments were very common and accounted for a high percentage by mass in about half the samples. However, due to the lack of diagnostic part among these remnants, no single species could be identified from the fresh material. Nevertheless, 28 squid taxa were identified from the large numbers of accumulated beaks. The families Gonatidae, Histioteuthidae and Cranchiidae were the most important either by number or by reconstituted mass (Table 42).

Fish

Fish was only found as unidentifiable flesh remains and no otoliths was discovered. The occurrence of the parasitic copepod *Sphyrion lumpi* might indicate scavenging on deep-sea cods Moridae or grenadiers Macrouridae.

Prey sizes

The crustacean prey species ranged in size from 15 to 30 mm in gammarids and 30 to 100 mm in decapods and mysids. Some parts of fish axial skeletons were estimated to be from 70-150-mm individuals. Several cephalopod species identified from the beaks included large specimens (DML >150 mm, mass >200 g) most probably found dead or moribund and ingested by pieces. Pooled prey species size distribution is broader and its upper limit greater in the winter breeding Greatwinged Petrel (Fig. 18) than in its two summer breeding congeners (Figs 16 & 17).

Comparison with previous studies

The prevalence of cephalopod remains in the stomach of Greatwinged Petrels throughout the Southern Ocean has long been reported in earlier studies (Falla 1937, Hagen 1952, Paulian 1953, Despin *et al.* 1972). Two previous quantitative studies have documented the diet of both subspecies, *P. m. macroptera* at Marion Island and the Greyfaced Petrel *P. m. gouldi* in northern

TABLE 41

THE DIET OF THE GREATWINGED PETREL AT THE CROZET ISLANDS (N=27)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.[a]	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**70.4**	**33**	**63.5**	**54.0**	**32.1**			
Copepods								
Sphyrion lumpi	3.7	4	7.7	5.4	3.2	30		1
Gammarid amphipods								
Eurythenes obesus	14.8	5	9.6	2.3	1.4	24 ± 7	(17-30)	5
E. gryllus	3.7	1	1.9	2.2	1.3	44		1
Cyphocaris challengeri	7.2	2	3.8	0.3	0.2	18	(15-20)	2
Unidentified	7.2	1	1.9	+	+			
Hyperiid amphipods								
Themisto gaudichaudii	3.7	1	1.9	0.2	0.1	18		1
Unidentified	3.7	1	1.9	+	+			
Mysids								
Gnathophausia gigas	25.9	3	5.8	14.4	8.6	62	(30-100)	3
Petalophthalmus armiger	3.7	1	1.9	0.7	0.4	44		1
Decapods								
Pasiphaea longispina	33.3	11	21.2	28.2	16.8	72 ± 20	(45-100)	9
Unidentified	7.2	3	5.8	0.3	0.2	24	(23-25)	2
Unidentified crustaceans	3.7	+	+	+	+			
CEPHALOPODS	**51.9**	**(14)**	**26.9**	**107.2**	**63.7**			
Unidentified	51.9	(14)	26.9	107.2	63.7			
FISH	**18.5**	**(5)**	**9.6**	**7.0**	**4.2**			
Unidentified	18.5	(5)	9.6	7.0	4.2	107	(70-150)	3

[a] numbers in parentheses indicate that the taxon appeared as fragments rather than complete individuals (see text under data processing)

TABLE 42

SUMMARY OF ACCUMULATED ITEMS IN GREAWINGED PETREL STOMACH CONTENTS (N=27)

Items	Number of items	Measurements (mm)[a]		Estimated body length (mm)[b]			Estimated body mass (g)	
		Mean±S.D. (range)	n	Mean	(range)		Mean	(range)
CEPHALOPODS								
Lower beaks	305							
Teuthoidea								
Onychoteuthis sp.	2	2.1 (2.1-2.2)	2	104	(102-105)		32	(30-33)
Moroteuthis knipovitchi	1	6.3	1	285			586	
Kondakovia longimana	2	6.8 (5.6-8.0)	2	296	(242-351)		612	(309-915)
Brachioteuthis picta	7	4.3±0.3 (3.9-4.8)	7	103	(95-113)		13	(12-16)
Gonatidae	1	5.8	1	205			181	
Gonatus antarcticus	36	6.0±0.8 (5.2-7.8)	36	214	(177-293)		218	(122-496)
Ancistrocheirus lesueuri	1	5.2	1	169			284	
Lycoteuthis sp.	14	4.0±0.3 (3.5-4.6)	14	87	(77-99)		36	(27-48)
Octopoteuthis sp.	1	8.9	1	153			182	
Lepidoteuthis sp.	1	5.7	1	237			118	
Histioteuthis spp. A	38	3.9±1.1 (2.0-6.7)	36	73	(32-134)		127	(26-392)
Histioteuthis spp. B	12	3.5±1.3 (2.2-6.3)	11	91	(56-161)		85	(29-236)
Alluroteuthis antarcticus	2	5.4 (5.2-5.6)	2	149	(143-154)		173	(157-189)
Mastigoteuthis sp.	3	5.1 (3.3-6.8)	3	124	(93-155)		95	(36-155)
Chiroteuthis sp.(small)	2	3.1 (2.4-3.9)	2	87	(69-106)		19	(7.9-30)
Chiroteuthis sp. (large)	5	6.3±1.1 (5.0-7.2)	4	165	(134-188)		118	(61-162)
C. imperator	6	4.7±0.7 (3.6-5.7)	6	127	(101-151)		55	(26-86)
"Batoteuthis sp."	1	3.8	1	109			56	
Liocranchia sp.	2	2.6 (2.5-2.8)	2	214	(204-223)		56	(51-62)
Megalocranchia sp.	11	6.7±1.2 (4.6-7.8)	10	399	(243-470)		151	(58-200)
Taonius pavo (small)	10	4.7±0.4 (4.1-5.3)	8	276	(243-310)		65	(50-83)
Taonius sp. (large)	53	7.2±0.7 (4.2-9.3)	51	430	(246-556)		168	(51-287)
Galiteuthis glacialis	1	4.7	1	204			77	
G. phyllura	4	4.6±1.7 (2.7-6.3)	4	200	(122-271)		86	(21-157)

Teuthowenia pellucida	4	4.8±0.2	(4.6-5.0)	4	210	(202-218)	83	(76-92)
Teuthowenia sp.	2	4.4	(3.6-5.2)	2	191	(159-223)	69	(42-97)
Mesonychoteuthis hamiltoni	1	3.1		1	137		28	
Unidentified oegopsids	5							
Eroded beaks	77							

[a] Lower Rostral Length
[b] Dorsal Mantle Length

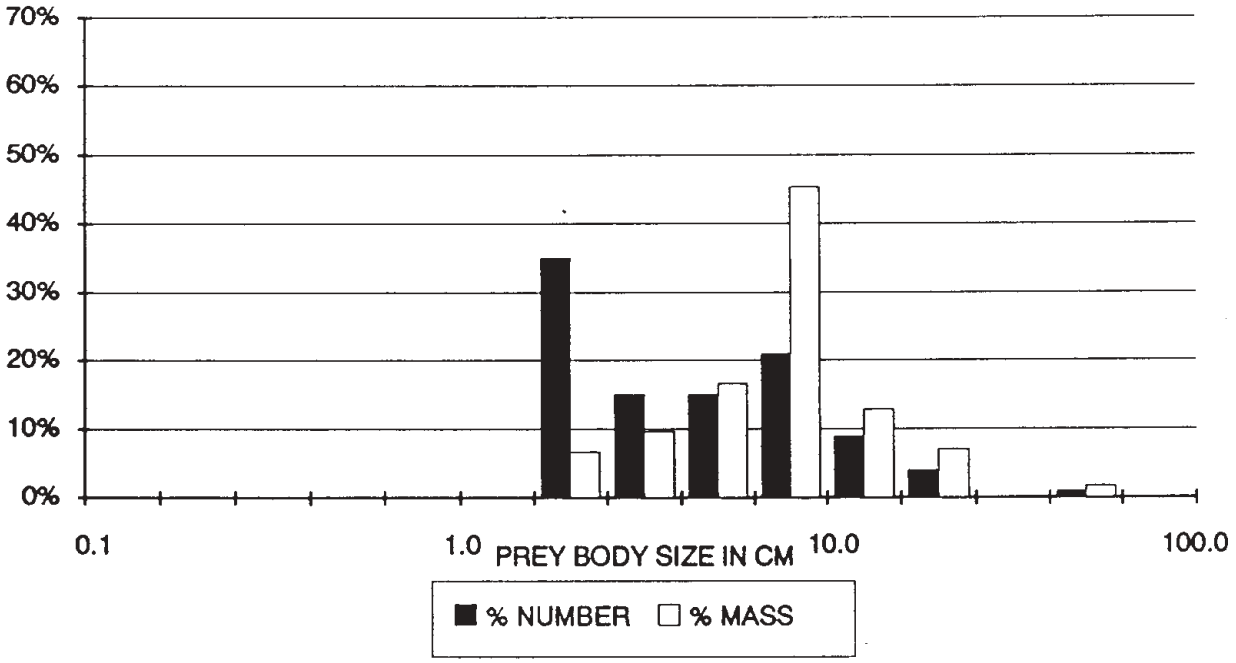

Figure 17
Prey-size distribution in the diet of the Softplumaged Petrel.

