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

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SUMMARY

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The diets of 27 seabird species have been investigated concurrently at the subantarctic Crozet Islands, southern Indian Ocean. The species dealt with in the study include penguins (four species), albatrosses (six species), petrels (11 species), storm petrels (three species), diving petrels (two species) and cormorant (one species) which virtually represents the whole pelagic seabird community breeding on these islands, since only the rarest species were not sampled. The stomach contents were collected using non-lethal methods combining spontaneous regurgitation and stomach-flushing techniques. The analytical procedure was designed to provide quantitative data on number, mass and body length distribution of every prey taxon occurring in any individual bird sample. The data are given for every bird species as occurrence, number, mass and body length of each prey type found in the fresh fraction (or food load), whereas accumulated diagnostic items are described separately to avoid most biases arising from differential digestion rates of these items. Pelagic divers, like the King *Aptenodytes patagonicus*, Macaroni *Eudyptes chrysolophus* and Rockhopper *E. chrysocome* Penguins and the two diving petrels, *Pelecanoides georgicus* and *P. urinatrix*, specialized on small, highly gregarious prey species including myctophid fishes (mainly *Electrona carlsbergi*, *Protomyctophum tenisoni* and *Krefftichthys anderssoni*) in the larger predators, as well as hyperiid amphipods (*Themisto gaudichaudii* and *Primno macropa*) and euphausiids (*Euphausia vallentini* and *Thysanoessa macrura/vicina*) in the smaller ones. The Gentoo Penguin *Pygoscelis papua* which forages both pelagically and benthically, included the euphausiid *Euphausia vallentini*, several myctophids and several notothenioids as important components of its diet. Surface-feeding birds as a whole displayed much a wider variety of prey types, both in terms of prey species and prey morphological and behavioural profiles. Furthermore, every surface-feeding species can also prey upon a broader array of prey types and sizes than divers generally do. Albatrosses basically fed on large sized non-gregarious organisms such as squids and fishes. In addition, the two sooty albatrosses *Phoebetria palpebrata* and *P. fusca* included in their food significant amounts of euphausiids, but also pieces of penguins and whole carcasses of petrels. The muscular non-luminescent onychoteuthid squid *Kondakovia longimana* was of prime importance in the food of the Wandering Albatross *Diomedea exulans*. The epipelagic squid *Todarodes fillipovae* was characteristic of the three mollymawk albatrosses *D. melanophrys*, *D. chrysostoma* and *D. chlororhynchos*, whereas the occurrence of oceanic deep-dwelling migratory squids was the rule in the diets of Wandering and the two sooty albatrosses. The two giant petrels *Macronectes giganteus* and *M. halli*, which are equivalent in size to albatrosses, were heavily dependant on penguin carrion and petrel carcasses for their food. The medium-sized petrels of the genus *Procellaria* and *Pterodroma* had mixed diets including fish, squid and crustaceans to various proportions. Oceanic deep-dwelling crustaceans, as well as a few fish and squid species, reported not to perform vertical diel migrations accounted for significant percentages by mass of the diet of the three gadfly petrels *Pterodroma* spp. The Pintado Petrel *Daption capense* displayed one of the most diversified diets, with nudibranchiate gastropods being important prey species and indicating very inshore feeding habitats. The Blue Petrel and the Salvin's *Pachyptila salvini* and Fairy *P. turtur* Prions were typically planktivorous species preying on a variety of euphausiids and hyperiids. Besides this common food basis their diets were complemented by squid, myctophid fishes and large nektonic crustaceans in the Blue Petrel, copepods in the Salvin's Prion and barnacle cypris larvae in the Fairy Prion. The three storm petrels displayed quite different food preferences with the Wilson's Storm Petrel *Oceanites oceanicus* preying on planktonic crustaceans, the Blackbellied Storm Petrel *Fregetta tropica* feeding on larger organisms and offal and the Greybacked Storm Petrel *Garrodia nereis* strictly specializing on cypris larvae of the southern barnacle *Lepas australis*. The only benthic diver of the community, the Imperial Cormorant *Phalacrocorax atriceps* preyed upon a wide array of demersal fishes (mainly the notothenioids *Lepidonotothen larseni*, *Paranotothenia magellanica*, *Dissostichus eleginoides*, *Notothenia acuta* and *Harpagifer* spp.) and invertebrates (the bivalve *Laternula elliptica*, the shrimp *Nauticaris marionis*, and several polychaetes). The presence of Antarctic Krill *Euphausia superba* in the diet of certain bird species, mainly the Lightmantled Sooty Albatross and the Whitechinned, Kerguelen and Blue Petrels, indicates southern feeding grounds and is in accordance with their known at-sea distributions. The amount of dietary overlap between bird species was investigated by using correspondence analysis on the importance by mass of every non-anecdotal prey species in the food of the birds, by calculating dietary overlap indices at the prey family level and by comparing prey size distributions. It has been observed that Crozet Island seabirds prey on a broader array of prey species than at higher latitudes, particularly at South Georgia where Antarctic Krill is the key species. Overlap indices were higher and prey size distributions were narrower and more similar within the diving guild (penguins, diving petrels and cormorant) than within the surface-feeding birds (albatrosses, petrels and storm petrels). Pairs or trios of congenerics displayed very high dietary similarity in terms of prey family and sizes. It is suggested that coexisting seabirds do not generally segregate by selecting certain prey species or sizes but that these two variables can express segregation mechanisms operating on other axes of the feeding niche, namely the feeding zones and habitats (spatial axis) and the breeding season (temporal axis). This study provides the basic dietary information for further studies of ecological segregation and role in the marine food web of the Crozet Island seabird community.

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INTRODUCTION

With 36 breeding species the Crozet Island seabird community is one of the most diversified in the world. Several groups of closely related species co-occur: four penguins, six species of albatrosses, four gadfly petrels, two prions and the Blue Petrel *Halobaena caerulea* and three storm petrels. Moreover, several pairs of sibling species also coexist: sooty albatrosses, giant petrels and diving petrels. In addition, in terms of food resources, there is no single micronektonic form that has such a key role in the epi- and mesopelagic food web around the Crozet Islands as does Antarctic Krill *Euphausia superba* at higher latitudes. This locality was thus considered as a ideal site for investigations of dietary segregation. Several comparative studies have been published on breeding cycles, behaviour, demography and at-sea distributions of Crozet seabirds (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). The present study was also designed with such comparisons in mind and describes the food of 27 seabird species, highlighting food partitioning within the whole community. Furthermore, this study provides detailed information to marine biologists interested in the epi- and mesopelagic food web around the Crozet Islands. Appendix 1 is designed so as to help the readers identify all the bird species that feed on a given prey taxa.

Previous accounts of the food of Crozet Island seabirds are mainly fragmentary and qualitative and came from works otherwise mostly dedicated to breeding biology. This paper reports on the food of the penguins (four species), albatrosses (six species), petrels (11 species), storm petrels (three species), diving petrels (two species) and cormorant (one species) breeding at the Crozet Islands. The diets of Kerguelen and Antarctic Terns *Sterna virgata* and *S. vittata*, Kelp Gull *Larus dominicanus* and Subantarctic Skua *Catharacta antarctica* have been studied using visual observations and/or analysis of pellets found at roosts and have been reported separately (Stahl & Weimerskirch 1981, Stahl & Mougin 1986a, b). The diets of the Kerguelen Pintail *Anas eatoni* and the Lesser Sheathbill *Chionis minor* are not considered here, since they have mostly terrestrial feeding habits.

In the species accounts section each seabird diet is successively detailed by prey occurrence, number, mass and body length, and the results compared to those obtained at other southern localities and discussed in terms of foraging methods and areas. The general discussion deals with food partitioning within the community. Appendix 1 allows the reader to find any information on the role of a given marine organism as a food resource for Crozet Island seabirds.

MATERIAL AND METHODS

Sampling

Stomach contents were collected at the Crozet Islands from breeding adults returning to the colonies or from recently fed chicks. Most albatrosses, petrels and storm petrels were sampled by spontaneous regurgitations as they were handled. Because some species regurgitated food as soon as they hit the mist-net, a plastic sheet was spread on the ground in order to collect the whole food load. Nevertheless, the extent to which spontaneous regurgitation provides the complete stomach contents is highly variable according to species (Schramm 1986, on gadfly petrels), chicks *vs* adults (Johnstone 1977, on giant petrels) or degree of stomach repletion (Duffy & Jackson 1986). Furthermore, penguins do not regurgitate at all. Therefore stomach flushing with water (Wilson 1984a, Offredo & Ridoux 1986) was used to collect samples from penguins and cormorants and to complete spontaneous regurgitations by albatrosses and petrels when needed. In accordance with the conclusions of Gales (1987), flushing was repeated until clear water and/or the presence of pebbles and squid beaks indicated complete stomach retrieval. For small species, the sampling method was modified by fitting a gastric sound onto a 250-ml syringe. Finally, South Georgia and Common Diving Petrels *Pelecanoides georgicus* and *P. urinatrix* could not be sampled by either regurgitation or flushing because of their tightly compacted stomach contents; both species were therefore stomach pumped through a gastric sound. Flushed samples were drained in the field and all samples were preserved in buffered formalin until sorting.

Sample processing

Fresh vs accumulated material

To avoid biases arising from differential retention times according to prey groups, quantitative analysis of the samples considered food items retained in the stomach for the same interval of time whatever prey type they belonged to. Thus only the fresh fraction, here called the food load, was quantitatively analysed. Hard-part remains provided additional information on squid and, to a lesser extent, fish species compositions but did not contribute to the overall number and mass analyses. To segregate between fresh and accumulated fractions the following criteria were used: any crustacean remain was considered in the food load except when the largest species (*Eurythenes gryllus, Pasiphaea longispina* and *Gnathophausia gigas*) occurred as small exoskeleton fragments which were believed to be mostly accumulated from previous meals; for fishes, all flesh remains as well as loose bones of smaller species (less than 100-mm Standard Length) were considered in the food load whereas loose bones of larger species and all loose otoliths were considered as accumulated items; cephalopod beaks in buccal masses were considered in the food load as were minute loose beaks (1-mm Lower Rostral Length or less), otherwise, loose beaks and gladii were considered as accumulated items.

Such a discrimination was defined somewhat subjectively as sorting was underway. However, there is reasonable agreement with the published data. Indeed, any remains of small fishes like pilchards or lantern fishes in seabird stomachs seem to disappear within a day or less (Furness *et al.* 1984, Jackson & Ryan 1986). School Whiting *Sillago bassensis* fed to various penguin species were found as loose vertebrae, otoliths and flesh fragments 16 h after the meal (Gales 1987). Eighty percent and 20% of krill eyes were still present after eight and 24 h, respectively, of digestion by Whitechinned Petrels (Jackson & Ryan 1986). In contrast, loose squid beaks were found in good condition 50 days after the last squid meal fed to a captive albatross (Furness *et al.* 1984) and three weeks in Whitechinned Petrels (Jackson & Ryan 1986). Finally, squid beaks were estimated to accumulate for as much as 170 to 230 days in stomachs of Wandering Albatross *Diomedea exulans* chicks (Clarke *et al.* 1981, Rodhouse *et al.* 1987). It thus appears that as far as fish and squid flesh and crustacean exoskeleton are concerned, retention times are of the same order of magnitude whereas squid beaks and, presumably, large fish bones, can accumulate for long periods.

Analysis by number

Prey number of a given taxon was generally estimated by counting diagnostic organs (crustacean heads or eyes, fish heads or caudal skeletons, squid buccal masses) throughout the whole food load. Nevertheless, subsampling was necessary for plankton- and micronekton-eating birds.

In planktivorous petrels (storm petrels, diving petrels, prions, Blue and Pintado Petrels) a Stempel pipette (a sub-sampling device used in planktonology) was used to take 5-ml subsamples from a homogeneous suspension of the food load of known total volume (sample + water volume = 250 ml). Prey items of a given taxon were counted in consecutive 5-ml subsamples (number of individuals in ith subsample was $n_{sp1,i}$; i=1 to x) until at least 30 items were encountered and total number N_{sp1} in the whole sample then extrapolated using:

$$N_{sp1} = (50/x) \text{ Sum } n_{sp1,i} \text{ (with Sum } n_{sp1,i} \geq 30) \qquad (1)$$

Such a sample splitter was not suitable for penguin stomach contents because of large sample and prey sizes. Consequently, numbers of abundant prey taxa in *Eudyptes* and *Pygoscelis* penguins were estimated from counts performed in quarter subsamples obtained with a Motoda Box (a sample splitter used in benthic ecology). Finally, King Penguin *Aptenodytes patagonicus* stomach contents were homogenized and split into 20-g subsamples from which numbers of the abundant prey taxa were estimated as in the Stempel pipette procedure, but replacing 50 in formula (1) by the number of 20-g subsamples obtained (i.e. drained sample mass divided by 20).

Prey sizes

Up to 30 length measurements per taxon and per sample were collected, both for prey size distribution analyses and original body mass calculations. Standard body lengths were measured on intact specimens and a diagnostic organ length (squid beaks, fish otoliths, jaws or caudal skeleton, crustaceans eyes or carapace) on damaged individuals. Measurements were as defined in Clarke (1986) for squid dorsal mantle length (DML) and lower rostral length (LRL), in Hecht (1987) for fish otolith length (OL) and in Fig. 1 for other diagnostic parts.

For food not occurring as discrete individuals (offal, some scavenged material) no length data could be obtained; consequently such material was weighed directly because recalculated individual biomass would have been meaningless.

Data processing

General

The number and mass analyses were performed on the food load excluding the accumulated fraction of the stomach content as defined above. For each sample-taxon, diagnostic organ lengths were converted into standard body lengths by using standard relationships. Then, both the converted lengths and the directly measured body lengths obtained from the rare intact specimens produced the length data set from which the corresponding prey body masses were computed. The contribution by mass of a prey taxon in a sample was then given by the number of individuals and the mean body mass of this taxon in the sample. For prey items obviously ingested in fragments the numbers are given in parentheses because they have less significance than for prey items swallowed whole (mostly in medium- to large-sized surface-feeding birds).

For every bird species, prey sizes are given as means ± standard deviation and ranges for each prey taxon. Additionally, an overall prey size distribution was also produced on a standardized logarithmic size scale allowing comparisons at the community level. For these histograms, all the prey species size distributions were summed after having been weighted according to the importance by number and by mass of each prey taxon considered (see examples in Fig. 2 and in each following species account).

Standard relationships

The equations used in this analytical procedure were those given by Clarke (1986 and other unpublished results) for relating squid LRL to DML and body mass and by Adams & Klages (1987), Brown & Klages (1987) and Hecht (1987) for the calculation of fish standard length and

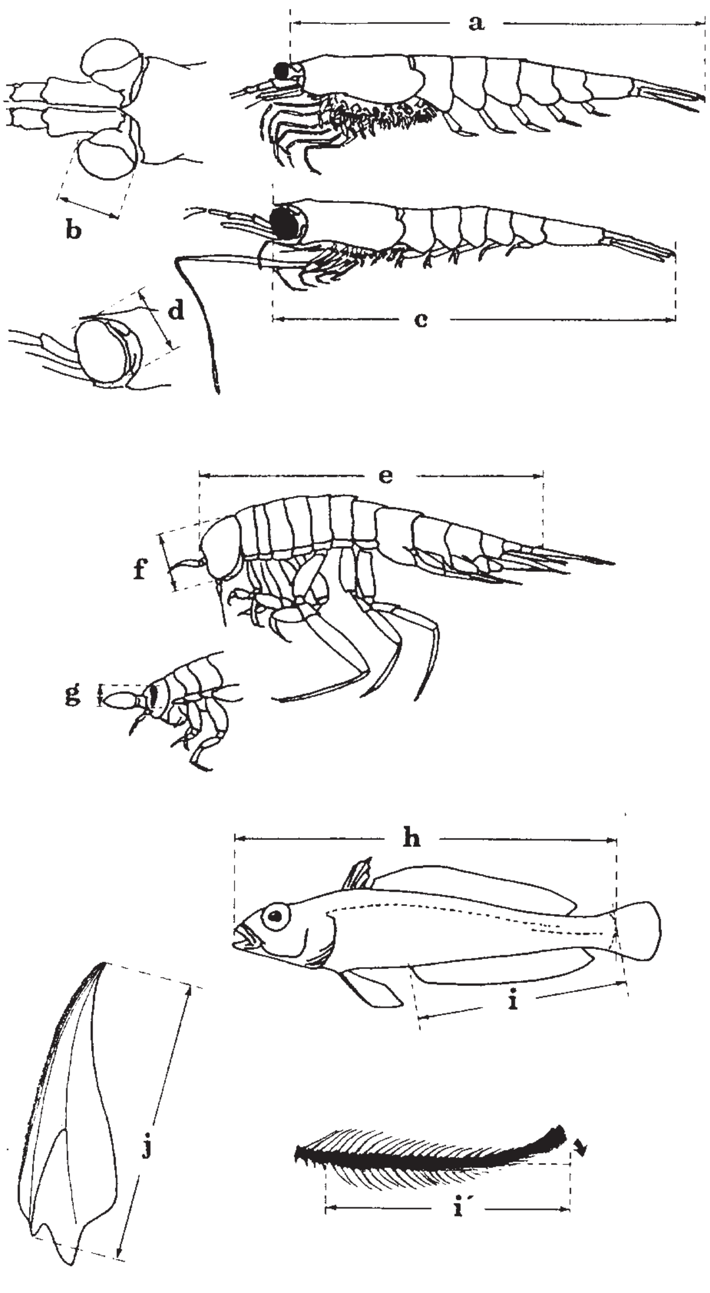

Figure 1

Standard measurements for fish and crustacean prey. **a** & **b**: body length and eye diameter of spheric-eyed euphausiids; **c** & **d**: body length and eye diameter of bilobed-eyed euphausiids; **e**: body length of amphipods; **f**: eye diameter of amphipods (*Vibilia* sp. excluded); **g**: eye diameter of *Vibilia* sp. **h** & **i**: standard and caudal length of fish; **i**: length of fish lower jaw (here, a myctophid jaw).

body mass from OL. For *Kondakovia longimana* less than 5.4-mm LRL the equation given by Adams & Brown (1987) was preferred to the one published in Clarke (1986) which in turn best fitted specimens larger than 5.4-mm LRL.

Otoliths were often dissolved by formalin (although buffered) and, consequently, alternative relationships had to be set up for various fish species from the measurements of other diagnostic parts (jaws or caudal skeletons). For most crustaceans preyed upon by seabirds at Crozet Islands no formulae for converting partial length measurements to total body length and mass exist. Therefore equations were developed from intact organisms found in the present collection of stomach samples. These specimens were blotted on tissue paper, weighed and measured for both standard and diagnostic organ lengths, prey from procellariiform seabirds being previously cleaned with a detergent in warm water to remove adhering oil and wax. When data were not obtained in sufficient numbers, only organ length/body length ratios and body mass/cubic body length ratios were calculated (assuming allometric growth); otherwise standard relationships were fitted (Appendix 2).

Species accounts

For every species studied the text gives a brief description of the samples, their general composition, the crustacean, fish and squid components of the diet and prey-size distributions. In addition, temporal variations in the diets of Macaroni *Eudyptes chrysolophus* and Gentoo *Pygoscelis papua* Penguins and the Imperial Cormorant *Phalacrocorax atriceps* are presented. Some details of foraging behaviour are given for the giant petrels *Macronectes* spp. and for the Imperial Cormorant.

Results are compared with data obtained at other localities, paying particular attention to how observed dietary variation fits prey-distribution patterns throughout the Southern Ocean. Results are then interpreted in the context of available information on foraging range and behaviour of the particular bird species and the known biological characteristics of its prey.

