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

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TABLE 53

WILSON'S STORM PETREL DIETS AT VARIOUS LOCALITIES

Localities[a]	Diets (% by mass, main prey species in brackets)					References
	Euphausiids	Amphipods	Other crustaceans	Fish	Other food types	
			Sub-Antarctic			
Crozet Isls. (46S) (c)	55.7 (1)	14.9 (4)	16.8 (5)	11.9	0.6	(this work)
South Georgia (54S) (c)	37.2 (2)	30.3 (4)	0.7	28.3 (6)	3.8 (8)	Croxall *et al.* 1988
			Antarctic continental slope and oceanic areas			
King George Isl. (62S) (c)	98 (2)	1 (4)	1			Wasilewski 1986[b]
Ross Sea (70S) (s)	36 (2)	+	+	15	49 (7,8)	Ainley *et al.* 1984[c]
			Antarctic continental shelf			
Adélie Land (66S) (c)	37 (3)	5	7	39	13 (9)	Ridoux & Offredo 1989

The main prey species are: (1) *Euphausia vallentini*, (2) *E. superba*, (3) *E. crystallorophias*, (4) *Themisto gaudichaudii*, (5) *Lepas australis*, (6) *Protomyctophum* spp., (7) polychaetes , (8) squids, (9) carrion

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

[b] percents by mass recalculated from analysis by number assuming the following individual body masses: 0.6 g for 43 mm long *E. superba*, 0.3 g for *E. crystallorophias*, 0.1 g for *T. gaudichaudii*, 0.5 g for fish larvae

[c] percents by mass within crustaceans recalculated from number analysis assuming the following individual body masses: 0.3 g for 35 mm long *E. superba*, 0.025 g for 10 mm long *Orchomene* spp. and other crustaceans

Unidentified organic material, mainly wax and blubber particles, formed nearly 40% by mass of Blackbellied Storm Petrel diet and constituted >50% of the food load in 20% of the samples (Table 54). Due to their small size, crustaceans were of secondary importance by mass although they outnumbered all other prey types pooled together. Crustaceans, however, constituted more than 50% by mass in seven out of 25 stomachs. Fish and squid remains complemented this diet. Pumice stones, plastic particles and expanded polystyrene balls occurred regularly.

Crustaceans

A variety of epiplanktonic taxa constituted the bulk of the crustacean part of the diet. The hyperiid *Themisto gaudichaudii* and the euphausiid *Euphausia vallentini* were important both by number and mass. *Lepas australis* accounted for more than half of all food items but, due to its minute body size, only constituted a small proportion by mass. Deep-sea crustaceans, the gammarid *Eurythenes obesus* and the mysid *Gnathophausia* sp., indicate at least partly offshore foraging zones.

Fish and cephalopods

No fresh remains of either squid or fish were identifiable to any taxonomic level. From the size of the eye-lenses, squid suckers and fish vertebrae the organisms from which they came were estimated to be rather large and, thus, to support scavenging. Pooled with the unidentified organic offal reported above (see general composition) this raises to 67% by mass the scavenged fraction of the food of the Blackbellied Storm Petrel.

Prey sizes

Crustaceans ranged from 2-25 mm body length whereas squid, fish and unidentifiable organic remains obviously came from much larger individuals (Fig. 24).

Comparison with previous studies

Only fragmentary and qualitative data on the diet of the Blackbellied Storm Petrel has been reported to date. At Kerguelen, squid eye-lenses and beaks were found as accumulated items in two stomachs (Paulian 1953). At Tristan da Cunha, very digested fragments of crustaceans as well as squid beaks and eye-lenses were found in five stomach contents (Hagen 1952).

Foraging range and behaviour

At sea, the species distribution is from 39° to 65°S (Bierman & Voous 1950, Thurston 1982, Ainley *et al.* 1984, Stahl 1987, Woehler *et al.* 1990) and broadly overlaps that of Wilson's Storm Petrel. However, in contrast with this latter species, the Blackbellied Storm Petrel is more abundant in the northern half of its range where it concentrates over subantarctic continental shelves (Jehl *et al.* 1979, Thurston 1982, Jouventin *et al.* 1988). At the Crozet Islands the species forages in neritic and oceanic waters as far as 100 km from the islands (Jouventin *et al.* 1988). Apart from a few deep-sea crustaceans (*E. obesus* and *Gnathophausia* sp.) there is little evidence of oceanic foraging from the diet of the birds breeding at the Crozet Islands.

The feeding techniques of the species are still little documented. Harper (1987) reported a single bird feeding exclusively by aerial dipping but shallow plunges and pattering are other likely foraging methods (Harper *et al.* 1985). The occurrence of inorganic floating particles and the importance by mass of unidentified organic fragments as well as squid and fish remains strongly support detritivorous feeding habits. Association with larger predators like other Procellariiformes (Stahl 1983) and Killer Whales (Ridoux 1987) that produce abundant offal as they eat allows this weak-beaked small bird (although large for storm petrel standards) to

TABLE 54

THE DIET OF THE BLACKBELLIED STORM PETREL DIET AT THE CROZET ISLANDS (N=25)

Prey Species	Occurrence %	Relative abundance No.[a]	Relative abundance %	Reconstituted mass (g)	Reconstituted mass %	Body length (mm) Mean ± S.D.	(range)	n
CRUSTACEANS	**92.0**	**191**	**93.2**	**5.4**	**33.3**			
Cirripeds								
Lepas australis (cypris)	36.0	55	26.8	0.1	0.5	2.4 ± 0.2	(2.0-2.8)	24
Gammarid amphipods								
Eurythenes obesus	12.0	3	1.5	0.6	3.9	17.0 ± 3.6	(13.0-20.0)	3
Hyperiid amphipods								
Themisto gaudichaudii	52.0	45	22.0	1.3	7.8	9.0 ± 5.5	(1.5-20.5)	30
Hyperiella antarctica	8.0	16	7.8	0.1	0.5	5.4 ± 1.3	(4.0-7.8)	6
Vibilia antarctica	8.0	2	1.0	0.1	0.4	9.8	(8.5-11.0)	2
Cyllopus lucasii	8.0	3	1.5	0.2	1.2	12.3	11.4-13.1)	3
Primno macropa	8.0	1	0.5	+	0.1	8.0		1
Unidentified	8.0	2	1.0	+	+			
Euphausiids								
Euphausia sp.	4.0	+	+	+	+			
E. vallentini	44.0	60	29.3	2.5	15.2	18.6 ± 4.3	(11.5-24.9)	60
Thysanoessa sp.	8.0	2	1.0	0.1	0.3	18.4		1
Mysids								
Gnathophausia sp.	8.0	2	1.0	0.5	3.0			
CEPHALOPODS	**8.0**	**(2)**	**1.0**	**1.0**	**6.1**			
Unidentified fragments	8.0	(2)	1.0	1.0	6.1			
FISH	**16.0**	**(2)**	**1.0**	**3.5**	**21.2**			
Unidentified fragments	16.0	(2)	1.0	3.5	21.2			
OTHER ORGANISMS	**40.0**	**(10)**	**4.9**	**6.5**	**39.4**			
Unidentified organic fragments	40.0	(10)	4.9	6.5	39.4			

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

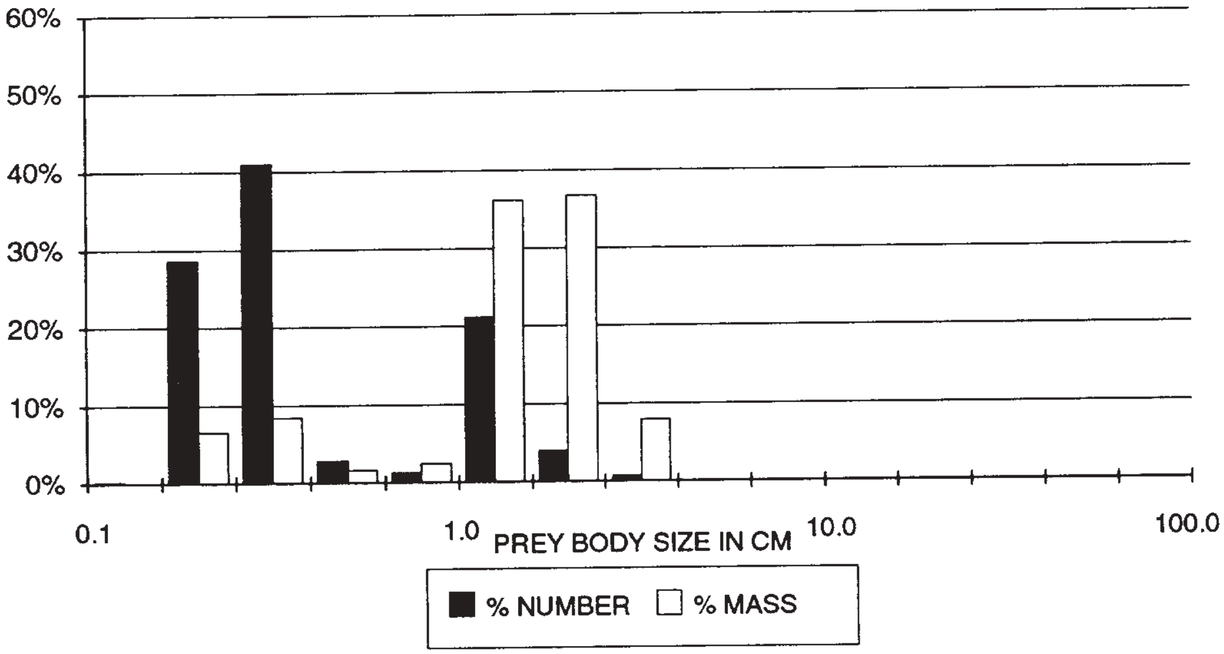

Figure 23
Prey-size distribution in the diet of Wilson's Storm Petrel.

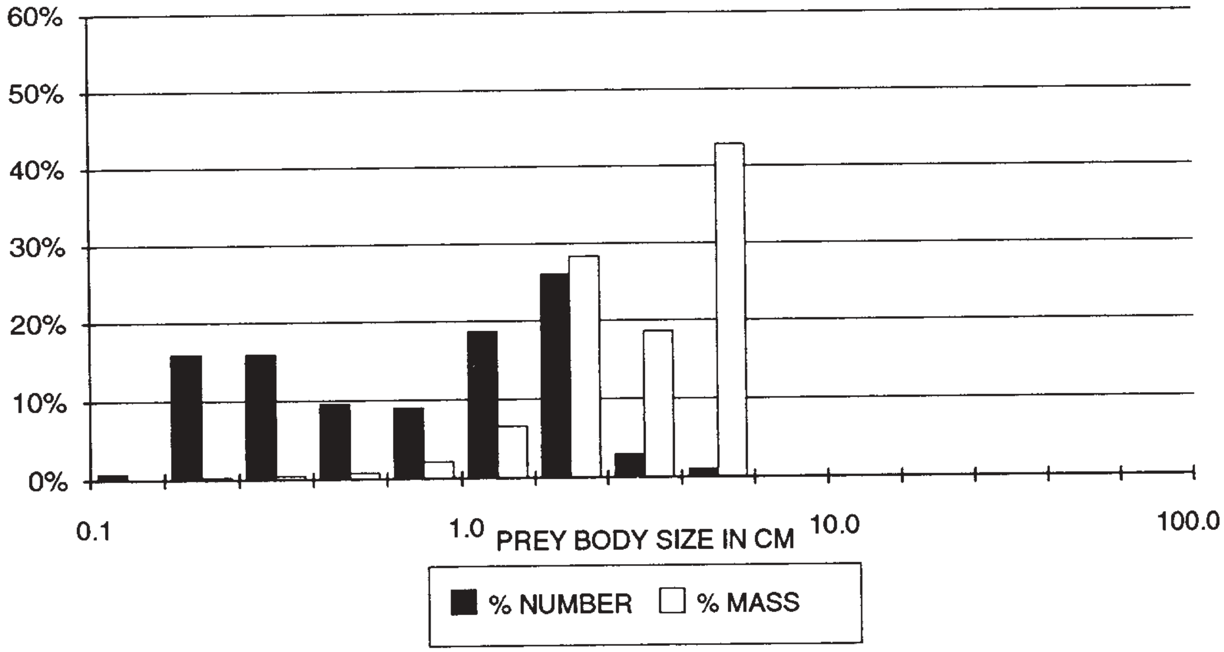

Figure 24
Prey-size distribution in the diet of the Blackbellied Storm Petrel.

obtain food from carcasses (penguins, large fish and squid) that would otherwise be unavailable.

GREYBACKED STORM PETREL *GARRODIA NEREIS*

Results

Samples

Only three stomach samples of this rare inconspicuous species were collected, two in January 1982 on Ile de l'Est and one on board ship over the western end of the Crozet continental shelf in February 1982.

Diet composition

The diet was dominated by both number and mass by cypris larvae of the thoracic barnacle *Lepas australis* (Table 55). Other prey species included isolated individuals of the hyperiids *Themisto gaudichaudii* and *Cyllopus lucasii*, the euphausiid *Euphausia vallentini* and some gonothecae of campanullariid hydrozoans. Prey size distribution was highly influenced by the dietary specialization on cirriped larvae and displayed a single peak at 2.4 mm (Fig. 25).

Comparison with previous studies

Dietary results from other localities are similar. A single stomach sample collected on East Island and full of cirripeds is the only previous information for the Crozet Island (Despin 1972). From 27 samples collected at Chatham Island, Imber (1981) estimated *L. australis* cypris larvae to constitute 85.5% by mass of the diet, the euphausiid *Nyctiphanes australis* and various hyperiid species reaching 7.3% and 6.8% by mass, respectively. The diet of birds from southern New Zealand, Antipodes Islands and the Prince Edwards Islands was similar (Imber 1981).

Foraging areas and methods

During their free-living pelagic existence cyprid larvae congregate in dense elongated swarms (J. Moyse pers. comm.) before settling on floating items during metamorphosis. Between the Subtropical and Antarctic Convergences (the distributional range of *L. australis*, Foster 1978), drifting rafts of *Macrocystis pyrifera* and *Durvillea antarctica* constitute a conspicuous micro-scale habitat at the sea-surface where both cyprids and stalked *L. australis* are likely to be found. Stahl (1983) showed that 74 % of Greyrumped Storm Petrels observed around the Crozet Islands were foraging over drifting kelp rafts. A similar association was observed at South Georgia (Jehl *et al.* 1979). This tiny species does not forage far out at sea in the Southern Atlantic (Thurston 1982) and is restricted to the continental shelf and slope around the Crozet Islands (Jouventin *et al.* 1988).

COMMON DIVING PETREL *PELECANOIDES URINATRIX*

Results

Samples

Adults caught as they landed back at their colony at ile de l'Est, Crozet Islands, during the period 19 November 1981 to 10 February 1982 were stomach-pumped. A total of 21 samples was collected. The first sample was obtained during incubation whereas all others were collected during chick rearing in January and early February. The mean reconstituted sample mass was 6.2 ± 4.4 g (1.0-20.4 g).

General composition

The food was consistently constituted of planktonic crustaceans. Chaetognaths and squid were rarely found and did not account for more than 0.5% by mass of any single sample.

TABLE 55

THE DIET OF THE GREYBACKED STORM 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**	**2327**	**100**	**3.8**	**100**			
Cirripeds								
Lepas australis (cypris larvae)	100	2308	99.2	3.5	94.8	2.4 ± 0.2	(2.0-3.1)	123
L. australis (post-larvae)	67	16	0.7	0.1	1.9	5.9 ± 2.0	(3.2-8.6)	6
Hyperiid amphipods								
Themisto gaudichaudii	33	1	+	+	+			
Cyllopus lucasii	33	1	+	0.1	1.6	12.2		1
Euphausiids								
Euphausia vallentini	33	1	+	0.1	1.6	22.6		1
OTHER ORGANISMS	**100**	+	+	+	+			
Hydrozoa								
Unidentified campanullariids	100	+	+	+	+			

Crustaceans

The most important crustacean prey taxa included four micronektonic forms, the euphausiids *Euphausia (vallentini)* and *Thysanoessa* sp. and the hyperiids *Themisto gaudichaudii* and *Primno macropa*. These species constituted the bulk of the food in every sample (Table 56). Composition varied little between samples and the three species, *Euphausia (vallentini)*, *Themisto gaudichaudii* and *Primno macropa*, were present in 81 to 95% of the samples. The euphausiids prevailed by mass (>50%) in 16 samples out of 21, *Euphausia (vallentini)* alone being dominant in 14, and the hyperiids prevailed in four samples. The proportions by mass of *T. gaudichaudii* and *P. macropa* were significantly correlated ($r=0.57$, $n=21$). Minor crustacean prey species included calanid copepods and cypris larvae of cirripeds.

Other organisms

The non-crustacean items in the diet were rare (Table 56). A single chaetognath and an unidentified squid larva were found.

Prey sizes

Prey sizes were highly homogeneous from one sample to another and ranged from 1.3-29 mm (Fig. 26).

Comparison with previous studies

Previous reports on the diet of Common Diving Petrels elsewhere agree well with the present results. At Gough Island, a single stomach contained euphausiids and one hyperiid amphipod (Williams & Imber 1982). At Whero Island, southern New Zealand, Richdale (1943) reported the presence of euphausiids whereas the hyperiid *Themisto gaudichaudii* was found at the Kerguelen Islands (Falla 1937, Paulian 1953). At Heard Island *Hyperiella antarctica* and the copepod *Euchaeta antarctica* were important food sources (Ealey 1954).

The only previous quantitative study was performed at South Georgia and euphausiids (most likely *Euphausia superba*) copepods and amphipods were estimated to account for 76%, 20% and 4% by volume, respectively (Payne & Prince 1979). Predation on swarming small epiplanktonic crustaceans thus appears as the rule throughout the Southern Ocean, with specific species composition reflecting the local availability.

Foraging range and behaviour

The diving petrels include four closely related species hardly identifiable at sea in areas of sympatry. At the Crozet Islands, the Common and the South Georgia Diving Petrels co-exist and were rarely discriminated in at-sea surveys. The discussion about at-sea distributions and foraging behaviour is therefore treated in the South Georgia Diving Petrel section below.

SOUTH GEORGIA DIVING PETREL
PELECANOIDES GEORGICUS

Results

Samples

The 23 stomach contents of South Georgia Diving Petrels were collected at Ile de l'Est, Crozet Islands, from 27 January to 16 February 1982. Adult birds were caught by night and their stomach contents removed by stomach pumping. Mean sample mass averaged 2.9 ± 1.6 g (1.0-6.7 g).