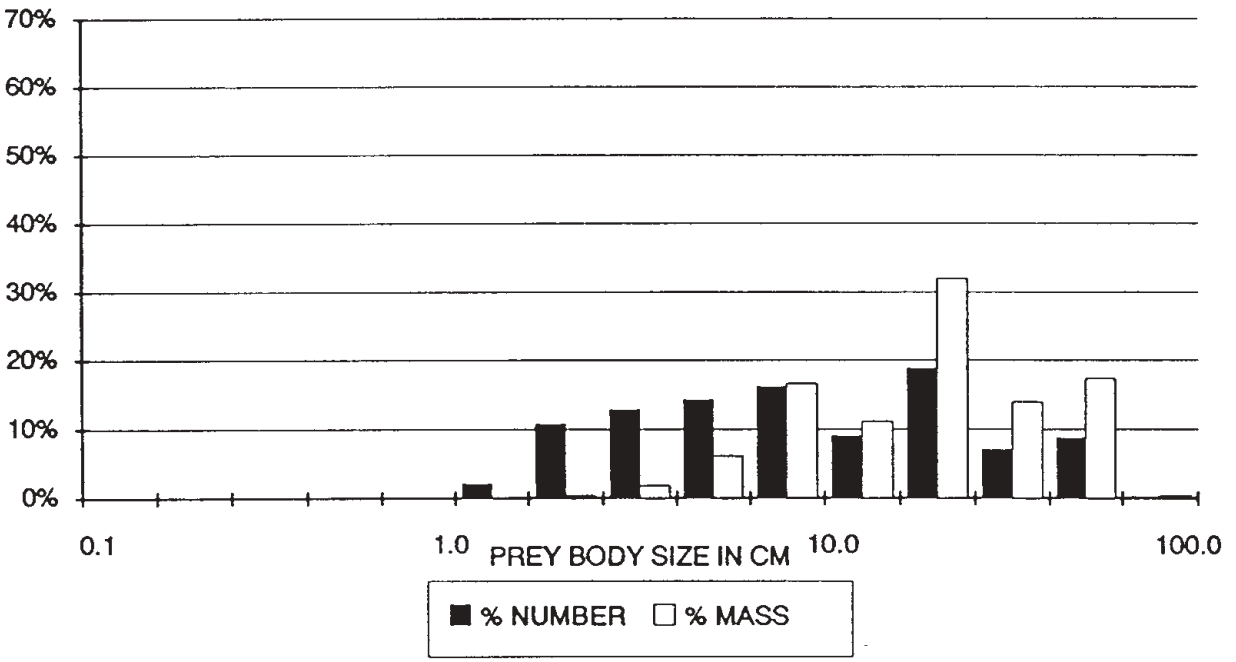

Figure 18
Prey-size distribution in the diet of the Greatwinged Petrel.

New Zealand (references in Table 38). The diets of Greatwinged Petrels are broadly similar irrespective of the subspecies or the locality. Cephalopods constituted the bulk of the food by mass in all three quantitative studies. Prey species diversity of squid is high (28 to 29 taxa each) with the same prevailing families: Gonatidae, Histioteuthidae and Cranchiidae. The species composition of the crustacean fraction is also similar from one study site to another and shows the importance of deep-dwelling nektonic forms. Although fish was less important by mass at the two subantarctic localities the taxonomic groups involved (Myctophidae and Moridae at Marion, indirect evidence of necrophagy on Moridae or Macrouridae from the observation of the parasitic copepod *Shyrion lumpi* at Crozet) fall within the broader species array reported from the diet of *P. m. gouldi* at the warm temperate locality of northern New Zealand. The octopods *Argonauta argo* and the decapod *Spirula spirula* as well as epipelagic euphausiids are the only prey groups of any importance specific to the northern locality. This pattern accords with the general distribution of deep-sea organisms which, unlike epipelagic communities, is mostly unaffected by the superficial oceanographic boundaries.

Foraging range and behaviour

Greatwinged Petrels forage from subtropical to cold temperate waters. In the Atlantic, the species is found from 24° to 36°S in December and as far south as 49°S in April (Bierman & Voous 1950). The New-Zealand subspecies, *P. m. gouldi*, is limited to areas where sea-surface temperature exceeds 10°C (Harper 1987). In the Crozet sector of the Southern Ocean the Greatwinged Petrel is found from 30° to 50°S in summer (the nonbreeding season for this species). In late February, as breeders come back to their colonies, the species forages between 200 and 700 km from the islands over deep (2500-3000 m) oceanic waters where sea-surface temperature is about 7°C (Stahl *et al.* 1985a, Stahl 1987).

Similar to the other *Pterodroma* petrels, Greatwinged Petrel abundance is negatively correlated to that of the Whitechinned Petrel and of the other large surface-feeding omnivorous species that forage extensively over the continental shelf (Stahl 1983, Stahl *et al.* 1985a, see discussion in the Kerguelen Petrel section). Consequently, its highly oceanic distribution is consistent with the prevalence of the meso- to bathypelagic prey species in its diet. Furthermore, the large squid species diversity is consistent with a northerly foraging dispersion with birds foraging potentially beyond the Subtropical Convergence lying at 43°S in this sector. Indeed, numerous squid families found in its food have clearly temperate or even subtropical affinities (Nesis 1987 and papers cited therein). This may be compared with the low squid species diversity found in the food of the Grey Petrel, the only other medium-sized winter-breeding petrel which, unlike the Greatwinged Petrel, is restricted to subantarctic and modified antarctic waters.

Surface seizing and dipping for live prey as well as scavenging are feeding methods reported for the Greatwinged Petrel (Imber 1973, Griffiths *et al.* 1982, Harper *et al.* 1985, Harper 1987). Off New Zealand, *P. m. gouldi* was observed feeding nocturnally on live squid about 200 mm long (i.e. 100 to 150-mm DML). An attempt at seizing a 400 mm-long specimen was unsuccessful (Harper 1987). If this value (converted in 200-300-mm DML) represents the limit for predation on live squid, then a substantial proportion of cephalopods ingested by Crozet Island Greatwinged Petrels (see Table 42) must have been scavenged at the sea surface. On the other hand, the frequent occurrence in the diet of vertically migrating and luminescent squid species argues for at least some nocturnal foraging, even though bioluminescence is now thought not to be

of assistance to nocturnal surface predators (Clarke *et al.* 1981, Rodhouse *et al.* 1987).

PINTADO PETREL *DAPTION CAPENSE*

Results

Samples

Due to very steep and scattered nesting sites combined with relatively small breeding populations only three stomach samples of Pintado Petrels were collected at Ile de la Possession, Crozet Islands. The samples were obtained in January 1982 and January 1983 during the chick-rearing period. The mean reconstituted mass of the samples was 10 g (4-14 g) whereas the mean number of prey items was 1542 (508-2925).

General composition

These three samples displayed very high prey species diversity (numbers of taxa per sample 16, 18 and 24) with crustacean taxa being predominant (12, 13, 19 crustacean taxa per sample). Moreover, crustaceans accounted for more than one half of the food load by mass. Fish and squid were found in two samples but did not account for high mass percentages.

Crustaceans

The main crustacean species were the euphausiids *Euphausia vallentini* and *Thysanoessa* sp. These species accounted each for *c.* 14% of the food load by mass. Of lesser importance were the hyperiids *Themisto gaudichaudii*, several gammarids and the large calanid copepod *Rhincalanus gigas* (Table 43). Other taxa were rare.

Fish, cephalopods and other food types

Numerous unidentified fish fry were found in one sample. In addition, some tiny octopodids also occurred in two samples. However, both prey groups were insignificant when analysed on a relative mass basis (Table 43). Other prey types included numerous gonothecae of a campanullariid hydrozoan, the chaetognath *Sagitta gazellae* and nudibranchiate gastropods. This last taxon was found in all three samples and constituted more than 60% by mass in one of them.

Prey sizes

Prey of Pintado Petrels were small, ranging from the minute halocyprid ostracods 1-2 mm long to arrow worms less than 37 mm long (Fig. 19). Most of the food came from prey individuals less than 20 mm body length, providing <0.01 to 0.1 g of food per prey item ingested.

Comparison with previous studies

Qualitative studies have demonstrated the variety of Pintado Petrel food sources. Squid beaks and offal arising from whaling activities were reported in its diet by Falla (1937). At Kerguelen, crustaceans, including the hyperiid *Themisto gaudichaudii*, were found in its food (Paulian 1953). At Terre Adélie crustaceans prevailed but squid and fish also occurred (Mougin 1968). In the African sector of the Southern Ocean the Pintado Petrel was considered as a squid eater (Griffiths 1982, Abrams 1985).

Several authors have quantified the food composition of the Pintado Petrel at various breeding sites or at sea (Table 44). Pintado Petrels caught at sea in oceanic and continental slope areas had mostly fed on squid whereas epipelagic crustaceans constituted the bulk of the diet of birds caught at the colonies (but see Ridoux & Offredo 1989 for possible methodological biases in processing squid remains). Antarctic Krill and Ice Krill *Euphausia*

TABLE 43

THE DIET OF THE PINTADO PETREL AT THE CROZET ISLANDS (N=3)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**100**	**4071**	**90.2**	**16.0**	**51.0**			
Ostracods								
Unidentified halocypridids	67	34	0.8	+	+	1.5 ± 0.1	(1.3-1.7)	18
Cirripeds								
Lepas australis (cypris larvae)	67	11	0.2	+	0.1	2.6 ± 0.6	(2.4-2.8)	7
Copepods								
Rhincalanus gigas	67	208	4.6	1.3	4.2	7.0 ± 0.6	(6.1-8.2)	19
Unidentified calanids	67	309	6.8	0.2	0.7	2.9 ± 0.5	(1.8-4.3)	41
Unidentified euchaetids	100	58	1.3	0.2	0.7	4.8 ± 1.2	(3.2-6.4)	13
Gammarid amphipods								
Parawaldeckia kidderi	33	37	0.8	0.3	1.0	7.2 ± 0.3	(7.0-7.5)	8
Unidentified lysianassids	33	4	0.1	0.1	0.3			
Pontogeneiella brevicornis	67	27	0.6	0.6	2.0	10.0 ± 1.0	(9.0-11.5)	6
Podocerus capillimanus	33	3	+	+	+	5.8 ± 0.8	(5.0-6.5)	3
Unidentified oedicerotids	33	4	0.1	+	+			
Unidentified	67	70	1.6	0.7	2.4	8.8 ± 1.8	(7.0-12.0)	6
Hyperiid amphipods								
Themisto gaudichaudii	100	259	5.7	1.1	3.6	4.9 ± 1.5	(2.0-7.5)	37
Hyperoche sp.	33	1	+	0.1	0.3	11.5		1
Hyperiella antarctica	67	9	0.2	+	0.1	4.6 ± 1.0	(2.3-5.5)	8
Cyllopus lucasii	33	1	+	+	0.1	10.5		1
Vibilia antarctica	67	3	0.1	0.1	0.2	8.0 ± 1.8	(6.0-9.1)	3
Primno macropa	67	35	0.8	0.5	1.5	6.6 ± 3.9	(1.7-13.9)	18
Euphausiids								
Euphausia vallentini	67	807	17.9	4.1	13.6	11.0 ± 2.1	(8.4-20.7)	74
E. triacantha	33	1020	22.6	1.2	4.0	7.8 ± 2.5	(4.0-13.9)	32
Euphausia sp.	67	182	4.0	0.2	0.6	6.8 ± 1.5	(4.5-10.3)	21

