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Fish and squid in the diet of king penguin chicks, *Aptenodytes patagonicus*, during winter at sub-antarctic Crozet Islands

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Abstract The diet of king penguins, *Aptenodytes patagonicus*, rearing chicks was studied during three consecutive austral winters (1990, 1991 and 1992) at Crozet Islands. The mean stomach content mass of the 47 samples was 503 g. Percentages of wet and reconstituted masses showed that both fishes (66 and 36%, respectively) and squid (34 and 64%) are important components of the winter diet. Juveniles of the demersal onychoteuthid squid *Moroteuthis ingens* form the bulk of the cephalopod diet, and this was the main prey by reconstituted mass (57%). Myctophid fish (lanternfishes) accounted for most of the fish diet, constituting together 32% by mass. The three main species of myctophids eaten in summer by king penguins were either very rare in winter (*Electrona carlsbergi*) or accounted for a smaller proportion of the diet (*Krefftichthys anderssoni* = 1.5% by mass and *Protomyctophum tenisoni* = 4.6%). Five other myctophids, which are rarely consumed in summer, contributed 24% of the diet by mass in winter (*Gymnoscopelus piabilis* = 18.1%, *Lampichthys procerus* = 2.4%, *G. nicholsi* = 1.3%, and *Metelectrona ventralis* and *Electrona subaspera* = 1.0%). The greater diversity of prey in winter suggests a more opportunistic feeding behaviour at a time probably marked by a change in prey availability. Both the known ecology of the fish and squid prey and the barely digested state of some items suggest that in winter breeding adults forage in the outer shelf, upper slope and oceanic areas in the close vicinity of the Crozet Islands to feed their chicks. Finally, using king penguins as biological samplers, the present work provides novel data on the previously unstudied mesopelagic/epibenthic marine community in waters surrounding the Crozet Islands. Seventeen myctophid fish have been identified to species level. These include several poorly known species in the southern Indian Ocean. The occurrence of small, nearly intact, cephalopods in the diet of king penguins suggests that spawning grounds of four squid species may be located near the Crozet Archipelago.

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Introduction

The king penguin *Aptenodytes patagonicus* is the most specialized sub-antarctic/antarctic seabird species preying almost exclusively on mesopelagic fishes and squid (Adams and Klages 1987; Sabourenkov 1992). Throughout its breeding range in the sub-antarctic, the king penguin in summer feeds mainly on three myctophid species, *Electrona carlsbergi*, *Krefftichthys anderssoni* and *Protomyctophum* spp., with only minor differences between localities (Adams and Klages 1987; Hindell 1988; Klages et al. 1990; Cherel and Ridoux 1992; Olsson and North 1996). In winter, changes in the diet are associated with a declining food supply to the chicks (Adams and Klages 1987; Hindell 1988). At this time, there is either a shift from *K. anderssoni* to *E. carlsbergi* as the major prey item in the southern Pacific Ocean (Macquarie Island; Hindell 1988), or a decrease in the dietary abundance of myctophid fishes and an increase in the importance of squids in the southern Indian Ocean (Marion Island: Adams and Klages 1987).

The population of king penguins is increasing at all censused breeding localities, including the Crozet

Archipelago (southern Indian Ocean), where half the world's population breeds (Guinet et al. 1995). Based on direct counts and satellite remote-sensing, the king penguin population of the Crozet Islands amounts to one million pairs, of which 70% breed at Iles aux Cochons, the largest colony in the world (Guinet et al. 1995). In 1985, predation on marine resources by breeding king penguins in waters surrounding the Crozet Islands was estimated to be 810000 tons, including 745000 tons of myctophid fish and 65000 tons of squid (Guinet et al. 1996). The king penguin is thus a major marine consumer in that part of the Southern Ocean, with an increasing impact on myctophid and squid populations over recent years.

The food of king penguins at the Crozet Islands in summer is now well documented (Cherel and Ridoux 1992; Ridoux 1994), and agrees with dietary studies from other breeding localities. On the other hand, a preliminary short note on the chick diet in winter 1990 clearly showed an increase in the proportion of squids eaten and a change in the fish prey (Cherel et al. 1993c). The aims of the present study were therefore: first, to examine the winter food of king penguins over three successive austral winters (1990, 1991, 1992) to investigate possible dietary seasonal variations of this major and specialized predator; second, to evaluate the consequences of such changes on the feeding ecology and nutrition of king penguins, because winter is a period of long foraging trips for the adults and, consequently, a period of food scarcity and long-term fasts for the chicks (Cherel et al. 1987); and third, to detail the mesopelagic fauna in Crozet waters by using penguins as biological samplers. While of primary importance in the nutrition of marine predators (Sabourenkov 1992; Ridoux 1994), the mesopelagic fauna has never been sampled in the vicinity of Crozet Archipelago, and its ichthyofauna is therefore virtually unknown.