General composition

Food was constituted primarily of planktonic crustaceans. Other prey groups, fish and squid, were only observed in three samples and never

TABLE 56

THE DIET OF THE COMMON DIVING PETREL AT THE CROZET ISLANDS (N=21)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**100.0**	**5701**	**100.0**	**130.8**	**100.0**			
Copepods								
Unidentified calanids	23.8	149	2.6	0.1	0.1	2.9 ± 0.7	(1.9-3.6)	12
Unidentified euchaetids	4.8	1	+	+	+	6.3		1
Cirripeds								
Lepas australis (cypris)	57.1	126	2.2	0.2	0.2	2.5 ± 0.2	(2.2-2.9)	68
Euphausiids								
Euphausia vallentini	95.2	3336	58.5	56.6	43.3	15.5 ± 3.7	(9.4-28.5)	221
Thysanoessa sp.	19.0	423	7.4	6.9	5.3	15.7 ± 2.8	(9.8-20.8)	29
Hyperiid amphipods								
Themisto gaudichaudii	81.0	960	16.8	33.8	25.8	12.7 ± 4.4	(4.7-19.8)	116
Primno macropa	95.2	705	12.4	33.1	25.3	11.2 ± 2.3	(7.1-17.7)	129
Unidentified	4.8	1	+	+	+			
CEPHALOPODS	**4.8**	+	+	+	+			
Unidentified	4.8	+	+	+	+			
OTHER ORGANISMS	**4.8**	**1**	+	+	+			
Chaetognaths								
Unidentified	4.8	1	+	+	+			

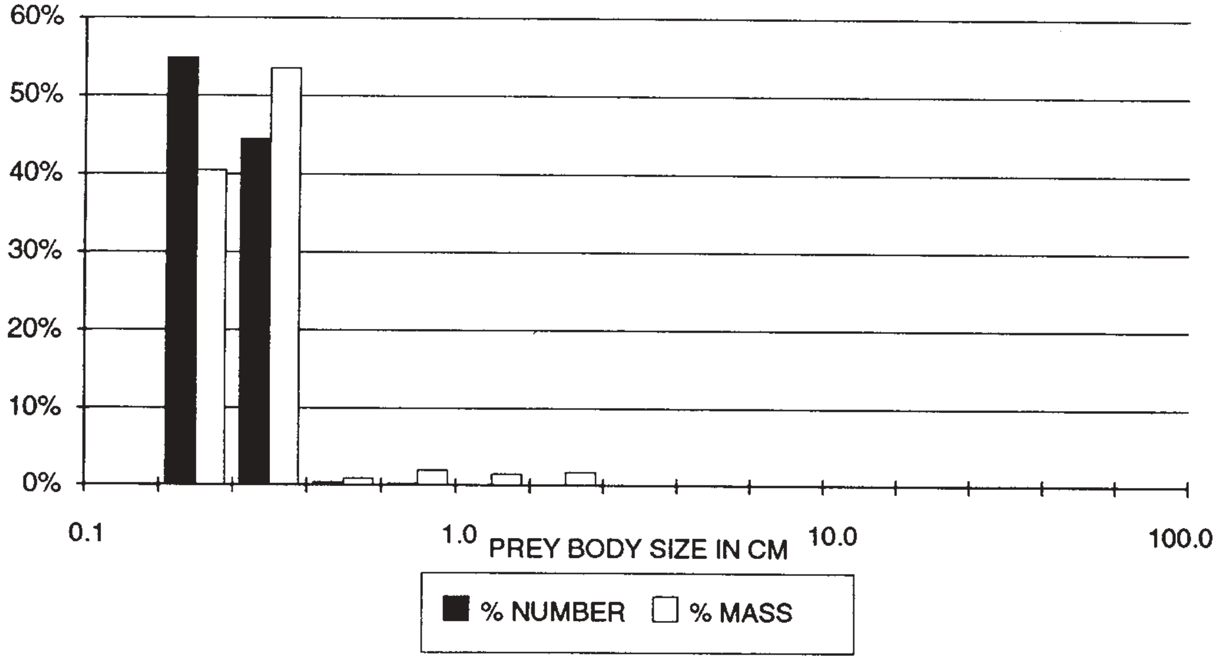

Figure 25
Prey-size distribution in the diet of the Greybacked Storm Petrel.

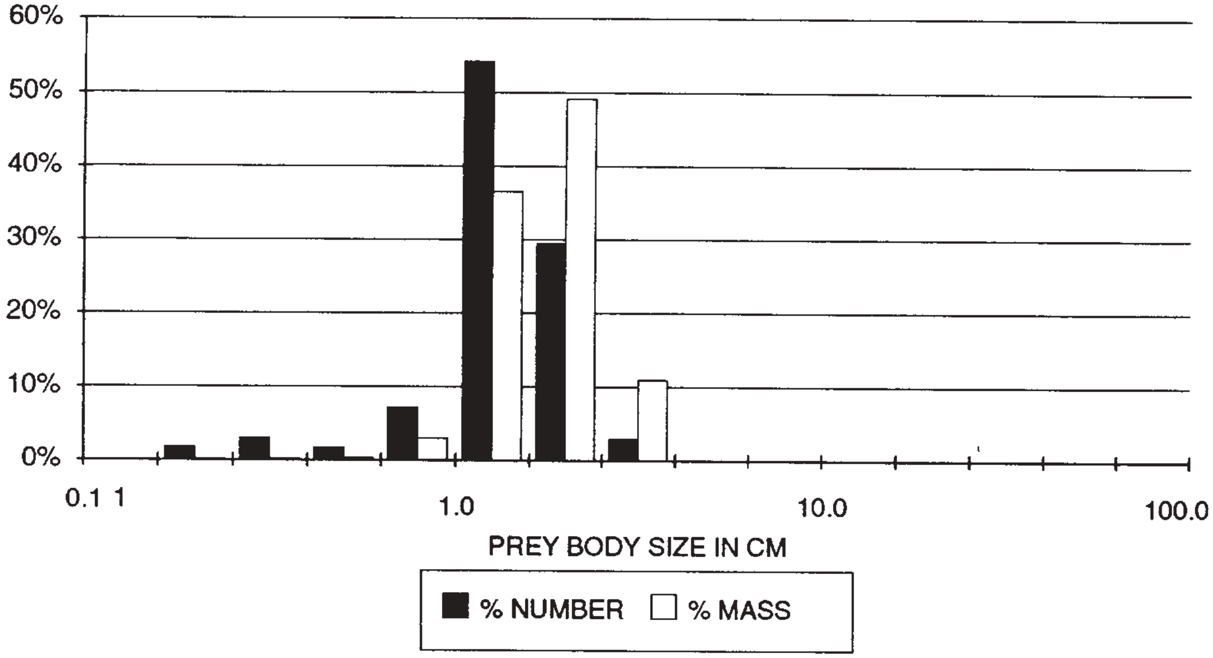

Figure 26
Prey-size distribution in the diet of the Common Diving Petrel.

accounted for more than 2% by mass of a single stomach content.

Crustaceans

The most important crustacean taxa were by far the euphausiids *Euphausia (vallentini)* and *Thysanoessa macroura/vicina* (Table 57) and accounted together for 90 to 100% by reconstituted mass of 18 of 23 samples. The two hyperiids *Themisto gaudichaudii* and *Primno macropa* complemented this crustacean diet. One sample consisted of 94% hyperids and three more consisted of between 20 to 50% by mass, the remainder containing less than 10%. *Primno macropa* was the dominant hyperiid and occurred alone in all but two samples in which hyperiids were found. Diet composition varied little between samples since the three prevailing species, *E. (vallentini)*, *Thysanoessa* spp. and *P. macropa*, were present in 78 to 100% of the samples. Copepods and cypris larvae occurred regularly but in very small numbers and due to their smaller size were of negligible importance in the diet.

Other organisms

One minute cephalopod and fish fry were found but represented an insignificant fraction of the diet.

Prey sizes

The crustaceans ranged in size from 2 mm-long copepods to 29 mm-long *Thysanoessa* sp. However, the bulk of the food came from individuals 10-20 mm long (Fig. 27).

Comparison with previous studies

Qualitative dietary observations report planktonic crustaceans as the main food of the South Georgia Diving Petrel. Matthews (1929) observed plankton in the food of the species around South Georgia. At Heard Island, 11 stomach contents were full of the copepod *Euchaeta antarctica* and the hyperiid *Themisto gaudichaudii* with *Hyperiella antarctica* and *Thysanoessa vicina* as prey of minor importance (Ealey 1954). Two South Georgia Diving Petrels caught in New Zealand had fed on euphausiids, fish and very young squid among which *Argonauta* sp., *Histioteuthis atlantica*, *Teuthowenia* sp. and *Chiroteuthis* sp. were identified (Imber & Nilsson 1980). Beyond the qualitative data the only previous study that attempted a quantification of the species diet estimated copepods, hyperiids and euphausiids to account for 68, 17 and 15% by volume, respectively at South Georgia (Payne & Prince 1979). This contrasts markedly with the results obtained at the Crozet Islands where copepods were absent.

Foraging range and behaviour

Diving petrels occur in Antarctic waters north of drifting sea ice (Murphy 1936, Thurston 1982, Stahl 1987, Woehler *et al.* 1990). The examination of specimens collected at sea showed a slight latitudinal shift between Common and South Georgia Diving Petrels; *P. georgicus* being observed from 46° to 60°S whereas *P. urinatrix* was not reported south of 56°S (Murphy 1936, Thurston 1982, Ainley *et al.* 1984). At-sea identifications gave similar conclusions (Stahl 1987). However, breeding birds have restricted foraging ranges around the islands: 28-37 km around South Georgia (Jehl *et al.* 1979) and less than 100 km at the Crozet Islands (Jouventin *et al.* 1988). This leads to very high concentrations over the continental shelf (Stahl *et al.* 1985a). The two sympatric species breeding at the Crozet Islands forage in rather distinct habitats. Although some overlap occurs, *P. georgicus* feeds in outer shelf and slope areas and *P. urinatrix* in inner shelf and coastal habitats (Jouventin *et al.* 1988). A similar habitat segregation was found in New Zealand (Imber & Nilsson 1980). Feeding techniques are identical in both species and consist of surface and pursuit diving and to a lesser extent surface seizing

TABLE 57

THE DIET OF THE SOUTH GEORGIA DIVING PETREL AT THE CROZET ISLANDS (N=23)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**100.0**	**4240**	**99.8**	**67.5**	**99.9**			
Copepods								
Unidentified calanids	13.0	12	0.3	+	+	3.0 ± 0.6	(2.1-3.6)	4
Cirripeds								
Lepas australis (cypris)	21.7	7	0.2	+	+	2.7 ± 0.2	(2.5-3.2)	7
Euphausiids								
Euphausia sp.	87.0	945	22.3	22.0	32.5	16.8 ± 3.5	(11.1-26.8)	107
Thysanoessa sp.	100.0	2986	70.3	32.2	47.7	13.8 ± 2.8	(8.3-28.6)	140
Hyperiid amphipods								
Themisto gaudichaudii	8.7	23	0.5	0.5	0.7	9.8 ± 2.9	(7.5-14.7)	5
Primno macropa	78.3	267	6.3	12.8	19.0	11.4 ± 1.3	(8.6-13.1)	46
CEPHALOPODS	**4.3**	+	+	+	+			
Unidentified squid larvae	4.3	+	+	+	+			
FISH	**13.0**	**7**	**0.2**	**0.1**	**0.1**			
Unidentified fry	13.0	7	0.2	0.1	0.1			

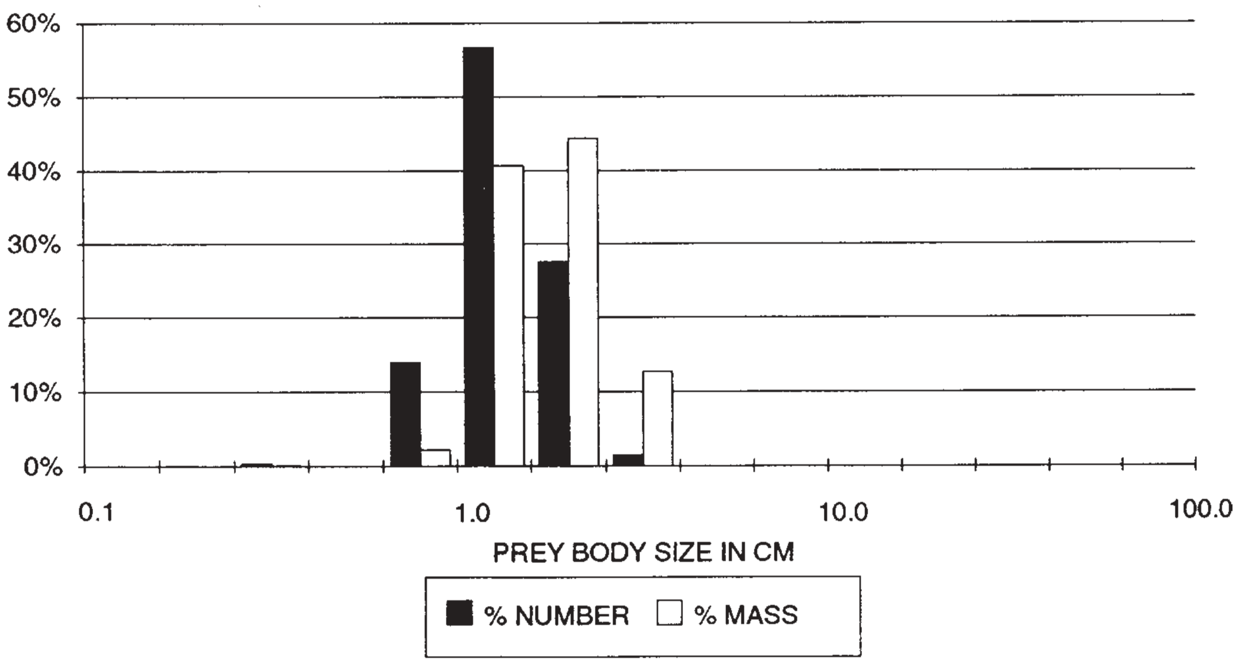

Figure 27
Prey-size distribution in the diet of the South Georgia Diving Petrel.

(Harper *et al.* 1985, Prince & Morgan 1987). Their broad similarities in terms of feeding ecology suggest that the difference found in the main crustacean prey species composition at the Crozet Islands should represent some medium scale and perhaps temporary differences in the composition of the epiplanktonic communities of outer shelf and slope habitats *vs* inner shelf and coastal habitats. The species assemblage *Euphausia (vallentini)* - *Thysanoessa* sp. - *P. macropa* probably dominates in offshore neritic areas and the trio *E. (vallentini)* - *T. gaudichaudii* - *P. macropa* should prevail in inshore zones.

IMPERIAL CORMORANT *PHALACROCORAX ATRICEPS*

Results

Samples

A total of 129 stomach contents of Imperial Cormorants was collected at Possession Island, Crozet Islands, from 4 January 1982 to 26 February 1983 at the average rate of 10 samples monthly (except in February and March 1982, Fig. 28). Average reconstituted mass was 68 ± 74 g (1 - 544 g) with lowest figures in March-May (minimum monthly average in April), intermediate values from June to February and a peak in December (Fig. 28a).

General composition

The food of the Imperial Cormorant showed a high species diversity with nine fish and 14 invertebrate taxa being identified. Although invertebrate taxa were found dominant in 45 out of 129 samples, fish accounted by far for the largest fraction of the diet by number (61.7%) and by reconstituted mass (82.2%). The samples in which invertebrates accounted for more than 50% by mass were significantly smaller than those dominated by fish (40 ± 33 g, range 1 - 139 g *vs.* 86 ± 87 g, range 5 to 544 g, respectively; $p < 0.001$).

Crustaceans

The main crustacean species was the hippolytid shrimp *Nauticaris marionis* (Table 58) which was found in 32.6% of the samples and contributed to as much as 100% reconstituted mass in some individual samples. The species occurred at low monthly average percent by mass all the year round (0.1 to 5.8%) but peaked at 47.9% by mass in May (Fig. 28b). Other crustacean prey taxa were minor component of the diet except in a single stomach content where the gammarid amphipod *Gondogeneia spinicoxa* constituted the bulk of the food.

Cephalopods

Only one small octopodid was found among the 3598 prey individuals of the collection.

Other invertebrates

Polychaetes, bivalves, priapulids, sea-spiders and sea-cucumbers were found as food items. Only the two former prey groups were significant in the diet of the Imperial Cormorant. The polychaetes, mainly represented by two taxa, the large nephtyid *Aglaophamus ornatus* and some smaller unidentified polynoids, occurred regularly in the diet and accounted for between 0.8 and 22.1% by reconstituted mass monthly. The bivalve *Laternula elliptica* occurred more irregularly being absent during five out of the 12 months studied. This species, however, contributed to as much as 64.0% reconstituted mass in October and 17.2% in November. Unlike for all other prey taxa, the birds did not ingest whole individuals of this species; instead they always tore the meaty siphon off, leaving the valves, mantle and viscera.