Thysanoessa sp.	100	961	21.3	4.3	14.2	9.0 ± 2.2	(3.6-13.0)	35
Stylocheiron sp.	33	17	0.4	0.4	1.4	16.4 ± 3.0	(11.3-20.6)	10
Mysids								
Boreomysis sp.	67	9	0.2	0.1	0.2	10.3 ± 1.9	(8.5-13.0)	5
Euchaetomera zurstrasseni	33	1	+	+	+	10.0		1
Isopods								
Unidentified sphaeromatids	33	1	+	+	+	4.5		1
CEPHALOPODS	**67**	**5**	**0.1**	**0.6**	**2.0**			
Octopods								
Unidentified octopodids	67	5	0.1	0.6	2.0	10.0		1
FISH	**67**	**184**	**4.1**	**0.6**	**2.0**			
Unidentified	67	184	4.1	0.6	2.0	10.0		1
OTHER ORGANISMS	**100**	**254**	**5.6**	**13.7**	**45.0**			
Hydrozoa								
Unidentified campanullariids	100	+	+	+	+			
Gastropods								
Unidentified nudibranchs	100	221	4.9	11.1	36.4	10.0		1
Chaetognaths								
Sagitta gazellae	100	33	0.7	2.1	7.0	28.2 ± 8.5	(20.0-37.0)	3
Unidentified organic fragments	33	+	+	0.5	1.6			

TABLE 44

PINTADO PETREL DIETS AT VARIOUS LOCALITIES

Localities[a]	Diets (% by mass, main prey species in brackets)					References
	Euphausiids	Other crustaceans	Fish	Squid	Other prey types	
			Sub-Antarctic			
Crozet Islands (46S) (c)	34 (1,2)	17 (5,6)	2	2	45 (9)	(this work)
			Antarctic continental slope and oceanic areas			
Signy Island (60S) (c)	64 (3)		15 (7)		21 (10)	Beck 1969[b]
Weddell Sea (60S) (s)	1		1	98		Bierman & Voous 1950[c]
Ross Sea (70S, oceanic) (s)	3 (3)			97		Ainley *et al.* 1984
			Antarctic continental shelf			
Adélie Land (66S) (c)	64 (3,4)	+	29	+	7 (11)	Ridoux & Offredo 1989
Prydz Bay (67S) (c)	76 (3)	1	23 (7)		+	Green 1986
Prydz Bay (67S) (c)	85 (3)	+	14 (8)	+		Arnould & Whitehead 1991

The main prey species are: (1) *Euphausia vallentini*, (2) *Thysanoessa* spp., (3) *E. superba*, (4) *E. crystallorophias*, (5) *Themisto gaudichaudii*, (6) gammarid amphipods, (7) nototheniids, (8) *Pleuragramma antarcticum* , (9) nudibranch gastropods, (10) various crustaceans, tunicates and pteropods, (11) carrion

[a] sampling details : collected at sea (s) or at the colonies (c)

[b] percents by mass recalculated by Croxall & Prince 1980

[c] percents by mass recalculated by Ainley *et al.* 1984

crystallorophias prevailed at the southernmost breeding sites complemented by substantial amounts of fish. The preliminary results obtained to date at the Crozets compare well with the other studies in terms of total mass percentages of crustaceans in the diet. The difference in species composition of the diet of Pintado Petrels throughout its latitudinal range fits the distribution of Subantarctic, Antarctic and Ice Krill, respectively throughout the latitudinal range of the Pintado Petrel. However, the diet of the Pintado Petrel at the Crozet Islands differs from the other localities in including high mass percentages of unusual prey types, mainly the nudibranchiate gastropods, and in the smaller average prey body size.

Foraging range and behaviour

Around the Crozet Islands the Pintado Petrel is associated to one coastal and two neritic seabird assemblages. The two latter assemblages were observed mostly in the western part of the archipelago where the shelf is broader (Stahl 1983). This petrel is known to forage in inshore habitats, including coastwards of the kelp beds to the surf zone, all the year round (Jouventin *et al.* 1982b, V. Ridoux unpubl. winter obs.). Therefore, Pintado Petrels of the eastern islands, from which the samples come, may therefore forage mostly in coastal habitats because the neritic zone is much narrower than it is around the western Crozet Islands. The importance of nudibranchs and the occurrence of hydrozoans, which both live on *Macrocystis pyrifera* kelp fronds, are consistent with such an inshore feeding behaviour.

Sightings from the coastline have shown that Pintado Petrels congregate opportunistically at any temporary small-scale food source. Such congregations occur around Killer Whales feeding close inshore (Ridoux 1987), carcasses of penguins and fish fed on by giant petrels or small-scale plankton swarms that sometimes occur in sheltered bays for a few hours during which plankton concentrations may be so high that chaetognaths and euphausiids were observed stranding alive (V. Ridoux unpubl. obs.). A similar feeding behaviour has been reported for other localities (Downes *et al.* 1959, Beck 1969). While scavenging, Pintado Petrels were seen associating with giant petrels at the same food source whereas Kelp Gulls *Larus dominicanus*, another inshore scavenger, were chased away by the giant petrels. On inshore planktonic swarms, Pintado Petrels foraged with Salvin's Prions.

In accordance with the variety of their prey, Pintado Petrels display various feeding techniques including surface seizing, shallow plunges, and filter feeding (Harper *et al.* 1985, Warham 1990). The smaller prey sizes observed at the Crozets than at other localities suggests that here filter feeding is likely to be an important feeding method. In addition, scavenging, although not supported by the dietary results, was observed directly.

BLUE PETREL *HALOBAENA CAERULEA*

Results

Samples

Thirty-three stomach contents of Blue Petrels were obtained at Ile de l'Est, Crozet Islands, from adults returning to the colonies in January 1982, at the end of the chick-rearing period. Birds were mist-netted by night and regurgitated food material as soon as they were handled. The mean reconstituted mass of the samples was 9 $\pm$ 6 g (1-28 g).

General composition

The Blue Petrel displayed a mixed diet dominated by micronektonic crustaceans (about 60% by mass) and complemented by squid and fish remnants representing 27 and 11% by mass, respectively. Other types of organisms in the diet

accounted for less than 2% by mass (Table 45). Crustaceans accounted for more than 50% of the mass of 23 samples out of 33, whereas squid, fish and gelatinous plankton dominated in five, three and one samples, respectively.

Crustaceans

Twenty-five crustacean taxa were identified, of which four amounted each to more than 5% by mass of the diet and included the hyperiid *Themisto gaudichaudii*, the euphausiids *Euphausia vallentini* and *Thysanoessa* spp. and the pasiphaeid shrimp *Pasiphaea longispina*. Epipelagic forms such as hyperiid amphipods and euphausiids dominated but several deep-dwelling taxa, amounting to 11.6% by mass of the diet, included the ostracod *Gigantocypris muelleri*, the gammarids *Eurythenes* spp., the mysids *Gnathophausia gigas* and *Pseudochalaraspidum* sp. and the decapod shrimp cited above. Also noteworthy was the frequent occurrence of Antarctic Krill.

On an individual sample basis, at least five taxa were found to account for more than 50% by mass including *Pasiphaea longispina* (five samples), *Euphausia vallentini* and *Thysanoessa* spp. (four samples each), *Themisto gaudichaudii* (three) and *Gnathophausia gigas* (one). In addition, the gammarid *Eurythenes gryllus* and Antarctic Krill ranked first in one sample each although they contributed somewhat less than 50% by mass to these samples.

Cephalopods, fish and other organisms

Squid occurred mostly as fragments of which only a few were identifiable. Only four beaks in buccal masses were found and identified as very small gonatids weighing *c.* 0.1 g. Other squid remains obviously came from much larger individuals since flesh fragments weighed 1-17 g. Fish also occurred as fragments, most often unidentifiable. However, six individuals found in the fresh fraction and 16 pairs of accumulated otoliths were all identified as pelagic species with four myctophids, the trichiurid *Paradiplospinus gracilis*, the melamphaid *Sio nordenskjoldii* and one bathylagid fish being identified (Tables 45, 46). Other prey organisms included salps and other unidentified gelatinous plankters, chaetognaths and insects (two types of moth and the assassin bug *Nabis capsiformis*). None of these was important either by number or by mass.

Prey sizes

Crustaceans ranged in length from 2-92 mm with most of the biomass arising from prey individuals over 10 mm in length (Table 44, Fig. 20). Fish were 2-120 mm long (Tables 45 & 46) but it was unclear whether they were ingested whole over the whole size range. Squid lengths were much less precisely known; however, it appeared that both small individuals (25 mm DML) and fragments of large ones (up to an estimated 150 mm DML, as suggested by pieces of gladii and arms) were caught.

Comparison with previous studies

Krill and squid were the only prey taxa reported in early qualitative studies. In the Atlantic sector of the Southern Ocean, five birds caught at sea between 57° and 66°S had fed on euphausiids and two others on squid (Bierman & Voous 1950). At Kerguelen, only eroded beaks and accumulated eye lenses of cephalopods were found in the stomachs of 12 birds collected at a breeding colony (Paulian 1953). Blue Petrels stranded ashore in Australia contained mainly squid remains but also some terrestrial insects (Brown *et al.* 1986).