Materials and methods

Fieldwork was carried out on Ile de la Possession, Crozet Archipelago (46°26'S; 51°45'E) during three successive winters (1990, 1991 and 1992) in the breeding colony of *Aptenodytes patagonicus* at La Baie du Marin. Stomach-flushing was used to sample 5 to 7 stomach contents of king penguins at weekly intervals during late June and early July, thus totalling 15 to 17 samples annually and 47 samples over the three years. Adult king penguins were randomly chosen from birds on arrival back at the colony after a foraging trip, but before they fed their single chick. Stomach contents were returned deep-frozen (−20°C) to Strasbourg, France, for analysis. Each sample was thawed, drained and weighed. Items that accumulate over time (eroded squid beaks and otoliths, stones) were discarded.

Sampling and determination and quantification of prey items was carried out according to Cherel and Ridoux (1992). Only otoliths enclosed in the cranium and beaks still within the buccal mass were measured. In two fish species (*Arctozenus risso* and *Paradiplospinus gracilis*), which possess small otoliths rarely found in samples, mandibles rather than otoliths were numbered and measured. Allometric equations given by Clarke (1986), Härkönen (1986), Adams and Klages (1987), Hindell (1988), Rodhouse and Yeatman (1990), Rodhouse et al. (1990), Williams and McEldowney (1990), Jackson (1995), Olsson and North (1996) and Cherel (unpublished data) were used to estimate the length and wet body mass of fish and squid prey. Where equations for certain species were not available, estimates were made from equations for closely related species or for species with a similar morphology. Systematic order follows Gon and Heemstra (1990) for fishes and Nesis (1987) for squid.

Data were compared for statistically significant differences using the Peritz' *F*-test (Harper 1984). Values are means ± SE unless otherwise stated.

Results

Meal size and general diet composition

The average wet mass (whole mass minus the mass of accumulated items) of the 47 stomach contents obtained from adult *Aptenodytes patagonicus* in winter was 503 ± 54 g (range = 29 to 1426 g). They contained, by number, 114 ± 23 (1 to 834) prey items, including 105 ± 23 (0 to 832) fishes and 8 ± 1 (0 to 47) squid. Fishes were therefore the most important food source by number (92.8% vs 7.2% for squid) and wet mass (66.1% vs 33.9%), but not by reconstituted mass (35.8% vs 64.2% for pooled samples). As previously noted (Cherel and Ridoux 1992), crustaceans were commonly found, but were considered to be fish prey secondarily ingested by the penguins.

A total of 5346 prey items was recovered from the 47 stomach contents (4959 fishes and 387 squid). Thirty-eight species or species groups of prey were identified, including 25 species of fishes and 13 of squid. The frequency of occurrence and number of prey items and the reconstituted mass of each taxon are given in Table 1, and size and wet mass are included in the following taxonomic section and in Figs. 1 to 3.

Taxonomic analysis of fish prey

Family Sternoptychidae.

Maurolicus cf. muelleri (Gmelin, 1789). A rare prey item, < 0.1% by number and reconstituted mass; two heads containing otoliths identical to those of *M. muelleri* from the North Atlantic (Härkönen 1986); otolith length (OL) = 1.2 and 1.5 mm, total length (TL) = 45 and 54 mm, body mass (M) = 0.6 and 1.1 g, respectively.

Family Paralepididae

Arctozenus risso (Bonaparte, 1840). An occasional prey species, < 1% by number and mass; previously identified as *Notolepis* sp. by Cherel and Ridoux (1992); mandible length = 7.4 to 13.0 mm (mean length = 9.5 mm, TL = 111 mm, M = 1.8 g), with only one large specimen (mandible length = 21.4 mm; Fig. 2).