Fish

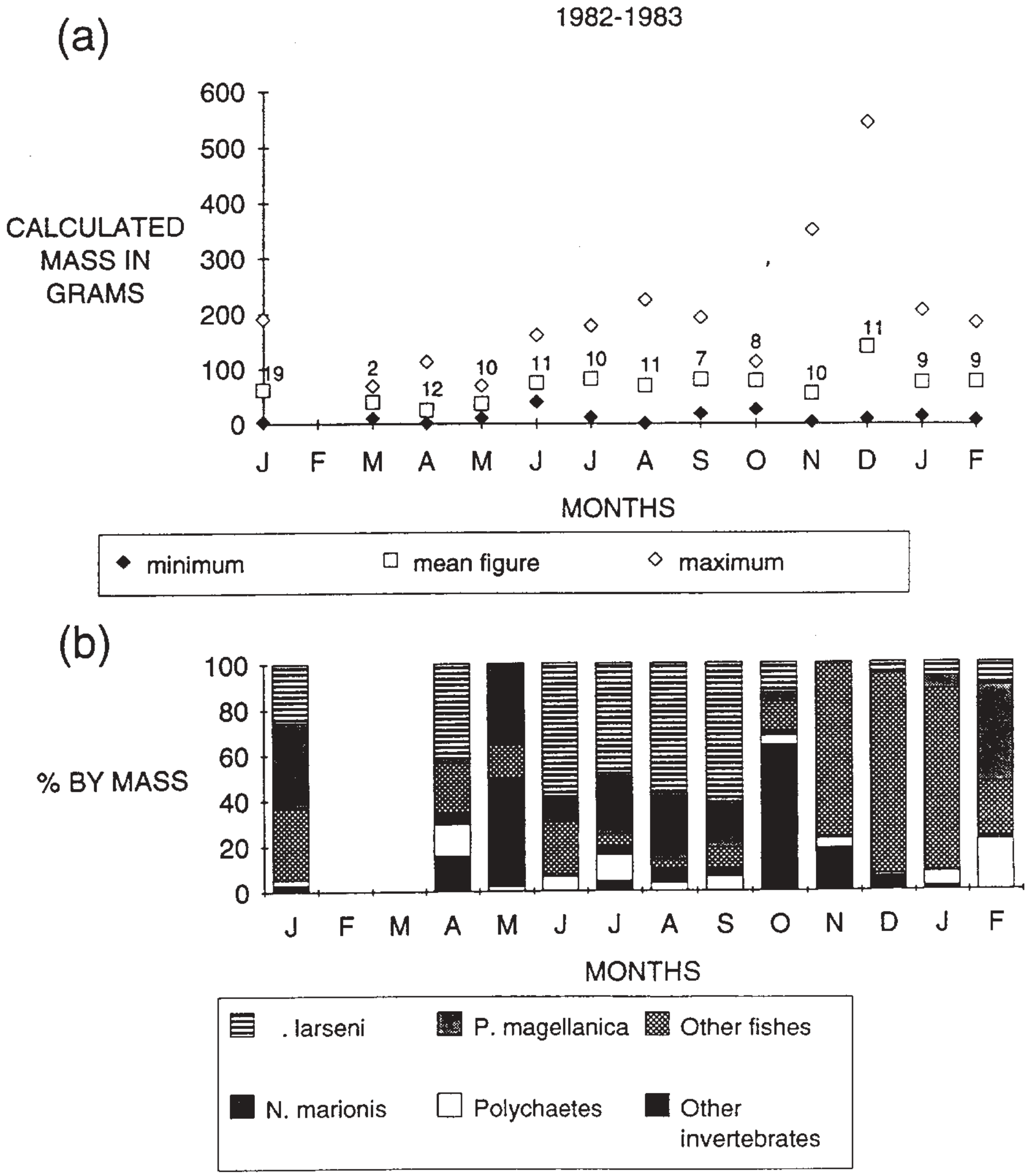

Figure 28

Seasonal variations in (**a**) reconstituted food mass and (**b**) food compositon in the Imperial Cormorant; numerals in (**a**) are sample sizes.

TABLE 58

THE DIET OF THE IMPERIAL CORMORANT AT THE CROZET ISLANDS (N = 129)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)		
	%	No.	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**36.4**	**554**	**15.4**	**341.1**	**3.8**			
Cirripeds								
Lepas australis	0.8	1	+	0.2	+	32		1
Isopods								
Astacilla marionis	1.6	2	+	0.2	+	12		1
Unidentified	1.6	2	+	+	+			
Gammarid amphipods								
Gondogeneia spinicoxa	5.4	62	1.8	13.2	0.1	20 ± 3	(15-26)	18
Unidentified lysianassids	1.6	2	0.1	0.2	+	20		1
Unidentified	1.6	2	0.1	0.5	+			
Decapods								
Nauticaris marionis	32.6	483	13.4	326.8	3.7	39 ± 6	(21-51)	210
CEPHALOPODS	**0.8**	**1**	**+**	**1.5**	**+**			
Octopods								
Unidentified octopodids	0.8	1	+	1.5	+	30		1
FISH	**95.3**	**2190**	**60.9**	**7319.4**	**82.1**			
Gadiformes								
Muraenolepis sp.	1.6	3	0.1	223.6	2.5	175 ± 106	(100-250)	3
Scorpaeniformes								
Zanchlorhynchus spinifer	13.2	21	0.6	41.9	0.5	40 ± 6	(31-50)	18
Perciformes								
Dissostichus eleginoides	5.4	20	0.6	1107.9	12.4	154 ± 92	(70-332)	7
Notothenia acuta	17.1	468	13.0	570.8	6.4	46 ± 21	(25-130)	127
Lepidonotothen squamifrons	5.4	40	1.1	606.4	6.8	80 ± 37	(37-148)	31
L. larseni	25.6	838	23.3	2342.1	26.3	60 ± 12	(36-200)	341
Paranotothenia magellanica	30.2	488	13.6	1631.5	18.3	58 ± 35	(17-250)	136

Unidentified nototheniids	20.2	79	2.2	460.7	5.2	68 ± 25	(30-140)	32
Harpagifer spinosus	17.8	102	2.8	115.4	1.3	33 ± 9	(20-71)	77
Harpagifer kerguelensis	10.1	61	1.7	126.9	1.4	43 ± 12	(22-62)	37
Unidentified harpagiferids	12.4	53	1.5	73.6	0.8	35 ± 12	(21-66)	42
Unidentified	9.3	17	0.5	18.6	0.2	43 ± 17	(20-70)	6
OTHER ORGANISMS	**51.2**	**855**	**23.7**	**1249.7**	**14.0**			
Polychaetes								
Aglaophamus ornatus	13.2	64	1.8	272.8	3.1	101 ± 37	(50-200)	22
Unidentified nereids	11.6	27	0.8	22.0	0.2	44 ± 12	(30-60)	8
Unidentified polynoids	29.5	567	15.8	239.8	2.7	31 ± 10	(25-45)	4
Bivalves								
Laternula elliptica[a]	14.7	189	5.3	679.5	7.6	29 ± 6	(22-37)	6
Priapulids								
Priapulus tuberculatospinosus	3.1	4	0.1	35.0	0.4	80		1
Holothurians								
Unidentified	0.8	1	+	0.6	+	45		1

[a] Only the siphons are ingested by the birds; consequently the lengths given are not total body length but only siphon lengths

Of the nine fish taxa, two nototheniids, *Lepidonotothen larseni* and *Paranotothenia magellanica*, contributed 44.6% by reconstituted mass of the Imperial Cormorant's diet. These species were found in 33 and 39 out of 129 samples, respectively but never co-occurred in any of them (significantly different from a distribution at random, chi-square=19.3, df=1). This difference was not related to any seasonal pattern. Both species displayed monthly variation in their contribution by mass to the diet ; a long interval of increased abundance occurred from June to September and again in January and February (Fig. 28b). The other nototheniid species showed a different pattern of occurrence with long periods of absence and short bursts of abundance in the diet of the imperial cormorant. *Dissostichus eleginoides* was abundant in November and December, *Lepidonotothen squamifrons* in December and *Notothenia acuta* in January. The harpagiferid *Harpagifer* spp. were preyed upon all year but never contributed over 9% by mass in the monthly average figures. *Muraenolepis (?orangiensis)* occurred only twice in January 1983 but, owing to its large size, accounted for a significant mass proportion in the monthly average value.

Prey sizes

Extreme prey body lengths were 12 and 332 mm (Fig. 29) but most fish were within 30 to 150 mm standard length. The mean individual body masses were 0.7 g for the shrimp *N. marionis*, 3.1 and 7.9 g, respectively for the two most important fish species *L. larseni* and *P. magellanica* and as much as 15 and 107 g for *L. squamifrons* and *D. eleginoides*.

Foraging behaviour

Observations performed from the shore provided additional data on several aspects of the imperial cormorant foraging behaviour. From December 1981 to March 1983, cormorants were observed most frequently foraging solitarily or, rarely, in very small groups (two to three birds) at every season. However, from mid November to mid December, eight observations of communal foraging with synchronized diving involved eight to 65 tightly grouped birds (28.5 ± 18.0 individuals per raft, inter-individual distances of the same order of magnitude as bird body length) were made. This communal fishing only occurred during a restricted period in selected sheltered bays beyond the *Macrocystis* kelp beds. During the same period the solitary foraging behaviour remained the rule in other coastal sectors and habitats.

On one occasion, water clarity in a shallow area (*c.* 5 m) allowed underwater behaviour to be observed during 10 successive dives. The bird dived directly from the surface to the bottom in an area of large boulders (0.5 to 2 m in diameter) where it systematically investigated the crevices between and under the rocks. It dived several times on the same boulder area before it swam horizontally underwater to a neighbouring boulder area and resumed its investigations. During this diving sequence the bird caught two fish (most probably *P. magellanica* about 100 mm long). These were caught in crevices by surprise without any pursuit and were swallowed at the surface.

Some diving parameters were investigated using a chronometer and a theodolite. Thirty-four dives by five birds were observed from a 35 m-high cliff in an area where the bottom was within 10 to 15 m from the surface. Dive and rest times were recorded as well as horizontal straight line distances swum underwater and at the surface (Table 59). Dive time was poorly correlated with straight-line distance swum underwater (r=0.17, n=28) in accordance with the highly sinuous search pattern described above. Rest time was significantly, although weakly, correlated with distance swum at the surface (r=0.39, n=29). Finally, rest time spent drifting at the surface was highly correlated with previous dive time (rest time = 1.22 x dive time - 51 s; r=0.89, n=23),

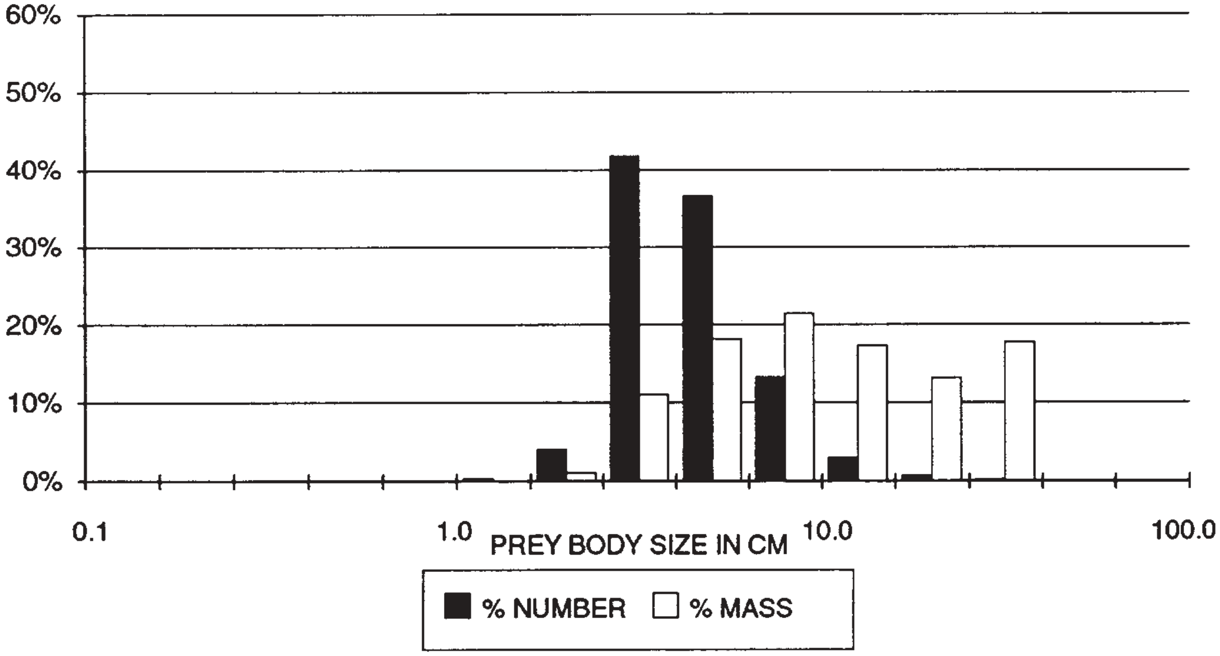

Figure 29

Prey-size distribution in the diet of the Imperial Cormorant.

TABLE 59

SOME DIVING PARAMETERS OF THE IMPERIAL CORMORANT

Parameters	Mean ± S.D.	(range)	n
Dive time (s)	103±18	(63-144)	31
Horizontal distance swum underwater (m)[a]	17.1±10.0	(1-32)	28
Rest time (s)	89±34	(30-189)	30
Horizontal distance swum at the surface between two dives (m)	12.9±7.0	(2-28)	29

[a] in straight line between diving and surfacing points

but less so when the bird actively swam towards another foraging area (r=0.68, n=29). It thus appeared as if a resting period was directly linked to the preceding effort (accordingly, rest time was not correlated at all with the following dive time; r=0.05). No prey was brought to the surface during these dive sequences but swallowing movements as well as beak cleaning at the surface were interpreted as possible signs of a successful dive; such behaviours occurred after nine out of 34 dives.

Comparison with previous studies

Invertebrates and benthic fishes have been recorded in numerous non-quantitative studies on the diet of the Imperial Cormorants (Table 60). Studies at Macquarie and Marion Islands have also showed the prevalence of benthic and demersal organisms in the food of the Imperial Cormorant (Table 61). The great diversity of prey species found at the Crozet Islands compares better with the results obtained at Marion Island than with those from Macquarie, where the diet is exclusively fish with only a few taxa identified. From the examination of hundreds of regurgitation casts, the Heard Island Imperial Cormorant population was reported to prey upon a wide variety of benthic invertebrates and coastal fish, among which polynoid polychaetes and nototheniid fish were the most common taxa (Green *et al.* 1990).

Foraging range and behaviour

Although the Imperial Cormorant is widely distributed in the Southern Ocean from Southern South America and the Antarctic Peninsula eastward to Macquarie Island, each island population is mostly sedentary and forages within a short distance of the coastline. This foraging radius is supposed to depend on local bathymetry. At Marion Island where there is virtually no continental shelf the species does not venture further than 450 m offshore (Cooper 1985) whereas at Crozet Islands, with a broader shelf, the Imperial Cormorant forages as far as 3 km out to sea (Stahl 1983). At Macquarie Island, Brothers (1985) considered the 50 m depth contour, *i.e.* about 1.1 km foraging radius, to be a limit for this benthic demersal feeder.

At Marion Island, the Imperial Cormorant forages either coastward or seaward of the *Macrocystis* belts or in scattered kelp beds but clearly avoids dense kelp areas (Cooper 1985). At the Crozet Islands the species forages mostly seaward of the kelp beds in summer but within the kelp beds in winter (U test, $p < 0.003$, data from Jouventin *et al.* 1981 and personal winter observations).

The dive durations recorded at the Crozet Islands are greater than that obtained at Marion Island in shallower waters, illustrating the relationship between dive duration and water depth observed by Cooper (1985). The dive/pause regression calculated from our observations is consistent with the ratio of 2.7 found for short dives (Cooper 1985) but leads to a ratio of *c.* 1 for dives longer than 130 s. Such a low dive/pause ratio may indicate that 130-140 s may be close to the maximum dive duration of the species. The mean dive duration found at Crozet for cormorants is of the same order of magnitude as mean values recorded *for Pygoscelis*, *Eudyptes* and *Spheniscus* penguins (Boersma 1976, Broni 1985, Wilson 1985, Trivelpiece *et al.* 1987).

One bird was caught in a net at a depth of 25 m (Conroy & Twelves 1972). Brothers (1985) estimated the maximum diving depth of Imperial Cormorants at 50 m. Such figures concur with the foraging habitat of the species since kelp is reported to grow within 10 to 20 m from the surface (Fischer & Hureau 1985) and cormorants are known to forage on either side of the kelp beds.

Prey species composition also fits these inshore foraging habits. The invertebrates, the harpagiferids and the nototheniids *Notothenia acuta* and *Paranotothenia magellanica* are

TABLE 60

QUALITATIVE DATA ON THE FOOD OF THE IMPERIAL CORMORANT

Localities	Prey types	References
Signy Island	1 *Notothenia neglecta*, 230-mm body length	Conroy & Twelves 1972
Antarctic Peninsula	Nototheniids (*N. kempi, Trematomus hanseni*), channichthyids, octopods, (*Pareledone turqueti, Bentheledone* sp.), crustaceans (*Euphausia superba*)	Schlatter & Moreno 1976
Marion Island	Harpagiferids[a], nototheniids (*N. macrocephala*), squid, decapod crustaceans (*N. marionis*), polychaetes	Blankley 1981
Ile de l'Est, Crozets	fish	Despin *et al.* 1972
Ile aux Cochons, Crozets	fish from a few to 200 mm in 19 stomachs, crustaceans in one stomach	Derenne *et al.* 1976
Kerguelen Islands	fish in eight stomachs	Falla 1937
Kerguelen Islands	fish and sea-urchins in two stomachs	Paulian 1953
Heard Island	Nototheniids in four stomachs	Falla 1937
Heard Island	Nototheniids, among which *N. cyanobranchia*	Downes *et al.* 1959

[a] doubtful identification according to Espitalier-Noël *et al.* 1988

TABLE 61

IMPERIAL CORMORANT DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in brackets)					References
	Crustaceans	Nototheniids	Other fish	Octopods	Other food types	
Marion Isl. (46S)	18.8 (1)	----------- 71.4 (2) ----------		7.1	2.7 (8)	Espitalier-Noel *et al.* 1988
Crozet Isls. (46S)	3.8 (1)	75.4 (3,4)	6.7 (6,7)	+	14.0 (8, 9)	(this work)
Macquarie Isl. (54S) 1985		91.7 (4,5)	8.3 (6)			Brothers

The main prey species are: (1) *Nauticaris marionis*, (2) *Notothenia squamifrons*, (3) *Lepidonotothen larseni*, (4) *Paranotothenia magellanica*, (5) unidentified nototheniids, (6) *Harpagifer* spp., (7) *Muraenolepis* sp., (8) polychaetes, (9) *Laternula elliptica* benthic to nektobenthic species of the sublittoral zone (Duhamel & Pletikosic 1983, Fischer & Hureau 1985). *Lepidonotothen squamifrons* and *Dissostichus eleginoides*, two large continental-slope-dwelling species, display coastal and nektonic habits during their first year(s) (Duhamel 1981, Kock *et al.* 1985). Finally, *Lepidonotothen larseni* is reported mostly from 90 to 360 m deep around the Crozet Islands (Duhamel & Pletikosic 1983) and should, therefore, be out of the cormorant's diving range. However, experimental catches performed to date in the area did not cover the sublittoral zone and failed to sample the age class 0 which prevails in the food of the cormorants. This suggests that *L. larseni* is also coastal during its first year(s) of life. Furthermore, its very distinct occurrence pattern in the food of the cormorant compared with that of *P. magellanica* (see results section) indicates that both species should dwell in distinct habitats. Presumably *P. magellanica* is a littoral nektobenthic fish mostly preyed upon from the kelp bed coastwards using the bottom investigation technique described above and juvenile *L. larseni* might have more offshore and nektonic habits and require other foraging methods still undocumented.