Two quantitative studies can be compared with the present results (Table 47). At South Georgia, fish dominated the diet of the Blue Petrel and Antarctic Krill (10-59 mm long), constituted the bulk of the crustacean fraction. This is consistent with the abundance of this krill species in the area. Squid constituted only a minor proportion

TABLE 45

THE DIET OF THE BLUE PETREL DIET AT THE CROZET ISLANDS (N=33)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.[a]	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**100.0**	**5924**	**98.8**	**177.5**	**60.9**			
Ostracods								
Gigantocypris muelleri	15.2	5	0.1	0.5	0.2	15		1
Copepods								
Unidentified calanoids	12.1	22	0.4	+	+	2.9 ± 0.1	(2.8-3.1)	5
Unidentified euchaetids	3.0	1	+	+	+	4.0		1
Rhincalanus gigas	3.0	2	+	+	+	6.2	(5.7-6.6)	2
Cirripeds								
Lepas australis (cypris larvae)	21.2	30	0.5	0.1	+	2.4 ± 0.2	(2.1-2.8)	18
L. australis (post-larvae)	6.1	2	+	0.1	+	6.0		1
Gammarid amphipods								
Eurythenes obesus	6.1	2	+	0.2	0.1	15.0	(12.0-18.0)	2
E. gryllus	6.1	1	+	5.0	1.7	80.0		1
Cyphocaris richardi	15.2	5	0.1	1.3	0.4	21.3	(17.5-25.0)	2
Unidentified[b]	9.1	4	0.1	2.5	0.9	24.0 ± 8.8	(12.0-33.0)	4
Hyperiid amphipods								
Themisto gaudichaudii	90.9	3025	50.5	33.7	11.6	8.8 ± 5.0	(1.9-20.3)	277
Hyperoche sp.	3.0	1	+	0.1	+	12.0		1
Hyperia sp.	6.1	3	+	0.3	0.1	10.3	(6.5-17.4)	3
Hyperiella antarctica	36.4	14	0.2	0.2	0.1	6.0 ± 1.8	(5.0-11.5)	12
Vibilia antarctica	48.5	177	3.0	4.9	1.7	9.6 ± 1.1	(7.2-11.5)	73
Cyllopus lucasii	51.5	121	2.0	5.4	1.8	10.6 ± 2.0	(5.8-17.0)	50
Primno macropa	12.1	6	0.1	0.2	0.1	11.5 ± 1.7	(10.0-13.9)	5
Unidentified	6.1	3	+	0.1	+	10.0		1
Euphausiids								
Euphausia vallentini	51.5	750	12.5	41.4	14.3	20.2 ± 3.2	(11.1-25.1)	159
E. superba	24.2	29	0.5	10.5	3.6	37.3 ± 5.5	(31.1-52.3)	24
Euphausia sp.	9.4	9	0.2	0.4	0.1	15.2 ± 6.5	(12.0-28.5)	6

Thysanoessa macrura/vicina	51.5	1693	28.3	41.5	14.3	16.4 ± 2.4	(13.0-26.2)	143
Mysids								
Gnathophausia sp.	12.1	3	0.1	5.9	2.0	66.0		1
? Pseudochalaraspidum sp.	3.0	1	+	2.4	0.8	70.0		1
Decapods								
Pasiphaea longispina	36.4	13	0.2	19.8	6.8	77.0 ± 13.4	(47.0-92.0)	11
Unidentified	3.0	1	+	1.0	0.3			
Isopods								
Unidentified	3.0	1	+	+	+	3.0		1
CEPHALOPODS	**69.7**	**(10)**	**0.2**	**79.9**	**27.2**			
Teuthoidea								
Unidentified gonatids	3.0	(4)	0.1	0.5	0.2			
Unidentified fragments	69.7	(6)	0.1	79.4	27.2			
FISH	**75.8**	**(32)**	**0.5**	**30.4**	**10.6**			
Myctophiformes								
Electrona carlsbergi	3.0	(1)	+	7.9	2.7	81.0		1
Protomyctophum tenisoni	6.1	(2)	+	2.3	0.8	42.0	(37.0-47.0)	2
P. normani	3.0	(1)	+	2.4	0.8	55.0		1
Krefftichthys anderssoni	3.0	(1)	+	1.3	0.4	45.0		1
Perciformes								
Paradiplospinus gracilis	3.0	(1)	+	3.0	1.0	100.0		1
Unidentified	57.6	(26)	0.4	13.5	4.6	57.0 ± 38.3	(20.0-120.0)	5
OTHER ORGANISMS	**33.3**	**33**	**0.6**	**4.4**	**1.6**			
Ctenophores								
Unidentified	18.2	17	0.3	3.7	1.3	20.0		1
Chaetognaths								
Sagitta gazellae	3.0	1	+	0.1	+			
Insects								
Unidentified pyraloids	3.0	1	+	0.1	+			
Unidentified noctuids	6.1	2	+	0.5	0.2	15.8	(13.5-18.0)	2
Nabis capsiformis	9.0	12	0.2	0.1	0.1	11.0	(11.0-11.0)	2

[a] numbers in parentheses indicate that the taxon appeared as fragments rather than complete individuals (see text under data processing)

[b] including 1 *Paracallisoma alberti* and 1 *Parandania boeki*

TABLE 46

SUMMARY OF ACCUMULATED ITEMS IN BLUE PETREL STOMACH CONTENTS (N=33)

Items	Number of items	Measurements (mm)[a]		Estimated body length (mm)[b]			Estimated body mass (g)	
		Mean ± S.D.	(range)	n	Mean	(range)	Mean	(range)
FISH								
Otoliths	16							
Electrona carlsbergi	3	3.65		1	81		7.9	
Protomyctophum tenisoni	3	1.57	(1.5-1.6)	3	40	(37-47)	1.0	(0.8-1.5)
P. normani	1	1.75		1	55		2.4	
Krefftichthys anderssoni	2	1.50	(1.4-1.6)	2	50	(45-54)	1.8	(1.3-2.3)
Unidentified myctophids	4							
Sio nordenskjoldii	1							
Bathylagus sp.	1							

[a] Otolith Length
[b] Standard Length

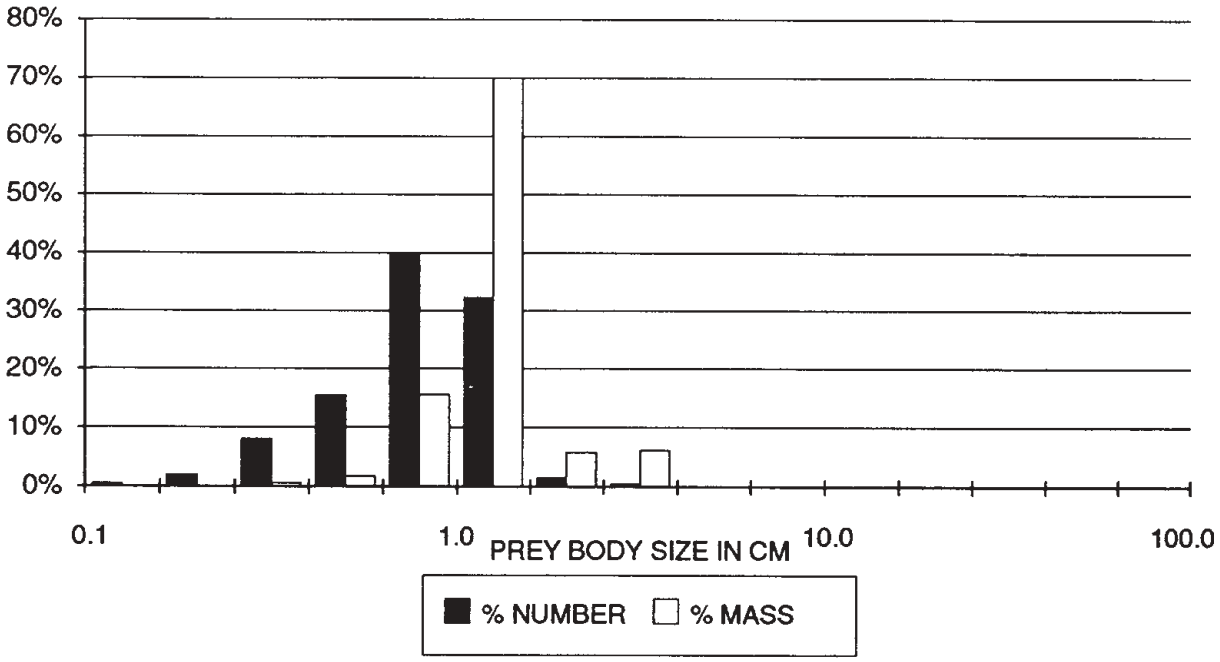

Figure 19
Prey-size distribution in the diet of the Pintado Petrel.

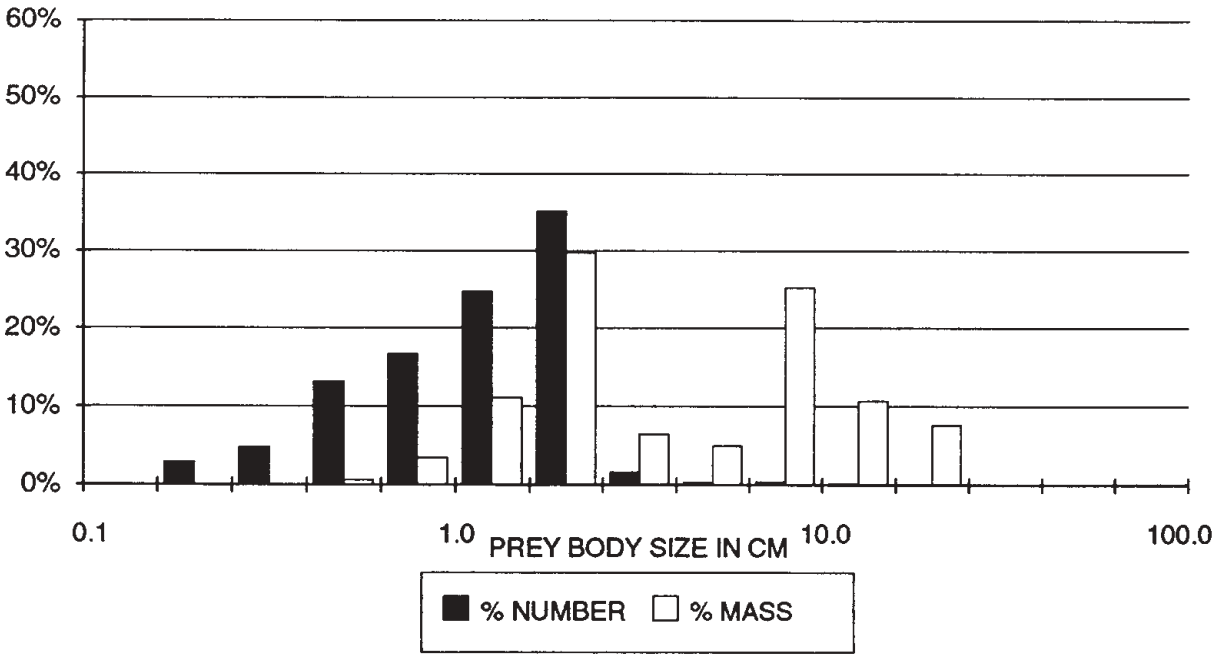

Figure 20
Prey-size distribution in the diet of the Blue Petrel.