Table 1 *Aptenodytes patagonicus*. Frequency of occurrence, numbers and reconstituted mass of prey items identified from stomach contents during winter (total for all 47 samples pooled) (*LRL* lower rostral length)

Species	Occurrence in stomachs		Prey items identified		Reconstituted mass	
	n	(%)	*n*	(%)	(g)	(%)
Fishes						
Sternoptychidae						
Maurolicus cf. *muelleri*	2	(4.3)	2	(< 0.1)	1.7	(< 0.1)
Paralepididae						
Arctozenus risso	11	(23.4)	23	(0.4)	122.5	(0.3)
Magnisudis prionosa	11	(23.4)	17	(0.3)	696.4	(1.6)
Myctophidae						
Electrona carlsbergi	3	(6.4)	6	(0.1)	63.2	(0.1)
Electrona subaspera	11	(23.4)	31	(0.6)	430.3	(1.0)
Gymnoscopelus nicholsi	22	(46.8)	226	(4.2)	584.3	(1.3)
Gymnoscopelus fraseri	4	(8.5)	4	(< 0.1)	22.2	(< 0.1)
Gymnoscopelus piabilis	25	(53.2)	341	(6.4)	8069.3	(18.1)
Krefftichthys anderssoni	15	(31.9)	949	(17.7)	659.0	(1.5)
Lampanyctus australis	2	(4.3)	2	(< 0.1)	23.0	(< 0.1)
Lampichthys procerus	28	(59.6)	531	(9.9)	1075.8	(2.4)
Metelectrona ventralis	20	(42.6)	78	(1.5)	463.8	(1.0)
Protomyctophum andriashevi	3	(6.4)	3	(< 0.1)	4.3	(< 0.1)
Protomyctophum bolini	26	(55.3)	182	(3.4)	134.7	(0.3)
Protomyctophum choriodon	20	(42.6)	64	(1.2)	524.2	(1.2)
Protomyctophum gemmatum	3	(6.4)	4	(< 0.1)	6.4	(< 0.1)
Protomyctophum normani	11	(23.4)	50	(0.9)	45.2	(0.1)
Protomyctophum tenisoni	28	(59.6)	2104	(39.3)	2056.5	(4.6)
Myctophidae sp. C	3	(6.4)	3	(< 0.1)	6.9	(< 0.1)
Myctophidae sp.	3	(6.4)	15	(0.3)	178.4	(0.4)
Ophidiidae						
Ophidiidae sp.	1	(2.1)	2	(< 0.1)	37.2	(< 0.1)
Nototheniidae						
Dissostichus eleginoides	2	(4.3)	2	(< 0.1)	180.7	(0.4)
Notothenioid juveniles[a]	10	(21.3)	265	(5.0)	37.5	(< 0.1)
Gempylidae						
Paradiplospinus gracilis	10	(21.3)	54	(1.0)	549.8	(1.2)
Unidentified fish	1	(2.1)	1	(< 0.1)	1.9	(< 0.1)
Squid						
Onychoteuthidae						
Moroteuthis ingens	23	(48.9)	64	(1.2)	25246.3	(56.5)
Moroteuthis knipovitchi (> 2 mm LRL)	9	(19.1)	32	(0.6)	1703.1	(3.8)
Moroteuthis ?knipovitchi (< 2 mm LRL)	25	(53.2)	137	(2.6)	244.1	(0.6)
Kondakovia longimana	6	(12.8)	40	(0.8)	308.8	(0.7)
Gonatidae						
Gonatus antarcticus	8	(17.0)	16	(0.3)	55.9	(0.1)
Histioteuthidae						
Histioteuthis macrohista	1	(2.1)	1	(< 0.1)	35.4	(< 0.1)
Histioteuthis atlantica	2	(4.3)	5	(< 0.1)	282.0	(0.6)
Neoteuthidae						
Alluroteuthis antarcticus	2	(4.3)	2	(< 0.1)	40.0	(< 0.1)
Brachioteuthidae						
Brachioteuthis sp.	1	(2.1)	1	(< 0.1)	12.3	(< 0.1)
Brachioteuthis ?riisei	9	(19.1)	13	(0.2)	57.6	(0.1)
Ommastrephidae						
Martialia hyadesi	2	(4.3)	2	(< 0.1)	637.9	(1.4)
Chiroteuthidae						
Chiroteuthis sp.	1	(2.1)	1	(< 0.1)	4.0	(< 0.1)
Unidentified squids	23	(48.9)	73	(1.4)	73.0	(0.2)
Total	–	–	5346	(100.0)	44675.4	(100.0)

[a] Include *D. eleginoides*, *Lepidonotothen larseni*, *Harpagifer spinosus*, and a unidentified fishes

Magnisudis prionosa (Rofen, 1963). An occasional large fish prey, < 1% by number, but contributing 1.6% by mass; OL = 3.1 to 6.3 mm, mean value at 4.5 mm (standard length, SL = 316 mm, M = 41.8 g).