DIETARY SEGREGATION

Comparability of the data within the community

In the systematic account the diets of the main seabirds breeding at the Crozet Islands have been described and discussed at the species level along two distinct perspectives: the geographical variability of the diet and the significance of the diet in terms of foraging habitats and techniques. The present section aims at comparing these dietary data interspecifically within the community.

The stomach samples analysed provide the first quantitative approach to Crozet Island seabird diets. Excluded species were mostly terrestrial or very rare ones. Particular attention was paid to interspecific comparability, especially as far as sorting and quantitative analysis are concerned. Indeed, the bases of the analytical procedures were the same irrespective of bird species. Furthermore, sampling took place in a limited period and at the two easternmost islands of the archipelago, separated by no more than 18 km, thus allowing interspecific comparisons from data obtained in as comparable environmental conditions as possible. Although a wealth of dietary studies of southern seabirds are now available, similarly-standardized dietary studies of Southern Ocean seabird communities remain scarce. Croxall & Prince (1980b) produced the first comparative study of seabird feeding ecology within a breeding community; however, the dietary data were compiled from various independently-designed studies that achieved different states of quantification, some of them being performed several hundred kilometres to the south of Bird Island, the main study site, and sampled during many separate breeding seasons. In the Southern Pacific and the Ross Sea a multi-species approach dealt with the food of three seabird species assemblages at sea in connection with three main habitats : oceanic, slope and shelf areas (Ainley *et al.* 1984). Later on, the small breeding community of Adélie Land was investigated using standardized quantitative methods (Offredo & Ridoux 1986, Ridoux & Offredo 1989). At Marion Island a considerable amount of data is now available for almost every breeding species and, although being produced by many distinct workers (see references in the synthetic tables of this paper), these studies mostly share common analytical principles and sampling location if not sampling periods. At other localities (the Falkland, King George, Gough, Heard and Macquarie Islands) dietary studies have been mostly restricted to penguins (references in the synthetic tables of the present paper). Amsterdam Island and Kerguelen Islands are the only southern ocean seabird communities that remain mostly undescribed in terms of seabird diets. This study does not always compare well with the other studies in terms of sample sizes for a given bird species. Instead, I have focused on the simultaneous appraisal of the whole community in terms of diets and on the comparability of the data obtained for each species.

The study is part of a broader research programme in community ecology undertaken at the Crozet Islands. Comparative studies of breeding cycles, behaviour, demography and at-sea distributions have already been published (Jouventin *et al.* 1982a,b, Jouventin *et al.* 1985, Stahl *et al.* 1985a, Weimerskirch *et al.* 1985, 1986, Stahl 1987, Weimerskirch *et al.* 1987, 1988, Jouventin & Weimerskirch 1988) and highlight some of the ways in which seabirds can share nesting sites and food resources in this community: mostly by differences in breeding seasons and habitats and by differences in foraging zones. In the following sections the dietary structure of the Crozet Island seabird community will be interpreted in the same context paying particular attention to whether the differences observed can be related to differences in morphological and energetic constraints of each bird species, segregation mechanisms operating on other dimensions of the trophic niche (space and time) and secondarily expressed in the diet, or segregation mechanisms operating by prey selection proper. The dietary structure of the community is described by three variables: prey taxa, prey size, and prey profile. For clarity the whole community is divided into two main guilds, the surface feeders and the divers. The surface feeders include the albatrosses, the petrels and the storm petrels and the divers include the penguins, the cormorant and the diving petrels. Although this dichotomy is the simplest way to classify the Crozet seabird community according to general foraging methods it should not hide the fact that overlap in feeding techniques exists between these two guilds. Indeed diving petrels can also seize prey at the surface whereas several petrels perform extensive dives in search of food (H. Weimerskirch unpubl. obs.).

Dietary structure of the community according to prey taxa

Correspondence analysis

With 27 bird species studied and 160 prey taxa identified only multivariate analysis can help in describing the dietary structure of the whole community in terms of prey taxa. Correspondence analysis, normally devised for the treatment of contingency tables, can also be used in species-sample tables provided that the data are positive and dimensionally homogeneous (Legendre & Legendre 1979). In this study, the species-sample table is a prey-bird table with data being either presence-absence, occurrence, abundance or indices of mass. Presence-absence and occurrence indices have been discarded because they are too rough descriptors of the diet compared to abundance and mass indices; furthermore they are very sensitive to the number of rare prey taxa and through them sample size in a given bird species. Abundance and mass indices are less sensitive to sample size. In this study only mass indices have been retained because they represent the energetic and selective advantages of feeding on a given prey better than do abundance indices. Only the 30 prey taxa accounting for more than 5% by mass in the diet of at least one bird species have been considered in the analyses. The mean reconstituted mass of a given prey taxon in the diet of each bird species (X) was transformed by log $(X+1)$ to lower heterogeneity (log) and avoid negative values $(X+1)$.

The first analysis deals with the entire community (Fig. 30). Only 33% of the total variability is explained by the first three axes. However, the distribution of bird species on the plot (for clarity prey are not shown in Fig. 30) can be considered as a preliminary approach to the dietary structure of the whole community. The Imperial cormorant

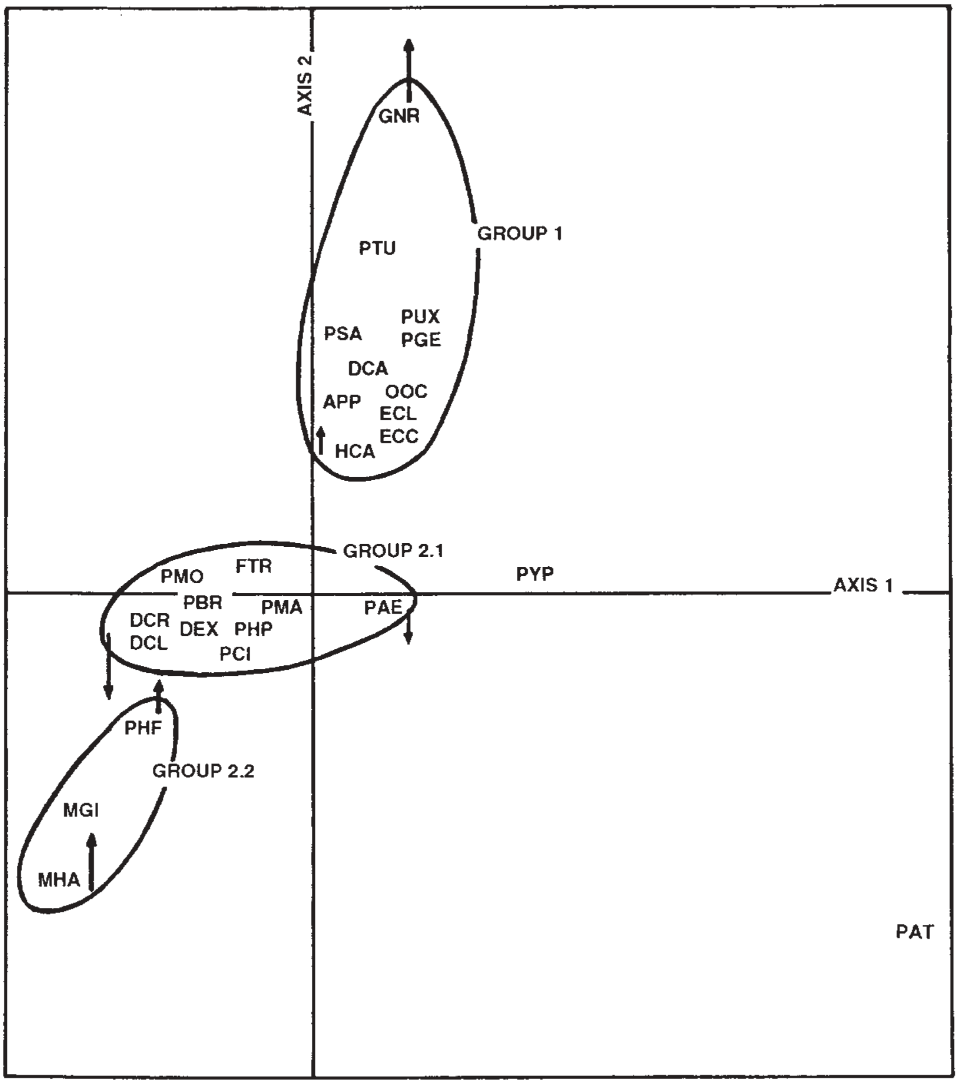

Figure 30

Correspondence analysis plot comparing the diets of seabirds breeding at the Crozet Islands. Analysis is performed on composition by mass of every species' average stomach content. Bird abbreviations as indicated in Appendix 3.

is well away from the rest of the community and is associated with benthic prey taxa, thus explaining most of the inertia of axis 1. Axis 2 separates two species groupings: the small surface feeders and the pelagic divers (together forming group 1) associated with planktonic and micronektonic prey taxa and the large surface feeders mostly associated with large nektonic taxa (group 2). The Gentoo Penguin is intermediate between the pelagic divers included in group 1 and the isolated Imperial Cormorant. Group 2 is split into two groups by the third axis: group 2.1 is mostly constituted of albatrosses and *Procellaria* and *Pterodroma* petrels that feed on nektonic squid, fish and crustaceans, whereas group 2.2 includes the giant petrels and the Sooty Albatross for which bird carcasses and offal are central in the diet. Noticeable is the situation of the Blackbellied Storm Petrel in group 2.1 together with the large surface feeders, whereas the other storm petrels are in group 1 with all the other small surface feeders. Within group 1 no particular feature is evidenced by the third axis.

A second analysis performed in the same manner as above on the diving guild (83% of total variability is explained by the first three axes) confirms the isolation of the cormorant and the intermediate position of the Gentoo Penguin (Fig. 31). It also illustrates the poor degree of dietary segregation achieved by the crested penguins and the diving petrels; indeed there is less difference within these pairs of congeners breeding sympatrically in summer than between the winter and the summer diets of the Gentoo Penguin (differences measured by the distances separating species on the plot).

Other analyses performed on the large-sized and small-sized surface feeders did not result in more information than shown in the first analysis and are therefore not illustrated here.

These correspondence analyses performed at the community level illustrate several trends. Some of them were intuitively expected: the benthic dwelling cormorant as well as the scavenging giant petrels (and, less expectedly, the Sooty Albatross) are isolated from the rest of the community. Similarly, the Gentoo Penguin which preys both on pelagic and benthic taxa is separated from the other penguins that feed exclusively on pelagic organisms.

Other trends were less obvious. The small-sized surface feeders and the pelagic divers are closely clustered in the same grouping characterized by micronektonic and planktonic prey taxa. The pairs and trios of congeneric species are generally plotted very closely (see mostly crested penguins, mollymawks, giant petrels and diving petrels and to a lesser extent prions and gadfly petrels). Only the Sooty Albatross is separated from its congener the Lightmantled Sooty Albatross. Not congeneric but very homogeneous in size and morphology, the storm petrels display the highest degree of segregation on the plot.

Overlap indices

The correspondence analysis is an exploratory tool allowing trends to be highlighted at the community level. However, it does not give a measurement of the dietary similarity between bird species. Overlap indices can give a measure of this similarity. Several indices have been proposed in the literature (*e.g.* Horn 1966, Baltz & Morejohn 1977) and produce significantly different overlap measurements from the same data set (Linton *et al.* 1987). It is therefore essential to compare measurements with values obtained in the same manner by other workers. Here, the overlap indices are calculated within both guilds (Tables 62 & 63) on the composition by mass at the family level using the formula proposed by Horn (1966), thus following Diamond (1983) and Adams & Brown (1989) for seabird communities.

The surface feeders display on average lower overlaps than the divers. This may reflect a better segregation within this guild but is also an

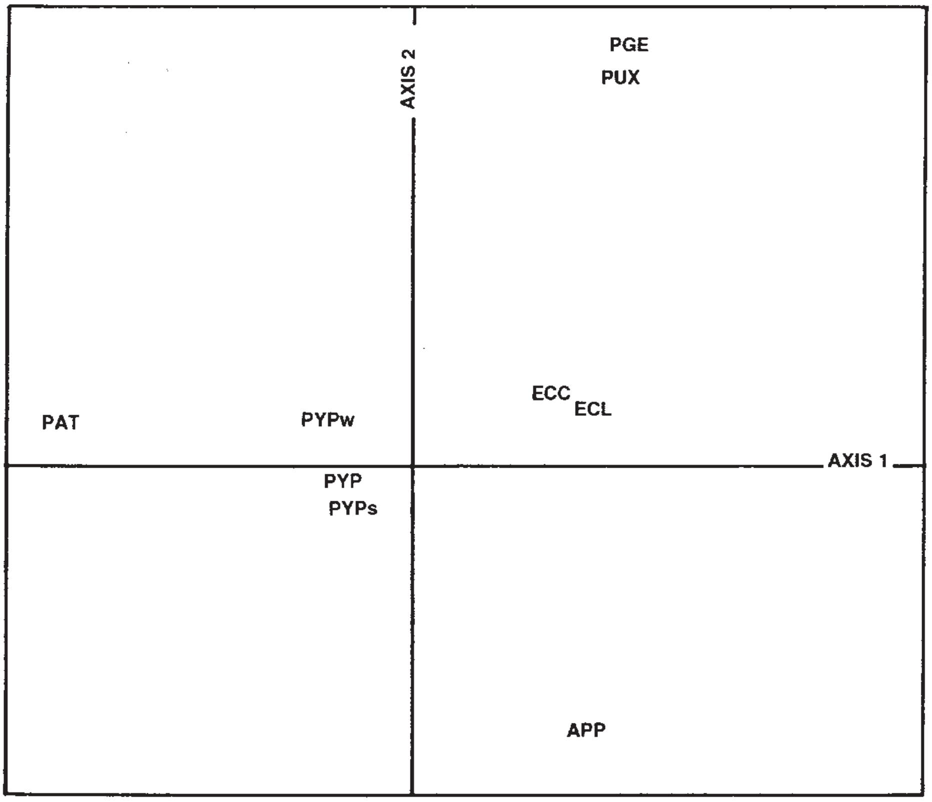

Figure 31
Correspondence analysis plot comparing the diets of diving seabirds at the Crozet Islands. Analysis is performed on composition by mass of every species' average stomach content. Bird abbreviations as indicated in Appendix 3.

TABLE 62

INDICES OF DIETARY OVERLAP IN THE DIVING GUILD

	APP	PYP	PYPw	PYPs	ECL	ECC	PAT	PUX	Mean	S.D.
PYP	0.30				all divers				0.44	0.38
PYPw	**0.06**					penguins			0.58	0.32
PYPs	**0.53**		**0.59**			diving petrels			0.84	
ECL	0.47	0.84	**0.71**	**0.80**						
ECC	0.15	0.91	**0.97**	**0.66**	0.80					
PAT	0.00	0.31	**0.07**	**0.28**	0.01	0.00				
PUX	0.00	0.71			0.76	0.79	0.00			
PGE	0.00	0.82			0.68	0.94	0.00	0.84		

The figures in bold compare winter and summer diets of the Gentoo Penguin to the other divers. These values do not contribute to the averages given in the upper right corner of the table (PYPw and PYPs mean Gentoo Penguin in winter and in summer, respectively)

Abbreviations are explained in Appendix 3

TABLE 63
INDICES OF DIETARY OVERLAP IN THE SURFACE-FEEDING GUILD

	DEX	DCL	DCR	PHF	PHP	MHA	MGI	PAE	PCI	PMA	PBR	PMO	DCA	HCA	PSA	PTU	OOC	FTR	GNR	PUX
DCL	0.18																		mean	S.D.
DCR	0.33	0.51																		
PHF	0.13	0.03	0.04											all surface feeders					0.15	0.20
PHP	0.84	0.17	0.27	0.19																
MHA	0.02	0.00	0.01	0.63	0.06									albatrosses and large petrels					0.21	0.24
MGI	0.04	0.06	0.01	0.61	0.08	0.99									albatrosses				0.27	0.25
PAE	0.44	0.49	0.12	0.12	0.58	0.00	0.05								giant petrels				0.99	
PCI	0.64	0.38	0.18	0.30	0.61	0.01	0.05	0.57							*Procellaria* petrels				0.57	
PMA	0.20	0.09	0.12	0.24	0.36	0.00	0.02	0.22	0.27						gadfly petrels				0.58	0.26
PBR	0.12	0.02	0.11	0.04	0.21	0.00	0.00	0.09	0.05	0.44										
PMO	0.02	0.09	0.23	0.04	0.07	0.00	0.00	0.04	0.01	0.42	0.88			small petrels					0.32	0.24
DCA	0.01	0.03	0.00	0.01	0.22	0.00	0.00	0.24	0.02	0.01	0.02	0.01			prions and Blue Petrel				0.51	0.24
HCA	0.25	0.00	0.10	0.07	0.51	0.00	0.01	0.41	0.21	0.19	0.22	0.21	0.57		storm petrels				0.20	0.20
PSA	0.07	0.04	0.02	0.01	0.15	0.00	0.00	0.16	0.06	0.02	0.01	0.07	0.31	0.52						
PTU	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.03	0.03	0.01	0.00	0.06	0.09	0.27	0.74					
OOC	0.04	0.16	0.00	0.01	0.33	0.00	0.01	0.42	0.09	0.02	0.03	0.01	0.65	0.79	0.41	0.27				
FTR	0.22	0.35	0.01	0.03	0.47	0.00	0.03	0.47	0.27	0.09	0.41	0.17	0.24	0.34	0.26	0.15	0.41			
GNR	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.50	0.19	0.01		
PUX	**0.00**	**0.00**	**0.00**	**0.01**	**0.24**	**0.00**	**0.00**	**0.26**	**0.00**	**0.00**	**0.02**	**0.03**	**0.57**	**0.75**	**0.65**	**0.46**	**0.83**	**0.32**	**0.02**	
PGE	**0.00**	**0.00**	**0.00**	**0.01**	**0.26**	**0.00**	**0.00**	**0.26**	**0.00**	**0.00**	**0.02**	**0.00**	**0.58**	**0.65**	**0.27**	**0.09**	**0.87**	**0.27**	**0.02**	**0.84**

Figures in bold compare the two diving petrels with the surface feeders.