KING PENGUIN *APTENODYTES PATAGONICUS*

Results

Samples

Thirty-two stomach contents were flushed from adult King Penguins returning to the colony at Possession Island, Crozet Islands, during late chick rearing, incubation and early chick brooding. Ten samples were collected from 28 October to 7 November 1980, 13 from 12 to 27 December 1980 and nine in early February 1981. Four additional samples were obtained on 28 May 1982, at the beginning of the winter fasting period. The mean reconstituted mass of the samples was 277 ± 156 g (33 - 628 g).

General composition

These samples contained mostly myctophid fish with smaller amounts of juvenile squid. Fish was dominant both by number and reconstituted mass (Table 1). However, the winter samples had a markedly high squid content (48.4% mass) compared with the low levels in summer (4.8% mass in early November, n=13 samples; 0.4% in December, n=10; 0.2% in early February, n=9).

Crustaceans

The crustaceans found in the King Penguin food were planktonic and were most likely released in the penguin stomach contents as the fish were digested. Noteworthy are also 62 stalked parasitic copepods, *Sarcotretes* sp. known to be frequently hosted by myctophid fish (Z. Kabata pers. comm.) and numerous cirolanid isopods

TABLE 1

THE DIET OF THE KING PENGUIN AT THE CROZET ISLANDS (N=36)

Prey Species	Occurrence %	Relative abundance No.	Relative abundance %	Reconstituted mass (g)	Reconstituted mass %	Body length[a] (mm) Mean ± S.D.	(range)	n
CEPHALOPODS	**86.1**	**101**	**1.8**	**861.6**	**7.6**			
Teuthoidea								
Moroteuthis knipovitchi	8.3	34	0.6	495.4	4.4	44 ± 30	(7-97)	33
Kondakovia longimana	33.3	14	0.3	242.8	2.1	60 ± 45	(9-132)	14
Onychoteuthidae spp.	5.6	2	+	3.9	+	21	(15-26)	2
Pholidoteuthis sp.	5.6	2	+	9.0	0.1	63	(61-65)	2
Gonatus antarcticus	13.9	5	0.1	21.3	0.2	82 ± 5	(74-88)	4
Unidentified gonatids	38.9	34	0.6	28.3	0.2	24 ± 7	(15-45)	27
Alluroteuthis antarcticus	8.3	5	0.1	50.1	0.4	45	(23-67)	2
Galiteuthis glacialis	5.6	4	0.1	9.6	0.1	54		1
Oegopsid A[b]	2.8	1	+	1.2	+	45		1
FISH	**100.0**	**5417**	**98.2**	**10445.2**	**92.4**			
Aulopiformes								
Unidentified paralepidids	50.0	42	0.8	123.4	1.1	127 ± 20	(70-167)	31
Magnisudis sp.	2.8	1	+	108.0	1.0	200		1
Myctophiformes								
Electrona carlsbergi	80.6	562	10.2	4026.9	35.6	78 ± 6	(39- 89)	422
Krefftichthys anderssoni	80.6	2433	44.1	3228.1	28.6	44 ± 8	(26- 64)	519
Protomyctophum tenisoni	83.3	2282	41.4	2759.6	24.4	43 ± 4	(30- 62)	519
P. normani	2.8	1	+	2.4	+	56		1
Gymnoscopelus nicholsi	8.3	12	0.2	177.9	1.6	98 ± 30	(45-136)	12
Unidentified myctophids	11.1	80	1.4	+	+			
Perciformes								
Paradiplospinus gracilis	5.6	2	+	18.9	0.2	184	(182-186)	2
Unidentified	8.3	2	+	+	+			

[a] Dorsal Mantle Length in squid, total body length for the other prey taxa ; [b] as in Adams & Klages 1987

which are mobile ectoparasites on fish. None of these crustaceans can be considered as prey of the King Penguin.

Fish

Fish species were identified by examining the jaws. Identification was confirmed with the otoliths where possible (preservation in buffered formalin prevented use of otoliths alone as diagnostic organs).

Three species of fish, *Electrona carlsbergi*, *Protomyctophum tenisoni* and *Krefftichthys anderssoni*, occurred in nearly all samples and accounted for high percentages by number and mass (Table 1). *P. tenisoni* was the only *Protomyctophum* identified from otoliths. These three taxa were found from November to February even though *K. anderssoni* partly replaced *P. tenisoni* as summer progressed. The four winter samples mostly consisted of *P. tenisoni* and two of them also contained substantial numbers of the myctophid *Gymnoscopelus nicholsi*. *E. carlsbergi* was absent in these winter samples. The other fish taxa (Paralepididae, Gempylidae) were too rare to show any significant seasonal variation in their occurrence.

Cephalopods

Squid found with flesh mostly belonged to three taxa, *Kondakovia longimana*, *Moroteuthis knipovitchi* and unidentified gonatids (Table 1). All were juvenile individuals of very small to moderate body sizes. Accumulated loose beaks allowed several hundred additional identifications and indicated the same prevalence of *K. longimana* and *M. knipovitchi* (Table 2). However, species composition differed between fresh and accumulated material in several respects. The tiny beaks of the young gonatids were absent from the accumulated fraction even though this taxa was fairly abundant as fresh material. Conversely, two taxa regularly found as loose beaks, Oegopsid A and Onychoteuthid A, were virtually absent in the fresh fraction. The very small and nearly transparent beaks of the young gonatids presumably had a shorter retention time in the stomach than larger and thicker beaks and were therefore absent in the accumulated fraction. The occurrence of the latter two taxa in the accumulated fraction was more likely a consequence of short-term variations in prey species composition, these squids having been preyed upon some weeks prior to and not during the sampling period.

Prey sizes

The prey size distributions showed quite a broad range from 20 to 200 mm standard length in fish and up 132 mm DML in squid (i.e. about half the total length of the animal). However, the bulk of the food came from items 40-to-100 mm-long which provided less than 1 to 10 g of food per individual caught (Fig. 2). Mean individual body masses of the most important prey species were 1.4 g for *K. anderssoni*, 1.2 g for *P. tenisoni* and 7.2 g for *E. carlsbergi*. Modal body length of the main myctophid species did not show any seasonal change throughout the sampling period.

Comparison with previous studies

Until recently our knowledge of King Penguin diet was fragmentary and merely qualitative. The species was considered a squid specialist because of the occurrence of numerous squid beaks in many stomachs otherwise empty of any fresh remains (Stonehouse 1960, Barrat 1976). A few nototheniid fish found on the ground in a colony were the only evidence of fish prey (Stonehouse 1960). From these qualitative data and other unpublished observations, squid were estimated to account for 70-90% by mass of the King Penguin diet at South Georgia, the remaining being fish (Croxall & Prince 1980b, 1982a). From the examination of the beaks, squid were reported as

TABLE 2

SUMMARY OF ACCUMULATED ITEMS IN KING PENGUIN STOMACH CONTENTS (N=36)

Items	Number of items	Measurements (mm)[a]			Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean ± S.D.	(range)	n	Mean	(range)	Mean	(range)
CEPHALOPODS								
Lower beaks	570							
Todarodes filippovae	1							
Onychoteuthis sp. A	73	5.0 ± 0.6	(3.8-5.9)	22	174	(88-248)	270.5	(100-467)
Moroteuthis knipovitchi	153	3.4 ± 1.3	(0.9-5.9)	113	(c)		117.5	(0.5-480)
Kondakovia longimana	83	3.9 ± 1.4	(1.2-8.0)	71	170	(47-349)	151.1	(3-904)
Unidentified gonatids	1	2.9		1	81		18.0	
Unidentified psychroteuthids	1	2.3		1	(c)		5.0	
Alluroteuthis antarcticus	2	2.8		1	79		35.5	
Taonius/Megalocranchia	7							
Teuthowenia pellucida	1	2.0		1	92		9.9	
Mesonychoteuthis hamiltoni	1	8.8		1	369		331.5	
Oegopsid A[d]	35	2.1 ± 0.3	(2.1-2.9)	25	120	(98-131)	20.8	(12-25)
Unidentified octopods	1							
Eroded beaks	211							

[a] Lower Rostral Length
[b] Dorsal Mantle Length
[c] available relationships inadequate for young specimens
[d] as in Adams & Klages 1987

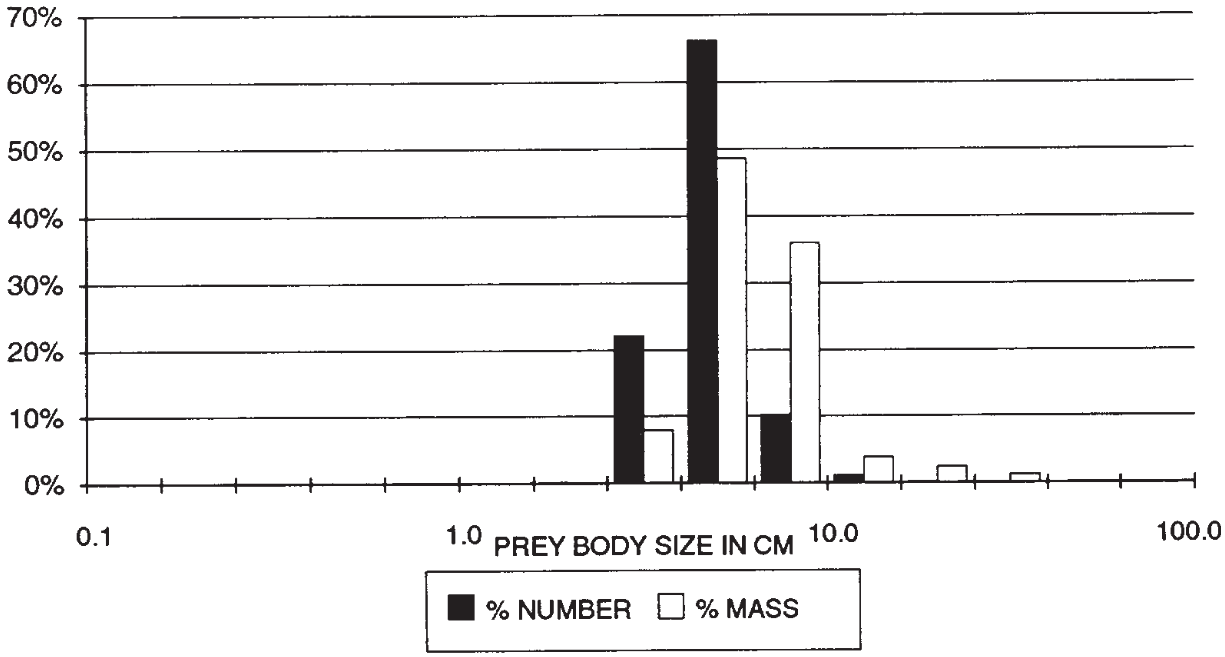

Figure 2

Prey-size distribution in the diet of the King Penguin.

420g-mean-body-mass *Todarodes aff. sagittatus* (M.R. Clarke, cited in Croxall & Lishman 1987).

From 1987 onwards, several studies have considerably changed these ideas. Indeed, studies undertaken at four localities in the Indian Ocean have described a consistent fish diet with small myctophids accounting for the bulk of the food (Table 3). The results obtained at the three northernmost localities are highly similar either in terms of general composition, prey species or prey sizes (Table 4). They show an overwhelming dominance of two to three myctophid species, *E. carlsbergi*, *P. tenisoni* and *K. anderssoni*, widely distributed throughout the Southern Ocean from south of the Antarctic Convergence to the Subtropical Convergence (Hulley 1981). The main differences between these localities relate largely to the higher prey diversity found at Crozet and Marion Islands (eight and 10 fish taxa respectively and 13 squid taxa largely overlapping between both localities) than at Macquarie Island (six fish and two squid taxa), and some discrepancies in seasonal patterns of occurrence. Adult *E. carlsbergi* were only preyed upon in winter at Macquarie Island. By contrast, both *E. carlsbergi* and *K. anderssoni* were eaten in summer at the Crozet Islands, *E. carlsbergi* being absent in winter. *K. anderssoni* peaked in spring at Marion Island and *E. carlsbergi* in summer.

Unique to Heard Island, the southernmost breeding locality, was the presence of a channichthyid fish *Champsocephalus gunnari* in the diet of the King Penguin. This prey species occurred in 25% of the samples and its high individual body mass (35.6 *vs* 8.1 and 1.9 g for *E. carlsbergi* and *K. anderssoni*, respectively; Klages *et al.* 1990) might compensate for its low importance by numbers. This discrepancy with the other localities studied accords well with the distribution of *C. gunnari*. The fish is abundant on the continental shelf of Heard-MacDonald but is absent north of the Kerguelen Islands (Fischer & Hureau 1985). Important local spawning grounds provide the penguins with numerous small pelagic fishes that switch later to a more demersal adult life style (Gon & Heemstra 1990). These pelagic shoaling fish are likely to display quite a similar "prey profile" to myctophids. The Macaroni Penguin *Eudyptes chrysolophus* which is partly a myctophid-eating penguin in the Indian Ocean (Cooper *et al.* 1990) also preys on young *C. gunnari* at Heard Island (Klages *et al.* 1989).

Foraging range and behaviour

The King Penguin occurs in subantarctic as well as ice-free antarctic waters (Ainley & Boekelheide 1983). In the Indian Ocean the species ranges from 43° to 54°S (Stahl 1987) and reaches 62°S in the Ross Sea (Ainley *et al.* 1984).

From data obtained at Marion Island (Adams 1987), average maximum foraging range of breeding King Penguins should not exceed 300 km and the actual foraging range was predicted to be 175 km when allowance is made for distance swum vertically during diving and for zigzag rather than straight line travelling (Wilson *et al.* 1989). Recently birds fitted with diving recorders were estimated to start feeding activity at an average of 28 km from their colony at Ile de la Possession (Kooyman *et al.* 1992). All these data indicate that they could easily reach oceanic waters beyond the continental slope but they probably do not feed as far north as the convergence zone located some 300 km north of the Crozets. Consistent with this, their major prey species, *K. anderssoni*, *E. carlsbergi*, *P. tenisoni* and *G. nicholsi*, belong to the broadly antarctic mesopelagic myctophid community (Hulley 1981) whereas the subantarctic and convergence zone species assemblages are only represented in the current study by a few *Protomyctophum normani/luciferum* and *Electrona subaspera*. Furthermore, the three major prey species are known to live at deeper depths in the northern part of their range since they are associated with cold water masses which flow in depth at low latitudes. They are usually caught within a few hundred metres from the surface south of the

TABLE 3

KING PENGUIN DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in brackets)				References
	Crustaceans	Myctophids	Other fish	Squid	
Marion Island (46S)	+	86.0 (1,2,3)	0.5 (5)	13.5 (8)	Adams & Klages 1987
Crozet Islands summer 1981(46S)		90.1 (1,2,3)	2.3 (5)	7.6 (8,9)	(this work)
Crozet Islands summer 1989 (46S)		89.3 (1,3)	10.6 (7)	0.1	Cherel & Ridoux 1992
Heard Island (53S)	+	------- 99.4 (1,3,4) ---------		0.6 (8)	Klages *et al.* 1990
Macquarie Island (54S)		92.2 (1,3)	5.7 (6)	2.2 (9)	Hindell 1988

The main prey species are: (1) *Krefftichthys anderssoni*, (2) *Protomyctophum tenisoni*, (3) *Electrona carlsbergi*, (4) *Champsocephalus gunnari*, (5) small paralepidids, (6) *Magnisudis prionosa*, (7) *Paradiplospinus gracilis*, (8) *Kondakovia longimana*, (9) *Moroteuthis* spp.

TABLE 4

ESTIMATED BODY SIZES OF MAJOR PREY SPECIES IN THE KING PENGUIN DIET AT VARIOUS LOCALITIES

Prey species and localities	Estimated body sizes (mm)		
	Mean ± S.D.	(range)	n
Krefftichthys anderssoni			
Marion	48 ± 10	(11 - 92)	2980
Crozets	44 ± 8	(26 - 64)	519
Macquarie	55	(19 - 80)	353
Heard	49 ± 10	(22 - 70)	442
Electrona carlsbergi			
Marion	82 ± 6	(17 - 101)	1332
Crozets	78 ± 6	(39 - 89)	422
Macquarie	76	(20 -120)	148
Heard	81 ± 9	(63 - 93)	28
Champsocephalus gunnari			
Heard	142 ± 27	(59 - 203)	51
Kondakovia longimana			
Marion	73 ± 26	(45 -273)	933
Crozets	109	(31 - 237)	18
Heard	78		1

Standard Length in fish, Dorsal Mantle Length in squid

References: Adams & Klages 1987, Hindell 1988a, Klages *et al.* 1990, present work latitude of the Crozet Islands whereas they live at 1000 m or deeper in the convergence zone (Hulley 1981). Consequently, they are more likely to be within the foraging depth of the King Penguin around and south of the islands than to the north of them.

The maximum recorded diving depths of King Penguins are second only to Emperor Penguins, *A. forsteri* (Kooyman & Davis 1987). Among 2595 dives by King Penguins recorded around South Georgia, 50% were below 50 m with a maximum at 240 m (Kooyman *et al.* 1982). Recently, King Penguins at the Crozet Islands have been shown to forage routinely between 100 and 300 m by repeated six to seven-minute dives separated by one to two-minute rests at the surface (Kooyman *et al.* 1992). At this locality prey mean body mass was 2.2 g (*K. anderssoni*: 1.4 g; *P. tenisoni*: 1.2 g; *E. carlsbergi*: 7.2 g), compared to 3.4 and 4.2 g at Marion and Macquarie Islands, respectively (Adams & Klages 1987, Hindell 1988). Assuming that their daily food requirements were 2.2 kg of myctophid fish and that they perform 100 to 170 dives per day (Kooyman *et al.* 1992), Crozet Island King Penguins must catch on average six to 10 mean prey individuals per dive or 1.8 to 3.1 *E. carlsbergi* per dive on average. Their major prey species are known to congregate in dense schools; particularly *E. carlsbergi* which constitutes the bulk of the Deep Scattering Layer in the Southern Pacific Ocean where it reaches densities as high as 0.2 to 0.4 individuals per cubic metre (Linkowski 1983). Assuming an arbitrary prey detection radius of one metre, an individual king penguin would find 6.3 to 12.6 *E. carlsbergi* per 10 m swum through the DSL or through any fish school of similar density. If a flat bottom part of a dive profile is an indication that feeding is underway (Kooyman *et al.* 1992) then 120 m (1 minute mean bottom time and 2 $m.s^{-1}$ swim speed) are swum per dive through a fish school thus allowing 76 to 151 *E. carlsbergi* to be detected. A 1.3 to 4.0% catching rate would allow the penguin to meet its energy requirements. Although this gross simulation is very speculative it suggests that the foraging behaviour of the King Penguin is mostly comparable to that of the plankton-eating penguins. These penguins also have to catch their prey at high rate per dive (Croxall & Lishman 1987, Croxall & Davis 1990) but only at a low rate per individual prey detected since they feed on abundant species living in predictable dense swarms. Such a feeding strategy contrasts with the one described for the King Penguin in South Georgia (see above) and with the occurrence of large squid beaks in the current samples. The degree of feeding behaviour plasticity should be investigated by simultaneous studies on the diet of individual birds of known status, their foraging behaviour and the availability of food resources.