Family Myctophidae

Electrona carlsbergi (Tåning, 1932). A rare prey in winter, 0.1% by number and mass; six specimens of the same size class; OL = 3.7 to 4.2 mm (SL = 88 mm, M = 10.5 g).

Electrona subaspera (Günther, 1864). An occasional prey item, < 1% by number and 1% by mass; OL = 1.9 to 4.0 mm, mode at 3.5 to 3.8 mm (mean SL in this mode = 96 mm, M = 16.9 g).

Gymnoscopelus nicholsi (Gilbert, 1911). A common prey that contributed 4.2 and 1.3% by number and mass, respectively; OL = 1.7 to 5.4 mm, mode at 2.0 to 2.5 mm (Fig. 1) (SL = 44 mm, M = 0.83 g).

Gymnoscopelus fraseri (Fraser-Brunner, 1931). A rare prey item, < 0.1% by number and mass; OL = 2.8 to 3.9 mm (SL = 78 mm, M = 5.5 g).

Gymnoscopelus piabilis (Whitley, 1931). An important item in winter that contributed 6.4 and 18.1% by number and mass, respectively; OL = 3.0 to 6.4 mm, mode at 5.0 to 5.5 mm (Fig. 1) (SL = 125 mm, M = 23.1 g).

Krefftichthys anderssoni (Lönnberg, 1905). A very common small fish in the diet, this species contributed 17.7% by number but only 1.5% by mass; OL = 0.5 to 1.8 mm, with two size classes (Fig. 1) at mode 0.8 to 1.0 mm (SL = 23 mm, M = 0.10 g) and at mode 1.4 to 1.6 mm (SL = 48 mm, M = 1.1 g).

Lampanyctus australis Tåning, 1932. A rare prey item, < 0.1% by number and mass; two specimens of similar size, OL = 2.7 and 2.8 mm (SL = 99 and 102 mm, M = 11.0 and 12.0 g), respectively.

Lampichthys procerus (Brauer, 1904). A common fish prey that contributed 9.9 and 2.4% by number and mass, respectively; OL = 1.9 to 3.6 mm, mode at 2.0 to 2.5 mm (Fig. 1) (SL = 53 mm, M = 1.7 g).

Metelectrona ventralis (Bekker, 1963). An occasional prey contributing 1.5% by number and 1.0% by mass; OL = 2.1 to 4.3 mm, mode at 3.5 to 4.0 mm (Fig. 1) (SL = 83 mm, M = 8.7 g).

Protomyctophum andriashevi Bekker, 1963. A rare prey species, with only 3 specimens found in the samples; OL = 1.8 to 2.1 mm (SL = 49 mm, M = 1.4 g).