Values in bold do not contribute to the average figures given in the upper right corner of the table.

Species abbreviations are explained in Appendix 3.

artifact related to the size of the table. Indeed, comparisons between closely related species (most likely to produce high overlap values) are concentrated on the diagonal of the table and their number increases with the number of birds included in the guild, whereas comparisons between taxonomically distant species (leading generally to low overlap values) are located on the surface below the diagonal and their number increases with the square of the number of bird species compared in the table. Therefore, large tables (studies on large guilds) are more likely to produce lower mean overlap indices than are smaller tables (studies on small guilds). Nevertheless, the difference noted between both guilds persists when comparing mean overlaps calculated on the diagonals of each tables (divers: 0.46 ± 0.37, n=6; surface feeders: 0.37 ± 0.29, n=18), although less markedly than on complete tables.

Within groups constituted of taxonomically related bird species the mean overlap indices are over 0.50 (Tables 62 & 63) with the highest values in pairs of congeneric species (see giant petrels: 0.99; Softplumaged and Kerguelen petrels: 0.88; diving petrels: 0.84; crested penguins: 0.80).

Interestingly, overlap indices are low within albatrosses and storm petrels and between the Greatwinged Petrel and the other two gadfly petrels. Particularly, in the albatrosses there is more overlap between the diets of the Wandering and the Lightmantled Sooty Albatrosses than between the congeneric Sooty and Lightmantled Sooty Albatrosses.

Specialized feeders have high overlaps with only one other bird species or none in their guild (giant petrels, Greybacked Storm Petrel, King Penguin, Imperial Cormorant), whereas poorly specialized feeders display significant overlaps with numerous other species, even with taxonomically and morphologically distant ones, in their guild (Wandering Albatross, Whitechinned Petrel, Blue Petrel, Blackbellied Storm Petrel) or in both guilds (the diving petrels, which have high overlap indices both with crested penguins and with most small surface-feeders).

Dietary structure of the community according to prey sizes

The prey size distributions for each bird species, shown as histograms in the species accounts, have been smoothed before being compared within each guild (Figs 32 & 33). Solid histograms give the frequency of each size class in number of individuals and open histograms are frequency distributions of reconstituted biomass. For bird species that feed on a broad array of size classes, the frequency distribution by number can be dramatically skewed towards the smaller sizes whereas the distribution by mass is skewed toward larger size classes. The culmen length (black dots) and the size of a theoretical prey weighing 20% of the bird body mass (empty circles) are also plotted. The culmen length is both an indication of the size of the bird and of its seizing ability. Twenty per cent of its own body mass is the maximum food load that a bird can lift (Croxall *et al.* 1984) and is here considered as a threshold beyond which partial ingestion must have occurred and which, therefore, suggests scavenging. On the other hand, this does not necessarily imply that every prey under this limit had been caught alive. This limit only helps in defining a conservative estimate of the scavenged part of the diet. For every seabird the size of a theoretical prey weighing 20% of the bird body mass is obtained graphically from Fig. 34 constructed from mean body length-body mass data of every prey taxa identified in this study.

The comparison of Figs 32 & 33 indicates that although both guilds include bird species in equivalent body mass ranges (120-14 000 g in divers, 30-10 000 g in surface feeders, see also culmen length in Figs 32 & 33) prey size ranges are quite different.

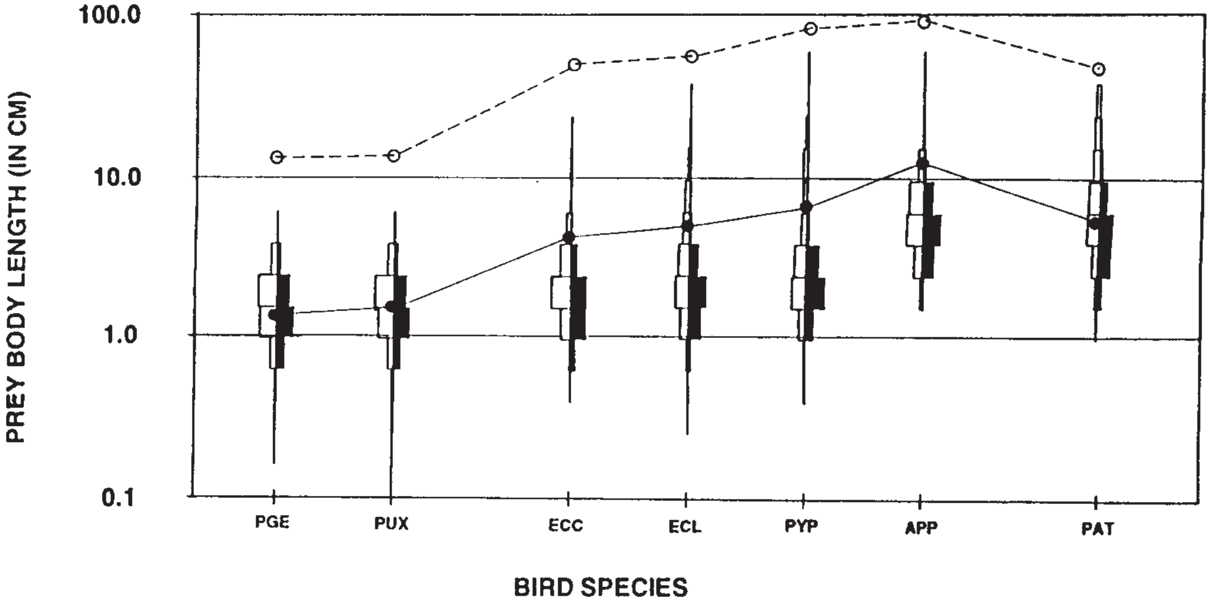

Figure 32

Prey-size distribution compared within diving seabirds breeding at the Crozet Islands. Black histograms are distributions by number, open histograms are distributions by mass, black dots are culmen lengths and open circles are the theoretical body length of a prey weighing 20% of the bird's body mass. Bird abbreviations as indicated in Appendix 3.

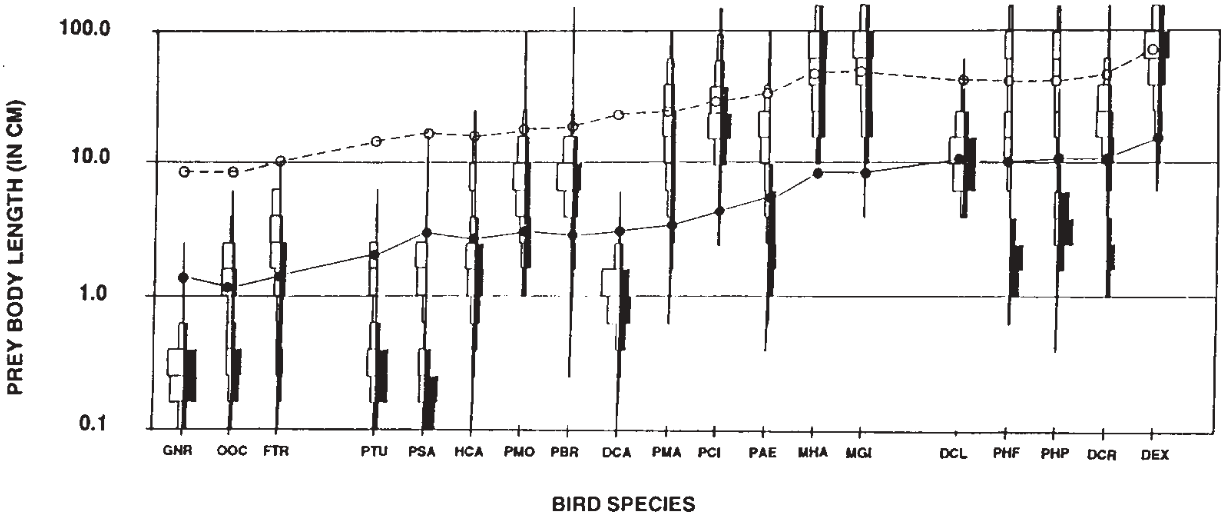

Figure 33

Prey-size distribution compared within surface-feeding seabirds breeding at the Crozet Islands. Black histograms are distributions by number, open histograms are distributions by mass, black dots are culmen lengths and open circles are the theoretical body length of a prey weighing 20% of the bird's body mass. Bird abbreviations as indicated in Appendix 3.

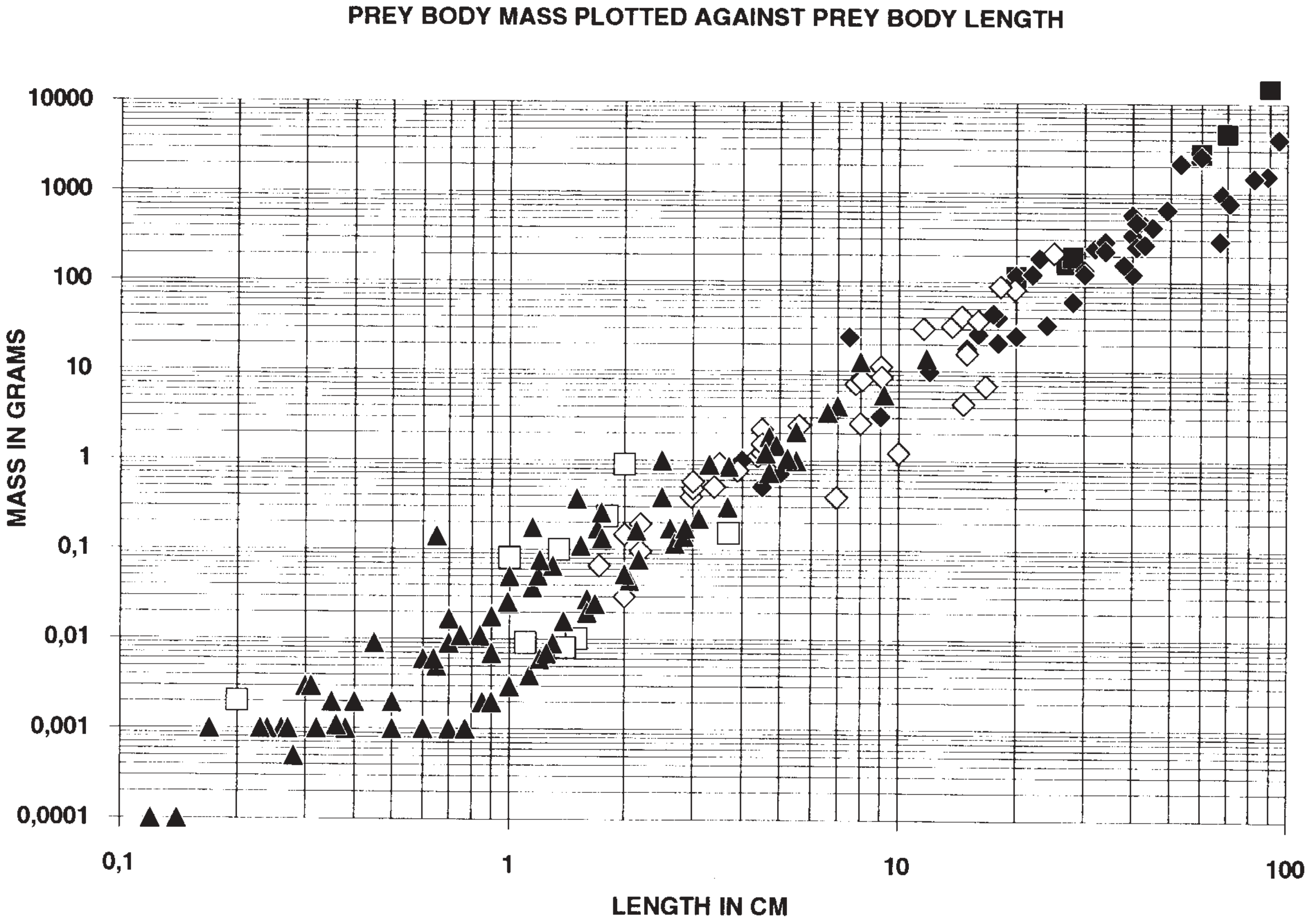

Figure 34

Prey body mass plotted against prey body length. Black triangles are custaceans, black diamonds are squid, black squares are birds, open diamonds are fish and open squares are other prey taxa.

Divers mostly prey on organisms between 10-100 mm long and only in the Imperial Cormorant does prey longer than 100 mm contribute a substantial proportion to the diet by mass. The whole prey size ranges exploited by divers are under the size limit that implies ingestion by fragments. Furthermore, in penguins the bulk of the food comes from prey shorter than the bird's culmen. Although the larger bird species feed on larger organisms than do smaller birds, their prey are much smaller than expected from the hypothesis of proportionality between beak size and prey size. This situation leads to a broad overlap of prey sizes throughout the guild, even between taxonomically and morphologically different species such as diving petrels and crested penguins. Pairs of congeneric species display nearly identical prey size distributions.

In contrast, surface feeders prey on organisms from 1 mm to over 100 cm. At the species level also, surface feeders display larger prey size ranges than do divers; the average ratio between minimum and maximum prey size is 1:30 in surface feeders as against 1:10 in divers. From the gadfly petrels to the albatrosses several species feed on organisms over their carrying capacity which suggests extensive scavenging. On the other hand, several birds forage on minute prey well below their bill size which indicates filtration. Thus the extended prey size ranges relative to bird size in surface feeders express their greater variety of feeding techniques compared to divers. On the whole, prey size increases faster than does bill size, suggesting that there is extensive room to allow segregation on the prey size axis of the niche in surface feeders. Actually, the prey size distributions in pairs and trios of congeners widely overlap and show that such a segregation does not generally operate (see sooty albatrosses, giant petrels, gadfly petrels, prions). The storm petrels, although not congeneric, are very homogeneous in body size and, unlike most other groups of similarly homogeneous birds in the guild, display quite an extensive degree of segregation in terms of prey sizes.

Dietary structure of the community according to prey profiles

In the two previous sections, the dietary structure of the community has been described along the two variables often considered to be the main dimensions along which dietary segregation can occur: the taxonomic nature of the food and the size of the organisms taken. The present section is an attempt to investigate the role of 'prey profile' in the dietary structure of the community. Prey profile is here defined as the set of prey characteristics allowing the bird to discriminate potential prey from non-prey items within all marine organisms met with while foraging at sea. The prey profile is therefore closely related to the species' feeding techniques, which are in turn dictated by morphological and energetic constraints on the one hand and by the competitive context on the other hand.

Clustering the prey taxa according to their profiles

The first step of the analysis is to cluster the different prey taxa in groups sharing a common prey profile. The characteristics considered as important components of the prey profile are body length, mobility, gregariousness, colour, photophores, association with a floating support, and association with benthic support. These features, certainly with other unsuspected ones, govern the detectability and availability of prey. Smell is also known to be important for several bird species (Hutchinson & Wenzel 1980, Jouventin & Robin 1984) and buoyancy of dead prey may also be critical (Lipinski & Jackson 1989); these features have nonetheless been ignored here because of the general lack of data concerning the vast array of prey identified in this study. Distributional characteristics of the prey are not considered either since they apply to habitat selection rather than to prey selection.

For each taxon the prey profile variables are coded as indicated in Table 64. Length is coded from the measurements done in the present study and the other variables are coded according to the literature (*e.g.* Marshall 1977, Mauchline 1980, Fisher & Hureau 1985, Nesis 1987, Gon & Heemstra 1990, P.M. Arnaud, M.R. Clarke, J. Moyse pers. comms concerning the prey profile of various prey groups from their own field observations). The matrix obtained is treated in a classification analysis whose aggregation criteria is the arithmetic average of the group calculated on the Pearson coefficient. At a similarity level of 60%, five clusters of prey taxa are recognized and can, in turn, be separated in sub-groups at 85% of similarity (Fig. 35).

These groupings can be interpreted from the characteristics that most contribute to their internal similarity and to their differences with the other groups:

Group A: small organisms living close to or fixed on a floating support, the typical A prey is the barnacle *Lepas australis*;

Group B: medium to large organisms living close to or fixed on the sea bottom with mobility low (B1) or nil (B2), the annelids and the bivalve *Laternula elliptica* are typical B1 and B2 prey respectively;

Group C: large organisms with mobility nil (offal and bird carcasses);

Group D: medium to large non gregarious organisms with medium to high mobility (D1), bright colour (D2) or photophores (D3), adult onychoteuthids and nototheniids are D1, the pelagic shrimp *Pasiphaea longispina* is D2 and the histioteuthids are D3 examples;

Group E: small to medium, gregarious to highly gregarious organisms (E1: medium size and medium gregariousness; E2: medium size, high gregariousness and photophores present; E3: small size, highly gregarious), post-larvae and early juveniles of squid and nototheniid fish are E1, euphausiids and myctophids are E2 and copepods are E3 examples. Although the hyperiid *Themisto gaudichaudii* bears no photophore it is related to type E2 for its otherwise great similarity with this group.

Prey profiles and seabird diets

For every bird species studied here the diet can be expressed as the relative importance by mass of each prey types defined above (Figs 36-38). Some evident trends then appear when one compares the diets within and between guilds. Pelagic divers (penguins and diving petrels) are all specialized on prey of type E, whereas benthic divers (Imperial Cormorant and, partly, Gentoo Penguin) concentrate on types B and D1 for their food.

Several surface feeders are also specialized on a given prey type. The Greybacked Storm Petrel (prey type A), the giant petrels (prey type C), the Kerguelen and Softplumaged Petrels (prey type D2) and the *Diomedea* albatrosses (prey type D1) each derives at least 75% by mass of its food from a single type of prey. The other surface feeders have more catholic diets in terms of prey profiles. The various subgroups of type D are dominant in the diets of the larger surface feeders (from gadfly petrels to albatrosses) and increasing proportions of prey belonging to type E constitute the diets of the smaller surface feeders. Consequently, in terms of prey profiles, the smaller surface feeders compare better with the divers than with the larger surface feeders.