MACARONI PENGUIN *EUDYPTES CHRYSOLOPHUS*

Results

Samples

The contents of 30 stomachs of Macaroni Penguins were collected in summer 1980-81 using the water-flushing method on adults returning to the colony at Possession Island, Crozet Islands. Three sets of 10 samples were collected corresponding to the incubation period, the early chick rearing and the crèche stage. The mean reconstituted mass of the samples was 126 ± 107 g and showed a marked increase during the sampling period (27 ± 27 g in November, 159 ± 119 g in December and 192 ± 78 g in January).

General composition

The food of the Macaroni Penguin consisted mainly of planktonic crustaceans (95.4% by number, 59.4% by reconstituted mass), with fish (28.0% by mass) and, to a lesser extent, squid (12.1% by mass) making up the remainder of the diet (Table 5). From an almost exclusively

TABLE 5

THE DIET OF THE MACARONI PENGUIN AT THE CROZET ISLANDS (N=30)

Prey Species	Occurrence %	Relative abundance No.	Relative abundance %	Reconstituted mass (g)	Reconstituted mass %	Body length[a] (mm) Mean ± S.D.	(range)	n
CRUSTACEANS	**100**	**42351**	**95.4**	**2571.4**	**60.9**			
Copepods								
Unidentified calanoids	6.7	6	+	+	+	6 ± 1	(4-8)	3
Hyperiid amphipods								
Cyllopus lucasii	6.7	2	+	0.1	+	11		1
Primno macropa	53.3	776	1.7	57.7	1.3	12 ± 3	(6-16)	21
Themisto gaudichaudii	100.0	11107	25.0	802.2	19.0	15 ± 3	(4-23)	384
Hyperiella antarctica	6.7	3	+	+	+	7		1
Hyperia (?galba)	6.7	3	+	0.8	+	18 ± 2	(16-20)	3
Hyperoche sp.	10.0	52	0.1	1.0	+	14 ± 2	(10-17)	11
Unidentified	10.0	3	+	+	+			
Gammarid amphipods								
Unidentified	3.3	1	+	+	+			
Euphausiids								
Euphausia vallentini	90.0	25056	56.5	1608.4	38.1	22 ± 3	(10-26)	391
Thysanoessa macrura/vicina	30.0	3025	6.8	33.7	0.8	14 ± 3	(8-19)	44
T. vicina	33.3	990	2.2	12.6	0.3	14 ± 1	(11-17)	42
T. macrura	40.0	903	2.0	35.9	0.8	18 ± 2	(12-22)	85
Stylocheiron abbreviatum	13.3	418	0.9	14.8	0.3	19 ± 2	(15-24)	17
Decapods								
Caridea larvae	13.3	3	+	2.0	0.1	24		1
Hoplophorid larvae	6.7	3	+	2.2	0.1	47	(44-50)	2
CEPHALOPODS	**80.0**	**425**	**1.0**	**415.2**	**9.8**			
Teuthoidea								
Kondakovia longimana	36.7	19	+	298.6	7.1	69	(11-127)	2
Pholidoteuthis sp.	3.3	1	+	14.7	0.3	77		1
Brachioteuthis sp.A	26.7	47	0.1	4.5	0.1	21 ± 2	(18-26)	14

Unidentified gonatids	70.0	347	0.8	69.4	1.6	31	(5-56)	2
Alluroteuthis antarcticus	10.0	7	+	11.9	0.3	21 ± 8	(13-36)	7
Octopoda								
Unidentified octopodids	3.3	2	+	6.4	0.2			
Argonauta argo	6.7	2	+	9.7	0.2			
FISH	**80.0**	**1580**	**3.6**	**1212.8**	**28.7**			
Aulopiformes								
Notolepis sp.	6.7	2	+	5.2	0.1	124	(122-126)	2
Paralepidid post-larvae	16.7	10	+	0.5	+	34 ± 4	(30-40)	6
Myctophiformes								
Electrona carlsbergi	20.0	51	0.1	348.1	8.2	76 ± 8	(49-90)	33
Krefftichthys anderssoni	40.0	524	1.2	781.1	18.5	46 ± 10	(28-78)	122
Protomyctophum tenisoni	6.7	13	+	20.9	0.5	47 ± 4	(43-59)	11
P. normani	3.3	1	+	4.1	0.1	68		1
Myctophid post-larvae	23.3	508	1.1	25.6	0.6	16 ± 2	(14-20)	9
Perciformes								
Lepidonotothen larseni	3.3	1	+	1.6	+	52		1
Nototheniid post-larvae	16.7	262	0.6	15.6	0.4	19 ± 4	(15-35)	23
Harpagiferid post-larvae	3.3	8	+	0.3	+	15		1
Unidentified	10.0	200	0.5	9.8	0.2			
OTHER ORGANISMS	**56.7**	**18**	**+**	**20.0**	**0.5**			
Chaetognaths								
Sagitta gazellae	3.3	1	+	+	+	22		1
Unidentified	56.7	17	+	20.0	0.5			

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

crustacean diet during the incubation and the early chick-rearing periods, Macaroni Penguins shifted to a more catholic diet in January during the crèche stage (Table 6).

Crustaceans

The main crustacean species were the euphausiid *Euphausia vallentini* and the hyperiid amphipod *Themisto gaudichaudii*. Fourteen other taxa of minor importance were also recorded (Table 5). *T. gaudichaudii* dominated the diet at the beginning of the sampling period (49.5% by mass in November and 30% in late December) and fell to a lower proportion during the crèche stage (10.3% by mass in late January). *E. vallentini* accounted for 36.9, 42.8 and 42.1% by mass, respectively, during these three periods. *Thysanoessa* spp. and *Stylocheiron abbreviatum* accounted for more than 10% by mass in only 3 samples out of 30 and for trace amounts in the others.

Fish

Myctophid and non-myctophid species occurred in very similar proportions in November (4.5 and 4.3%, respectively) but the former, mainly *Krefftichthys anderssoni* and *Electrona carlsbergi*, reached much higher percentages later in the season (16.5% in December, 39.6% by late January) while non-myctophid taxa virtually disappeared.

Cephalopods

The most numerous cephalopods were tiny gonatid squids less than 0.2 g individual body mass. However, *Kondakovia longimana* accounted for the bulk of the cephalopod fraction by mass due to its larger body size (Table 5). The examination of accumulated squid material (Table 7) led to similar conclusions. The smaller proportion of the mostly transparent gonatid beaks in this fraction probably reflects their shorter retention time in the stomach. No seasonal trend was evident in the occurrence of these taxa throughout the sampling period.

Prey sizes

Prey sizes ranged from 4 to 126 mm; however, most of the prey were between 10 and 50 mm long and their body mass ranged from *c.* 0.05 to 2.0 g (Fig. 3). The mean body mass of the three most important prey species *K. anderssoni*, *E. vallentini* and *T. gaudichaudii* were 1.6, 0.06 and 0.07 g, respectively.

Comparison with previous studies

The prevalence of planktonic crustaceans in the food of the Macaroni Penguin (including the Royal Penguin *E. schlegeli*) has long been reported (see a synthesis in Appendix 1 of Cooper *et al.* 1990). The often enormous concentrations of Macaroni/Royal Penguins at various breeding localities have motivated a number of quantitative dietary studies aimed at assessing their role in the marine food web (Table 8). These studies have confirmed the key role of euphausiid crustaceans in their food at two Atlantic localities where Antarctic Krill is highly abundant (e.g. Hampton 1983, Fischer & Hureau, 1985 for krill distribution). In the Indian sector of the Southern Ocean, this large krill species does not occur at such an abundance in the vicinity of the main breeding grounds of Macaroni/Royal Penguins and no alternative single species of the micronektonic community dominates the pelagic ecosystem. Consequently, Indian Ocean Macaroni Penguins show a more catholic diet with a variety of micronektonic forms (10-to-100 mm organisms). Prey include widely distributed species such as *E. vallentini*, *Thysanoessa macrura*, *T. gaudichaudii*, *K. anderssoni* and *Protomyctophum tenisoni*, found from the convergence zone south to the limit of the East-Wind Drift (prey species distributions in Baker 1965, Kane 1966, Nemoto & Yoo 1970, Casanova 1980, Hulley 1981, Fischer & Hureau 1985). These species are abundant prey items for

TABLE 6

TEMPORAL VARIATIONS IN THE DIET OF THE MACARONI PENGUIN DURING THE BREEDING SEASON

Periods	Diet (% by reconstituted mass)				Number of samples
	Crustaceans	Fish	Cephalopods	Others	
Incubation	88.0	8.9	3.1	+	10
Chick brooding	77.5	17.5	5.0	+	10
Crèche	58.4	39.8	1.8	+	10

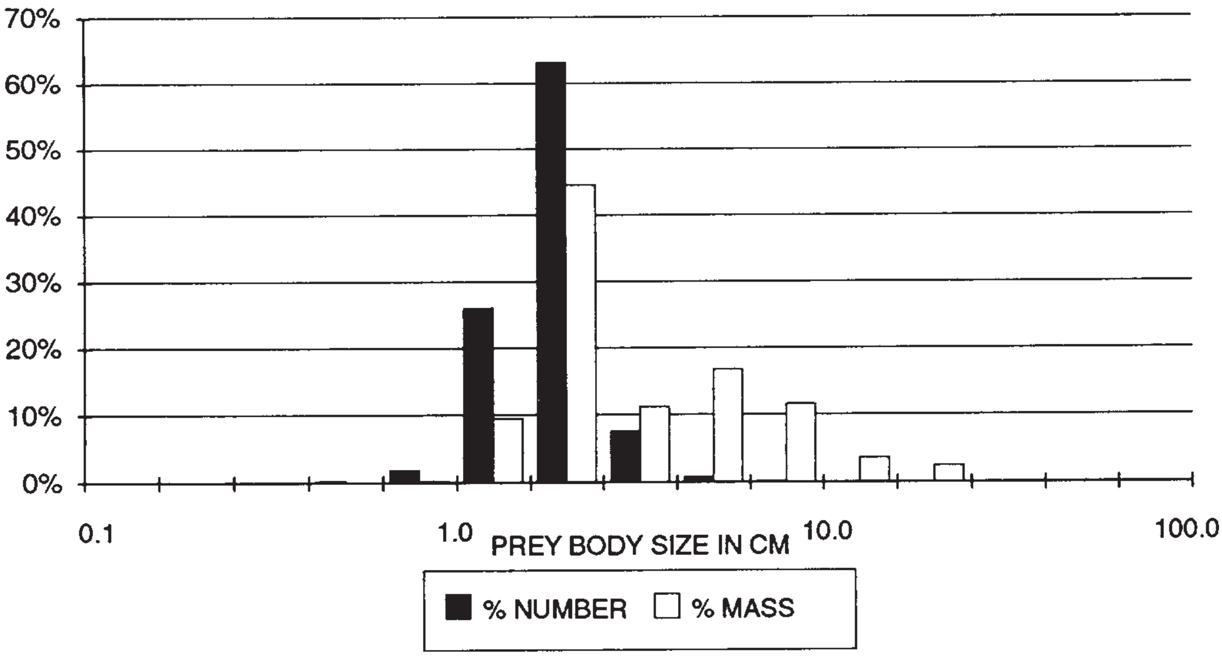

Figure 3

Prey-size distribution in the diet of the Macaroni Penguin.

TABLE 7

SUMMARY OF ACCUMULATED ITEMS IN MACARONI PENGUIN STOMACH CONTENTS (N = 30)

Items	Number of items	Measurements (mm)[a]			Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean ± S.D.	(range)	n	Mean	(range)	Mean	(range)
CEPHALOPODS								
Lower beaks	75							
Moroteuthis knipovitchi	2	2.2	(1.6-2.8)	2	c		19.6	(4.8-34.3)
Kondakovia longimana	19	2.0 ± 0.9	(0.7-4.3)	19	85	(27-185)	25.6	(0.7-142.0)
Brachioteuthis sp.	4	0.5	(0.4-0.5)	4	26	(25-27)	0.6	(0.5-0.7)
Gonatidae spp.	43	0.8 ± 0.2	(0.5-1.3)	43	c		0.3	(0.1-1.3)
Gonatus antarcticus	1	1.3		1	11		1.1	
Alluroteuthis antarcticus	6	0.8 ± 0.3	(0.4-1.5)	6	23	(12-40)	2.0	(0.3-6.6)

[a] Lower Rostral Length in squid
[b] Dorsal Mantle Length in squid
[c] available relationships inadequate for young specimens

TABLE 8

MACARONI/ROYAL PENGUIN DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in parentheses)					References
	Euphausiids	Other crustaceans	Fish	Squid	Other food types	
	Eudyptes (chrysolophus) chrysolophus, Atlantic sector					
South Georgia (54S)	95-98 (1)	+	2-5			Croxall & Prince 1980
South Shetland (62S)	75.0 (1,3)		25.0			Croxall & Furse 1980
	Eudyptes (chrysolophus) chrysolophus, Indian sector					
Marion Island (46S)	------- 70 (2,5,6) -------		18 (8)	12 (12)		Brown & Klages 1987
Crozet Islands (46S)	40.4 (2)	20.5 (6)	28.7 (9)	9.8 (12,13)	0.5	(this work)
Heard Island (53S)	------- 76.8 (2,3,6) -------		23.2 (9,11)	+		Klages *et al.* 1989
	Eudyptes (chrysolophus) schlegeli					
Macquarie Island (54S)	14.5 (2,4)	4.3 (6,7)	58.0 (9)	23.2		Horne 1985[a]
Macquarie Island (54S)	51.3 (2,4)		45.7 (9,10)	3.0 (14)		Hindell 1989

The main prey species are: (1) *Euphausia superba*, (2) *E. vallentini*, (3) *Thysanoessa macrura*, (4) *T. gregaria*, (5) *Nauticaris marionis*, (6) *Themisto gaudichaudii*, (7) *Primno macropa*, (8) *Protomyctophum tenisoni*, (9) *Krefftichthys anderssoni*, (10) *Electrona carlsbergi*, (11) *Champsocephalus gunnari*, (12) *Kondakovia longimana*, (13) gonatids, (14) *Martialia hyadesi*

[a] the squid component of the diet is calculated here as the complement of the crustacean and fish fractions since the author did not give the squid percent by mass

Macaroni Penguins at most localities in the Indian sector, as well as the locally important predatory fish *Champsocephalus gunnari* at Heard Island.

Beyond the taxonomic diversity described above, these major prey species share several important features defining their prey profile: moderate to small size (*c.* 20 to 120 mm body length), living in dense swarms, present within 100 m or less from the surface.

Foraging range and behaviour

The at-sea distribution of Macaroni Penguins is poorly known. In the Indian sector of the Southern Ocean the species has been observed from 45° to 56°S in both shelf and oceanic regions (Stahl 1987). The maximum foraging range has been estimated using feeding frequency (or measured time spent at sea) and swim speed data plus various assumed correction factors to be 60-100 km around South Georgia (Croxall *et al.* 1984), and 95 km (Williams & Siegfried 1980) or 59 to 303 km around Marion Island (data from five birds fitted with speed meters, swim speed = 7.5 km/h, Brown 1987). Similar estimations performed from data obtained at Ile de l'Est, Crozet Islands, gave a maximum foraging range of 215 km from the colony (swim speed 5.2 km/h, mean feeding trip 3.45 days; Stahl *et al.* 1985). However, observations at sea have shown that Crozet breeding birds mostly forage in shelf and slope habitats within 30-50 km of the coasts (Stahl *et al.* 1985a, Ridoux *et al.* 1988). Little is known of the composition of the micronektonic community over the shelf and slope compared to that of oceanic areas around the Crozet Islands. However, as far as crustacean species are concerned, the food of the Macaroni Penguin is similar to that of other shelf predators such as Salvin's Prion, *Pachyptila salvini* and the diving-petrels *Pelecanoides* spp. (see relevant sections in this study). On the other hand the myctophids *K. anderssoni* and *E. carlsbergi* are ubiquitous species in the area reaching, at least by night, the 100 m surface layer where sea surface temperature is below 5° to 6C (Hulley 1981, Gon & Heemstra 1990). The former species is also reported from the upper water layer over submarine seamounts (Lubimova *et al.* 1983, *in litt.*) and is a prey of the neritic channichthyid *Champsocephalus gunnari* (Duhamel & Hureau 1982) thus indicating that it also occurs in neritic habitats.

The diving performances of Macaroni Penguins have been recently investigated in South Georgia and displayed clear-cut day-night variations related to the nycthemeral vertical migration of Antarctic Krill, with shallow dives at night (*c.* 20 m) and deep dives during the day (down to 100 m; Croxall *et al.* 1988). All the species recorded in its food are known to occur within these depths. The Macaroni Penguin was estimated to need adult Antarctic Krill swarms of density no less than 9-22 individuals per cubic metres to meet its own and chick energy requirements (Croxall & Davis 1990). Relying on the smaller *Euphausia vallentini* (mean body mass 0.06 g) and *Themisto gaudichaudii* (mean body mass 0.07 g) around the Crozet Islands, Macaroni Penguins would need swarm densities about 20 times higher. By contrast, bird feeding on the myctophid *K. anderssoni* (mean body mass 1.6 g) of higher energetic value (7.0 kJ/g , Clarke & Prince 1980, Cherel & Ridoux 1992) would necessitate much lower shoal density.

SOUTHERN ROCKHOPPER PENGUIN *EUDYPTES CHRYSOCOME CHRYSOCOME*

Results

Samples

Seventeen stomach contents were collected, using the water-flushing method, from adult birds returning to the colony between 30 November 1980 and 31 January 1981, 14 of which were obtained in January during the chick-brooding period. The mean reconstituted mass of the samples was 64 ± 71 g (3 - 268 g).

General composition

The food of the Rockhopper Penguin was dominated by planktonic crustaceans (98.4% by number, 73.1% by reconstituted mass), mainly euphausiids. Fish and squid only accounted for small proportions of the diet (Table 9). On an individual basis, 14 samples were constituted of >50% crustaceans. Two samples were predominantly fish, and only one predominantly squid.

Crustaceans

The dominant species was *Euphausia vallentini* which appeared in every sample but one and accounted for >50% reconstituted mass in 12 out of 17 samples. Ten additional crustacean taxa were recorded of which only *Themisto gaudichaudii* and *Thysanoessa macrura/vicina* contributed substantially to any single sample.

Cephalopods

The most abundant cephalopod was the same post-larval gonatid squid as were found in the Macaroni Penguin samples, accounting for as much as 43.9 and 47.9% by mass in two samples. Although it was much less numerous, the cranchiid *Galiteuthis/Teuthowenia* constituted the bulk of the cephalopod fraction by mass throughout the collection due to its larger body size (Table 9).

Fish

Myctophids, mainly *Krefftichthys anderssoni*, represented the major part of the fish fraction by number and by reconstituted mass (Table 9). Other families were of minor importance.

Prey sizes

The prey ranged in size from 9 mm-long *Thysanoessa vicina* to a 147 mm-long *Paradiplospinus gracilis* and a 78 mm-DML *K. longimana* (total length about twice as much as DML). These extreme values are far out of the normal size range because 95% of the prey individuals were within 10 to 60 mm body length (Fig. 4), which represents *c.* 0.02 to 3.0 g food intake per individual prey caught. Mean body mass of the two most important prey species, *K. anderssoni* and *E. vallentini*, which accounted together for as much as 75% by mass, were 1.7 and 0.04 g, respectively.