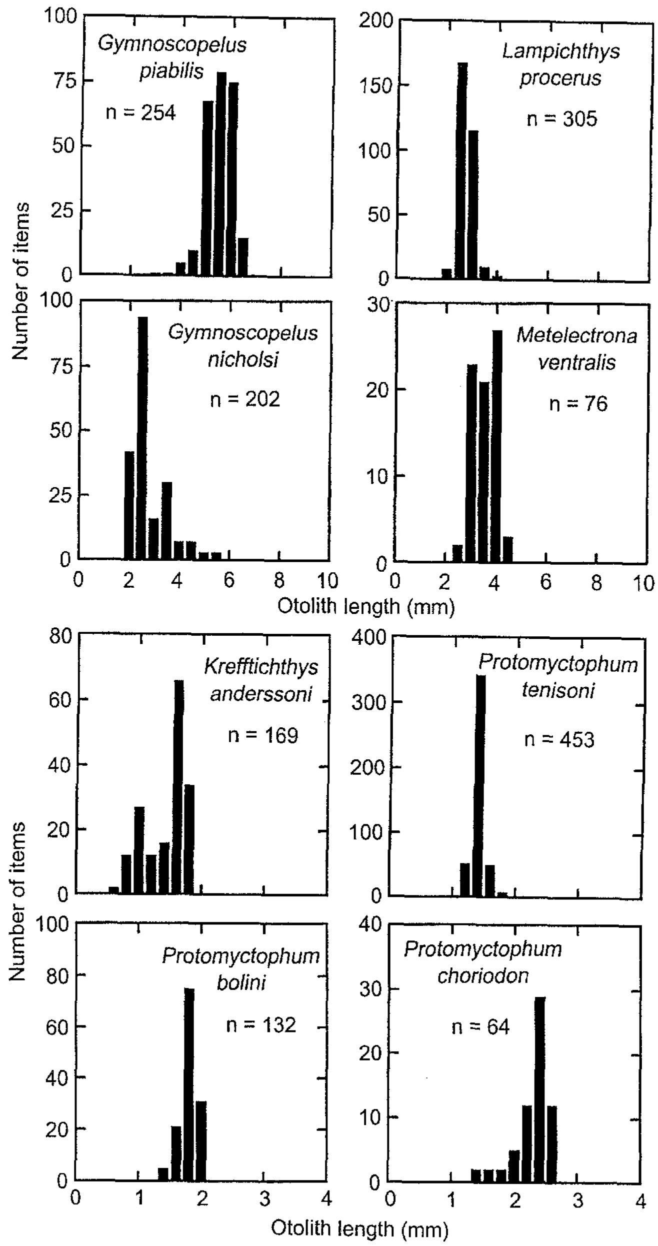

Fig. 1 *Aptenodytes patagonicus.* Number of otoliths of myctophid fishes in stomach contents of king penguin chicks at Crozet Islands during winter as a function of otolith length. Note different scales of abscissas

Protomyctophum bolini (Fraser-Brunner, 1949). A common prey item that contributed 3.4% by number but < 1% by mass; OL = 1.3 to 2.0 mm, mode at 1.6 to 1.8 mm (Fig. 1) (SL = 40 mm, M = 0.89 g).

Protomyctophum choriodon Hulley, 1981. An occasional prey item that contributed 1.2% by number and mass; OL = 1.3 to 2.6 mm, mode at 2.2 to 2.4 mm (Fig. 1) (SL = 81 mm, M = 9.0 g). Otoliths of this species were formerly misidentified as *Protomyctophum normani* (Cherel and Ridoux 1992).

Protomyctophum gemmatum Hulley, 1981. A rare prey species, with only four specimens found in the samples; OL = 2.6 to 2.8 mm (SL = 48 mm, M = 1.6 g).

Protomyctophum normani (Tåning, 1932). An occasional prey which contributed < 1% by number and mass. Otolith length ranged from 1.3 to 1.7 mm, with a mode at 1.4 to 1.6 mm (SL = 37 mm, M = 0.83 g).

Protomyctophum tenisoni (Norman, 1930). The most abundant prey species in winter; this species contributed 39.4% by number, but, owing to its small size, only 4.6% by mass; OL = 1.1 to 1.8 mm, mode at 1.2 to 1.4 mm (Fig. 1) (SL = 40 mm, M = 0.92 g).

Myctophidae *sp. C.* An unidentified species of myctophid, with otoliths clearly different in shape and size from the species listed above. Myctophidae sp. C was a rare prey item (< 0.1% by number and mass) of small size, all OL being 1.7 mm.

Family Ophidiidae

Two specimens of an unidentified species of this family were found in one sample. They were nearly intact, thus allowing the measurement of their standard length (183 and 184 mm, respectively) and body mass (18.6 g each).

Family Nototheniidae

Dissostichus eleginoides Smitt, 1898. A rare prey species, with only two specimens recorded; OL = 4.9 and 5.5 mm (SL = 169 and 214 mm, M = 57.9 and 122.9 g), respectively.

Juveniles of suborder Notothenioid. Juvenile fishes were common prey items for king penguins in winter; they contributed 5.0% by number but < 0.1% by mass. Most of them were at an advanced stage of digestion, thus precluding species identification. However, a few better preserved specimens indicated the presence of at least three different species, the Nototheniidae *Dissostichus eleginoides* and *Lepidonotothen larseni* (Lönnberg, 1905), and the Harpagiferidae *Harpagifer spinosus* Hureau, Louis, Tomo and Ozouf 1980. Two *L. larseni* had a 21 to 23 mm SL for a 0.11 g body mass, and the SL and M of ten specimens of *H. spinosus* ranged between 19 and 22 mm, and 0.11 and 0.20 g, respectively.