In both guilds, pairs of congeneric species display comparable food type preferences. The only marked exception to this generality is the Greatwinged Petrel whose diet is more diversified than those of its two congeners, the Kerguelen and the Softplumaged Petrels. The storm petrels also have clearly different food preferences in

TABLE 64

CODE VALUES FOR PREY PROFILE VARIABLES

Variables	Conditions	Codes
Body length	less than 1 cm	0
	from 1 to 10 cm	1
	more than 10 cm	2
Mobility	mostly immobile	0
	low escaping ability	1
	powerful swimmer	2
Swarm	isolated individuals	0
	small swarms	1
	important swarms	2
Photophores	no	0
	some (less than 10)	1
	numerous	2
Colour	mimetic	0
	bright colour	1
Floating support	not associated with floating support	0
	living close to or fixed on floating support	1
Benthic support	not associated with sea bottom	0
	living close to or fixed on benthic support	1

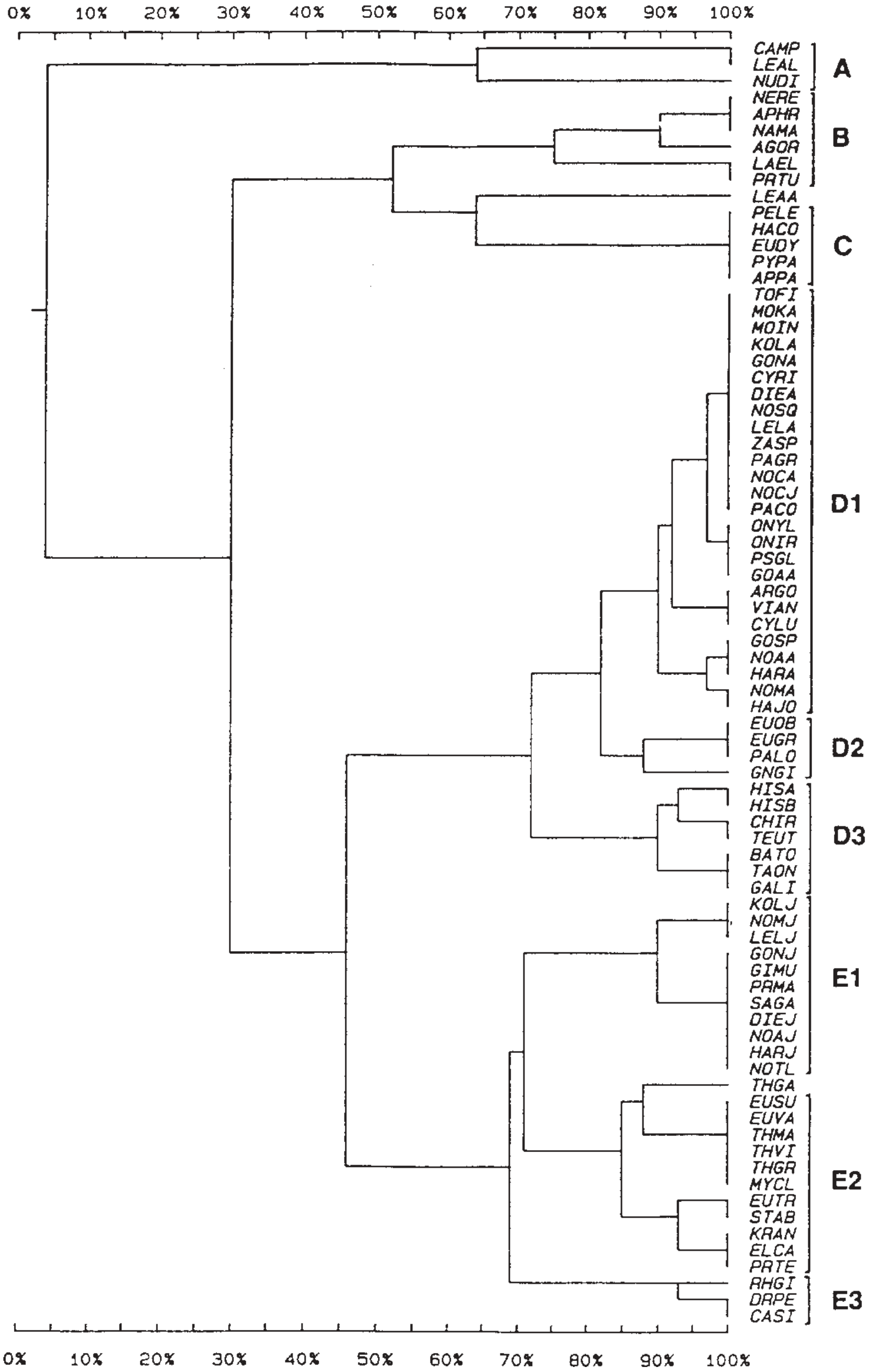

Figure 35

Classification dendrogram of the prey taxa showing prey groups of similar profiles. Abbreviations as indicated in Appendix 3.

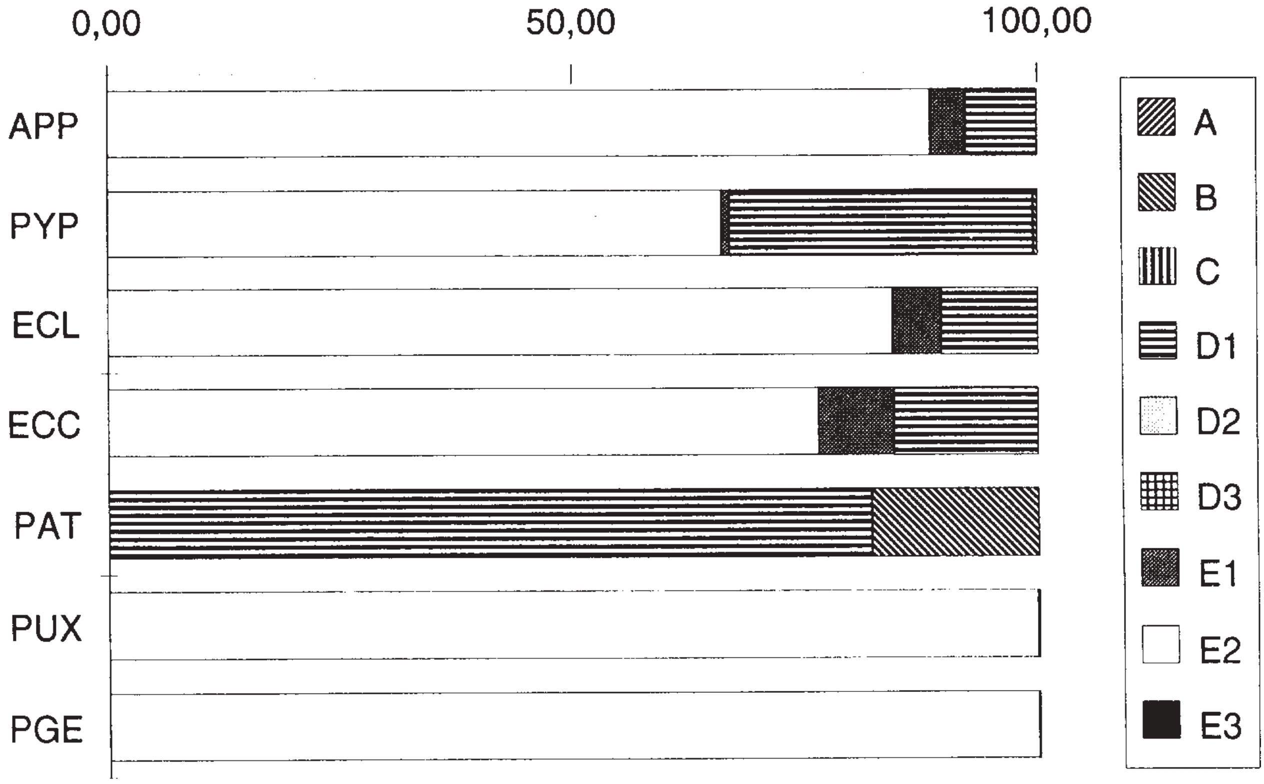

Figure 36

Relative importance by mass of the different prey groups in the diet of diving seabirds at the Crozet Islands. Abbreviations as indicated in Appendix 3.

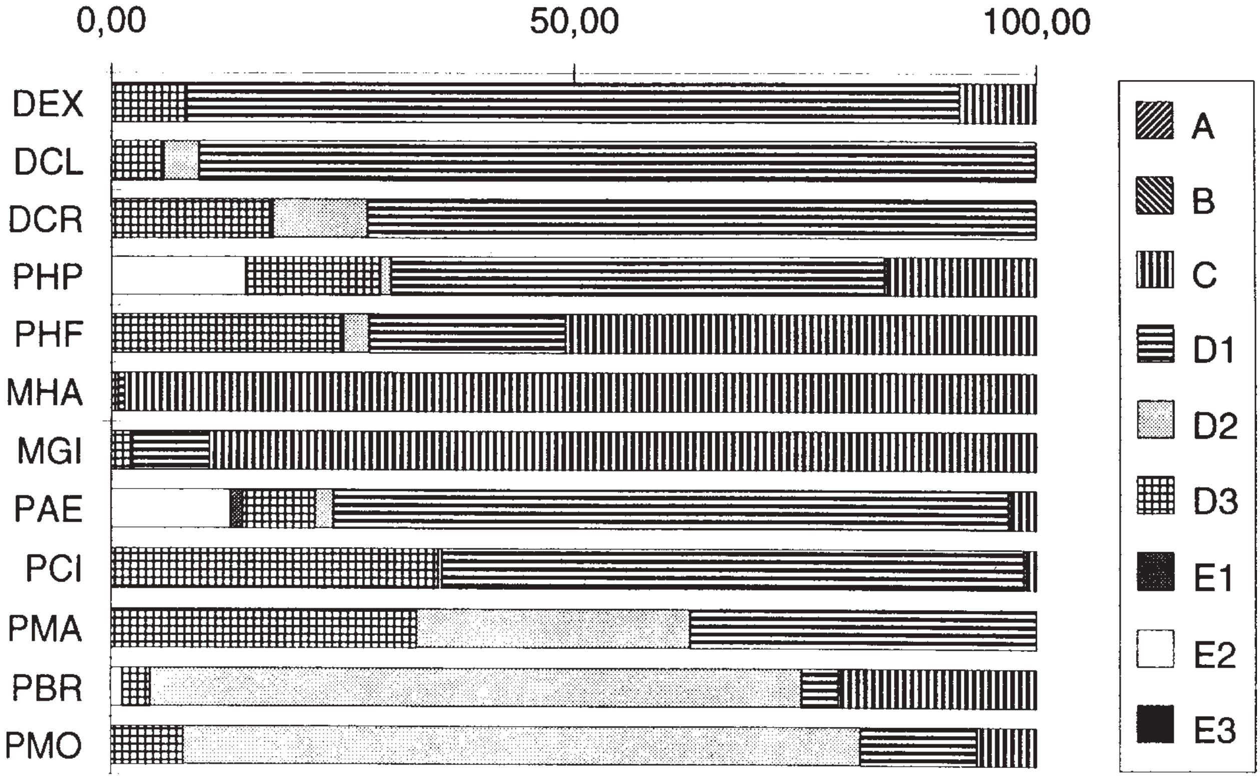

Figure 37

Relative importance by mass of the different prey groups in the diet of the larger surface-feeding seabirds at the Crozet Islands. Abbreviations as indicted in Appendix 3.

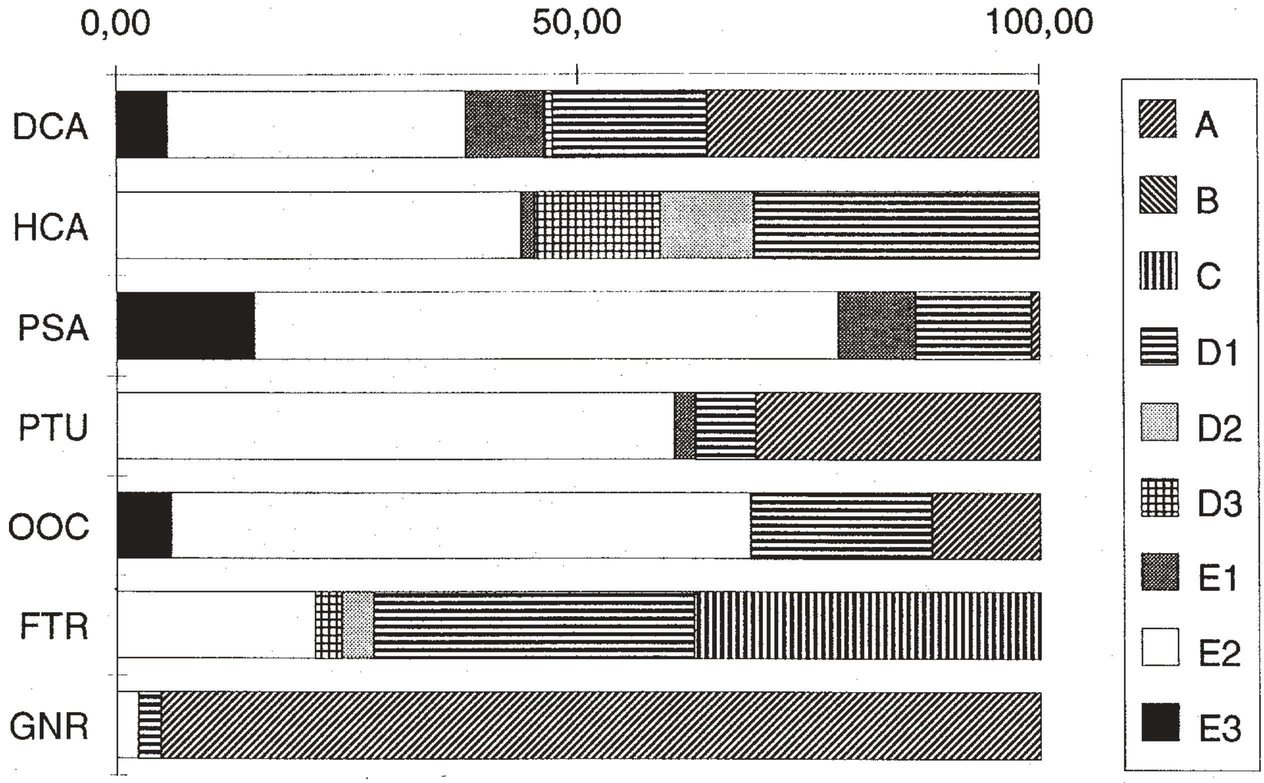

Figure 38

Relative importance by mass of the different prey groups in the diet of the smaller surface-feeding seabirds at the Crozet Islands. Abbreviations as indicated in Appendix 3.

terms of prey types with E2 being dominant in the food of the Wilson's Storm Petrel, a mixture of C, D1 and E2 for the Blackbellied Storm Petrel and only type A prey in the diet of the Greybacked Storm Petrel.

Discussion

Previous community studies

There are rather few studies of seabird diets involving complete communities or at least large fractions of communities. These have been undertaken at various latitudes from the North Sea (Pearson 1968) to South Georgia (Croxall & Prince 1980) in the Atlantic Ocean, as well as in tropical regions of the Pacific and Indian Oceans (Christmas Islands, Ashmole & Ashmole, 1968; the Galápagos Islands, Harris 1977; Hawaii, Harrison *et al.* 1983; the Seychelles, Diamond 1983). All these studies dealt with large parts of island seabird communities and are comparable in their design to the present one. However, the analytical procedures and therefore the descriptions of the diets were not identical, thus leading to difficulties in comparing directly results obtained at the community level. Besides these land-based studies, research in the Ross Sea by Ainley *et al.* (1984) provides dietary comparisons within seabird assemblages collected at sea in three distinct habitats: the continental shelf, the continental slope and the oceanic zones.

These studies did not lead to clear-cut conclusions about the extent of dietary segregation or the amount of dietary overlap within seabird communities. Pearson (1968) reported extensive similarities in the taxa and the size classes exploited by terns, gulls, cormorants and alcids at the Farne Islands, North Sea, and suggested that the resource, mainly constituted of young sand-eels *Ammodytes* sp. and herrings *Clupea harengus* was plentiful in summer and thus allowed several bird species, quite different taxonomically and morphologically, to feed on it without competition. At tropical Christmas Island, bird populations have been much reduced since the arrival of humans (Ashmole & Ashmole 1967). Nonetheless, these authors considered that past competition for food within the seabird community was highlighted by segregating mechanisms still observable today. These mechanisms include selection of different prey taxa by taxonomically distant bird species and differences in prey sizes between closely related seabirds. At the Galápagos Islands, the feeding ecology of 18 bird species out of 19 was studied (Harris 1977). Seabirds there appeared better segregated in terms of diets than at Christmas Island. This may arise from the greater diversity of bird species studied and also from the greater diversity of marine habitats in the vicinity of the archipelago. Indeed, these islands are surrounded by three main water masses with different values of productivity and inhabited by different planktonic and nektonic communities thus offering to predatory birds more possibilities of dietary segregation (or at least more chance that segregation operating on foraging ranges and behaviours would be expressed in the diets) than in the homogeneous environment of Christmas Island. According to the author the dietary differences observed are the consequences of differences in feeding techniques and foraging zones and periods. At Aldabra and Cousin Atolls, Seychelles Islands, oceanic-foraging species appeared poorly segregated whereas neritic feeders differed substantially in their food habits (Diamond 1983). It was therefore suggested that this situation was an expression of the diversity of prey. By comparison with Pearson's (1968) results at the Farne Islands, Diamond concluded that whatever the amount of food available (seasonally plentiful in the North Sea, thinly scattered year round in the tropics) the extent of segregation is an image of prey diversity. In the North Western Hawaiian Islands, Harrison *et al.* (1983) have very thoroughly studied the diets of 18 seabird species but, because of a general lack of data on prey abundance at sea, have not discussed the dietary differences and overlaps observed in the light of segregation concepts. However, in accordance with Diamond's observations, they found that neritic feeders had more diversified diets than did oceanic species. In the Southern Ocean the only community adequately studied to date is South Georgia (Croxall & Prince 1980). Although their approach was more general than the other studies reviewed here and than the current study, which have focused on diets, these authors have illustrated the variety of ways in which dietary segregation can occur. Birds can thus differ by their diets, diving depths or breeding seasons in the diving guild and additionally by foraging ranges, nocturnal *versus* diurnal foraging and feeding techniques in the surface-feeding guild. These mechanisms can operate alone or variously combined to achieve a complete ecological segregation.