Comparison with previous studies

Numerous reports have already highlighted the importance of pelagic crustaceans in the diet of Rockhopper Penguins (synthesis in Appendix 1 of *Cooper et al.* 1990). Recently, much effort have been devoted to the quantification of the Rockhopper Penguin's diet in localities where it is particularly abundant and/or where it breeds sympatrically with Macaroni/Royal Penguins (Table 10). It appears that pelagic crustaceans, mostly euphausiids, form the basis of its food at most localities, ranging from 70 to 92% by mass. However, at Beauchêne Island, Falkland Islands, juvenile squid *Illex argentinus* accounted for 53% by mass of its food. The main species preyed upon at each site concord well with the known distribution of euphausiids in the Southern Ocean: *Euphausia lucens* and *Thysanoessa gregaria* at and north of the Antarctic Convergence and *E. vallentini* and *T. macrura/vicina* at and south of it (e.g. Baker 1965, Casanova 1980, Fischer & Hureau 1985 for euphausiid distributions). In the Indian sector, squid, myctophids and juvenile nototheniids provide a significant proportion of the diet, matching the general distribution patterns of these prey groups. The importance of the post-larval ommastrephid *I. argentinus* in the food of Rockhopper Penguins at Beauchêne Island is consistent with the abundance of this squid on the Patagonian shelf where it is the target species of an extensive fishery. Experimental catches

TABLE 9

THE DIET OF THE ROCKHOPPER PENGUIN AT THE CROZET ISLANDS (N=17)

Prey Species	Occurrence %	Relative abundance No.	Relative abundance %	Reconstituted mass (g)	Reconstituted mass %	Body length[a] (mm) Mean ± S.D.	(range)	n
CRUSTACEANS	**100**	**25258**	**98.4**	**879.5**	**71.3**			
Copepods								
Unidentified calanoids	5.9	1	+	+	+	7		1
Cirripeds								
Lepas australis	5.9	1	+	+	+	6		1
Hyperiid amphipods								
Primno macropa	41.2	29	0.1	2.5	0.2	14 ± 1	(12-15)	7
Themisto gaudichaudii	64.1	172	0.7	26.7	2.2	19 ± 6	(10-28)	24
Unidentified	17.6	3	+	+	+			
Isopods								
Serolis latifrons	5.9	2	+	0.3	+	12		1
Unidentified	5.9	7	+	+	+			
Euphausiids								
Euphausia vallentini	94.1	18838	73.5	797.5	64.6	18 ± 4	(9-25)	313
Thysanoessa macrura/vicina	58.8	3655	14.3	29.0	2.3	13 ± 3	(7-18)	46
T. vicina	17.6	2440	9.5	19.6	1.6	13 ± 2	(9-17)	24
T. gregaria	11.8	110	0.4	3.9	0.3	18 ± 2	(16-20)	10
CEPHALOPODS	**76.5**	**281**	**1.0**	**212.6**	**17.2**			
Teuthoidea								
Kondakovia longimana	5.9	1	+	12.3	1.0	49		1
Unidentified onychoteuthids	5.9	1	+	0.5	+	22		1
Pholidoteuthis sp.	11.8	2	+	17.6	1.5	73	(64-81)	2
Brachioteuthis sp.A	11.8	9	+	3.6	0.3	23	(20-25)	6
Unidentified gonatids	35.3	237	0.9	49.5	4.0	33	(5-60)	2
Alluroteuthis antarcticus	11.8	2	+	3.2	0.3	23	(18-27)	2
Galiteuthis/Teuthowenia	35.3	25	0.1	112.1	9.1	63	(39-122)	23
Octopoda								

Argonauta argo	17.6	4	+	13.8	1.1			
FISH	**76.5**	**100**	**0.4**	**141.2**	**11.4**			
Aulopiformes								
Notolepis sp.	5.9	2	+	4.9	0.4	122		1
Myctophiformes								
Krefftichthys anderssoni	29.4	70	0.3	128.1	10.4	50 ± 7	(34-60)	46
Myctophid post-larvae	5.9	8	+	0.8	0.1	20 ± 2	(17-25)	8
Perciformes								
Paranotothenia magellanica	5.9	1	+	1.5	0.1	45		1
Paradiplospinus gracilis	5.9	1	+	4.3	0.4	147		1
Unidentified	47.1	18	0.1	1.6	0.1	15		1
OTHER ORGANISMS	**23.5**	**5**	**+**	**1.3**	**0.1**			
Chaetognaths								
Sagitta gazellae	17.6	5	+	0.3	+	25		1
Unidentified	17.6	+	+	1.0	0.1			

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

TABLE 10

ROCKHOPPER PENGUIN DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in brackets)					References
	Euphausiids	Other crustaceans	Fish	Squid	Other food types	
	Eudyptes (chrysocome) moseleyi					
Gough Island (40S)	---------- 92 (1,3) ----------		6 (7)	2 (11)	+	Klages *et al.* 1988
	Eudyptes (chrysocome) chrysocome, Atlantic sector					
Beauchène Island (52S)	45.1 (1,3,4)	+ (6)	1.9	53.0 (12*)		Croxall *et al.* 1985
	Eudyptes (chrysocome) chrysocome, Indian sector					
Marion Island (46S)	-------- 84.4 (4,5) ---------		10.6 (8,9)	5.0 (13,14)		Brown & Klages 1987
Crozet Islands (46S)	66.3 (3)	6.8 (6)	11.7 (8)	15.1 (15)	0.1	(this work)
Heard Island (53S)	90.8 (4,2)	+ (6)	8.0 (8)	1.2		Klages *et al.* 1989
Macquarie Island (54S)	70 (4)	+	17 (10)	13		Horne 1985[b]
Macquarie Island (54S)	69.1 (4)	0.3	28.6 (8)	1.7 (16)		Hindell 1989

The main prey species are: (1) *Thysanoessa gregaria*, (2) *T. macrura*, (3) *Euphausia lucens*, (4) *E. vallentini*, (5) *Nauticaris marionis*, (6) *Themisto gaudichaudii*, (7) unidentified larvae, (8) *Krefftichthys anderssoni*, (9) *Protomyctophum tenisoni*, (10) *Notothenia* sp., (11) Ommastrephidae, (12) *Illex argentinus*, (13) Onychoteuthidae, (14) Octopoda, (15) Gonatidae, (16) *Martialia hyadesi*

[a] identification in the original paper modified according to P. Ward pers. comm.

[b] the squid component of the diet is calculated here as the complement of the crustacean and fish fractions since the author did not give the squid percent by mass

performed in summer have shown that very young squid were at that time one of the most important components of the micronektonic community (Strange 1982). This corresponds to the spawning season of *I. argentinus* (December to March - Roper & Sweeney 1984). Such squid are likely to have quite a similar prey profile as euphausiids: i.e. small body size, moderate velocity and high gregariousness. Among the major prey species, mean body lengths range from 17 mm-long *E. lucens* (0.024 g per individual) at Beauchène Island to 55 mm-DML ommastrephids (12.4 g mean mass) at Gough Island and, in between, include 18 mm-long *E. vallentini* (*c.* 0.05 g) and 1-to-70 mm-long *K. anderssoni* (0.02 to 5 g) at various Indian sector localities (references as in Table 10).

Foraging range and behaviour

The Rockhopper Penguin is widely distributed in the Indian and Atlantic sectors of the Southern Ocean, from temperate islands (*E. c. moseleyi*) to most sub-antarctic islands (*E. c. chrysocome*). The at-sea distribution of non-breeders is still unknown but their absence on the islands suggests an oceanic dispersal. On the other hand, breeding birds are considered mainly to be neritic feeders around the Crozet Islands with most observations at sea being within 30 km of the shore (Stahl 1987, Ridoux *et al.* 1988). Speedmeters fitted on breeding birds during the chick-rearing period have shown that the maximum foraging ranges were less than 24 km for 12-hour feeding bouts, between 30 and 50 km for 36-hour feeding bouts and up to 157 km when the bird spent three days at sea (swimming speed 7.4 km/h, Brown 1987).

The precise diving performances of the Rockhopper Penguin remain unknown. Little Penguins *Eudyptula minor* have been recorded diving to 69 m (Montague 1985), consequently the Rockhopper Penguin's small size does not rule out the possibility that it might reach significant depths. However, in terms of main crustacean prey species and sizes, its diet shows many similarities with surface and sub-surface feeders such as the Salvin's Prion, Blue Petrel *Halobaena caerulea*, and the diving petrels *Pelecanoides* spp., (see relevant sections in this study), therefore suggesting shallow foraging depths.

GENTOO PENGUIN *PYGOSCELIS PAPUA*

Results

Samples

The stomach contents of 23 Gentoo Penguins were collected from 7 November 1980 to 5 January 1981 using the water-flushing method on adults returning to Possession Island, Crozet Islands. Ninety-four additional samples were similarly obtained from 29 May 1982 to 23 December 1982 at a monthly mean rate of 12 samples (range 7-16). These latter samples corresponded to the whole breeding season of 1982. The birds were caught on their path from the landing beach to the colony and consequently their breeding status was not assessed. This minimized disturbance at the breeding site for this shy species.

The mean reconstituted mass of the samples was 135 $\pm$ 127 g (6-593 g) and displayed significant seasonal variation, being lower in winter, during incubation, than in spring and summer, during the chick-rearing period (Fig. 5a). However, much heterogeneity presumably arose from the fact that the samples were collected from birds of unknown breeding status. Results obtained in summer 1980-81 did not significantly differ from those of the following year.

General composition

The food of the Gentoo Penguin was characterized by its high species diversity with 14 fish and 31 invertebrate taxa identified. The diet by reconstituted mass comprised 54.2%

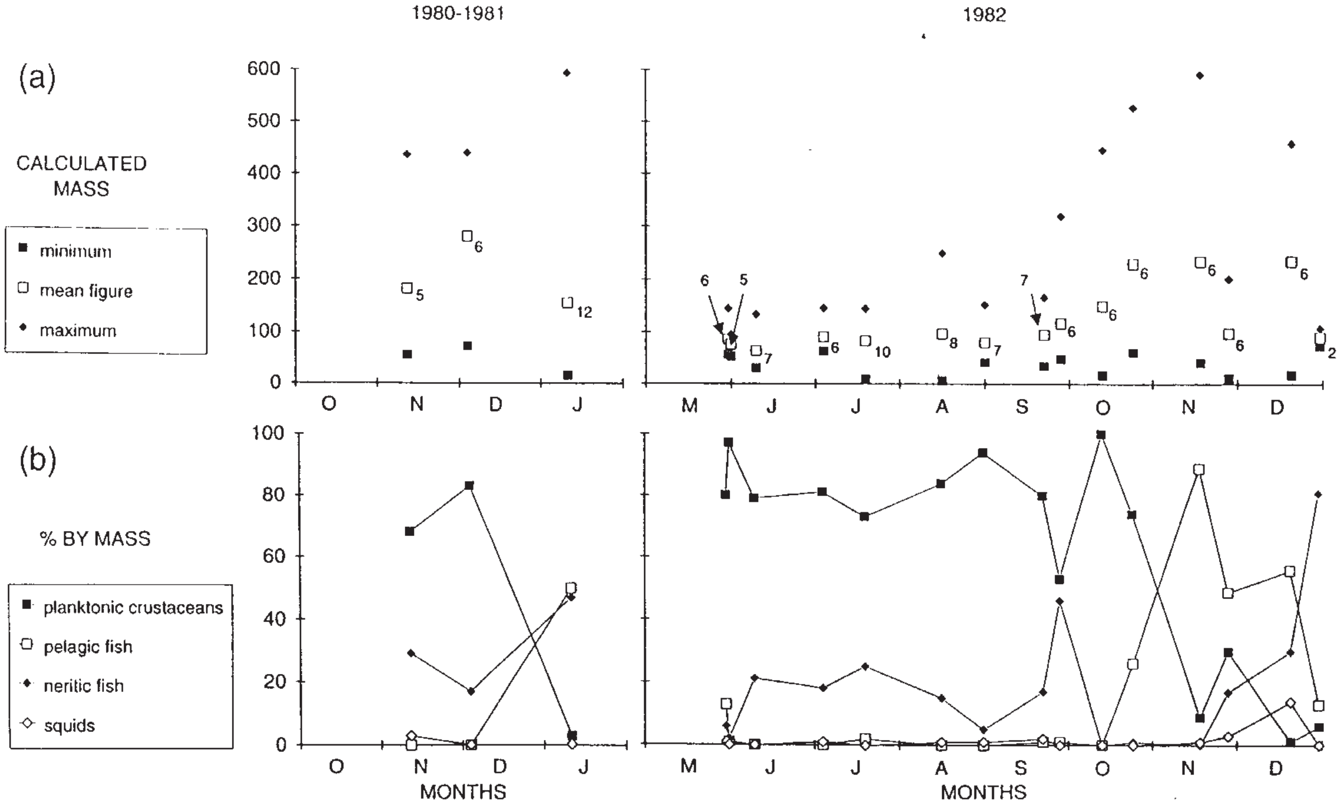

Figure 5

Seasonal variations in (**a**) reconstituted food mass and (**b**) food composition in the Gentoo Penguin; numerals in (**a**) are sample sizes.

crustaceans, 43.9% fish and 1.8% cephalopods (Table 11) and showed important seasonal variation with high crustacean figures in winter and increasing amounts of fish in spring and summer (Fig. 5b). Year-to-year variations in the summer diets in 1980-81 and 1982 (Table 12) may be partly a consequence of the high day-to-day variability observed within both summer sets of samples. The winter sample collection showed much more consistency from one sampling date to another (Fig. 5b).

Crustaceans

Although 21 crustacean taxa were identified, only one, the Subantarctic Krill *Euphausia vallentini*, formed a significant proportion of the food of the Gentoo Penguin. It accounted for 53.5% by reconstituted mass, being mostly prevalent in winter and early spring but also on the first two sampling dates of the 1980-81 summer. Among the other crustacean prey, the hyppolytid shrimp *Nauticaris marionis* was the only one that occurred at significant mass levels in any single sample. Other taxa of micronektonic crustaceans appeared merely as by-catches in samples dominated by *E. vallentini* whereas benthic crustaceans (isopods, some gammarid amphipods) were mostly found in samples dominated by neritic fish.

Cephalopods

Cephalopod prey were found in the diet of the Gentoo Penguin all the year round but never provided an important food source in any season (Fig. 5b); the apparent increase observed in early December was due entirely to a single unusually large-sized onychoteuthid squid (195.3 g reconstituted body mass). Beside this species, young specimens of *Kondakovia longimana*, unidentified onychoteuthids and octopodids occurred in numerous samples as incidental catches but never as the main prey species. Few loose beaks were found as accumulated items. The range of species was similar to those found in the fresh fraction except for the smallest taxa whose largely transparent beaks were unlikely to accumulate in the stomachs to the same extent as larger ones (Table 13).

Fish

Unlike crustaceans, the fish fraction displayed an eclectic composition with several species being important, at least seasonally. Among the pelagic fish, the family Myctophidae was by far the most important and displayed dramatic seasonal changes. The large *Gymnoscopelus nicholsi* and the small *Krefftichthys anderssoni* and *Protomyctophum tenisoni* mostly appeared as target species in late spring and summer samples although both latter species also occurred in small numbers as by-catches among Subantarctic Krill in winter. Another pelagic fish, the gempylid *Paradiplospinus gracilis*, had a highly seasonal occurrence pattern, being present in only six summer samples and accounting for more than 50% by mass in five of them. The demersal fish of the family Nototheniidae appeared all the year round with two important species, *Dissostichus eleginoides* and *Lepidonotothen larseni*. They constituted the bulk of the food in numerous summer samples, often associated with pelagic fish taxa, as well as in a few winter ones. They also appeared as incidental catches in krill-dominated winter samples. On average, nototheniids and the other demersal fish families regularly accounted for 15-20% by mass of the winter diet (until mid October) but showed tremendous day-to-day variations in summer (0 - 85% by mass, Fig. 5b).

Young *Zanchlorhynchus spinifer* mostly appeared in the diet as incidental catches in winter samples dominated by *E. vallentini*. Other fish taxa were of minor importance.

Prey sizes

The prey ranged from 4 to 49 mm total length in crustaceans, 6 to 50 mm DML in cephalopods,

TABLE 11

THE DIET OF THE GENTOO PENGUIN AT THE CROZET ISLANDS (N=116)

Prey Species	Occurrence %	Relative abundance No.	Relative abundance %	Reconstituted mass (g)	Reconstituted mass %	Body length[a] (mm) Mean ± S.D.	(range)	n
CRUSTACEANS	**94.8**	**102369**	**98.4**	**8585.9**	**54.2**			
Copepods								
Unidentified	9.5	569	0.5	5.7	+	8		1
Gammarid amphipods								
Gondogeneia spinicoxa	0.9	1	+	0.2	+	20		1
Unidentified lysianassid	0.9	1	+	0.1	+			
Unidentified	8.6	12	+	0.7	+	12 ± 4	(4-15)	6
Hyperiid amphipods								
Themisto gaudichaudii	19.0	163	0.2	5.1	+	16 ± 3	(6-26)	70
Hyperoche sp.	0.9	1	+	0.1	+	11		1
Hyperia sp.	0.9	1	+	0.3	+	15		1
Hyperiella antarctica	1.7	24	+	0.4	+	9 ± 4	(5-13)	10
Primno macropa	0.9	1	+	0.1	+	15		1
Cyllopus lucasii	0.9	2	+	0.2	+	22	(20-25)	2
Unidentified	1.7	4	+	+	+	20		1
Isopods								
Unidentified	3.5	8	+	2.8	+	11	(9-12)	3
Euphausiids								
Euphausia vallentini	89.7	101332	97.4	8478.3	53.5	23 ± 2	(16-30)	2338
E. triacantha	6.9	7	+	1.4	+	36 ± 6	(24-42)	14
E. longirostris	2.6	3	+	1.5	+	27		1
E. similis	11.2	47	+	9.4	0.1	35 ± 4	(29-44)	29
Thysanoessa sp.	6.0	33	+	0.7	+	16	(13-18)	3
Stylocheiron abbreviatum	2.6	3	+	1.5	+	28	(27-28)	2
Unidentified	0.9	6	+	+	+			
Decapods								
Nauticaris marionis	6.9	151	0.1	77.4	0.5	35 ± 7	(16-49)	33
Unidentified	0.9	+	+	+	+			
CEPHALOPODS	**33.6**	**141**	**0.1**	**292.9**	**1.8**			

Teuthoidea								
Kondakovia longimana	14.7	29	+	58.5	0.4	21 ± 12	(6-50)	29
Onychoteuthis sp. A	0.9	1	+	195.3	1.2	149		1
Moroteuthis sp.	1.7	2	+	5.2	+	27	(22-32)	2
Onychoteuthidae spp.	7.8	15	+	14.5	0.1	12 ± 8	(5-31)	15
Gonatus antarcticus	1.7	4	+	0.4	+			
Unidentified gonatids	3.4	9	+	0.8	+			
Alluroteuthis antarcticus	1.7	4	+	0.5	+	16 ± 5	(11-21)	4
Brachioteuthis sp.	0.9	1	+	0.5	+	24		1
Unidentified	0.9	65	0.1	6.0	+			
Octopoda								
Unidentified octopodids	6.0	11	+	11.2	0.1	10 ± 1	(8-11)	10
FISH	**74.1**	**1494**	**1.4**	**6958.3**	**43.9**			
Myctophiformes								
Gymnoscopelus nicholsi	13.8	214	0.2	2246.8	14.2	91 ± 30	(30-138)	129
Krefftichthys anderssoni	12.9	77	0.1	64.2	0.4	35 ± 5	(20-44)	38
Protomyctophum (tenisoni)	14.7	601	0.6	804.2	5.1	45 ± 3	(32-62)	209
P. normani	2.6	3	+	21.9	0.1	85	(82-91)	3
Gadiformes								
Muraenolepis sp.	0.9	1	+	15.7	0.1	150		1
Scorpaeniformes								
Zanchlorhynchus spinifer	11.2	17	+	43.3	0.3	41 ± 26	(30-116)	13
Perciformes								
Dissostichus eleginoides	10.3	56	0.1	823.8	5.2	96 ± 68	(20-250)	22
Notothenia acuta	0.9	2	+	2.2	+	44		2
Lepidonotothen larseni	25.0	353	0.3	1607.2	10.1	73 ± 20	(40-145)	174
Paranotothenia magellanica	2.6	3	+	169.6	1.1	152	(125-182)	3
Unidentified nototheneids	13.8	75	0.1	102.4	0.6	32 ± 32	(18-160)	35
Harpagifer spinosus	2.6	11	+	5.2	+	28 ± 3	(22-35)	10
Unidentified harpagiferids	3.4	5	+	3.1	+	32 ± 10	(20-45)	5
Paradiplospinus gracilis	5.2	31	+	644.8	4.1	230 ± 24	(190-280)	16
Unidentified	18.1	45	+	403.9	2.5	62 ± 62	(20-280)	19
OTHER ORGANISMS	**3.5**	**25**	**+**	**5.4**	**+**			
Chaetognaths								
Sagitta gazellae	3.5	25	+	5.4	+	42 ± 5	(35-50)	13