Family Gempylidae

Paradiplospinus gracilis (Brauer, 1906). An occasional fish prey, that contributed 1.0 and 1.2% by number and mass, respectively; mandible length = 11.2 to 16.5 mm, mode at 14.0 to 15.0 mm (Fig. 2) (SL = 206 mm, M = 7.3 g); three specimens of larger size: mandible length = 21.5, 29.6 and 30.0 mm, respectively.

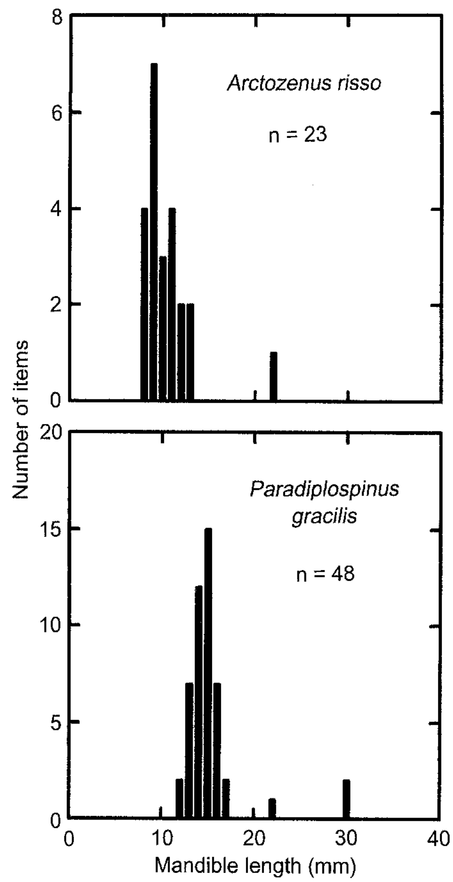

Fig. 2 *Aptenodytes patagonicus.* Number of mandibles of paralepidid fishes in stomach contents of king penguin chicks at Crozet Islands during winter as a function of mandible length

Taxonomic analysis of squid prey

Family Onychoteuthidae

Moroteuthis ingens (Smith, 1881). This species constituted the main prey by mass in winter, accounting alone for 56.8% of the whole reconstituted mass, but only 1.2% by number; lower rostral length (LRL) = 4.3 to 8.7 mm, main mode at 5.0 to 5.5 mm, and a discrete mode at 8.0 to 8.5 mm (Fig. 3). The use of sex-specific allometric equations (Jackson 1995) indicates that the first mode corresponded to male and female squids of 227 mm (M = 328 g) and 206 mm (M = 310 g) dorsal mantle length (ML), respectively, and the second mode to specimens with a ML of 300 mm (M = 741 g) and 340 mm (M = 1344 g), respectively.

Moroteuthis knipovitchi Filippova, 1972 – > 2 mm LRL. An occasional squid prey; < 1% by number but

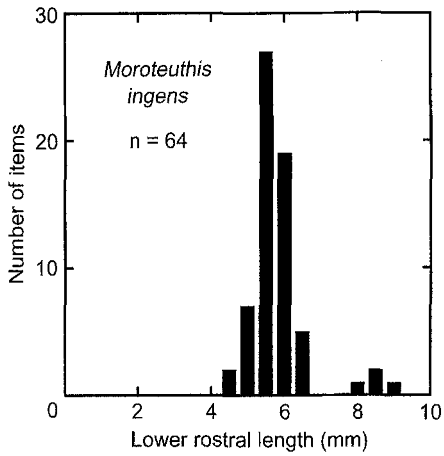

Fig. 3 *Aptenodytes patagonicus*. Number of lower beaks of onychoteuthid squid *Moroteuthis ingens* in stomach contents of king penguin chicks at Crozet Islands during winter as a function of lower rostral length

contributing 3.8% by mass; LRL = 2.0 to 3.9 mm, mode at 3.5 to 4.0 mm (ML = 134 mm, M = 95.4 g).