The only comparative dietary study performed at sea showed that surface-feeding birds collected in the same habitat could display very high dietary overlaps irrespective of their taxonomic relationships or their morphological similarity (Ainley *et al.* 1984). For instance, birds as different as the Lightmantled Sooty Albatross and the Antarctic Prion collected in the same foraging habitat displayed a very extensive dietary overlap. This suggests that, at least in some cases, birds feeding in the same habitat show little specialization.

The dietary structure observed in the Correspondence Analysis plot and the amount of similarity measured by overlap indices in this study suggest a greater degree of segregation here than at several other localities. Indeed, very high overlap values were only found for pairs of congeneric species and average overlaps calculated within each guild are rather low compared to values obtained at Cousin and Aldabra Atolls for tropical surface feeders (Diamond 1983), at the Farne Islands (Pearson 1968, indices calculated by Diamond 1983) or at the oceanic and slope habitats of the Ross Sea (Ainley *et al.* 1984, in this case the indices are not directly comparable, being calculated on number rather than mass data, however the comparison of overlap index orders of magnitude between their study and the present one is strongly indicative, if not statistically valid). This difference with other localities may derive from various reasons.

Firstly, the array of bird species studied here is larger and taxonomically and morphologically more diversified than in any previous study. Consequently, foraging strategies developed in the Crozet seabird community are more diversified; accordingly average dietary overlap indices are lower than elsewhere.

Secondly, foraging habitats attainable by birds breeding at the Crozet Islands are more diversified than in other studies. Within foraging ranges of the oceanic bird species breeding there (albatrosses, gadfly petrels) major hydrographic boundaries separate several water masses from the subtropical waters to the seasonal ice zone; these water masses are associated with distinct planktonic and nektonic communities. This variety of marine habitats enhances the probability that segregation according to foraging distances is expressed in the diets. Such a possibility is reduced in the tropical seabird community at the Seychelles since the latitudinal gradient of sea surface temperature is much less definite in the tropics than at subantarctic latitudes. Consequently, tropical oceanic seabirds can feed on very similar prey communities in a radius of one thousand kilometres from their breeding site. At the Farne Islands the situation is mostly comparable but for other reasons. The various seabird species breeding there can hardly reach distinct water masses because of their reduced foraging ranges (generally less than 50 km).

Finally, in Ainley *et al.* (1984), it was the purpose of the study to investigate the ecology at sea of seabirds in three distinct habitats of the Ross Sea. Consequently birds were collected in three homogeneous marine habitats and the extent of dietary overlap within the slope and oceanic zones were exceedingly high even between as distant species as the Lightmantled Sooty Albatross and the Antarctic Prion. This study is an interesting counterpart of the land-based dietary studies since, only in this case, is the effect of prey availability in a given marine habitat isolated from food selection proper by the birds. Indeed, in land-based studies partition of foraging habitats and prey selection *sensu stricto* combine in shaping the food composition observed in stomach contents brought to the colony. If, as demonstrated by Ainley *et al.* (1984) in the Ross Sea, prey selection is so low that even taxonomically and morphologically very different seabirds prey upon the same resource when they are in the same foraging habitat, then the dietary differences observed at the Crozet Islands community level would mainly indicate that the dietary segregation operates by partition of feeding habitats (and microhabitats) between coexisting species. Such a segregation would barely be observable in the diets of seabird communities breeding in more homogeneous oceans. This may explain the high overlap values found in tropical oceanic foraging species (Diamond 1983, Harrison *et al.* 1983) and does not exclude the possibility that these birds actually segregate according to foraging zones.

Summary of mechanisms allowing dietary segregation in the Crozet Island seabird community

Sympatric species can achieve a high degree of dietary segregation through mechanisms operating on the various dimensions of the trophic niche. These axes are mainly diet itself, foraging habitats and techniques and the phenology of breeding seasons which govern the season of peak consumption by a given species (see Croxall & Prince 1980 and the other studies cited above). At the Crozet Islands these mechanisms have been studied (e.g. Stahl 1983, Jouventin *et al.* 1985, Stahl *et al.* 1985a,b, Weimerskirch *et al.* 1986, 1988). I will not review here all such studies but their main conclusions are compared to the present dietary data.

The albatrosses, the largest surface feeders, can forage at very great distances from their nests using their energetically inexpensive flight. Doing this, they are able to segregate very efficiently according to foraging grounds and they are known to forage in very distinct habitats (Stahl 1983, Weimerskirch *et al.* 1986, 1988). Additionally, they are also suspected to feed at different periods of the day, the *Diomedea* albatross being mainly diurnal foragers and the *Phoebetria* albatrosses nocturnal. These distinct foraging habits are expressed in the composition of their diets by several key species indicating particular habitats: Antarctic Krill for southern feeding grounds in the Lightmantled Sooty Albatross, numerous temperate to sub-tropical squid taxa indicating northern feeding zones in the Sooty Albatross and the ommastrephid squid *Todarodes filipovae* indicating diurnal foraging in neritic and/or productive oceanic areas by mollymawks (see relevant sections of this study). This partition seems efficient enough to allow these species to breed almost simultaneously. Apart from the Wandering Albatross, distinguished by its year-long breeding cycle, the other five species breed in summer and the differences in their reproduction schedules are very small (a few weeks) relative to the total length of their breeding cycle (six months).

The gadfly and *Procellaria* petrels also perform extensive foraging trips at sea. However, within each genus they are less segregated than are albatrosses in terms of habitats because all gadfly petrels mostly forage in food-depleted oceanic areas and *Procellaria* petrels generally feed in productive neritic and oceanic zones. In both genera, species breed in opposite seasons (Jouventin *et al.* 1985, 1988) and, in the case of the gadfly petrels, where two of the three species studied here breed in summer, segregation is maintained by latitudinal differences in their at-sea distributions (Stahl 1983, Jouventin *et al.* 1988). Unlike albatrosses, the diet of the two summer-breeding species (Kerguelen and Softplumaged Petrels) segregated according to foraging latitudes is not characterized by notable differences in prey species composition. This may be a consequence of their dietary specialization on deep-sea crustaceans whose species distributions are weakly affected by surface oceanographic boundaries.

Excepting the Blue Petrel which is ecologically intermediate between gadfly petrels and prions and can forage very far from its colonies, the small surface feeders are energetically unable to perform these long far-ranging feeding trips known for the larger species (Pennycuick *et al.* 1984). They are also poorly adapted to forage in food-depleted habitats. Consequently, they concentrate on abundant and predictable food sources situated within *c.* 200 km from their nests (Croxall *et al.* 1984). There is therefore less room for them to segregate spatially. In the prey size ranges that small surface feeders can exploit easily, these predictably gregarious prey taxa are mostly planktonic and micronektonic crustaceans whose abundance or availability in surface layers of the ocean is highly seasonal (synthesis in Smith & Schnack-Schiel 1990). Therefore, dietary segregation can hardly be achieved by differences in the reproduction period either and, indeed, none of these species breeds in winter; being all present at the colonies from November to March (Jouventin *et al.* 1985, 1988). It could be expected in such a case that segregation would operate through food selection since spatial and temporal shifts are not possible. Within the prions such a segregation looks very marginal since their index of dietary overlap, calculated at the prey family level, is high and their prey size distributions are mostly similar.

In contrast, storm petrels segregate more clearly. These three species are considered do be under the strongest energetic constraints within the surface feeders due to their very small body size (Pennycuick *et al.* 1984, Pennycuick 1987). They can segregate less than any other species in the community according to foraging ranges and indeed they forage at almost identical distances from the islands (Stahl 1983, Jouventin *et al.* 1988). The seasonal abundance of their food resources also impairs, more strongly than for the other surface feeders, any possibility of temporal shifts in their breeding seasons, actually known to overlap widely (Jouventin *et al.* 1985). Interestingly, food appears to be the main axis of the trophic niche on which these species segregate. Their diets differ in terms of prey taxa, prey sizes and prey profiles to a greater extent than in any group of closely related surface feeders of the Crozet Islands seabird community. The Greybacked Storm Petrel concentrates its predation on larvae of the cirriped *Lepas australis*, the Wilson's Storm Petrel feeds on planktonic and micronektonic crustaceans and the Blackbellied Storm Petrel specializes on nektonic crustaceans and offal. These dietary specializations are most probably the effect of a fine-scale spacial segregation as well as behavioural specializations. Within their overlapping foraging ranges storm petrels differentiate by feeding in distinct habitats: drifting kelp rafts for the Greybacked Storm Petrel, neritic areas for the Wilson's Storm Petrel and deeper zones for the Blackbellied Storm petrel (Stahl 1983, Stahl *et al.* 1985, Jouventin *et al.* 1988). In addition, the Blackbellied Storm Petrel is also attracted by larger predators (see species account above).

Divers also have more energy constraints than do large surface feeders. Volant divers are shaped in such a way that their flight costs are high and the penguins' underwater 'flight' is associated with high thermoregulation and mechanical costs (Pennycuick 1987). Pelagic penguins and diving petrels are to some extent in a comparable situation as the small surface feeders. Due to their energetic constraints they must concentrate on gregarious predictable food source within *c.* 150-200 km of their nests. This resource again consists of micronektonic forms whose availability in the surface layer is seasonal. Due to its larger size the King Penguin is able to dive deeper (Kooyman *et al.* 1992) and preys upon myctophid fishes available within 300 m of the sea surface. The smaller crested penguins and the diving petrels reach shallower depths and mostly feed on crustaceans. There is apparently little room for them to segregate either spatially, temporally and even by foraging methods. Indeed, they all breed in summer with very little temporal shift between congeneric species relative to total durations of the cycles (Jouventin *et al.* 1985, 1988, Stahl *et al.* 1985b) and their distributions at sea are mostly in neritic and slope habitats. Accordingly, these four species display extensive overlap both in terms of prey taxa, prey sizes and prey profiles exploited. They, at least the diving petrels, also have extensive dietary overlaps with the smaller surface feeders.

However, the overlap indices are calculated at the family level, following Diamond (1983) in order to allow inter-community comparisons, and therefore hide differences in the compositions of the diets described at the species level. When one examines more closely the micronektonic species assemblages exploited by each of these divers, and also by the prions and Blue Petrel, several consistent trends arise. All these seabirds extensively prey upon various species of euphausiids and hyperiids ranging in size from 10-25 mm, thus their high overlap values. However, *Euphausia vallentini* largely prevails in the euphausiid species assemblages exploited by Gentoo, Macaroni and Rockhopper Penguins and Common Diving Petrels whereas a mixture of *E. vallentini* and *Thysanoessa* spp. in equivalent proportions characterizes the diet of the Blue Petrel, the prions and the South Georgia Diving Petrel. The hyperiid species assemblages are largely dominated by *Themisto gaudichaudii* in crested penguins and Blue Petrel and by *Primno macropa* in the South Georgia Diving Petrel, both species contributing rather equally to the hyperiid diets of prions and Common Diving Petrels. It is suggested that these differences in the micronektonic species assemblages express fine differences in feeding habitats operating within the limits of the continental shelf and slope areas. Indeed, at-sea observations suggest that small-scale spatial segregation occurs within the congeneric pairs of crested penguins and diving petrels; Rockhopper Penguin and Common Diving petrel being inner shelf foragers and Macaroni Penguin and South Georgia Diving Petrel feeding on the outer shelf area (Stahl 1983, Jouventin *et al.* 1988, Ridoux *et al.* 1988). Unfortunately, small-scale distribution patterns of the main micronektonic communities are not sufficiently documented around the Crozet Islands and this lack of data makes more detailed inferences from the dietary results rather speculative. A better knowledge of bird behaviour at sea, combined with more information on the small-scale heterogeneity of their food resources would help in better understanding the precise manner in which neritic feeding birds, both surface feeders and divers, partition food in summer at the Crozet Islands.

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APPENDIX 1

SUMMARY OF ALL PREY SPECIES AND THEIR IMPORTANCE AS FOOD TO CROZET ISLAND SEABIRDS

Prey species	Bird species[a]
CNIDARIANS	
Campanulariidae	*DCA*, *PSA*, *OOC*, *GNR*,
CTENOPHORES	
unidentified	*PAE*, HCA,
GASTROPODS	
Nudibranchiate	**DCA**,
Limacina sp.	*OOC*,
BIVALVES	
Laternula elliptica	PAT,
CEPHALOPODS	
SEPIOIDEA	
Sepiidae	*PAE*,
TEUTHOIDEA	
Architeuthis sp.	*DEX*, *PHF*,
Todarodes filippovae	*APP*, *PYP*, DME, **DCR**, **DCL**, *PAE*, *PMO*,
Onychoteuthis spp.	*APP*, *PYP*,*DEX*, *PHP*, *PHF*, *MHA*, *MGI*, *PMA*, PSA,
Moroteuthis robsoni	*DEX*, *PHF*,
M. ingens	DEX, PHP, *MHA*, *MGI*, PCI,
M. knipovitchi	APP, *PYP*, DEX, *DCR*, *PHP*, PHF, *MHA*, PAE,*PMA*,
Kondakovia longimana	APP, ECL, ECC, *PYP*, **DEX**, **DCR**, **PHP**, PHF, MHA, *MGI*, *PAE*, *PBR*, *PMA*,
Pholidoteuthis sp.	*APP*, *ECL*, *ECC*,
Psychroteuthis spp.	*APP*, *DEX*, *DME*, *DCR*, *PHP*, *MGI*,
P. glacialis	**PHP**,
Brachioteuthis (picta)	*ECL*, *ECC*, *PYP*, *DEX*, *PCI*, *PBR*, *PMA*, PTU,
unidentified gonatid	*APP*, ECL, ECC, *PYP*, *PMA*, *HCA*, *PSA*, PTU,
Gonatus antarcticus	*APP*, DEX, *DCR*, PHP, PHF, *MHA*, PAE, PCI, PMA,
Ancistrocheirus lesueuri	*DEX*, *PHF*, *PMA*,
Lycoteuthis spp.	*DEX*, *DCR*, *PHP*, *PHF*, *MHA*, *PAE*, *PMO*, *PMA*,
Octopoteuthis sp.	*DEX*, *PHF*, *PMA*,
Taningia sp.	*DEX*, *PHF*,
Lepidoteuthis sp.	*DEX*, *PHF*, *PMA*,
Histioteuthis sp. *A*	DEX, *DCR*, PHF, *PAE*, *PBR*, PMA,
Histioteuthis sp. *B*	*DEX*, PHF, *PAE*, PMA,
H.eltaninae	DEX, *DCR*, PHP, **PHF**, PCI, *PBR*, *PMO*,
Alluroteuthis antarcticus	*APP*, *ECL*, *ECC*, *PYP*, DEX, *DCR*, *PHP*, PHF, *PMA*,
Bathyteuthis abyssicola	*PBR*, *PMO*,
Cycloteuthis sp.	*DEX*, *PHP*, *PHF*,

Mastigoteuthis spp.	*DEX*, *PHP*, *PHF*, *PMA*,
Chiroteuthis spp.	*DEX*, *DME*, *DCR*, *PHP*, *PHF*, *PCI*, PMA,
C. imperator	*DCR*, *PHF*, *PAE*, *PMA*,
"*Batoteuthis* sp."	DCR, PHP, PHF, *MGI*, PBR, *PMA*,
Liocranchia sp.	*PMA*,
Bathothauma sp.	*PHP*, *PHF*, *PAE*,
Megalocranchia sp.	*APP*, *DEX*, *PHP*, *PAE*, *PMA*,
Taonius sp. (large)	*DEX*, *PHF*, *PAE*, *PBR*, PMA,
T. pavo (small A)	*DEX*, *PHF*, *PAE*, *PMO*, *PMA*,
T. pavo (small B)	*DEX*, *PHF*,
Teuthowenia megalops	*DEX*,
T. pellucida	*APP*, *DCR*, *MGI*, *PMA*,
Teuthowenia sp.	*PBR*, *PMA*,
Galiteuthis glacialis	*APP*, *PYP*, DEX, DCR, **PHP**, **PHF**, PAE, *PMA*,
G. phyllura	*PMA*,
Galiteuthis/Teuthowenia	*ECC*,
Mesonychoteuthis hamiltoni	*APP*, *DEX*, *PHP*, *PHF*, *PMA*,
"Oegopsid A"	*APP*, *PAE*,
unidentified oegopsids	*DEX*, **DCR**, **DCL**, **PHF**, **PHP**, *MHA*, **PAE**, **PCI**, PBR, **PMO**, **PMA**, **HCA**, PSA, *FTR*, *PUX*, *PGE*,
OCTOPODA	
Octopodidae	*APP*, *ECL*, *PYP*, *PAT*, *PAE*, *DCA*,
Argonauta argo	*ECL*, ECC,
POLYCHAETES	
Nereidae	*PAT*,
Polynoidae	PAT,
Aglaophamus ornatus	PAT,
PRIAPULIDS	
Priapulus tuberculatospinosus	*PAT*,
PYCNOGONIDS	
Pycnogonum platylophum	*PAT*,
CRUSTACEANS	
OSTRACODS	
Halocyprididae	*DCA*, *PSA*,
Gigantocypris muelleri	*PBR*, *HCA*,
COPEPODS	
unidentified calanoids	*ECL*, *ECC*, *PYP*, *DCA*, *HCA*, PSA, OOC, *PUX*, *PGE*,
Euchaetidae	*DCA*, *HCA*, *PUX*,
Rhincalanus gigas	DCA, *HCA*, PSA,
Drepanopus pectinatus	**PSA**,
Calanus simillimus	PSA,
Sphyrion lumpi	*DEX*, *MHA*, *PCI*, PMA,
Sarcotretes sp.	*APP*,
Lernaeenicus sp.	*APP*,
unidentified harpacticoids	*PSA*,
CIRRIPEDS	