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

TABLE 12

SEASONAL VARIATIONS IN THE DIET OF THE GENTOO PENGUIN

Prey taxa	Diet (% by mass)		
	1st summer Nov. 1980- Jan 1981	Winter May 1982- Oct. 1982	2nd summer Nov. 1982- Dec. 1982
Crustaceans			
Euphausia vallentini	46.3	79.3	8.9
other crustaceans	0.2	1.1	0.2
Cephalopods			
all species combined	0.6	0.5	6.3
Fish			
Gymnoscopelus nicholsi	20.6	0.6	33.0
other myctophids	0.0	4.5	15.1
Paradiplospinus gracilis	0.3	0.0	17.6
Dissostichus eleginoides	9.2	1.2	8.8
Lepidonotothen larseni	20.3	5.8	7.1
minor nototheniids and other demersal fish families	2.2	7.0	3.1

TABLE 13

SUMMARY OF ACCUMULATED ITEMS IN GENTOO PENGUIN STOMACH CONTENTS (N=116)

Items	Number of items	Measurements (mm)[a]		n	Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean±S.D.	(range)		Mean	(range)	Mean	(range)
CEPHALOPODS								
Lower beaks	22							
Todarodes sp.	2	6.9	(6.8-6.9)	2	272	(270-274)	505.6	(495-516)
Onychoteuthis sp. A	2	6.0	(5.8-6.2)	2	253	(232-274)	454.2	(401-507)
Moroteuthis knipovitchi	6	5.6±0.5	(4.9-6.3)	6	213	(137-285)	403.9	(243-586)
Kondakovia longimana	6	2.9±1.5	(1.1-4.6)	6	85	(19-149)	77.2	(1.3-195)
Brachioteuthis picta	1	2.2		1	60		5.1	
? *Brachioteuthis* sp.	2	2.6	(2.5-2.6)	2	68	(67-69)	6.5	(6.3-6.7)
Galiteuthis glacialis	3	1.1	(1.0-1.2)	3	57	(55-60)	2.6	(2.3-2.9)

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

with an extreme value of 149 mm DML, and 20 to 280 mm standard length in fish. However, 95% of all prey items were between 10 and 130 mm long (Fig. 6) and weighed 0.06 to 25 g per individual.

Comparison with previous studies

Studies have long reported the presence of krill and coastal dwelling nototheniid fish in the food of the Gentoo Penguin (Matthews 1929, Ealey 1954, Conroy & Twelves 1972, White & Conroy 1975). However, in the last decade a number of quantitative studies has been performed on this widely distributed species at its most important breeding localities (Table 14). In Southern Atlantic localities, where Antarctic Krill is plentiful, Gentoo Penguins, as do most other top predators, rely largely on this small prey species for their food. This is often complemented with demersal nototheniid fish (sometimes as much as *c.* 50% by mass). However, successive studies performed at King George Island have shown that important year-to-year and monthly variations can occur (Jablonski 1985, Table 14). Williams (1991) also showed significant year-to-year variations in the winter diet as well as intraspecific sexual differences, males consuming more fish than females.

At all Indo-pacific localities no single species of pelagic organism compares with Antarctic Krill in terms of biomass available for predators. Accordingly Gentoo Penguins here switch to various alternative food resources: the shrimp *Nauticaris marionis* and the nototheniid fish *Notothenia squamifrons* at Marion Island, Subantarctic Krill and a mixture of pelagic and demersal fish taxa at the Crozet Islands, and mostly fish, either pelagic or demersal, at the southernmost localities of Heard and Macquarie Islands. At Kerguelen Islands, preliminary results obtained at open-sea study sites compare better with these two latter islands, whereas data from in-fjord study sites have more similarities with the two northernmost localities of the Indian sector and are consistent with the lower fish density observed in the fjords (J.C. Hureau cited in Bost & Jouventin 1990). Another case of small scale geographical variation was found between two sites studied at Macquarie Island. The dietary coefficient of demersal fish taxa during the non-breeding season increased with the width of the continental shelf; however, this discrepancy disappeared during the chick-rearing period (Hindell 1989).

Dramatic temporal variations have also been documented at most of these localities. At Macquarie Island several myctophid species and one nototheniid successively prevail in the food of Gentoo Penguins from April to November at a nearly monthly time scale (Hindell 1989). At the Crozet Islands, *E. vallentini* dominated the diet of Gentoo Penguins from May to October. The summer diet investigated during two different seasons was considerably more variable (Fig. 5b). This might account for a great part of the year-to-year variation observed since rather few sampling dates per year were involved in the comparison. This small-scale temporal and geographical variability observed in the food of the Gentoo Penguin contrasts with the greater consistency found in the diets of the other sub-Antarctic penguins (see relevant sections in this study and references cited therein). The variability of the gentoo penguin diet is comparable to that observed in the food of the coastal-dwelling Imperial Cormorant at the Crozet Islands (see Fig. 28b). Such a variability is consistent with the more patchy distribution of demersal and benthic organisms that contribute to the diet of Gentoo Penguins at most localities.

Foraging range and behaviour

The Gentoo Penguin breeds at every subantarctic island south of 46°S southwards to 65°S on the Antarctic Peninsula (Wilson 1983). Despite this broad latitudinal range the species is rarely observed far out at sea (Jehl *et al.* 1979, Thurston 1982, Stahl 1987). Around the Crozet Islands,

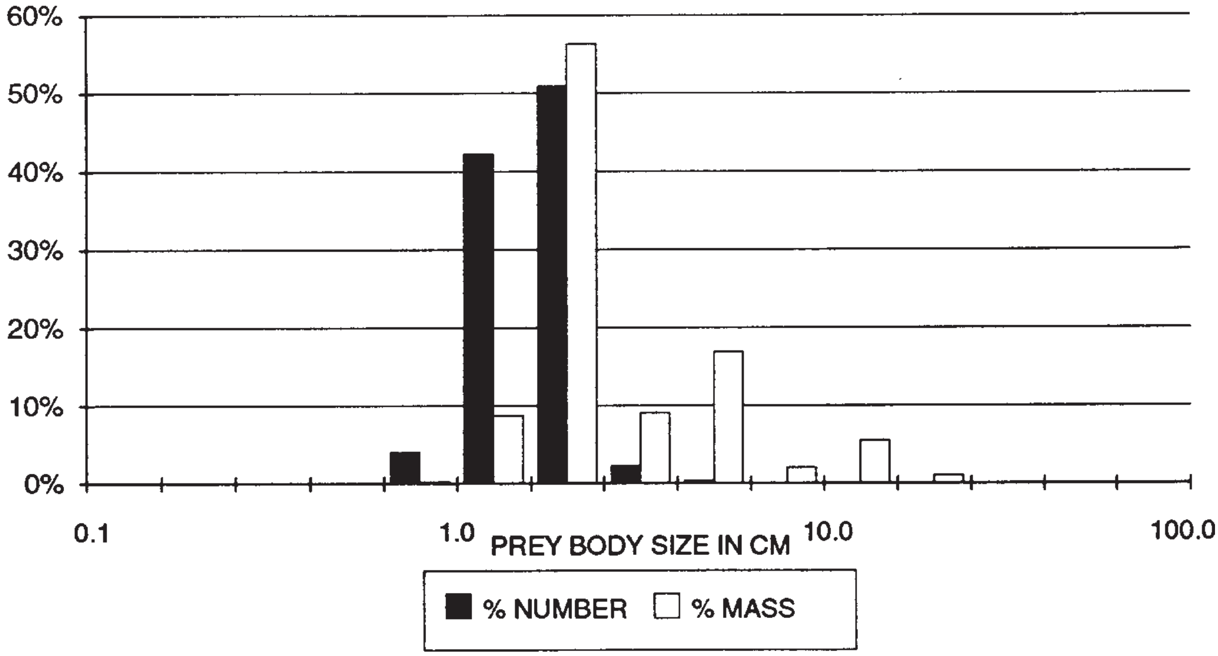

Figure 4

Prey-size distribution in the diet of the Rockhopper Penguin.

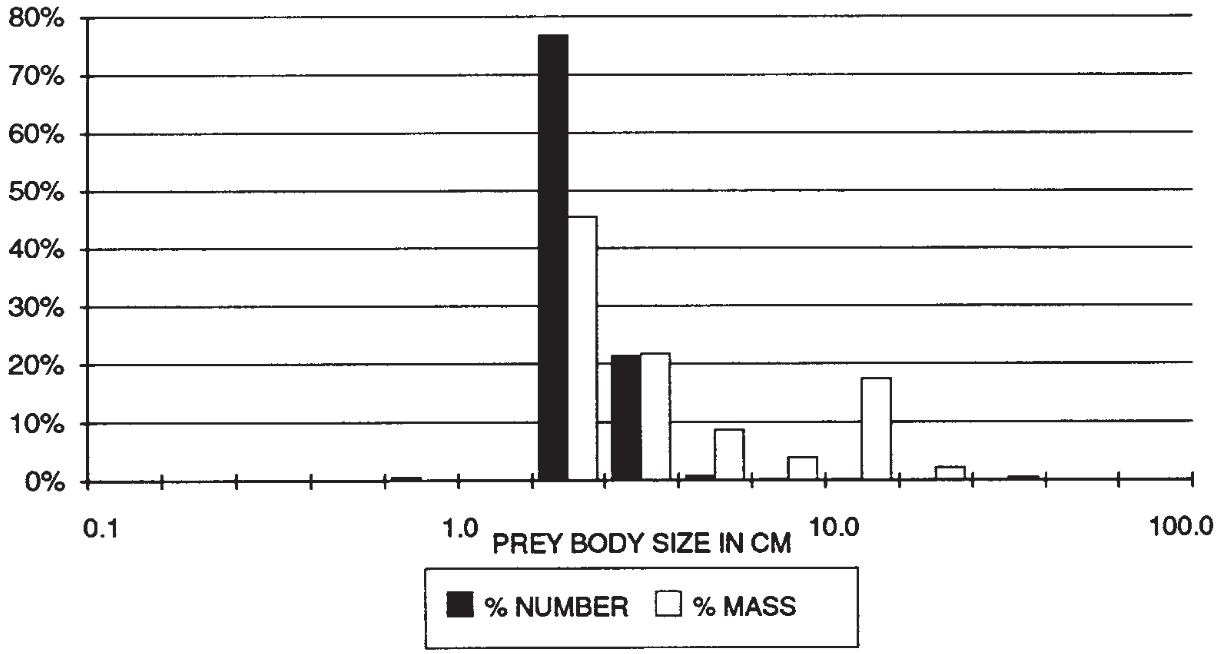

Figure 6

Prey-size distribution in the diet of the Gentoo Penguin.

TABLE 14

GENTOO PENGUIN DIETS AT VARIOUS LOCALITIES

Localities (sampling details)	Diets (% by mass, main prey species in brackets) Crustaceans	Pelagic fish	Neritic fish	Cephalopods	Other food types	References
			Atlantic sector			
King George Isl. (60S) (Nov. 1977-Feb.1978)	84.6 (1)		15.4 (9)			Volkman *et al.* 1980
King George Isl. (Dec. 1978-Jul. 1981)	50.9 (1)		48.6		0.5	Jablonski 1985
South Georgia (52S) (Dec. 1976 - Feb.1977)	67 (1)		33 (11,12,13)	+		Croxall & Prince 1980
South Georgia (May - Sept. 1987)	66.5 (1)	1.0 (5)	32.4 (12,13)			Williams 1991[a]
South Georgia (May - Sept. 1988)	98.0 (1)	+	2.0 (12, 13)			Williams 1991[a]
			Indian sector			
Marion Isl. (46S) (Sep. 1982)	30 (3)	+	70 (10)	+		La Cock *et al.* 1984
Marion Isl. (March 1984-March 1985)	44.4 (2,3)	---------- 53.5 (10) ----------		2.1		Adams & Klages 1989
Marion Isl. (Sep. - Oct. 1984)	46.2 (3)		53.2 (10)	0.6		Adams & Wilson 1987
Crozet Isls. (46S) (Nov. 1980 to Jan. 1981)	46.5 (2)	20.9 (6)	31.7 (12,15)	0.6 (18)		(this work)
Crozet Isls. (Nov. - Dec. 1982)	9.1 (2)	65.7 (6,7,8)	19.0 (12,15)	6.3		(this work)
Crozet Isls. (May - Oct. 1982)	80.4 (2)	5.1 (7)	14.0 (12)	0.5 (18)	+	(this work)

Kerguelen Isls. (51S, fjords)	85	---------- 12 ----------		0	3	preliminary results, Bost & Jouventin 1991
Kerguelen Isls. (open sea)	20	---------- 70 ----------		6	4	preliminary results, Bost & Jouventin 1991
Heard Isl. (53S) (Dec.1986-Jan. 1987)	7.8 (2)	----- 90.5 (4,8,16) ----		1.7 (18)		Klages *et al.* 1990
		Pacific sector				
Macquarie Isl. (54S) (Apr. - Nov. 1985)	0.1	62.9 (4,5,6)	18.4 (14)	18.6 (17,19)		Hindell 1989

The main prey species are: (1) *Euphausia superba*, (2) *E. vallentini*, (3) *Nauticaris marionis*, (4) *Krefftichthys anderssoni*, (5) *Electrona carlsbergi*, (6) *Gymnoscopelus nicholsi*, (7) *Protomyctophum tenisoni*, (8) *Paradiplospinus gracilis*, (9) *Pleuragramma antarctica*, (10) *Notothenia squamifrons*, (11) *N. rossii*, (12) *Lepidonotothen larseni*, (13) *Champsocephalus gunnari*, (14) *Paranotothenia magellanica*, (15) *Dissostichus eleginoides*, (16) unidentified nototheniids, (17) *Moroteuthis* spp., (18) *Kondakovia longimana*, (19) *Martialia hyadesi*

[a] composition by mass of the prey consumed in winter using fish mass calculated from otoliths lengths; see also details of monthly variations and intraspecific sexual differences in the original paper (fish being predominantly eaten by males)

Gentoo Penguins are associated with two feeding habitats. One is neritic and the other is the oceanic waters located within 40 km of the islands (i.e. off areas of narrow continental shelf; Stahl 1983). Accordingly, the prey taken includes benthic (*N. marionis*, harpagiferids, some nototheniids), neritic (*D. eleginoides*, *L. larseni*) and oceanic (myctophids, gempylid) prey species. *E. vallentini* is an ubiquitous pelagic species and is therefore a poor indicator of fine-scale feeding habitat.

The low degree of food digestion, the high nest relief and chick-feeding frequencies are all evidence of the coastal feeding habits of Gentoo Penguins (Croxall & Prince 1980a, Volkman *et al.* 1980, Jablonski 1985, Trivelpiece *et al.* 1987, Bost & Jouventin 1990, Klages *et al.* 1990). Direct observations (Jablonski 1985) as well as calculations from nest relief intervals, chick-feeding frequency, swim speed data and preliminary activity budgets at sea suggest a maximum foraging range and a foraging habitat radius of 24 km and 17 km, respectively at King George Island (Trivelpiece *et al.* 1987). Similar investigations gave estimated median traveling distances of 13.8 and 30.7 km for two different study sites at Marion Island with shrimp-feeding birds swimming shorter distances than did fish feeders (Adams & Wilson 1987). These figures indicate quite inshore feeding habitats when allowance is made for swimming to and from the feeding area and some degree of zigzagging while searching for patchily distributed demersal prey.

Maximum diving depths of the Gentoo Penguin were 100 m at Signy Island (bird caught in net, Conroy & Twelves 1972) and ranged from less than 20 to 70 m at Marion Island (capillary recorders, Adams & Brown 1983). Seven Gentoo Penguins out of 10 dived deeper than 100 m at Esperanza Bay, Antarctic Peninsula (Wilson 1989). The maximum dive time ever recorded was seven minutes (Scholander 1940) but modal routine dive durations were one minute in very shallow waters (Kooyman 1975) or two minutes at King George Island (Trivelpiece *et al.*1987).

Depth histograms recorded during routine foraging dives showed that krill-eating birds foraged preferentially within 60 m of the surface whereas fish eaters ranged from 30 to 100 m deep off South Georgia (Croxall *et al.* 1988). The capture of these two prey types requires distinct feeding strategies (Croxall *et al.* 1988). Antarctic Krill (0.4 to 1.2 g mean body mass) were estimated to be required at rates of 15 to 49 individual per dive (a crested penguin strategy) and fish (74 g mean body mass) at 0.2 to 0.4 individuals per dive (a cormorant strategy). Around the Crozet Islands, predation on the local euphausiid *E. vallentini* is likely to occur in the first tens of metres. Prey-catching rates should be about 15 times higher than at South Georgia to allow for the difference in individual body mass (i.e. 225 to 750 individuals per dives for 0.08 g mean-body-mass *E. vallentini*). Similarly, fish predation is also likely on deeper dives since *Dissostichus eleginoides* and *Lepidonotothen larseni* are mostly abundant below 50 m (Duhamel & Pletikosic 1983) and *Gymnoscopelus nicholsi* is a bentho-pelagic myctophid (Hulley 1981). However, deep dives should not be over-emphasized since these three species are supposed to have more epipelagic habits during their first years of life. The size distributions of both nototheniids in the food of the Gentoo Penguin suggests a diet of juvenile fish (Duhamel 1981, Hulley 1981, Kock *et al.* 1985, see also discussion in the Imperial Cormorant section). Additionally, all these fish species have been reported to prey on the epipelagic *E. vallentini* (Duhamel & Pletikosic 1983, pers. obs. from intact fish specimens found in the samples) and must therefore occur sometimes at relatively shallow depths.

WANDERING ALBATROSS *DIOMEDEA EXULANS*

Results

Samples

The stomach contents of 37 Wandering Albatrosses were collected at Ile de la Possession, Crozet Islands, from 16 August to 23 October 1982. The samples were obtained from chicks previously observed being fed and then induced to regurgitate into a bucket.

The samples contained an average of 482 ± 297 g (60-1100 g) of stomach oil and 297 ± 339 g (0-1600 g) of identifiable fresh material. Accumulated prey hard parts, mainly squid beaks and fish bones, also occurred but were not weighed; neither was the fine unidentifiable fraction lost through the 250 μ-mesh sieve.