Moroteuthis ?knipovitchi Filippova, 1972 – < 2 mm LRL. A common prey item that contributed 2.6% by number but < 1% by mass. The measured ML of 20 specimens averaged 24 ± 3 mm (range = 11 to 60 mm). A doubt remains on the species identification due to the small to very small size of these squids. Hooks on the tentacular clubs together with beak morphology are indicative of Onychoteuthidae, whereas no marginal suckers on the tentacular clubs and a smooth mantle skin suggest *M. knipovitchi.*

Kondakovia longimana Filippova, 1972. An occasional prey item, < 1% by number and mass; LRL = 1.2 to 5.1 mm, mode at 1.0 to 1.5 mm (ML = 24 mm, M = 1.4 g); largest specimen: ML = 166 mm and M = 117 g.

Family Gonatidae

Gonatus antarcticus Lönnberg, 1898. Fifteen small specimens identified from the flesh, and one larger arm crown without buccal mass; small specimens, LRL = 1.7 to 2.2 mm (ML = 35 mm, M = 4.0 g).

Family Histioteuthidae

Histioteuthis macrohista N. Voss, 1969. One barely digested specimen; LRL = 2.4 mm (ML = 39 mm, M = 35.4 g).

Histioteuthis atlantica (Hoyle, 1885). A rare prey species; four well-preserved specimens; LRL = 2.8 to 3.3 mm (ML = 56 mm; M = 69.9 g); one smaller individual; LRL = 0.7 mm (ML = 18 mm, M = 2.5 g).

Family Neoteuthidae

Alluroteuthis antarcticus Odhner, 1923. Two specimens; one very small (LRL = < 1 mm) and one larger (LRL = 2.3 mm, ML = 71 mm, M = 39.0 g).

Family Brachioteuthidae

The genus *Brachioteuthis* is in need of revision. Two different species have been collected in Kerguelen waters. One species is marked by a narrow mantle, a rhomboidal fin, a rugose skin resembling that of *Moroteuthis ingens*, and expanded tentacular clubs. According to Nesis (1987), this species is *B. picta*. However, unlike the lower beak of *B. ?picta* from the Atlantic sector (Rodhouse et al. 1992), the beak of both the Kerguelen species and the specimen eaten by king penguins at the Crozet Islands has a distinct thickened lateral ridge. We therefore called it *Brachioteuthis* sp. The second species, *B. ?riisei*, is characterized by a wider mantle, a heart-shaped fin, a smooth skin, narrow tentacular clubs, and by a lower beak with no ridge on the lateral wall.

Brachioteuthis sp. One large individual, LRL = 4.0 mm (ML = 97 mm, M = 12.3 g).

Brachioteuthis ?riisei, (Steenstrup, 1882). Seven small and six large specimens; 0.2 and 0.1% by number and mass, respectively; large individuals: LRL = 2.4 to 3.6 mm (ML = 75 mm, M = 7.8 g).

Family Ommastrephidae

Martialia hyadesi Rochebrune and Mabille, 1889. Two specimens; LRL = 4.7 and 5.9 mm (ML = 241 and 275 mm, M = 249 and 389 g).

Family Chiroteuthidae

Chiroteuthis sp. One head without buccal mass, thus precluding the calculation of ML and M of this single specimen.

Interannual variation in meal size and prey-class constituents

No significant interannual differences were found in either the number of items per sample and the mass per sample or in the number of fishes and squid per sample

Table 2 *Aptenodytes patagonicus*. Interannual changes in mass (= wet mass minus mass of accumulated items) and in general diet composition of stomach contents during winter. Data are means ± SE. Values in same column *not* sharing a common superscript letter are significantly different ($P < 0.05$)

Year	(*n*)	Total content		Fishes			Squid		
		no. of items	mass (g)	no. of items	mass (g)	% mass	no. of items	mass (g)	% mass
1990	(15)	54 ± 13^a	623 ± 84^a	49 ± 13^a	296 ± 75^a	42.6 ± 8.6^a	6 ± 1^a	327 ± 62^a	57.4 ± 8.6^a
1991	(17)	111 ± 31^a	456 ± 106^a	105 ± 29^a	383 ± 102^a	86.0 ± 6.4^b	7 ± 3^a	73 ± 32^b	14.0 ± 6.4^b
1992	(15)	174 ± 60^a	437 ± 84^a	163 ± 60^a	312 ± 69^a	$69.3 \pm 8.6^{a,b}$	12 ± 3^a	125 ± 49^b	$30.7 \pm 8.6^{a,b}$
Average value for all three winters combined	(47)	114 ± 23	503 ± 54	105 ± 23	333 ± 49	66.8 ± 5.2	8 ± 1	171 ± 32	33.2 ± 5.2