TABLE 47

BLUE PETREL DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in brackets)					References
	Euphausiids	Other crustaceans	Fish	Squid	Other prey types	
Marion Island (46S)	44.8 (2)	14.7 (4)	21.2 (7)	15.7 (9)	3.6 (10)	Steele & Klages 1986
Crozet Islands (46S)	32.3 (1,2)	28.6 (5,6)	10.6 (7)	27.2	1.6 (11)	(this work)
South Georgia (52S)	35.8 (3)	6.0	58.3 (7)	0.3		Prince 1980, modified by Prince & Morgan 1987

The main prey species are: (1) *Thysanoessa* spp., (2) *Euphausia vallentini* , (3) *E. superba,* (4) *Themisto gaudichaudii*, (5) *Pasiphaea longispina,* (6) *Cyllopus* sp. and Gammaridae, (7) Myctophidae, (8) Nototheniidae, (9) Onychoteuthidae, (10) insects, (11) salps and other gelatinous plankters

of the diet. The diet of the Blue Petrel at Marion Island was similar to that determined for the Crozet Islands.

Foraging range and behaviour

The distribution of the Blue Petrel at sea is circumpolar but restricted to antarctic waters (Bierman & Voous 1950, Ainley *et al.* 1984). In the Crozet sector of the Southern Ocean, in February, *i.e.* soon after the chicks have fledged, the species is associated with low sea-surface temperatures (0-2°C) about 2000 km south of the islands (Stahl 1987). In September the species forages at lower latitudes where sea-surface temperature is 5°C (Stahl *et al.* 1985a). Blue Petrels are rarely observed in neritic areas around the Crozets, instead mostly foraging over oceanic zones. Although breeding populations tend to forage somewhat north of nonbreeding birds, the occurrence of Antarctic Krill in the food delivered to chicks at Crozet Islands indicates long southward foraging trips to at least 55°S. This latitude is the northern limit at which Antarctic Krill is likely to be caught in any numbers (from euphausiid distributions in John 1936, Baker 1965). From other evidence such as the amount of stomach oil or the occurrence of pumice stones, the Blue Petrel was also considered to forage in offshore waters to the south of South Georgia (Prince 1980a, Croxall & Prince 1980b). Its foraging radius was estimated to be 670 km against 240 km for the Antarctic Prion *Pachyptila desolata* (Croxall *et al.* 1984). The occurrence of deep-sea forms (*Gigantocypris muelleri, Eurythenes* spp., *Pasiphaea longispina, Gnathophausia gigas, Pseudochalaraspidum* sp., and *Sio nordenskjoldii*) in the diet of the Blue Petrel at the Crozet Islands is additional evidence of oceanic foraging and suggests an intermediate feeding niche between a typical prion and a gadfly petrel diets (epiplanktonic crustaceans and deep-sea nektonic crustaceans, respectively ; see also discussion in Kerguelen and Softplumaged Petrel sections above). In contrast to this evidence of offshore feeding areas, Falla (1937) observed Blue Petrels feeding in the kelp beds at Kerguelen.

The feeding methods of the Blue Petrel are not known in detail. Surface seizing appears the most common method of feeding followed by dipping and rarely diving (Bierman & Voous 1950, Harper *et al.* 1985, J.C. Stahl unpubl. data). In areas where plankton is plentiful Blue Petrels forage in large flocks, similar to prions, and may associate with large whales whose swimming movements drive planktonic organisms to the surface (Bierman & Voous 1950). In areas of thinly scattered prey the Blue Petrel switches to solitary aerial feeding methods, a gadfly petrel behaviour (J.-C. Stahl unpubl. data). Such a plasticity in foraging methods accords well with the dietary composition which includes prey taxa typical of both prions and gadfly petrels (see relevant sections in this work).

Although a minor component in the diet, the occurrence of insects in the Blue Petrel diet warrants comments. Terrestrial insects have been reported in the diet of Blue Petrels from three localities, Marion and Crozets (noctuid and pyraloid moths and the assassin bug *Nabis capsiformis*) and the coasts of Victoria, Australia, (Coleoptera) (Brown *et al.* 1986, Steele & Klages 1986, Steele & Crafford 1987, this study). These taxa do not belong to the fauna of any subantarctic island. The assassin bug is a pantropical species known from all three southern continents. These insects must have been driven easterly by dominant winds from nearby continental masses. Their occurrence in good condition in the food of the Blue Petrel suggests that a steady flux of live wind-driven insects reaches the Crozet Island sector and perhaps even farther south. Insects have also been recorded from stomach samples of Salvin's Prions and Kerguelen Petrels (this study).

SALVIN'S PRION *PACHYPTILA SALVINI*

Results

Samples

The stomach contents of 33 Salvin's Prions were collected at Ile de l'Est from 12 January to 18 February 1982 during the early chick-rearing period. Adults were mist-netted as they flew back to their nests and induced to regurgitate their food load. The mean reconstituted mass of the samples was 10 $\pm$ 8 g (6-41 g).

General composition

The diet of Salvin's Prions was dominated by planktonic crustaceans in the analyses by number and mass (Table 48). Squid, fish and other organisms, mainly arrow worms, accounted for small numbers of items but constituted a larger proportion of the diet by mass. On an individual sample basis, non-crustacean prey taxa accounted for more than 50% by mass in only three out of 33 samples (one with arrow worms and two with squid).

Crustaceans

Twentytwo crustacean taxa were identified from the food of Salvin's Prions. Copepods were extremely numerous, tens of thousands being counted from several individual samples (maximum 130 000 copepods in one sample). This group accounted for more than 90% of all prey individuals. The two most important species were the calanids *Drepanopus pectinatus* and *Calanus simillimus*. However, copepods comprised only 15% by mass of the diet. In contrast, all other crustacean species appeared at very low to negligible percents by number. However, owing to their generally much larger body sizes compared to copepods, several of them, including the hyperiids *Themisto gaudichaudii* and *Primno macropa* and the euphausiids *Euphausia vallentini* and *Thysanoessa* spp., constituted a significant proportion of the diet by mass. Of these prey taxa *T. gaudichaudii* ranked first by reconstituted mass comprising 41.3% of the diet. On an individual sample basis *T. gaudichaudii* dominated by mass in 12 of 33 stomachs and, albeit being below 50% by mass, ranked first in four others. Copepods, *P. macropa* and *Thysanoessa* spp. accounted for more than 50% by mass in five, three and two samples, respectively. *C. lucasii* and *E. vallentini* dominated in one sample each.

Other organisms

Other prey organisms of Salvin's Prions included squid, fish, hydrozoan gonothecae, the arrow worm *Sagitta gazellae* and the assassin bug *Nabis capsiformis*. The most important prey were squid which dominated in two stomachs and chaetognaths which dominated in one sample and ranked first, although being below 50% by mass, in another one. Squid and fish mostly occurred as fragments from which few beaks and no otoliths allowing identification were found (Table 48, plus one loose beak of *Onychoteuthis* sp. 11 mm estimated DML, 0.4 g estimated body mass).

Prey sizes

Prey body lengths ranged from 1-25 mm in crustaceans and up to 70 mm in other groups (Table 48, Fig. 21). Although, due to the huge number of copepods, the size distribution by number was heavily skewed towards the size classes less than 5 mm, *c.* 80% by mass of the food was contributed by prey over 10 mm.

Comparison with previous studies

Previous qualitative data have shown the importance of euphausiids and hyperiids at every sampling site as well as the occasional occurrence of squid, fishes and pteropods in the diet of Salvin's Prion (Bierman & Voous 1950, Mougin 1975, Grindley & Lane 1979). The only quantitative work, carried out at the Marion Island, estimated the composition by mass to be

TABLE 48

THE SALVIN'S PRION DIET AT THE CROZET ISLANDS (N=33)

Prey Species	Occurrence	Relative abundance		mass		Reconstituted body length[b] (mm)		
	%	No.[a]	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**100.0**	**319039**	**99.9**	**277.1**	**87.7**			
Ostracods								
Unidentified halocypridids	3.0	2	+	+	+	1.6	(1.5-1.7)	2
Copepods								
Drepanopus pectinatus	72.7	256500	84.7	27.4	8.7	1.6 ± 0.2	(1.2-2.6)	300
Calanus simillimus	39.4	13200	4.3	8.4	2.7	3.0 ± 0.4	(1.4-3.8)	162
Rhincalanus gigas	9.1	23	+	0.1	+	6.3 ± 1.2	(3.8-4.6)	15
Unidentified calanoids	18.2	34600	11.4	11.1	3.5			
Unidentified harpacticoids	6.1	11	+	+	+	0.7	(0.7-0.8)	4
Cirripeds								
Lepas autralis (cypris larvae)	57.6	1767	0.5	2.9	0.9	2.4 ± 0.2	(2.0-2.9)	181
L. australis (post-larvae)	3.0	1	+	+	+	3.5		1
Gammarid amphipods								
Gondogeneia ushuaiae	15.2	294	0.1	4.3	1.4	8.2 ± 1.7	(4.0-10.5)	25
Uristes murrayi	3.0	25	+	2.6	0.8	16.8 ± 1.3	(15.0-18.0)	5
Unidentified ischyrocerids	6.1	3	+	+	+			
Unidentified	27.3	122	+	3.2	1.0	9.0 ± 7.3	(5.0-25.0)	5
Hyperiid amphipods								
Themisto gaudichaudii	97.0	9237	2.9	130.5	41.3	9.4 ± 5.9	(1.3-21.5)	438
Hyperoche sp.	3.0	2	+	+	+	7.0	(7.0-7.0)	2
Hyperiella antarctica	24.2	92	+	1.6	0.5	5.9 ± 1.1	(4.3-9.0)	26
Vibilia antarctica	48.5	84	+	2.3	0.7	9.6 ± 0.8	(8.2-11.9)	66
Cyllopus lucasii	48.5	180	0.1	10.3	3.3	10.9 ± 1.7	(7.0-14.2)	50
Primno macropa	72.7	818	0.2	30.9	9.8	10.7 ± 2.6	(4.8-15.4)	98
Megalanceola sp.	3.0	1	+	1.6	0.5	46.0		1
Unidentified	6.1	4	+	+	+			
Mysids								
Gnathophausia gigas	3.0	1	+	+	+			