Lepas australis	*ECC*, *PAT*, *DCA*, *HCA*, PSA, **PTU**, **OOC**, *FTR*, **GNR**, *PUX*, *PGE*,
MYSIDS	
unidentified	*OOC*,
? Pseudochalaraspidum sp.	*HCA*,
Gnathophausia gigas	*DME*, DCR, *DCL*, *PHP*, PHF, *PAE*, *PCI*, **PBR**, PMO, PMA, HCA, *PSA*, FTR,
G. ingens	*MGI*,
Petalophthalmus armiger	*PMA*,
Euchaetomera zurstrasseni	*DCA*,
Boreomysis sp.	*DCA*,
ISOPODS	
Serolis latifrons	*ECC*, *PAT*,
Cirolanidae	*APP*,
Sphaeromatidae	*DCA*,
Astacilla sp.	*PAT*,
Bopyridae	*PTU*,
AMPHIPODS	
Gondogeneia spinicoxa	*PYP*, PAT,
G. ushuaiae	*PSA*,
Pontogeneiella brevicornis	DCA,
Cyphocaris challengeri	*PMA*,
C. richardi	PBR, *HCA*,
Eurythenes obesus	*PHP*, *PAE*, PBR, **PMO**, PMA, *HCA*, FTR,
E. gryllus	*DCR*, PHF, **PBR**, *PMA*, HCA,
Paracallisoma alberti	*PBR*, *HCA*,
Parawaldeckia kidderi	DCA,
Uristes murrayi	*PSA*,
Lysianassidae n. sp.	*DCA*,
Oedicerotidae n.sp.	*DCA*,
Podocerus capillimanus	*DCA*,
Parandania boecki	*HCA*,
Hyperiella antarctica	*ECL*, *PYP*, *PBR*, *DCA*, *HCA*, *PSA*, *PTU*, *OOC*, *FTR*,
Hyperia sp.	*ECL*, *PYP*, *PHF*, *HCA*, *PTU*,
Hyperoche sp.	*ECL*, *PYP*, *DCA*, *HCA*, *PSA*,
Themisto gaudichaudii	**ECL**, ECC, *PYP*, *DCR*, *PHP*, *PHF*, PAE, *PBR*, *PMO*, *PMA*, DCA, **HCA**, **PSA**, **PTU**, OOC, FTR, *GNR*, **PUX**, *PGE*,
Vibilia antarctica	*ECL*, *PBR*, *DCA*, HCA, *PSA*, *PTU*, OOC, *FTR*,
Cyllopus lucasii	*ECL*, *PYP*, *PBR*, *DCA*, HCA, PSA, PTU, FTR, *GNR*,
Primno macropa	ECL, *ECC*, *PYP*, DCA, *HCA*, **PSA**, **PTU**, OOC, *FTR*, **PUX**, **PGE**,
Megalanceola sp.	*PSA*,
Lanceola sp.	*PBR*,
EUPHAUSIIDS	
Euphausia superba	**PHP**, *PHF*, **PAE**, PBR, HCA,

E. vallentini	**ECL**, **ECC**, **PYP**, *PHP*, *PHF*, *PAE*, **DCA**, **HCA**, PSA, *PTU*, **OOC**, **FTR**, *GNR*, **PUX**, **PGE**,
E. triacantha	*PYP*, DCA, *OOC*,
E. longirostris	*PYP*,
E. similis	*PYP*,
Thysanoessa sp.	**DCA**, **HCA**, PSA, PTU, *OOC*, *FTR*, PUX, **PGE**,
Thysanoessa macrura	ECL, ECC, *PYP*,
T. vicina	ECL, ECC,
T. gregaria	*ECC*,
Stylocheiron abbreviatum	*ECL*, *PYP*, DCA,
DECAPODS	
Caridea	*ECL*, *PYP*,
Pasiphaea longispina	DCR, *PHP*, *PHF*, PAE, **PBR**, **PMO**, **PMA**, HCA,
Nauticaris marionis	*PYP*, **PAT**,
INSECTS	
unidentified	*PBR*,
Nabis capsiformis	*HCA*, *PSA*,
Pyraloidea	*HCA*,
Noctuellidae	*HCA*,
ECHINODERMS	
Holothurians	*PAT*,
CHAETOGNATHS	
unidentified	*PUX*,
Sagitta gazellae	*ECL*, *ECC*, *PYP*, DCA, *HCA*, PSA,
Eukrohnia hamata	*OOC*,
FISHES	
UNIDENTIFIED	**DEX**, **DME**, *DCR*, **DCL**, **PHP**, PHF, MGI, **PAE**, **PCI**, *PBR*, *PMO*, PMA, DCA, HCA, PSA, *PTU*, **OOC**, **FTR**,
SALMONIFORMES	
Bathylagus sp.	*HCA*,
AULOPIFORMES	
Paralepididae	APP, *ECL*, *ECC*, *PBR*,
Magnisudis (prionosa)	APP, PAE,
MYCTOPHIFORMES	
Electrona carlsbergi	**APP**, ECL, *PBR*, HCA,
E. subaspera	*APP*,
Gymnoscopelus nicholsi	*APP*, **PYP**,
Protomyctophum (tenisoni)	**APP**, *ECL*, PYP, HCA,
P. normani	*APP*, *ECL*, *PYP*, *HCA*,
Krefftichthys anderssoni	**APP**, **ECL**, **ECC**, *PYP*, HCA,
unidentified	*PAE*, *HCA*,
GADIFORMES	
Muraenolepis (orangiensis)	*PYP*, PAT,
Halargyreus johnsoni	PCI,
BERYCIFORMES	
Sio nordenskjoldii	*HCA*,

Melamphaes sp.	*PMO*,
SCORPAENIFORMES	
Zanchlorhynchus spinifer	*PYP*, *PAT*,
PERCIFORMES	
Dissostichus eleginoides	PYP, **PAT**,
Notothenia acuta	*PYP*, **PAT**,
Lepidonotothen squamifrons	PAT, PHF,
L. larseni	*ECL*, PYP, **PAT**,
Paranotothenia magellanica	*ECC*, PYP, **PAT**,
Nototheniidae	*ECL*, *PYP*, PAT, PAE,
Harpagifer spinosus	*PYP*, PAT,
H. kerguelenensis	PAT,
Harpagiferidae	*ECL*, *PYP*, PAT,
Paradiplospinus gracilis	*APP*, *ECC*, PYP, *PHF*, *HCA*,
BIRDS	
SPHENISCIFORMES	
unidentified	DME, *DCR*, PHP, **MHA**, **MGI**,
Aptenodytes patagonicus	MHA, MGI,
Eudyptes spp.	**PHF**, **MHA**, MGI,
PROCELLARIIFORMES	
unidentified	MHA, MGI,
Pachyptila salvini	**PHF**, MHA, MGI,
P. turtur	*PHF*, *MHA*,
Halobaena caerulea	*MGI*,
Pelecanoides urinatrix	MHA, MGI,
P. georgicus	*MGI*,
CARRION (other than birds, fish and squid)	
unidentified	DEX, PHP, PAE, *PCI*, **PBR**, PMO, **FTR**,

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[a] For every taxon the initials of the bird species in which it occurs are given. Bold capitals are used when the prey taxon is a major food component for the bird (>10% either by number or by mass), standard capitals correspond to secondary food sources (from 1 to 10% by number or by mass) and italics indicate rarely-taken prey

Bird initials are as indicated in Appendix 3

APPENDIX 2

STANDARD RELATIONSHIPS USED IN THE COMPUTATION OF PREY TOTAL BODY LENGTH AND RECONSTITUTED BIOMASS FROM THE MEASUREMENTS OF VARIOUS DIAGNOSTIC PARTS

Prey taxa	Conversion formulae[a] Y = f(X)	r	n	(Y range)
FISH				
Myctophiformes				
Electrona carlsbergi	BL=5.8 JL		27	(6.7-9.0)
Krefftichthys anderssoni	BL=7.4 JL		3	(2.7-3.2)
Protomyctophum tenisoni	BL=6.0 JL		2	(4.2-4.8)
Gymnoscopelus nicholsi	BL=5.3 JL		8	(10.7-12.7)
(BL calculations from Otolith Lengths and BM calculations were performed using published relationships in Adams & Klages 1987, Brown & Klages 1987, Hecht 1987)				
Perciformes				
Notothenia acuta	BL = 1.87CL - 0.24	0.99	17	(2.7 - 9.1)
	$BM = 0.0071\ BL^{3.40}$	0.99	16	(0.2 - 13.1)
Paranotothenia magellanica	BL = 2.08CL - 0.57	0.99	14	(3.5 - 24.5)
	$BM = 0.0198\ BL^{2.90}$	0.95	16	(0.7 - 412.8)
Lepidonotothen squamifrons	BL = 2.00 CL - 0.52	0.99	9	(4.7 - 14.8)
	$BM = 0.0092\ BL^{3.27}$	0.99	8	(1.7 - 60.0)
L. larseni	BL = 1.63CL + 0.34	0.99	23	(4.4 - 13.2)
	$BM = 0.0098\ BL^{3.12}$	0.99	21	(1.1 - 26.5)
Harpagifer spinosus	BL = 2.13 CL - 0.29	0.99	29	(2.1 - 7.1)
	$BM = 0.0136\ BL^{3.36}$	0.99	31	(0.2 - 7.9)
H. kerguelensis	BL = 1.99 CL - 0.13	0.99	10	(2.2 - 5.8)
	$BM = 0.0139\ BL^{3.35}$	0.99	18	(0.2 - 4.8)
Zanchlorhynchus spinifer	BL = 3.38 CL - 0.76	0.98	5	(3.5 - 4.8)
	$BM = 0.0061\ BL^{4.13}$	0.97	5	(1.0 - 4.0)
Paradiplospinus gracilis	BL/JL = 15		9	(19.0 -26.0)
CRUSTACEANS				
Cirripeds				
Lepas australis (cypris larvae)	$BM/BL^3 = 0.11$		11	(0.21 - 0.28)
Copepods				
Rhyncalanus gigas	$BM/BL^3 = 0.018$		20	(0.70 - 0.85)
other calanoids	$BM/BL^3 = 0.024$		168	(0.22 - 0.36)
Amphipods				
Gondogeneiella spinicoxa	$BM = 0.02\ BL^{3.01}$	0.97	8	(0.8 - 0.34)
Eurythenes obesus	$BM/BL^3 = 0.03$		3	(0.2 - 2.1)
E. gryllus	$BM/BL^3 = 0.025$		1	(14.3)
Cyphocaris richardi	$BM/BL^3 = 0.025$		1	(0.32)

Themisto gaudichaudii	$BL = 0.56 ED - 0.15$	0.99	118	(0.3 - 2.1)
	$BM = 0.0224 BL^{2.6}$		34	(0.01 - 0.09)
Hyperia sp./*Hyperoche* sp.	$BL = 0.36 ED + 0.12$	0.95	6	(0.7 - 1.9)
Primno macropa	$BL = 0.76 ED - 0.13$	0.99	56	(0.2 - 1.3)
	$BM/BL^3 = 0.03$		1	(0.04)
Vibilia antarctica	$BL = 0.94 ED + 0.44$	0.84	37	(0.6 - 1.3)
	$BM/BL^3 = 0.03$			
Cyllopus lucasii	$BL = 0.56 ED + 0.08$	0.92	13	(0.9 - 1.3)
	$BM/BL^3 = 0.034$		2	(0.04 - 0.07)
Mysids				
Gnathophausia gigas	$BL/TL = 2.45$		4	(4.2 - 11.8)
	$BM/BL^3 = 0.012$		4	(1.5 - 15.0)
Euphausiids				
Euphausia vallentini	$BL = 1.74 ED + 0.07$	0.98	151	(0.8 - 2.7)
	$BM = 0.00316 BL^{3.8}$		25	(0.01 - 0.11)
E. superba	$BL = 1.93 ED + 0.60$	0.95	10	(3.3 - 5.0)
	$BM/BL^3 = 0.0074$		4	(0.32 -0.46)
Thysanoessa spp.	$BL = 1.56 ED - 0.42$	0.97	15	(0.5 - 2.1)
	$BM = 0.00251 BL^{4.4}$		10	(0.01 - 0.05)
Stylocheiron abbreviatum	$BL = 1.42 ED - 0.50$	0.93	13	(1.5 - 2.2)
Decapods				
Nauticaris marionis	$BM = 0.0053 BL^{3.54}$	0.98	30	(0.3 - 2.2)
Pasiphaea longispina	$BL/TL = 2.63$		2	(8.0 - 8.7)
	$BL/ED = 4.18$		2	(8.0 - 8.7)
	$BM/BL^3 = 0.007$		2	(4.0 - 4.1)
OTHER ORGANISMS				
Chaetognaths				
Sagitta gazellae	$BM/BL^3 = 0.0027$		3	(0.2 - 0.5)
Polychaetes				
Aglaophamus ornatus	$BM = 0.0167 BL^{2.33}$	0.98	6	(1.5 - 20.0)

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[a] Variables and units are: BL body length in cm; JL jaw length in cm; CL caudal length in cm; TL thoracic length in cm; ED eye diameter in mm; BM body mass in g

APPENDIX 3

(a)

LIST OF VERNACULAR AND SCIENTIFIC NAMES OF BIRDS AND THEIR ABBREVIATED FORMS (THREE CAPITALS) USED IN FIGURES AND TABLES

King Penguin	*Aptenodytes patagonicus*	APP
Gentoo Penguin	*Pygoscelis papua*	PYP
Macaroni Penguin	*Eudyptes chrysolophus*	ECL
Rockhopper Penguin	*Eudyptes chrysocome*	ECC
Wandering Albatross	*Diomedea exulans*	DEX
Blackbrowed Albatross	*Diomedea melanophrys*	DME
Greyheaded Albatross	*Diomedea chrysostoma*	DCR
Yellownosed Albatross	*Diomedea chlororhynchos*	DCL
Sooty Albatross	*Phoebetria fusca*	PHF
Lightmantled Sooty Albatross	*Phoebetria palpebrata*	PHP
Northern Giant Petrel	*Macronectes halli*	MHA
Southern Giant Petrel	*Macronectes giganteus*	MGI
Pintado Petrel	*Daption capense*	DCA
Whitechinned Petrel	*Procellaria aequinoctialis*	PAE
Grey Petrel	*Procellaria cinerea*	PCI
Greatwinged Petrel	*Pterodroma macroptera*	PMA
Kerguelen Petrel	*Pterodroma brevirostris*	PBR
Softplumaged Petrel	*Pterodroma mollis*	PMO
Blue Petrel	*Halobaena caerulea*	HCA
Salvin's Prion	*Pachyptila salvini*	PSA
Fairy Prion	*Pachyptila turtur*	PTU
Wilson's Storm Petrel	*Oceanites oceanicus*	OOC
Blackbellied Storm Petrel	*Fregetta tropica*	FTR
Greybacked Storm Petrel	*Garrodia nereis*	GNR
Common Diving Petrel	*Pelecanoides urinatrix*	PUX
South Georgia Diving Petrel	*Pelecanoides georgicus*	PGE
Imperial Cormorant	*Phalacrocorax atriceps*	PAT

(b)

LIST OF THE MAIN PREY SPECIES AND THEIR ABBREVIATED FORMS (FOUR CAPITALS) USED IN TABLES AND FIGURES

Campanulariidae	CAMP
Drepanopus pectinatus	DRPE
Calanus simillimus	CASI
Rhincalanus gigas	RHGI
Other copepods	COPE
Lepas australis (larvae, adults)	LEAU (LEAL, LEAA)
Gigantocypris muelleri	GIMU
Euphausia vallentini	EUVA
Euphausia superba	EUSU
Euphausia triacantha	EUTR
Thysanoessa spp.	THYS
Thysanoessa vicina	THVI
Thysanoessa macrura	THMA
Thysanoessa gregaria	THGR
Stylocheiron abbreviatum	STAB
Themisto gaudichaudii	THGA
Cyllopus lucasii	CYLU
Vibilia antarctica	VIAN
Primno macropa	PRMA
Other planktonic crustaceans	CRPK
Cyphocaris richardi	CYRI
Eurythenes spp.	EURY
Eurythenes obesus	EUOB
Eurythenes gryllus	EUGR
Gnathophausia gigas	GNGI
Pasiphaea longispina	PALO
Other nektonic crustaceans	CRNK
Gondogeneia spinicoxa	GOSP
Nauticaris marionis	NAMA
Benthic crustaceans	CRBT
Kondakovia longimana (juveniles, adults)	KOLO (KOLJ, KOLA)
Moroteuthis knipovitchi (juveniles, adults)	MOKN (MOKJ, MOKA)
Moroteuthis ingens	MOIN
Kondakovia/Moroteuthis	KOMO
Onychoteuthis sp. "large"	ONYL
Todarodes filippovae	TOFI
Psychroteuthis glacialis	PSGL
Gonatus antarcticus (juveniles, adults)	GOAN (GOAJ, GOAA)
Unidentified gonatids (juveniles, adults)	GONA (GONJ, GONA)
Batoteuthis sp.	BATO

Chiroteuthis spp.	CHIR
Histioteuthis spp. (type A, type B)	HIST (HISA, HISB)
Taonius sp.	TAON
Teuthowenia spp.	TEUT
Galiteuthis glacialis	GALI
Argonauta argo	ARGO
Other cephalopods	CEPH
Nudibranchs	NUDI
Laternula elliptica	LAEL
Nereidae	NERE
Aphroditidae (=Polynoidae)	APHR
Aglaophamus ornatus	AGOR
Priapulus tuberculatospinosus	PRTU
Other benthic invertebrates	INBT
Sagitta gazellae	SAGA
Other invertebrates	INVE
Paralepis coregonoides	PACO
Notolepis sp. (larvae, adults)	NOTO (NOTL, NOTA)
Electrona carlsbergi	ELCA
Krefftichtys anderssoni	KRAN
Gymnoscopelus nicholsi	GYNI
Protomyctophum tenisoni	PRTE
Krefftichthys/Protomyctophum	KRPR
Myctophid larvae	MYCL
Paradiplospinus gracilis	PAGR
Other pelagic fishes	PEFI
Dissostichus eleginoides (juveniles, adults)	DIEL (DIEJ , DIEA)
Notothenia (Lepidonotothen) squamifrons	NOSQ
Lepidonotothen larseni (juveniles, adults)	LELA (LELJ , LELA)
Notothenia (Paranotothenia) magellanica	NOMA (NOMJ, NOMA)
Notothenia acuta (juveniles, adults)	NOAC (NOAJ, NOAA)
Harpagifer spp. (juveniles, adults)	HARP (HARJ, HARA)
Halargyreus johnsoni	HAJO
Other benthic fish	BTFI
Unidentified fish	FISH
Eudyptes spp.	EUDY
Aptenodytes patagonicus	APPA
Pygoscelis papua	PYPA
Unidentified penguins	PENG
Pachyptila spp. (including *Halobaena caerulea*)	PACH
Pelecanoides spp.	PELE
Unidentified offal	OFFA