General composition

The food of the Wandering Albatross was dominated by squid by number and by mass (Table 15). In terms of individual samples, squid accounted for more than 50% by mass in 31 out of 37 samples, fish and carrion prevailing in four and two stomachs, respectively.

Crustaceans

No free-living crustacean was found as prey of the Wandering Albatross (Table 15). The only crustacean components of its diet were four stalked parasitic copepods *Sphyrion lumpi*, most likely to have been ingested with their hosts, fish of the families Macrouridae or Moridae.

Cephalopods

Cephalopod prey occurred as fragments of mantle, fins or heads from which diagnostic organs were not always found. However, within the 26 beaks found as fresh material (in buccal masses) the onychoteuthid *Kondakovia longimana* predominated by number and mass (Table 15). Examination of the numerous accumulated squid beaks found in the stomach samples and one additional pellet regurgitated at the nest site showed much a broader species diversity than the fresh fraction would indicate. Both fresh and accumulated food remains were dominated by *K. longimana* in number and reconstituted mass (Table 16). The two other onychoteuthids *Moroteuthis ingens* and *M. knipovitchi* were distant second and third in abundance by estimated biomass whereas the family Histioteuthidae was second by number and only fourth by mass due to their smaller mean size.

Fish and other organisms

Fish always appeared as unidentifiable fragments. The occurrence of the parasitic copepod suggested that grenadiers (Macrouridae) or deep-sea cods (Moridae) might have been preyed upon or scavenged by the Wandering Albatross. *Sphyrion lumpi* is hosted by several deep-sea fish families of which only these two are known in the area (Z. Kabata pers. comm.). In the Grey Petrel diet *Shyrion lumpi* was found together with fish remains identified as the morid *Halargyreus johnsoni* (see below).

Shapeless pieces of blubber, presumably scavenged from dead whales because of their thickness, accounted for a significant fraction of the food in five samples. Penguin feathers were found as accumulated items.

Prey sizes

The food of the Wandering Albatross consisted largely of fragments rather than complete prey individuals; accordingly prey size data were scarce. However, the prey sizes ranged from 44 to 911 mm estimated DML for squid (Tables 15 & 16) and 100 to 350 mm for fish. Size distribution is given in Fig. 7 for all prey types pooled.

Comparison with other studies

TABLE 15

THE DIET OF THE WANDERING ALBATROSS AT THE CROZET ISLANDS (N=37)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length[b] (mm)		
	%	No.[a]	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**2.8**	**4**	**6.3**	**5**	**0.1**			
Copepods								
Sphyrion lumpi	2.8	4	6.3	5	0.1			
CEPHALOPODS	**91.7**	**(40)**	**63.5**	**7290**	**76.7**			
Teuthoidea								
Kondakovia longimana	38.9	(19)	30.2	5750	60.5	502	(444-569)	19
Moroteuthis knipovitchi	2.8	(1)	1.6	250	2.6	385		1
Lycoteuthis sp. A	2.8	(1)	1.6	50	0.5	991		1
Megalocranchia sp.	2.8	(1)	1.6	180	1.9	467		1
Taonius pavo (large)	2.8	(1)	1.6	150	1.6	420		1
"*Batoteuthis* sp."[c]	5.6	(2)	3.2	120	1.3	112	(102-122)	2
Unidentified	51.7	(15)	23.8	790	8.3			
FISH	**27.7**	**(10)**	**15.9**	**1420**	**14.9**			
Unidentified	27.7	(10)	15.9	1420	14.9	233 ± 98	(100-350)	6
OTHER ORGANISMS	**25.0**	**(9)**	**14.3**	**795**	**8.4**			
Carrion	25.0	(9)	14.3	795	8.4			

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

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

[c] taxon awaiting final identification (see text under Lightmantled Sooty Albatross)

TABLE 16

SUMMARY OF ACCUMULATED ITEMS IN WANDERING ALBATROSS STOMACH CONTENTS (37 STOMACHS AND 1 PELLET)

Items	Number of items	Measurements (mm)[a]			Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean±S.D.	(range)	n	Mean	(range)	Mean	(range)
CEPHALOPODS								
Lower beaks	1277							
Architeuthis sp.	3							
Onychoteuthis sp. (large)	4	3.3±0.3	(2.9-3.6)	4	172	(149-188)	152	(94-196)
Onychoteuthis sp. (ridge)	1	4.5		1	246		466	
Moroteuthis robsoni	2	8.8	(8.7-8.8)	2	543	(537-548)	1852	(1815-1889)
M. ingens	60	9.4±1.1	(7.1-11.5)	43	616	(369-832)	2553	(891-4819)
M. knipovitchi	43	7.1±0.9	(5.5-8.7)	40	365	(200-536)	929	(369-1807)
Kondakovia longimana	650	12.7±1.1	(10.2-15.4)	133	559	(451-682)	3701	(1918-6549)
Psychroteuthis glacialis	1	6.9		1			90	
Psychroteuthis sp. A	1	4.6		1			30	
Psychroteuthis sp.	1							
Brachioteuthis sp.	1	3.8		1	93		11	
Gonatus antarcticus	24	5.9±0.6	(5.0-7.8)	22	210	(170-291)	201	(109-486)
Ancistrocheirus lesueuri	5	7.9±1.5	(5.5-9.3)	5	279	(182-338)	1424	(351-2318)
Lycoteuthis sp. A	1	4.0		1	86		35	
Octopoteuthis sp.	4	9.9±1.1	(8.3-10.7)	4	172	(144-185)	240	(159-282)
Taningia sp.	5	14.4±2.8	(10.1-17.8)	5	524	(201-782)	4234	(1128-7886)
Lepidoteuthis sp.	2	17.6	(13.8-21.4)	2	750	(589-911)	5122	(2056-8189)
Histioteuthis spp. A	87	5.3±1.1	(2.6-7.6)	85	105	(44-154)	250	(44-527)
Histioteuthis spp. B								
(including *H. eltaninae*)	187	3.8±1.1	(2.2-6.8)	91	96	(56-176)	91	(29-282)
Alluroteuthis antarcticus	21	5.3±0.3	(4.7-5.8)	21	146	(130-162)	166	(123-215)
Cycloteuthis sp.	11	13.7±1.9	(11.2-16.6)	10			1111	(731-1583)
Mastigoteuthis sp. A	6	7.3±1.2	(5.5-8.7)	6	211	(158-251)	392	(161-611)
Mastigoteuthis sp. O	2	5.8	(5.7-5.9)	2	167	(165-170)	191	(183-200)

Chiroteuthis sp. (small)	3	4.9	(4.0-5.8)	2	132	(110-154)	63	(34-91)
Chiroteuthis sp. (large)	8	7.2±0.6	(6.2-7.9)	8	188	(164-205)	165	(110-208)
C. imperator	3	4.9	(4.3-5.9)	3	131	(118-156)	59	(42-95)
"*Batoteuthis* sp. "	22	3.9±0.4	(2.9-4.6)	22	113	(82-132)	64	(25-97)
Bathothauma sp.	2	3.7	(3.5-3.8)	2	196	(185-205)	53	(48-59)
Taonius sp. (large)	8	8.5±2.1	(4.7-10.3)	8	507	(275-620)	251	(64-363)
T. pavo (small A)	6	4.9±0.2	(4.6-5.1)	6	290	(270-300)	72	(62-77)
T. pavo (small B)	1	6.5		1	386		131	
Teuthowenia/Megalocranchia	2	8.3	(7.8-8.8)	2	350	(331-369)	293	(255-332)
Galiteuthis glacialis	60	5.2±0.6	(3.4-6.1)	50	223	(153-259)	98	(37-140)
Mesonychoteuthis hamiltoni	1	11.9		1	498		682	
Unidentified	6							
Eroded beaks	33							
FISH								
Unidentified bones and vertebrae	+ +							

a Lower Rostral Length
b Dorsal Mantle Length
+ + present but not quantified

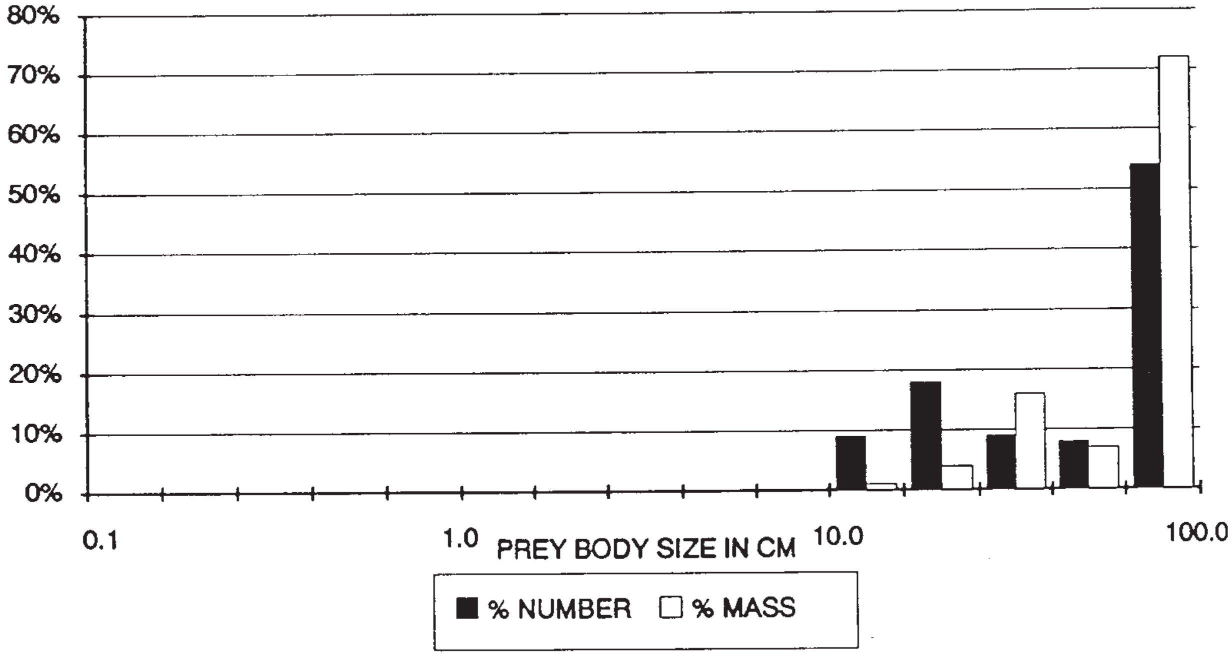

Figure 7

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

The abundance of squid material in the stomachs of the Wandering Albatrosses was emphasized in all the other studies. These studies also reported the occurrence of a variety of other food sources including fish (Matthews 1929, Mougin 1970a, Imber & Russ 1975, Williams & Imber 1982), seal and whale fragments (Falla 1937, Hagen 1952, Paulian 1953) or offal obtained from vessels (Bierman & Voous 1950). Additionally, krill has been recently reported as a possible food source for the Wandering Albatross (Harper 1987).

Quantified dietary data deal with three localities: South Georgia, Marion Island and the Crozet Islands (Table 17). Croxall & Prince (1980), using earlier data from Tickell (1968), estimated the composition by mass of the Wandering Albatross diet at South Georgia to be largely dominated by squid. More recent studies have shown squid and fish amounting to equal percent by mass (Croxall & Prince unpublished, cited in Prince & Morgan 1987) thus contrasting with the prevalence by mass of the squid prey at the Crozets.

The abundant accumulated beaks generally found in stomach contents and regurgitation casts of the Wandering Albatross have motivated numerous studies on the squid part of its diet. At both temperate localities studied, southern New Zealand and Gough Island, the family Histioteuthidae prevails by number (Imber & Russ 1975, Williams & Imber 1982). At least at the former site, the analysis by reconstituted biomass gives a catholic species assemblage with Onychoteuthidae ranking first at 37% wet mass and Histioteuthidae and Cranchiidae second and third at 23 and 13%, respectively. Nine other cephalopod families accounting for the remaining 27%. In contrast, studies from the three subantarctic localities, South Georgia (Clarke *et al.* 1981, Rodhouse *et al.* 1987), Marion (Imber & Berruti 1981, Cooper *et al.* 1992) and Crozet Islands (this study), all have highlighted the key role of the family Onychoteuthidae (mainly *K. longimana*) which accounted for between 53 and 96% by reconstituted mass according to localities, with Cranchiidae and Histioteuthidae being distant second and third at Marion Island and Ommastrephidae second at South Georgia. At South Georgia year-to-year variations in the species composition were consistent with squid availability inferred from variations in krill abundance. Indeed after a summer krill crash, antarctic squid species, that rely on Antarctic krill for their own food, were less important in the diet of the albatrosses than in previous seasons, being partly replaced by temperate species, mainly the ommastrephid *Illex (?argentinus)* (Rodhouse *et al.* 1987).

The fish part of the diet has only been investigated with any detail at South Georgia, the only locality where fish has been shown to reach comparable or even slightly higher wet mass percent than cephalopods. The chaenichthyids *Pseudochaenichthyis georgianus* and *Chaenocephalus aceratus* as well as the eel-cod *Muraenolepis microps* were the most important species by mass. The family Macrouridae accounted for a significant proportion of the diet by number (27%) and although its reconstituted mass was not given it is unlikely that it was negligible. The merlucciid *Macruronus novaezelandiae* and the morid *Halargyreus johnsoni* were found in the diet of the Wandering Albatross in New Zealand (Imber & Russ 1975) whereas the latter was only suspected from the occurrence of specific parasitic copepod at the Crozet Islands (this work).

Foraging range and behaviour

The Wandering Albatross has a very broad latitudinal range from 35° to 65°S in the Indian Sector and as far north as 18°S in the cold waters of the Benguela Current. However, the peaks of abundance are in subtropical to temperate waters and in antarctic waters (Bierman & Voous 1950, Woehler *et al.* 1990). Around the Crozet Islands the Wandering Albatross forages in both neritic

TABLE 17

WANDERING ALBATROSS DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in brackets)				References
	Crustaceans	Squid	Fish	Carrion	
South Georgia (52S)	0.2	39.5 (1,2)	41.5 (4,5,6,7)	18.8	Croxall & Prince unpubl., cited in Prince & Morgan 1987, Croxall *et al.* 1988, Rodhouse *et al.* 1987
Marion Island (46S)	0.1	58.6 (1,3)	36.5 (7)	4.8 (8)	Cooper *et al.* 1992
Crozet Islands (46S)	+	79.7 (1,3)	13.0	7.3	(this work)

The main prey species are: (1) *Kondakovia longimana*, (2) *Illex sp.*, (3) *Moroteuthis spp.*, (4) *Pseudochaenichthys georgianus*, (5) *Chaenocephalus aceratus*, (6) *Muraenolepis microps*, (7) Macrouridae sp., (8) cetacean and oceanic habitats with a slight preference for continental shelf and slope areas and for temperate waters (Weimerskirch *et al.* 1986). At the Kerguelen Islands the species forages preferentially in the vicinity of the Antarctic Divergence (Weimerskirch *et al.* 1988). Breeding adults were reported to forage as far as 1000 km from the colony in the South Atlantic (Jehl *et al.* 1979) and one dyed bird breeding at the Kerguelen Islands was observed at 1420 km from its nest (Weimerskirch *et al.* 1988). Recent satellite-tracking experiments (Jouventin & Weimerskirch 1990) have shown that Wandering Albatrosses incubating at the Crozet Islands foraged as far north as subtropical waters and as far south as the antarctic pack-ice, thus crossing several major water mass boundaries. Some fragmentary data indicated that brooding birds performed shorter feeding trips and mostly foraged over the shelf and slope around the Crozet Islands. The extent of the foraging zone during late chick rearing (corresponding to samples reported here) remains undocumented but can be expected to be intermediate between the incubating and the brooding periods. Consequently, Wandering Albatrosses, at least during incubation and possibly during late chick rearing, prey upon several squid communities from subtropical to pack-ice areas. This accords with the very high squid species diversity found in their diets at every locality studied to date (Imber & Russ 1975, Clarke *et al.* 1981, Imber & Berruti 1981, Rodhouse *et al.* 1987, Cooper *et al.* 1992, this study).

The Wandering Albatross feeding techniques mostly involve surface seizing, shallow plunging being rare (Harper 1987, Harper *et al.* 1985). The large size of the Wandering Albatross allows birds to compete successfully with all other albatrosses and giant petrels even when they do not arrive first at a food source (Weimerskirch *et al.* 1986, Harper 1987).

Scavenging is also reported since the species is known to follow trawlers and other vessels as well as Sperm Whales *Physeter macrocephalus*; however, the extent to which the species is dependant on floating dead or moribund fish and squid for its food is still disputed. It has been suggested that most of the fish diet of the Wandering Albatross at South Georgia is derived from scavenging around the numerous trawlers operating in the area in winter (Croxall & Prince 1987). The small proportion by mass of fish in its food at the Crozet Islands would thus accord with this hypothesis since it is consistent with the absence of fishing fleets over the surrounding shelf. However, scavenging behind trawlers as the main fish source for Wandering Albatrosses at South Georgia was disputed by Croxall *et al.* (1988) since they failed to identify in significant numbers the principal target species of the fishery from the otoliths collected in albatross regurgitations.

Similarly, the circumstances in which the Wandering Albatross feeds on the large-sized, swift-swimming and often deep-dwelling squid which constitute the bulk of its food are also unclear. The abundance in its food of photophore-bearing vertically-migrating squids were arguments put forward to support the hypothesis of nocturnal feeding on live specimens (Imber & Berruti 1975). Harper (1987) reported that 93% of observations of feeding Wandering Albatrosses occurred nocturnally. However, Clarke *et al.* (1981) pointed out that in most bioluminescent squid the photophores help in hiding the outline of the animal seen from below and were mostly invisible from above; additionally, *K. longimana* and the other onychoteuthids, which constitute the bulk the species' diet at all subantarctic localities, are not luminescent. Consequently these authors, followed by Rodhouse *et al.* (1987), suggested scavenging to be the dominant feeding technique and that fragments or whole corpses of deep-dwelling squid were brought to the surface as a consequence of various phenomena as Sperm Whale regurgitations (observed by Clarke *et al.* 1981), post-breeding mass mortality of squid after they had congregated close to the surface for mating and spawning (Rodhouse *et al.* 1987) and probably other, still undescribed, mechanisms. The scavenging hypothesis concurs with the observations made around the Crozet Islands (Weimerskirch *et al.* 1986). The use of appropriate activity recorders would help in quantifying the relative importance of nocturnal feeding on live squid versus diurnal scavenging (Prince & Morgan 1987).

YELLOWNOSED ALBATROSS *DIOMEDEA CHLORORHYNCHOS*

GREYHEADED ALBATROSS *DIOMEDEA CHRYSOSTOMA*

BLACKBROWED ALBATROSS *DIOMEDEA MELANOPHRYS*

Results

Samples

None of the three mollymawks breeding at the Crozet Islands (the shy albatross *D. cauta*, a fourth species recently found breeding at Ile aux Pingouins is only represented by a few pairs and was not discovered at the time of sampling) breeds in significant and readily accessible numbers at Ile de la Possession. The most important colonies, discovered in the last decade, are located at Ile de l'Est and at the barely accessible western islands of Ile aux Pingouins and Ilots des Apôtres (Jouventin *et al.* 1984). They have been visited only rarely. Consequently dietary information has come either from fragmentary stomach samples regurgitated by chicks as they were handled for other scientific purposes (Blackbrowed and Greyheaded Albatrosses, Ile de l'Est, February 1982) or from nine complete stomach contents obtained during a single one-day visit to Ile aux Pingouins (Yellownosed Albatross, February 1982). Owing to these poor sampling conditions only cumulative number and mass compositions are given.