Euphausiids								
Euphausia vallentini	39.4	669	0.2	19.0	6.0	15.5 ± 4.1	(9.0-25.1)	82
Euphausia sp.	27.3	47	+	0.3	0.1	12.3 ± 3.6	(5.9-21.6)	33
Thysanoessa sp.	57.6	1311	0.4	20.0	6.3	14.9 ± 5.9	(3.6-25.4)	155
Unidentified	12.1	44	+	0.6	0.2			
Isopods								
Unidentified	3.0	1	+	+	+	4.2		1
CEPHALOPODS	**24.2**	**(10)**	+	**11.2**	**3.5**			
Teuthoidea								
Unidentified onychoteuthids	6.1	2	+	6.8	2.1	47.0	(22.0-71.0)	2
Unidentified gonatids	3.0	2	+	0.4	0.1			
Unidentified frements	12.1	(6)	+	4.0	1.3			
FISH	**36.4**	**(17)**	+	**7.0**	**2.2**			
Unidentified	36.4	(17)	+	7.0	2.2			
OTHER ORGANISMS	**48.5**	**249**	+	**20.6**	**6.5**			
Hydrozoa								
Unidentified campanullariids	15.2	+	+	+	+			
Gastropods								
Unidentified	3.0	1	+	+	+			
Chaetognaths								
Sagitta gazellae	33.3	245	+	20.6	6.5	31.3 ± 1.3	(30.0-33.0)	4
Insects								
Nabis capsiformis	3.0	3	+	+	+	11.0		1

[a] Numbers in parentheses indicate that the taxon appeared as fragments rather than complete individuals (see text under data processing)

[b] Dorsal Mantle Length for squid, total body length for the other prey taxa

44.2% crustaceans, 41.9% fish and 13.9% squid (Gartshore *et al.* 1988, Table 49). The main crustaceans were *Themisto gaudichaudii* and *Euphausia vallentini* which accounted respectively for 66.6% and 25.2% by mass of the crustacean fraction. Squid present in the diet were juvenile onychoteuthids 8-46 mm DML. All identified fishes were the myctophid species *Electrona carlsbergi* (56-83 mm long) and *Protomyctophum tenisoni* (41-67 mm long). The absence of copepods is another noticeable feature of the diet of Salvin's Prions at Marion Island.

In common with Salvin's Prion, two other prion species have enlarged beaks fitted with lamellae under the upper mandible, namely the Broadbilled *P. vittata* and Antarctic *P. desolata* Prions. These three species constitute a complex whose systematic level is still controversial (see Cox 1980 and Harper 1980 for taxonomic considerations, also synthesis in Warham 1990). They can hardly be discriminated at sea and presumably have similar food requirements and foraging abilities. Consequently, previous reports on the diets of the other two species are summarized below and in Table 49.

Qualitative dietary results showed a broad spectrum of prey in the diet of the Antarctic Prion and a wide overlap with the prey array of Salvin's Prion. Prey include unidentified plankton (Matthews 1929), squids and pteropods (Falla 1937), amphipods (Paulian 1953), amphipods and pteropods (Ealey 1954), amphipods and fish (Harper unpubl. data cited in Imber 1981). In the Ross Sea and the southern Atlantic Ocean, Antarctic Prions collected at sea had stomachs full of Antarctic Krill 8-23 mm long (Ainley *et al.* 1984, Harper 1987). The only quantitative study, performed in South Georgia, highlighted the importance by mass of planktonic crustaceans in the diet of the Antarctic Prion. Prey included 56.9% by mass Antarctic Krill (5-60 mm), 31.5% copepods (1-11 mm), 4.5 % *Themisto gaudichaudii* (2-18 mm), 4.7% other crustaceans, 1.8% fish and 0.6% squid (Prince 1980a).

The occurrence of copepods in the diet of the Broadbilled Prion has been emphasized at every study site (Richdale 1944, Imber 1981). At Chatham Islands, copepods (1.3-4.1 mm) accounted for 70% by mass of the diet, whereas the euphausiid *Nyctiphanes australis* and various amphipods constituted the bulk of the remaining 30% (Imber 1981). At Gough Island, 150 stomach samples collected over four seasons were analysed for frequency of occurrence and prey body length (Klages & Cooper 1992). Copepods appeared in all samples but one and the hyperiids *Platyscelus ovoides* and *Themisto gaudichaudii* ranked second and third in importance respectively. Number and mass were not given but copepods were reported to constitute "the bulk of each sample" (Klages & Cooper 1992). However, differences in prey body size and individual mass suggest that non-copepod prey groups may be significant in mass composition since mean body masses of hyperiids were 25 times greater than that of copepods (calculated from length data given in Klages & Cooper 1992 and regressions in Appendix 1 of this work).

Foraging range and behaviour

In the south western Indian Ocean, Salvin's Prions are associated with modified Antarctic waters located between the Antarctic Convergence and the Polar Front (Stahl 1983). At the Crozet Islands the species forages opportunistically in a variety of habitats characterized by high plankton abundance in either inshore or offshore waters. Salvin's Prions can concentrate as close to the coastline as the kelp bed area where plankton occasionally aggregates (Jouventin *et al.* 1982b, pers. obs.). Similar observations have been made for Antarctic Prions at Heard Island (Downes *et al.* 1959). Salvin's Prions also forage over the continental shelf and slope, particularly in the western Crozet Islands where drifting waters form eddies and turbulences as they meet these shallow areas. In oceanic zones, the Salvin's/Antarctic Prion complex is also strongly associated with the

TABLE 49

SALVIN'S AND ALLIED PRION DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in brackets)					References
	Copepods	Euphausiids	Amphipods	Other crustaceans	Other Food types	
			Broadbilled Prion *Pachyptila vittata*			
Chatham Islands (45S)	70.0 (1)	5.8 (5)	19.7 (9)	1.3	3.1	Imber 1980
			Salvin's Prion *Pachyptila salvini*			
Marion Island (46S)		11.2 (6)	32.6 (10)	0.4	55.6 (12,13,14)	Gartshore *et al.* 1988
Crozet Islands (46S)	14.9 (2)	12.6 (6,8)	59.3 (10)	1.0 (11)	12.2 (15)	(this work)
			Antarctic Prion *Pachyptila desolata*			
South Georgia (52S)	31.5 (3,4)	57.3 (7)	8.2 (10)	0.8	2.4	Prince 1980

The main prey species are: (1) *Calanus tonsus*, (2) *Drepanopus pectinatus*, (3) *Rhincalanus gigas*, (4) *Calanoides acutus*, (5) *Nyctiphanes australis*, (6) *Euphausia vallentini*, (7) *Thysanoessa* spp., (8) *E. superba*, (9) *Platyscelus ovoides*, (10) *Themisto gaudichaudii*, (11) *Lepas australis*, (12) *Protomyctophum tenisoni*, (13) *Electrona carlsbergi*, (14) Onychoteuthidae, (15) *Sagitta gazellae*

Subtropical and Antarctic Convergences to the north of the Crozet and Kerguelen Islands (Stahl *et al.* 1985a). Finally, drifting kelp rafts (Stahl 1983, Harper 1987 for Antarctic Prion) and baleen whale pods (Griffiths 1982) are small-scale foraging habitats utilized by Salvin's/Antarctic Prions.

With their enlarged bill fitted with lamellae and therefore specialized for filter feeding one would expect prions of the *P. vittata* complex to be restricted to foraging in this specialized manner. Although they feed by filtration and hydroplaning (as defined in Harper *et al.* 1985) to a greater extent than other petrels, only 18% of Antarctic Prions observed in the southern Pacific and Atlantic Oceans were actually filtering their food out of the water or hydroplaning. As many as 71% were recorded surface-seizing. This is the least specialized procellariiform feeding technique (Harper 1987). Consistently, prey types likely to be efficiently preyed upon with filtering methods, namely copepods and other small plankters, rarely constituted the bulk of their food by mass even though prions of the *vittata* group generally had higher copepod component in their food than the sympatrically breeding Fairy Prion and Blue Petrel (Tables 47, 49 & 51). For example, at South Georgia copepods accounted for 31% by mass of the diet of the Antarctic Prion but only 3.6% of the diet of Blue Petrels and Fairy Prions. At the Crozet Islands copepods accounted for 15% by mass of the diet of Salvin's Prions against 0% in Fairy Prions and Blue Petrels (this study). Copepods were absent from the diet of both Salvin's Prions and Blue Petrels at the Prince Edward Islands (Steele & Klages 1986, Gartshore *et al.* 1988). The Broadbilled Prion, which displays the most specialized beak of all filtering prions, has also been reported to rely on copepods for its food to the greatest extent within prions (Imber 1981, Klages & Cooper 1992).

Comparisons of body sizes of a given prey species taken by both prions with specialized beaks and prions without (or Blue Petrels) should reveal significant differences because of the specialized feeding behaviour of Broadbilled Prions. Prince (1980a) found that Blue Petrels preyed upon larger individuals than did Antarctic Prions. However, at the Crozet Islands no general trend was evident and although some prey species indeed occurred at smaller sizes in Salvin's Prion than in Blue Petrel samples (see *Euphausia vallentini*) or in Fairy Prion samples (see *Themisto gaudichaudii*) others did not. These prey size differences are probably a consequence of differences in prey size availability in the different foraging zones rather than the effect of prey size selection.

FAIRY PRION *PACHYPTILA TURTUR*

Results

Samples

Only six stomach samples of Fairy Prions were collected at Ile de l'Est, Crozet Islands, from 26 January to 16 February 1982 during the early chick-rearing period. The mean reconstituted mass was 7 ± 4 g (3-10 g).

General composition

The food of the Fairy Prion consisted almost exclusively of crustaceans (Table 50). Cephalopods, fish and chaetognaths were only minor components of the diet either by frequency of occurrence, numbers or mass. The prevalence of planktonic crustaceans was observed in every individual sample of the collection.

Crustaceans

Cypris larvae and stalked juveniles of the barnacle *Lepas australis* predominated by number whereas the hyperiids *Themisto gaudichaudii* and *Primno macropa* largely prevailed by reconstituted mass (Table 50). Other crustacean taxa including several hyperiids and two euphausiids were of

TABLE 50

THE DIET OF THE FAIRY PRION AT THE CROZET ISLANDS (N=6)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**100**	**11280**	**99.9**	**50.0**	**95.4**			
Cirripeds								
Lepas australis (cypris)	100	9964	88.3	15.3	29.2	2.4 ± 0.2	(1.7-2.9)	183
L. australis (post -larvae)	83	535	4.7	0.8	1.5	3.4 ± 1.2	(1.9-10.0)	128
Gammarid amphipods								
Unidentified lysianassid	17	1	+	+	+	18.0		1
Hyperiid amphipods								
Themisto gaudichaudii	67	388	3.4	23.7	45.2	13.5 ± 5.6	(2.4-21.3)	145
Hyperia sp.	17	1	+	+	0.1	9.3		1
Hyperiella antarctica	17	2	+	+	0.1	5.1	(4.5-5.6)	2
Vibilia antarctica	33	8	0.1	0.3	0.5	10.7 ± 1.6	(9.3-14.4)	7
Cyllopus lucasii	50	28	0.3	1.7	3.2	12.1 ± 1.1	(9.1-14.9)	26
Primno macropa	67	305	2.7	7.4	14.1	9.1 ± 1.5	(5.4-12.4)	79
Unidentified	50	3	+	+	+			
Euphausiids								
Euphausia vallentini	50	9	0.1	0.2	0.4	16.1 ± 1.8	(13.6-19.0)	9
Thysanoessa sp.	17	35	0.3	0.6	1.1	15.0 ± 2.0	(12.2-17.8)	18
Isopods								
Unidentified bopyrid	17	1	+	+	+	3.4		1
CEPHALOPODS	**33**	**4**	+	**2.4**	**4.6**			
Teuthoidea								
Brachioteuthis sp.	17	1	+	1.3	2.5	32.5		1
Unidentified gonatids	17	3	+	1.1	2.1			
FISH	**50**	**3**	+	+	+			
Unidentified	50	3	+	+	+			
OTHER ORGANISMS	**50**	**3**	+	+	**0.1**			
Chaetognaths								
Sagitta gazellae	50	3	+	+	0.1	16.7	(15.0-20.0)	3

minor importance. On an individual basis cypris larvae dominated in three samples, *T. gaudichaudii* in two and *P. macropa* in one.

Other organisms

Unidentified fish fry, minute squid, among which *Brachioteuthis* sp. A and unidentified gonatids were found, as well as the chaetognath *Sagitta gazellae* occurred in the diet but none accounted for a significant proportion by mass of any individual sample.

Prey sizes

The prey of the Fairy Prion ranged from 1.7 mm-long cypris larvae to 21 mm-long *Themisto gaudichaudii*. However, the bulk of the diet by mass consisted of prey 10-20 mm long (Fig. 22, Table 50). The fish and squid were often not ingested whole, however, they apparently came from rather small individuals and were not necessarily scavenged at the surface.

Comparison with previous studies

The results of this study contrast with earlier studies since they indicate the huge numerical importance of *Lepas australis* and, despite its minute size, its significant proportion by mass. In New Zealand and Australia, squid, euphausiids and hyperiid amphipods were recorded and included the ubiquitous hyperiid *Themisto gaudichaudii* and the local euphausiid *Nyctiphanes australis* (Harper 1976, Vernon 1978, Morgan & Ritz 1982). Quantitative studies performed in New Zealand (Imber 1981) and at South Georgia (Prince & Copestake 1990) concur with the present results with planktonic crustaceans predominating at all three localities (Table 51). Specific composition differs greatly from one site to another, mainly due to differences in local prey species availability. For example *Nyctiphanes australis* predominates in New Zealand, *Themisto gaudichaudii* at the Crozets and *Euphausia superba* at South Georgia. However, in the light of the other two studies the very low figure for *E. vallentini* in Fairy Prion diet at the Crozets is surprising since Subantarctic Krill is an important food source for several abundant planktivorous seabirds of this community. It may be an indication of very specific foraging habitats but needs to be confirmed from a larger sample collection.

Foraging range and behaviour

During the breeding season, Fairy Prions mostly forage between 50 and 100 km from the Crozet Islands over water 300-1000 m deep. This corresponds roughly to the continental slope (Stahl 1983). Accordingly, the species most important prey species form also a significant proportion of the food of other shelf and slope planktivores (see *Eudyptes* penguins, other prions, diving petrels, storm petrels in relevant sections of this study) although the very low importance by mass of euphausiids contrasts with the other neritic predators. Unfortunately, no data on small-scale variations in the composition of the Crozet shelf and slope micronekton can be compared with these specific dietary differences.

Barnacle larvae and recently settled juveniles found in Fairy Prion diet also occur in the diet of the Greyrumped Storm Petrel *Garrodia nereis* (see below). In accordance with its specialized diet this latter species associates frequently with drifting seaweed rafts when foraging (Stahl 1983). No similar association has been observed for Fairy Prions and the circumstances in which barnacle larvae are taken are unclear. A significant fraction of these barnacles displayed flattened antenules surrounded by glueing secretion or even antenule peduncle transformed into a stalk. This indicates that metamorphosis was under way and consequently that the barnacle had been preyed upon on or very close to a floating support. Algal fragments attached to several clumps of stalked individuals are further evidence to support this assumption and were not observed in Greyrumped Storm Petrel samples.

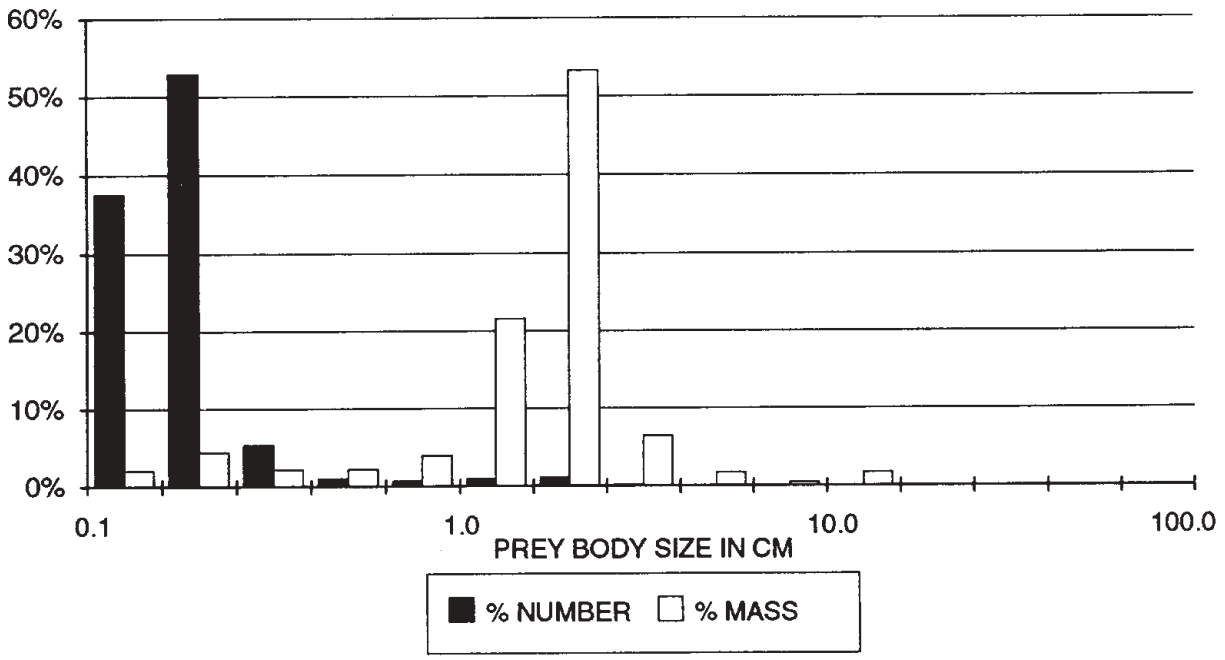

Figure 21
Prey-size distribution in the diet of the Salvin's Prion.

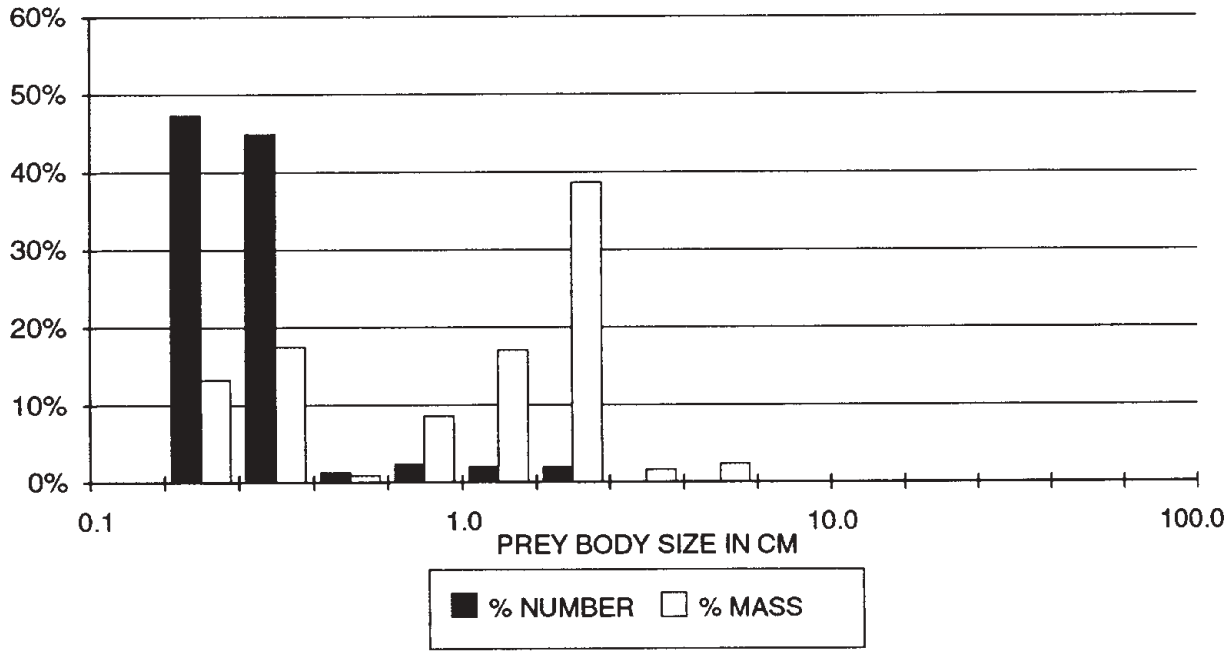

Figure 22
Prey-size distribution in the diet of the Fairy Prion.