General composition

The identifiable fresh fragments were mostly squid and less importantly crustaceans in the Greyheaded Albatross, a mixture of squid and fish in equal proportions in the Yellownosed Albatross (Table 18) and mostly fish in the Blackbrowed Albatross. Oil accounted for *c.* 25% by mass of the samples in all three species.

Crustaceans

Large mesopelagic species like the lophogastrid mysid *Gnathophausia gigas*, the pasiphaeid shrimp *Pasiphaea longispina* and the lysianassid amphipods *Eurythenes* spp. were the typical crustacean prey for all mollymawks. They accounted for as much as 8.8% by reconstituted mass in the Greyheaded Albatross but for lesser proportions in the other species. Other crustacean prey groups include copepods found in a single Yellownosed Albatross sample and the hyperiid *Themisto gaudichaudii* regularly observed in the food of the Greyheaded Albatross. The copepods were found with fish remains and were very likely to be fish prey rather than albatross prey. The same may apply for *T. gaudichaudii* in Greyheaded Albatross diet samples.

Cephalopods

Cephalopod prey items include fresh fragments of the ommastrephid *Todarodes filippovae* and the onychoteuthid *Kondakovia longimana* in Greyheaded and only the ommastrephid in Yellownosed Albatrosses. No fresh remains of cephalopods were found in Blackbrowed Albatrosses. Accumulated loose beaks were found in all three species, although in greater number and diversity in the Greyheaded Albatross than in its two congeners (Table 19). *T. filippovae* was thus confirmed as an important prey species for the three mollymawks, being the

TABLE 18

THE DIETS OF GREYHEADED AND YELLOWNOSED ALBATROSSES AT THE CROZET ISLANDS

Prey Species	Greyheaded Albatross				Yellownosed Albatross			
	Relative abundance %	Mass %	Body length[a] (mm) mean ± S.D.(range)	n	Relative abundance %	Mass %	Body length[a] (mm) mean ± S.D.(range)	n
CRUSTACEANS	**73.4**	**10.7**			**13.3**	**3.8**		
Gammarid amphipods								
Eurythenes gryllus	1.7	0.3	52	2				
Hyperiid amphipods								
Themisto gaudichaudii	43.3	0.2	19 ± 1 (18-23)	15				
Mysids								
Gnathophausia gigas	6.7	4.9	115	1	6.7	3.8		
Unidentified mysids					6.7	+		
Decapods								
Pasiphaea longispina	21.7	5.3	97 ± 5 (90-105)	7				
Unidentified					+	+		
CEPHALOPODS	**20.0**	**89.3**			**13.3**	**38.0**		
Teuthoidea								
Todarodes filippovae[b]	15.0	53.6	130 (110-170)	3	10.0	26.6	111 ± 26 (80-150)	5
Kondakovia longimana	1.7	3.2	360	1				
Unidentified	3.3	36.4			3.3	11.4		
FISH	**6.7**	+			**73.3**	**58.2**		
Unidentified	6.7	+			73.3	58.2		

[a] Dorsal Mantle Length for squids, total body length for the other prey taxa

[b] Recent examination of fresh material suggests that confusion with *Martialia hyadesi* may have occurred (note added by author at proof stage)

TABLE 19

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

Items	Number of items	Measurements (mm)[a]			Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean±S.D.	(range)	n	Mean	(range)	Mean	(range)
	Greyheaded Albatross *Diomedea chrysostoma*							
CEPHALOPODS								
Upper beaks	362							
Lower beaks	253							
Todarodes filippovae	101	4.0±0.8	(2.5-7.8)	47	153	(94-311)	120	(31-730)
Moroteuthis knipovitchi	2	6.9	(6.9-6.9)	2	349	(348-350)	810	(806-814)
Kondakovia longimana	26	9.5±3.0	(2.8-13.2)	18	417	(121-583)	1918	(41-4108)
Psychroteuthis sp.	1							
Gonatus antarcticus	1	5.5		1	191		148	
Lycoteuthis sp. A	1	3.3		1	72		23	
Histioteuthis sp.A	1							
Histioteuthis eltaninae	4	3.4±0.3	(3.1-3.8)	4	88	(79-97)	72	(58-87)
Alluroteuthis antarcticus	1	4.8		1	133		131	
Chiroteuthis sp. (large)	1	6.4		1	169		121	
Chiroteuthis imperator	1	4.3		1	115		39	
"*Batoteuthis* sp."	25	4.0±0.3	(3.3-4.4)	18	116	(94-126)	68	(37-86)
Teuthowenia pellucida	2	5.3	(5.2-5.4)	2	229	(224-235)	104	(98-110)
Galiteuthis glacialis	64	5.0±0.4	(4.1-5.7)	59	215	(177-243)	89	(55-119)
Eroded beaks	12							
SEABIRDS								
Penguin feathers	numerous							
	Blackbrowed Albatross *Diomedea melanophrys*							
CEPHALOPODS								
Upper beaks	17							

Lower beaks	9							
Todarodes filippovae[c]	7	4.3	(3.9-4.6)	3	164	(150-177)	132	(103-159)
Psychroteuthis sp.	1							
Chiroteuthis sp. (small)	1	4.6		1	124		48	
SEABIRDS								
Penguin feathers	very numerous							
	Yellownosed Albatross *Diomedea chlororhynchos*							
CEPHALOPODS								
Upper beaks	9							
Lower beaks	8							
Todarodes filippovae[c]	8	4.2	(4.1-4.3)	2	162	(156-167)	125	(114-135)

[a] Lower Rostral Length
[b] Dorsal Mantle Length
[c] The examination of recent samples suggests that *T. filippovae* and *Martiala hyadesi* may have been pooled under the name *T. filippovae* (author's note added at proof stage)

most important either by number or estimated biomass in Blackbrowed and Yellownosed Albatrosses and the first by number and only second by mass, after the large onychoteuthid *K. longimana*, in the Greyheaded Albatross.

Fish

Although some fish fragments were present in most of the samples and even dominated the diet by mass in the Blackbrowed Albatross, no individual could be identified or even assigned with any safety to a family. From remains of axial skeletons these fish were estimated to range from 150 to 300 mm standard length.

Other prey groups

Numerous penguin feathers were found as accumulated items in the stomach contents of Blackbrowed Albatrosses, indicating some degree of scavenging behaviour.

Prey sizes

Observed DML of some well preserved *T. filippovae* were 130 $\pm$ 35 mm (110-170 mm; n=3) in Greyheaded and 111 $\pm$ 26 mm (80-150 mm; n=5) in Yellownosed Albatrosses.

Pooled prey size distributions are given for the Greyheaded and the Yellownosed Albatrosses in Figs 8 and 9 and indicate a broader range of prey sizes in the former species.

Comparison with other studies

Descriptive studies have shown the large variety of food sources used by mollymawks: unspecified fish and squid at Heard Island (Downes *et al.* 1959), the fish *Notopogon lilliei* up to 200 mm long around Tristan da Cunha (Hagen 1952), floating offal, crustaceans and gelatinous plankton in the southern Pacific (Harper 1987), cephalopods, krill, other crustaceans, salps, fish and birds at South Georgia (Tickell 1964). Similarly, at South Georgia (Matthews 1929, Tickell 1964) and the Crozet Islands (Despin *et al.* 1972), cephalopods together with krill, other crustaceans, salps, lampreys, fish and seabirds were recorded from the stomachs of Greyheaded Albatrosses. Reported in the diet of the Yellownosed Albatross have been the flying fish *Cypselurus furcatus*, the Snoek, *Thyrsites atun*, and a few deep-sea crustaceans at Amsterdam Island (Paulian 1953, Segonzac 1972), squid at Gough Island (Williams & Imber 1982) or a mixture of fish, among which 100-210 mm-long *Scomberesox saurus*, with 150-mm squid and large bathypelagic crustaceans such as *Eurythenes obesus* and some pasiphaeid shrimps at Tristan da Cunha (Hagen 1952). These records highlight the opportunist feeding behaviour of these albatrosses.

The only comparative study was conducted in South Georgia and showed a broad dietary overlap between the Blackbrowed and the Greyheaded Albatrosses (Prince 1980b, Prince & Morgan 1987). Nevertheless, fish and krill accounted for a significantly higher percentage by mass in Blackbrowed than in Greyheaded Albatrosses, whereas squid and lampreys were dominant in Greyheaded Albatrosses (Table 20). At Marion Island, fish prevailed by mass in the diet of the Greyheaded Albatross whereas squid was of secondary importance, accounting for only one-third of the food. The ommastrephid *Todarodes (sagittatus)* was shown to account for 76 and 91% by reconstituted mass of the cephalopods preyed upon by the Blackbrowed and Greyheaded Albatrosses, respectively at South Georgia (Clarke & Prince 1981). The same key role was held by the onychoteuthid *Kondakovia longimana* in the squid diet of Greyheaded and Yellownosed Albatrosses at the Prince Edward Islands (Brooke & Klages 1986). The decreasing extent of the continental shelf and slope at South Georgia, the Crozet Islands and Marion Island may partly account for the differences observed in the most abundant squid species since the family Ommastrephidae occurs

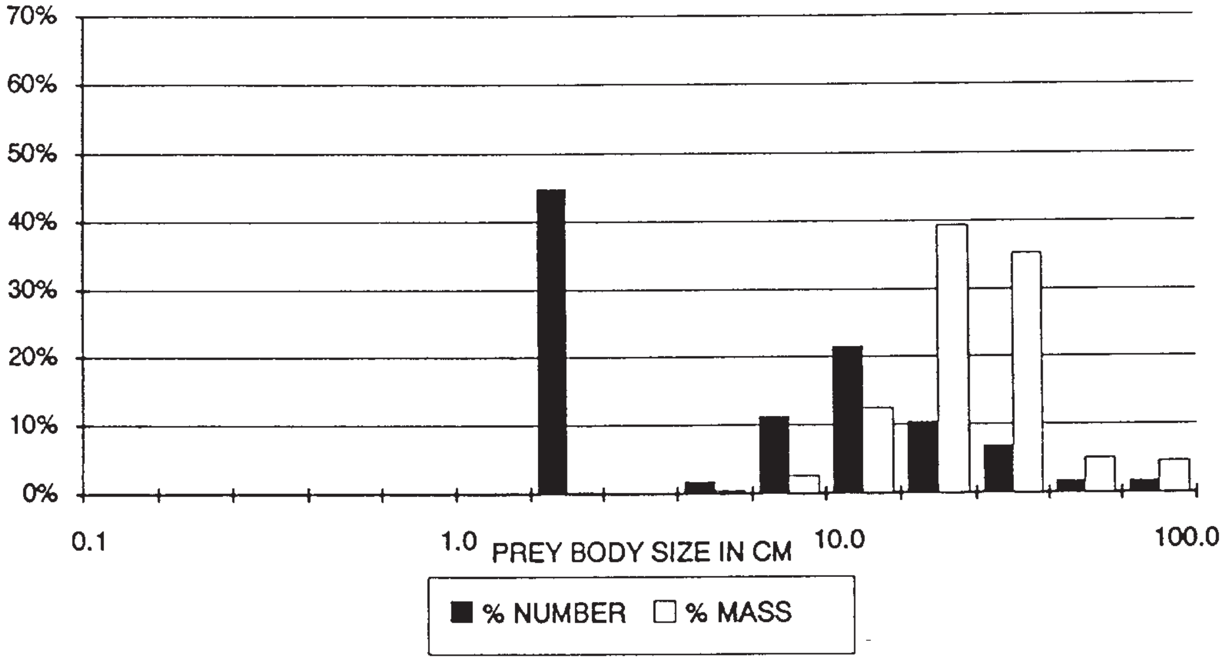

Figure 8

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

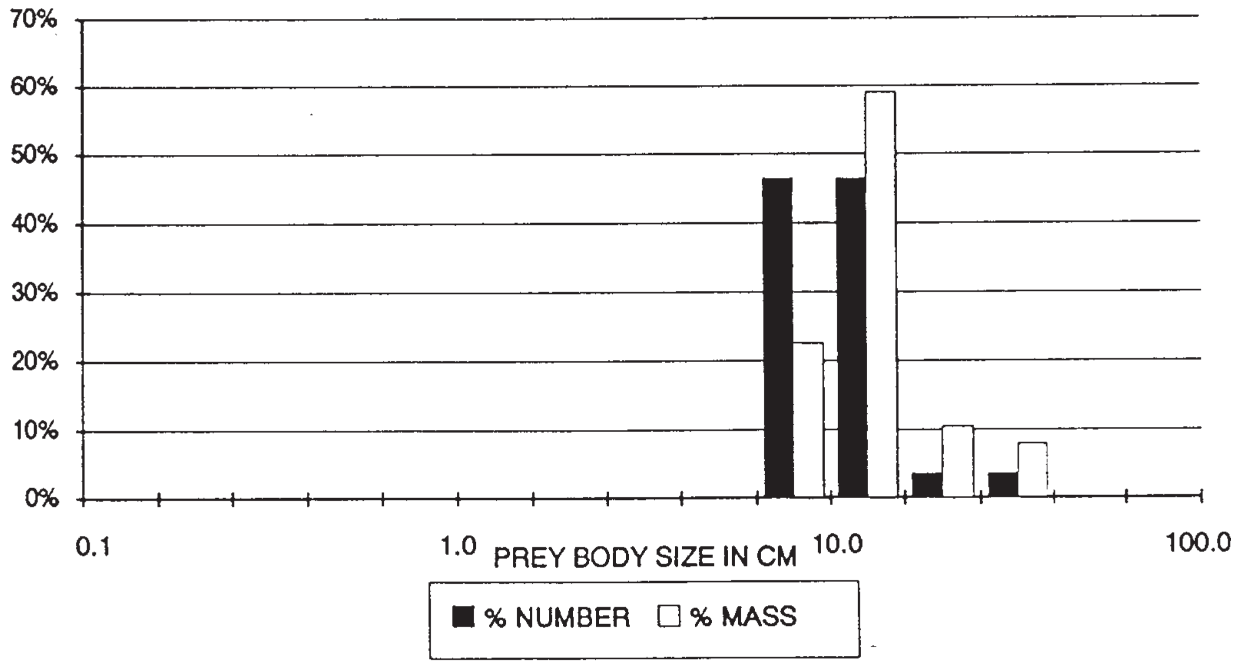

Figure 9

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

TABLE 20

MOLLYMAWK DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in brackets)					References
	Crustaceans	Fish	Squid	Carrion	Other food types	
	Blackbrowed Albatross *Diomedea melanophrys*					
South Georgia (52S)	39.9 (1)	39.5 (4)	20.6 (6)			Prince 1980, Prince & Morgan 1987
Crozet Islands (46S)	+	+ + +	+ (7)	+ + (10)		(this work)
	Greyheaded Albatross *Diomedea chrysostoma*					
South Georgia (52S)	16.5 (1)	34.5 (4,5)	49.0 (6)			Prince 1980, Prince & Morgan 1987
Marion Island (46S)	3.0	58.0	34.2 (8,9)	4.7 (10,11)	0.2	Hunter & Klages 1989
Crozet Islands (46S)	9.0 (2,3)	+	91.0 (7,8)	+		(this work)
	Yellownosed Albatross *Diomedea chlororhynchos*					
Crozet Islands (46S)	3.8 (3)	58.2	38.0 (7)			(this work)

The main prey species are: (1) *Euphausia superba*, (2) *Pasiphaea longispina*, (3) *Gnathophausia gigas*, (4) unidentified fish, (5) *Geotria australis*, (6) *Todarodes (? sagittatus)*, (7) *T. filippovae*, (8) *Kondakovia longimana* , (9) *Histioteuthis eltaninae*, (10) penguins, (11) seals mainly in neritic waters whereas *K. longimana* is an oceanic species (Clarke 1966, Roper *et al.* 1984).

Foraging range and behaviour

In the Southern Indian Ocean the three mollymawks display very distinct at-sea distributions: Yellownosed Albatross from 35° to 45°S, Blackbrowed Albatross from 40° to 55°S and Greyheaded Albatross from 40° to 65°S (Weimerskirch *et al.* 1986, Stahl 1987). Furthermore, in terms of foraging habitats a significant segregation also occurs. Blackbrowed Albatrosses concentrate feeding on the continental shelves (Stahl *et al.* 1985a) from the slope to the immediate vicinity of the coasts (Jouventin *et al.* 1981) whereas the other two species were never observed feeding in inshore waters but forage largely in productive oceanic areas like the subtropical and antarctic convergence zones (Yellownosed Albatross) and southwards to the Antarctic Polar Front and the antarctic waters (Greyheaded Albatross) (Stahl *et al.* 1985a, Weimerskirch *et al.* 1986). These at-sea distributions agree well with studies performed in other sectors of the Southern Ocean (Jehl *et al.* 1979, Harper 1987, Weimerskich *et al.* 1988). One Greyheaded Albatross marked at South Georgia was observed 850 km southward (Prince & Francis 1984) and several breeders of the same species from Kerguelen Islands were controlled close to the Antarctic Divergence 1850 km south of their colony. Blackbrowed Albatrosses at the same locality were not seen further than 500 km from their colony and never observed in oceanic areas (Weimerskirch *et al.* 1988). Although the foraging range of the Yellownosed Albatross is not known with much accuracy, breeders at the Crozet Islands are likely to forage at or north of the convergence zone since it is the only species clearly associated with warm waters in February when the adults raise their chicks (Stahl *et al.* 1985a). There is unexpectedly little evidence from dietary analysis that matches the clear-cut differences in at-sea distributions; however, poor sample size may partly explain this.

The three mollymawks display similar feeding methods (Harper *et al.* 1985). The Blackbrowed Albatross is estimated to feed mainly by surface seizing (98%) during daylight hours (78%, Harper 1987). Mainly daylight feeding remains debated for the other species. Indeed Greyheaded Albatrosses fitted with activity recorders have been demonstrated to spent three times as much time sitting on the water by night than by day (Prince & Francis 1984). These authors concluded that Greyheaded Albatrosses ate by night. By contrast at-sea observations led other workers to the conclusion that *Diomedea* spp. albatrosses were mostly diurnal scavengers (Weimerskirch *et al.* 1986). One of the arguments supporting the nocturnal hypothesis is the occurrence in the food of the albatrosses of numerous bathy- to mesopelagic oceanic squid. These squid are known to perform nycthemeral vertical migrations leading them close to the surface where they feed on planktonic and micronektonic forms concentrating there during the night. At the Crozet Islands, the squid diet of the three mollymawks is characterized by the importance of the family Ommastrephidae. This family is only weakly, if at all, represented in the food of the other three species of albatrosses (see sections dealing with Wandering, Sooty and Lightmantled Sooty Albatrosses). This peculiarity may indicate some foraging behavioural traits shared by all three mollymawks that separate them from the other albatrosses. Of the squid species found in the food of the Crozet Island albatrosses, *T. filippovae* is the species which undergoes the least vertical migrations (from the surface to 100 m) and is therefore most likely to be found by day close to the surface. This genus is also more abundant over shelf and slope areas as well as in the most productive oceanic zones (Roper *et al.* 1984, and partly inferred from information on *T. sagittatus* and *T. pacificus*, Clarke 1966, Roper & Young 1975). Its abundance in the squid diets of the three

Crozet Island mollymawks suggests some degree of diurnal foraging in the highly productive neritic or oceanic habitats. Feeding at twilight may provide a compromise between the abundance of squids at the surface and their detectability (as previously suggested by Clarke & Prince 1981 and West & Imber 1986). Further investigations on bird activity at sea and squid vertical distributions are required to clearly elucidate this point.