TABLE 51

FAIRY PRION DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in brackets)					References
	Euphausiids	Amphipods	Other crustaceans	Fish	Squid	
Stephens Island, N.Z. (40S)	99.0 (1)	0.3 (4)		0.7		Imber 1981
Crozet Islands (46S)	1.5 (2)	63.2 (4,5)	30.7 (6)	+	4.6	(this work)
South Georgia (52S)	76.8 (3)	15.1 (4)	4.0 (7)	2.7	1.3	Prince & Copestake 1990

The main prey species are: (1) *Nyctiphanes australis,* (2) *Euphausia vallentini* and *Thysanoessa sp.,* (3) *E. superba,* (4) *Themisto gaudichaudii*, (5) *Primno macropa,* (6) *Lepas australis*,, (7) *Rhincalanus gigas*.

An alternative hypothesis to predation on algal rafts is that Fairy Prions in the Crozet sector mainly forage over frontal zones or eddies where planktonic organisms of low mobility and detritic material including algal particles are likely to accumulate. This hypothesis accords with foraging in slope areas (Stahl 1983) since such medium-size eddies are often observed where the western drift is deflected and perturbated by submarine topography.

WILSON'S STORM PETREL *OCEANITES OCEANICUS*

Results

Samples

The stomach contents of 15 Wilson's Storm Petrels were collected at Ile de l'Est, Crozet Islands, from 14 January to 1 March 1982, i.e. during late incubation and early chick rearing periods. Adult birds were mist-netted by night as they returned to their nests and regurgitated on handling. The mean reconstituted mass was 0.3 $\pm$ 0.4 g (0.0-1.7 g).

General composition

The diet of Wilson's Storm Petrels was dominated by planktonic crustaceans when considered in terms of frequency of occurrence, number or mass (Table 52). Fish fry were of secondary importance and never accounted for a significant proportion of the diet by mass in any stomach content. Other prey groups were of minor importance and included planktonic gastropods, arrow worms and hydroids, which indicated predation on floating algae.

Crustaceans

The most important crustacean prey groups in the analysis by number were copepods and cyprid larvae of cirripeds. However, owing to their very small body size, they were only of secondary importance in the analysis by mass. Hyperiids, among which *Themisto gaudichaudii* and *Vibilia antarctica* ranked first, collectively accounted for *c.* 15% of the diet by reconstituted mass. However, they always co-occurred with other prey groups which dominated the sample by mass. Euphausiids, mostly *Euphausia vallentini*, ranked fourth in the numerical analysis but accounted for more than one half of the food load pooled over the whole collection. This species dominated the diet composition by reconstituted mass in seven out of 15 samples.

Fish

Unidentified fish fry occurred in three samples and amounted to a significant part of the food load in only one.

Prey sizes

Prey sizes ranged from 1-29 mm long corresponding to 0.01-0.1 g per individual caught (Fig. 23).

Comparison with previous studies

Qualitative data on the food of Wilson's Storm Petrels at numerous southern localities show a wide array of prey taxa. Two birds collected in the Atlantic sector contained accumulated squid beaks, eye lenses and gladii (Bierman & Voous 1950). At the Kerguelen Islands, only tiny squid beaks and eye lenses were reported by Paulian (1953), whereas the hyperiid *Themisto gaudichaudii* and floating offal from the whaling industry were found in the diet of Wilson's Storm Petrel by Falla (1937). The latter report concurs with observations at South Georgia, another important whaling station (Matthews 1929). Seven birds caught at sea in the loose pack ice of the Atlantic sector had fed on squid, planktonic crustaceans, including *Euphausia* sp., and oily offal (Falla 1937). At Signy Island, Antarctic Krill was the main prey species (Roberts 1940,

TABLE 52

THE DIET OF WILSON'S STORM PETREL AT THE CROZET ISLANDS (N=15)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**100.0**	**937**	**80.3**	**4.5**	**87.5**			
Copepods								
Unidentified calanoids	26.7	316	27.1	0.3	4.9	3.1 ± 0.4	(2.0-4.0)	34
Cirripeds								
Lepas australis (cypris larvae)	66.7	420	36.0	0.6	11.9	2.4 ± 0.2	(1.3-3.0)	163
Hyperiid amphipods								
Themisto gaudichaudii	46.7	35	3.0	0.4	8.3	5.2 ± 3.6	(2.7-19.2)	30
Hyperiella antarctica	13.3	6	0.5	+	0.4	4.6 ± 0.8	(3.7-5.3)	3
Vibilia antarctica	13.3	9	0.8	0.3	4.9	9.7 ± 0.6	(8.8-10.4)	9
Primno macropa	26.7	35	3.0	0.1	1.2	3.4 ± 1.4	(1.7-7.9)	30
Unidentified	20.0	3	0.3	+	0.1			
Euphausiids								
Euphausia vallentini	53.3	98	8.4	2.8	54.7	16.8 ± 4.5	(7.7-28.7)	98
E. triacantha	6.7	8	0.7	+	0.2	7.1 ± 3.0	(2.4-11.6)	8
Thysanoessa sp.	20.0	6	0.5	+	0.8	10.5 ± 2.6	(8.8-10.4)	6
Mysids								
Unidentified	6.7	1	0.1	+	+	12.0		1
FISH	**20.0**	**190**	**16.3**	**0.6**	**11.9**			
Unidentified	20.0	190	16.3	0.6	11.9	10.0		1
OTHER ORGANISMS	**26.7**	**40**	**3.4**	**+**	**0.6**			
Hydrozoa								
Unidentified campanulariid	6.7	+	+	+	+			
Gastropods								
Limacina sp.	20.0	39	3.3	+	0.6	2.0		1
Chaetognaths								
Eukrohnia hamata	6.7	1	+	+	+	14.0		1

Beck & Brown 1972, Croxall & Prince 1980b), whereas at South Georgia the myctophids *Protomyctophum bolini* and *P. normani* were identified from otoliths, their length being estimated to be 63-84 mm (Croxall & North 1988).

Prior to the present study, four recent quantitative studies have been performed at different localities: the Ross Sea, South Georgia, King George Island and Adélie Land (Table 53). These studies showed quite differing food preferences from one study site to another. Euphausiids and hyperiids prevailed at both subantarctic localities, Antarctic krill alone accounted for nearly the whole biomass at King George Island. More catholic diets including krill, fish, squid and carrion, were found at both Antarctic Continent study sites.

Foraging range and behaviour

During the breeding season, Wilson's Storm Petrels are reported from 35°S to the coasts of the Antarctic Continent with the exception of the southern part of the Ross Sea (Bierman & Voous 1950, Ainley *et al.* 1984, Stahl 1987). Within this broad distribution range the species mostly forages over continental shelves and slopes at subantarctic latitudes and loose pack-ice and polynia around the Antarctic Continent (Jehl *et al.* 1979, Zink 1981, Thurston 1982, Stahl 1983, Ainley *et al.* 1984, Jouventin *et al.* 1988). Breeding birds at the Crozet Islands do not forage farther than 100 km from the colonies and are often sighted feeding in inshore waters as close to the coastline as the surf area. This is particularly the case during the late chick-rearing period (Stahl 1983, Jouventin *et al.* 1982b). Nevertheless, no prey species found in its diet at the Crozet Islands are clear indicators of coastal foraging. This shift to coastal foraging in late summer may involve only a small proportion of the population. The crustacean component of the diet of Wilson's Storm Petrel is consistent with neritic feeding habitats. The prey species that prevail in its diet also constitute the bulk of the food of several important micronektonic feeders of the shelf area such as crested penguins, prions, and diving petrels (see relevant sections of this study).

Wilson's Storm Petrel has exclusively aerial and diurnal feeding habits which include dipping (73% of the sightings) and pattering (27%, Harper 1987). The planktonic forms which constitute its diet at the Crozet Islands are all small slow-swimming organisms readily seized by this small petrel. In contrast, predation on larger fish and squid reported from other localities suggests scavenging, consistent with its attraction to fishing and whaling activities. The diet of Wilson's Storm Petrel at the Crozet Islands gave no evidence of scavenging but direct observations showed the species to be associated with large Procellariiformes (Stahl 1983) and Killer Whales (Ridoux 1987). Furthermore, the broad range of prey sizes (maximum food intake per individual prey caught ranges from 0.1 g at the Crozets to 3.9 g at South Georgia), combined with the variety of food types reported from the different localities, suggests a very adaptable feeding strategy according to local food resources.

BLACKBELLIED STORM PETREL *FREGETTA TROPICA*

Results

Samples

Of the 25 stomach contents of Blackbellied Storm Petrels collected at Ile de l'Est, Crozet Islands, four were obtained from 20 October 1981 to 28 January 1982 during the incubation period and 21 in February 1982 as chicks were being raised. The reconstituted mass of the samples amounted to 0.7 ± 0.8 g (0.0-3.4 g).

General composition