LIGHTMANTLED SOOTY ALBATROSS *PHOEBETRIA PALPEBRATA*

Results

Samples

The stomach contents of 31 Lightmantled Sooty Albatrosses were collected from 5 January to 28 May 1982 (27 samples) and between 13 and 21 March 1983 at Ile de la Possession, Crozet Islands. All of them but the first four samples, which were collected from adults birds using the water-flushing method, were obtained from regurgitations of chicks. The total mass of the regurgitated samples ranged from 240 to 1495 g but the identifiable fresh fraction ranged only 0 to 572 g (130 $\pm$ 133 g). The remainder of the samples comprised unidentifiable liquid, oil and accumulated items. Two samples contained no fresh fraction. They were discarded from quantitative results but included in the analysis of accumulated material.

General composition

Squid accounted for 56.4% by wet mass of the food of the Lightmantled Sooty Albatross (Table 21). Crustaceans dominated the diet by numbers but, due to their small sizes, only constituted 16.0% by mass of the food; similar to the proportion of carrion. Fish only represented 10.9% by wet mass of the diet. Analysed on the basis of individual samples, squid, crustaceans, carrion and fish accounted for at least 50% by mass in 17, six, four and two samples, respectively.

Crustaceans

Antarctic Krill made up almost the whole reconstituted mass of the crustacean part of the diet (Table 21). Other taxa included epiplanktonic forms such as *E. vallentini* and the hyperiid *Themisto gaudichaudii* and mesopelagic taxa such as the lophogastrid mysid *Gnathophausia gigas* and the pasiphaeid shrimp *Pasiphaea longispina*.

Cephalopods

Cephalopods occurred mostly as fragments of mantle, arms, tentacles and fins and were seldom identifiable. Ten beaks recovered from buccal masses allowed four taxa to be identified in the fresh fraction. The onychoteuthids *Kondakovia longimana* and *Moroteuthis ingens* were the most important by mass (Table 21).

Eighteen taxa were identified from accumulated beaks in stomach samples and six casts regurgitated at the nest (Table 22). The cranchiid *Galiteuthis glacialis* was the most numerous, accounting for more than 50% of all identified beaks, followed by *K. longimana*, *Psychroteuthis* sp., *Histioteuthis eltaninae* and a species provisionally called "*Batoteuthis* sp." for the similarity of its beak to the beak of the rare *B. skolops* (Young & Roper 1968) and still awaiting final identification. *K. longimana* largely prevailed by reconstituted mass.

Fish and other organisms

No fish were identified from either fresh or accumulated material. Carrion was identified as penguin skin scraps, unidentified viscera and sea mammal blubber. Penguin feathers were recorded from both the accumulated fraction of the samples and the pellets.

TABLE 21

THE DIET OF THE LIGHTMANTLED SOOTY ALBATROSS AT THE CROZET ISLANDS (N=29)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length[b] (mm)		
	%	No.[a]	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**41.4**	**1031**	**96.8**	**565.5**	**16.0**			
Gammarid amphipods								
Eurythenes obesus	10.3	3	0.3	11.5	0.3	41	(30-50)	4
Hyperiid amphipods								
Themisto gaudichaudii	10.3	22	2.1	1	+	11 ± 5	(6-22)	17
Euphausiids								
Euphausia superba	27.6	949	89.1	519	14.7	37 ± 6	(28-50)	66
E. vallentini	3.4	50	4.7	3	0.1	20 ± 2	(17-23)	10
Mysid								
Gnathophausia gigas	10.3	2	0.2	20	0.6	120	(110-130)	2
Decapods								
Pasiphaea longispina	10.3	5	0.5	11	0.3	85		1
CEPHALOPODS	**75.9**	**(25)**	**2.4**	**1990**	**56.3**			
Teuthoidea								
Kondakovia longimana	13.8	(4)	0.4	565	16.0	456	(205-591)	4
Moroteuthis ingens	3.4	1	0.1	395	11.1	367		1
Galiteuthis glacialis	3.4	(4)	0.4	110	3.1	211	(200-230)	4
"*Batoteuthis* sp."	3.4	(1)	0.1	130	3.7	109		1
Unidentified	51.7	(15)	1.4	790	22.4			
FISH	**13.8**	**(4)**	**0.4**	**385**	**10.9**			
Unidentified	13.8	(4)	0.4	385	10.9	188 ± 67	(100-250)	5
OTHER ORGANISMS	**20.7**	**(6)**	**0.6**	**590**	**16.7**			
Carrion								
Penguins	76.9	(2)	0.2	85	2.4			
Mammals	3.4	(1)	0.1	160	4.5			
Unidentified	10.3	(3)	0.3	345	9.8			

[a] numbers in brackets indicate that the taxon appeared as fragments rather than complete individuals

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

TABLE 22

SUMMARY OF ACCUMULATED ITEMS IN LIGHTMANTLED SOOTY ALBATROSS STOMACH CONTENTS (31 STOMACHS AND SIX PELLETS)

Items	Number of items	Measurements (mm)[a]			Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean ± S.D.	(range)	n	Mean	(range)	Mean	(range)
CEPHALOPODS								
Lower beaks	672							
Onychoteuthis sp.	2	6.5	(6.4-6.6)	2	366	(362-371)	1794	(1717-1870)
Moroteuthis ingens	2	8.2	(8.0-8.5)	2	486	(459-512)	1487	(1329-1645)
M. knipovitchi	6	7.0±0.5	(6.6-7.8)	6	361	(311-438)	871	(672-1216)
Kondakovia longimana	69	8.7±2.9	(3.1-14.4)	62	380	(131-637)	1543	(53-5344)
Psychroteuthis glacialis	76	7.2±0.5	(6.0-8.3)	73			102	(62-148)
Psychroteuthis sp.	4	4.6	(4.6-4.7)	4			30	(29-31)
Gonatus antarcticus	7	5.9±0.3	(5.4-6.2)	6	210	(188-220)	194	(143-220)
Lycoteuthis sp. A	2	3.9	(3.5-4.2)	2	84	(78-91)	33	(28-39)
Histioteuthis eltaninae	51	3.3±0.3	(2.7-4.0)	49	85	(68-102)	66	(43-95)
Alluroteuthis antarcticus	14	5.6±0.6	(4.6-6.5)	12	155	(127-181)	194	(115-282)
Cycloteuthis sp.	1	11.4		1	352		755	
Mastigoteuthis sp.	1	6.4		1	184		252	
Chiroteuthis sp. (small)	1	4.9		1	131		57	
Chiroteuthis sp. (large)	1	5.7		1	150		84	
"*Batoteuthis* sp."	59	4.2±0.3	(3.1-4.9)	56	120	(89-141)	76	(32-118)
Bathothauma sp.	2	3.4	(3.3-3.5)	2	185	(181-188)	47	(45-49)
Megalocranchia sp.	2	7.4	(7.1-7.8)	2	434	(412-457)	214	(188-240)
Galiteuthis glacialis	359	5.0±0.3	(4.2-5.7)	105	218	(183-246)	92	(59-123)
Mesonychoteuthis hamiltoni	2	10.1	(7.8-12.3)	2	423	(332-514)	496	(257-735)
Eroded beaks	11							
SEABIRDS								
Penguin feathers	numerous							

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

Prey sizes

The prey ranged in size from 6 to 130 mm body length in crustaceans, 100 to 250 mm estimated length in fish and 109 to 591 mm DML in squid (Table 21, size distributions for all species pooled in Fig. 10). However, Antarctic Krill was the smallest prey species that had any importance in the diet composition by mass (body size from 28 to 50 mm). Analysis of accumulated squid beaks showed slightly an extended DML range (68 to 637 mm, Table 22) compared with the data obtained from fresh squid material.

Comparison with other studies

Previous reports have already highlighted the role of cephalopods in the food of the Lightmantled Sooty Albatross (Matthews 1929, Paulian 1953) with various other prey types complementing the diet including krill, amphipods and prions *Pachyptila desolata* (at sea in the South Atlantic and Weddell Sea, Falla 1937), crustaceans and fish (Heard Island, Downes *et al.* 1959) and crustaceans, fish and mammal remains (Crozet Islands, Mougin 1970b). In the Southern Pacific and the Ross Sea, two Lightmantled Sooty Albatrosses caught at sea had exclusively fed on krill (Ainley *et al.* 1984).

The only previous quantitative study of the diet of the Lightmantled Sooty Albatross was undertaken at South Georgia and showed a similar diet (Table 23) after allowance is made for the higher wet mass contribution of Antarctic Krill. This high proportion of krill is consistent with the huge abundance of the species around South Georgia. The squid component of the diet of this albatross at Crozet and Marion Islands was similar, with *K. longimana* and, to a lesser extent other onychoteuthids, largely prevailing by mass, several taonine cranchiids being second and the glacial squid *Psychroteuthis glacialis* third (Berruti & Harcus 1978 and references in Table 23). On the other hand, squid species composition in the food of the Lightmantled Sooty Albatross at South Georgia was distinctive in the prevalence, by reconstituted mass, of *P. glacialis*. This species was twice as important as *Galiteuthis/Teuthowenia* which ranked second and was four times as important as *K. longimana*. This difference accords well with the higher latitude of South Georgia and its proximity to pack ice which is there deflected northward by the Weddell Drift. The glacial squid whose habitat is mainly in the pack ice area are therefore more readily exploitable by birds breeding at South Georgia some 1000 km to the north, than at Crozet and Marion Islands which are located 2000 km north of the summer sea-ice limit.

Foraging range and behaviour

The Lightmantled Sooty Albatross is known from subantarctic waters to the pack-ice area *i.e.* 41° to 67°S and its abundance peaks in the antarctic waters between 56° and 67°S with immature birds remaining in the southern part of this range (Bierman & Voous 1950, Ainley *et al.* 1984, Weimerskirch *et al.* 1985, Stahl 1987, Woehler *et al.* 1990). Around the Crozet Islands this albatross does not forage over the shelf and seems restricted to southern oceanic waters. There are no direct evidence of long distance foraging trips to the south. However, the frequency of occurrence of Antarctic Krill and the presence of the glacial squid *P. glacialis* in the diet suggests that birds engaged in breeding duties at the Crozet Islands regularly forage south of 55°S and occasionally as far as *c.* 60°S or more during the chick-rearing period.

The Lightmantled Sooty Albatross was reported (Harper 1987) to feed exclusively during daylight hours by surface seizing (78%), filtration for krill (15%) or shallow plunging (7%). On the other hand Weimerskirch *et al.* (1985) have suggested that *Phoebetria* albatrosses, unlike *Diomedea* species, were mainly nocturnal feeders. Obviously further investigations and the use of activity recorders are necessary to elucidate this point (see also discussion under mollymawks

TABLE 23

LIGHTMANTLED SOOTY ALBATROSS DIETS AT VARIOUS LOCALITIES

Localities	Diets (% by mass, main prey species in brackets)					References
	Euphausiids	Other crustaceans	Fish	Squid	Carrion	
South Georgia (52S)	35.5 (1)	4.0 (2)	10.9 (4)	45.5 (5,6,7)	4.1 (8)	Thomas 1982, modified by Prince & Morgan 1987
Crozet Islands (46S)	14.8 (1)	1.2 (3)	10.9	56.4 (6,7)	16.7 (9)	(this work)

The main prey species are: (1) *Euphausia superba*, (2) decapods, (3) decapods and mysids, (4) myctophids and nototheniids, (5) *Psychroteuthis glacialis*, (6) *Kondakovia longimana*, (7) *Galiteuthis* spp., (8) penguins and prions , (9) penguins and mammals above). Finally, scavenging appears as an important feeding method at the Crozet Islands since fragments of seabirds, marine mammals and very large squid specimens (up to a 5.3-kg *Kondakovia longimana*) contribute significantly to its diet.

SOOTY ALBATROSS *PHOEBETRIA FUSCA*

Results

Samples

The stomach contents of 31 Sooty Albatrosses were collected from 15 March 1982 to 4 April 1982. Spontaneous regurgitations of chicks were complemented by samples obtained using the water-flushing method. Eleven stomach contained oil, other liquid material and accumulated items with no fresh material. The mean reconstituted mass of the solid fraction was 105 $\pm$ 76 g (1-207 g) in the 20 samples in which solid material occurred.

General composition

The food of the Sooty Albatross consisted mostly of carrion and squids with fish and crustaceans being of minor importance in the analysis by mass (Table 24). Crustaceans prevailed when samples were analysed on the basis of numerical abundance. On an individual stomach basis, carrion, squid, crustaceans and fish accounted for more than 50% by mass in respectively eight, seven, four and one samples out of 20.

Crustaceans

Epipelagic forms such as the euphausiids *Euphausia superba* and *E. vallentini* and the hyperiid *Themisto gaudichaudii* were the most numerous taxa whereas several large-sized deep-sea species prevailed by mass (Table 24). The latter included the gammarid *Eurythenes gryllus*, the mysid *Gnathophausia gigas* and the shrimp *Pasiphaea longispina*. Three of the four samples dominated by crustaceans contained these deep-dwelling forms.

Cephalopods

Cephalopod prey always occurred as fragments and no one complete specimen was found. Consequently, diagnostic organs were not present in every sample in which squid occurred. Ten beaks in buccal masses were identified as belonging to four species, the most common being *Histioteuthis eltaninae* (Table 24). Accumulated material found in the stomach samples and in 13 pellets regurgitated at the nest site, included 1161 lower beaks from 30 distinct taxa (Table 25). The most numerous were the cranchiid *Galiteuthis glacialis*, the family Histioteuthidae and "*Batoteuthis* sp." (see the Lightmantled Sooty Albatross section for identification). The most important taxa by reconstituted mass were *G. glacialis* and the two large-sized onychoteuthids *Kondakovia longimana* and *Moroteuthis knipovitchi*.

Fish and carrion

Fish remains included diagnostic organs in only two samples, with *Notothenia squamifrons* and *Paradiplospinus gracilis* being identified. Bird carrion constituted about one half of the Sooty Albatross diet, with penguins *Eudyptes* spp. and prions *Pachyptila* spp. accounting for similar mass percentages. Prions were either ingested whole or in pieces. Fish bones and bird feathers were also found as accumulated items.

Prey sizes

Prey sizes ranged from 14 to 130 mm body length in crustaceans, 50 to 360 mm standard length in fish and from 30 to 727 mm estimated DML in squids (Tables 24 and 25, size distributions for all species pooled in Fig. 11).

Comparison with other studies

TABLE 24

THE DIET OF THE SOOTY ALBATROSS AT THE CROZET ISLANDS (N=20)

Prey Species	Occurrence	Relative abundance		Reconstituted mass		Body length (mm)[b]		
	%	No.[a]	%	(g)	%	Mean ± S.D.	(range)	n
CRUSTACEANS	**50.0**	**227**	**87.3**	**57.8**	**2.7**			
Gammarid amphipods								
Eurythenes gryllus	5.0	1	0.4	18.0	0.8	85		1
Hyperiid amphipods								
Themisto gaudichaudii	15.0	23	8.8	2.6	0.1	19 ± 2	(14-22)	13
Hyperia sp.	5.0	1	0.4	+	+			
Euphausiids								
Euphausia superba	5.0	5	1.9	2.7	0.1	41 ± 3	(37-47)	5
E. vallentini	10.0	191	73.5	5.8	0.3	17 ± 1	(15-20)	21
Mysids								
Gnathophausia gigas	25.0	4	1.5	21.2	1.0	81 ± 37	(42-130)	4
Decapods								
Pasiphaea longispina	10.0	2	0.8	7.5	0.4	100		1
CEPHALOPODS	**50.0**	**(15)**	**5.8**	**855.0**	**40.5**			
Teuthoidea								
Architeuthis sp.	5.0	(1)	0.4	80.0	3.8			
Kondakovia longimana	5.0	(1)	0.4	30.0	1.4			
Gonatus antarcticus	5.0	(1)	0.4	200.0	9.5			
Histioteuthis eltaninae	25.0	(7)	2.7	235.0	11.1	58		1
Unidentified	25.0	(5)	1.9	310.0	14.7			
FISH	**35.0**	**(7)**	**2.7**	**115.0**	**5.5**			
Perciformes								
Lepidonotothen squamifrons	5.0	(1)	0.4	80.0	3.8	200		1
Paradiplospinus gracilis	5.0	(1)	0.4	5.0	0.3	360		1
Unidentified	25.0	(5)	1.9	30.0	1.4	146 ± 64	(50-200)	5

OTHER ORGANISMS	**55.0**	**(11)**	**4.2**	**1080.0**	**51.2**
Carrion					
Eudyptes sp.	25.0	(5)	1.9	620.0	29.4
Pachyptila salvini	25.0	(5)	1.9	440.0	20.9
P. turtur	5.0	(1)	0.4	20.0	0.9

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

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

TABLE 25

SUMMARY OF ACCUMULATED ITEMS IN SOOTY ALBATROSS STOMACH CONTENTS (31 STOMACHS AND 13 PELLETS)

Items	Number of items	Measurements (mm)[a]			Estimated body length (mm)[b]		Estimated body mass (g)	
		Mean ± S.D.	(range)	n	Mean	(range)	Mean	(range)
CEPHALOPODS								
Lower beaks	1163							
Architeuthis sp.	2	5.4	(4.2-6.6)	2	266	(195-337)	542	(123-961)
Onychoteuthis sp. (small)	1	2.1		1	97		26	
Onychoteuthis sp. (large)	3	3.9	(3.8-3.9)	3	207	(200-211)	265	(238-283)
Onychoteuthis sp. (ridge)	4	6.4 ± 0.6	(5.6-7.0)	4	364	(313-399)	1823	(1048-2417)
Moroteuthis robsoni	1	8.3		1	499		1565	
M. knipovitchi	50	7.0 ± 0.5	(5.9-8.2)	45	353	(247-485)	848	(477-1475)
Kondakovia longimana	27	10.0 ± 3.3	(2.4-15.4)	26	438	(101-680)	2284	(25-6498)
Gonatus antarcticus	8	6.0 ± 0.7	(5.3-7.4)	8	212	(186-276)	208	(138-415)
Ancistrocheirus lesueuri	1	6.5		1	224		645	
Lycoteuthis sp.	1	4.0		1	91		40	
Lycoteuthis sp. A	2	3.5	(2.9-4.2)	2	78	(66-91)	29	(18-40)
Octopoteuthis sp.	1	11.5		1	199		334	
Taningia sp.	2	12.5	(12.1-12.8)	2	381	(356-406)	2341	(2130-2553)
Lepidoteuthis sp.	1	17.1		1	727		3998	
Histioteuthis spp. A	104	4.7 ± 1.3	(2.0-7.8)	98	91	(30-16)	198	(24-566)
Histioteuthis spp. B (including *H. eltaninae*)	179	3.4 ± 0.6	(2.7-6.4)	152	88	(69-166)	73	(44-250)
Alluroteuthis antarcticus	10	5.0 ± 0.3	(4.6-5.5)	8	140	(130-153)	149	(118-185)
Cycloteuthis sp.	1	11.5		1	357		775	
Mastigoteuthis sp. A	7	7.0 ± 0.6	(6.1-7.9)	7	202	(177-229)	332	(224-466)
Chiroteuthis sp. (small)	2	3.8	(3.3-4.3)	2	105	(93-117)	30	(21-40)
Chiroteuthis sp. (large)	6	6.0 ± 1.0	(4.6-7.1)	6	159	(124-186)	106	(49-157)
C. imperator	2	4.0	(2.9-5.1)	2	110	(83-137)	39	(14-65)
"*Batoteuthis* sp. "	159	4.2 ± 0.3	(3.2-5.0)	60	121	(91-142)	78	(34-121)

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