Table 3 *Aptenodytes patagonicus*. Interannual changes in percentages by number and reconstituted mass, and in otolith length or lower rostral length of main prey items of king penguin chicks during winter. Data are means ± SD with *n* in parentheses. Values in same row *not* sharing a common superscript letter are significantly different ($P < 0.05$)

	% by number			% by reconstituted mass			Otolith length or lower rostral length (mm)		
	1990	1991	1992	1990	1991	1992	1990	1991	1992
Fishes									
Gymnoscopelus nicholsi	4.3	6.4	2.6	1.4	1.3	1.2	(32) 3.16 ± 0.96^a	(103) 2.32 ± 0.53^b	(67) 2.60 ± 0.75^c
Gymnoscopelus piabilis	5.1	12.5	2.4	5.7	45.1	10.2	(35) 5.30 ± 0.45^a	(159) 5.26 ± 0.50^a	(60) 5.21 ± 0.72^a
Krefftichthys anderssoni	1.9	27.3	15.8	< 0.1	4.2	0.9	(11) 1.36 ± 0.22^a	(76) 1.39 ± 0.26^a	(82) 1.27 ± 0.37^a
Lampichthys procerus	7.1	3.0	15.9	0.7	1.0	5.8	(59) 2.55 ± 0.38^a	(57) 2.56 ± 0.29^a	(189) 2.43 ± 0.20^b
Metelectrona ventralis	1.9	0.8	1.8	0.6	0.8	1.8	(16) 3.47 ± 0.42^a	(16) 3.36 ± 0.43^a	(44) 3.21 ± 0.46^a
Protomyctophum bolini	11.3	2.6	1.5	0.3	0.4	0.2	(44) 1.75 ± 0.09^a	(50) 1.67 ± 0.16^b	(38) 1.68 ± 0.09^b
Protomyctophum choriodon	3.6	0.2	1.2	1.0	0.4	2.1	(30) 2.05 ± 0.29^a	(4) 2.38 ± 0.15^b	(30) 2.32 ± 0.15^b
Protomyctophum tenisoni	27.7	33.7	47.2	1.2	5.3	7.9	(79) 1.29 ± 0.08^a	(163) 1.35 ± 0.12^a	(211) 1.28 ± 0.07^a
Squid									
Moroteuthis ingens	4.7	0.6	0.5	75.6	29.8	55.6	(39) 5.43 ± 0.40^a	(12) 5.15 ± 0.44^a	(13) 6.53 ± 1.23^b

(Table 2). However, there was a trend for wet mass to be higher in 1990, and for the number of items to increase over the three years.

While the wet mass of fishes did not vary significantly, the wet mass of squid was 4.5 and 2.6 times higher in 1990 than in 1991 and 1992, respectively (Table 2). This difference was mainly due to a larger proportion of *Moroteuthis ingens* in the diet during winter 1990. At this time, *M. ingens* contributed 5% (< 1% in 1991 and 1992) and 76% (30% in 1991 and 56% in 1992) by number and reconstituted mass, respectively (Table 3). Several myctophid species also showed interannual variations in number and mass. For example, 1991 and 1992 were marked, respectively, by the importance of *Gymnoscopelus piabilis* (13 and 45% by number and mass, respectively) and *Lampichthys procerus* (16 and 6%) in the diet of king penguin chicks. On the other hand, few *Krefftichthys anderssoni* occurred in 1990, whereas *Protomyctophum tenisoni* was always the most abundant prey item over the three winters (28 to 47% by number).

Interannual differences in size were observed in 5 out of 9 of the main prey items (Table 3). Mean otolith length of *Lampichthys procerus* was smaller in 1992, and that of *Protomyctophum bolini* and *P. choriodon* was smaller in 1990. Lower rostral length of *Moroteuthis ingens* was on average larger in 1992, because four larger (adult) squids had been consumed by penguins during that period.

General comments on prey species

Ten prey species, including eight species of fish (*Gymnoscopelus nicholsi, G. piabilis, Krefftichthys anderssoni, Lampichthys procerus, Metelectrona ventralis, Protomyctophum bolini, P. choriodon* and *P. tenisoni*) and two of squid (*Moroteuthis ingens* and *M. ?knipovitchi*) occurred in > 30% of the samples. Taken together, these common prey species contributed 87.5 and 87.4% by number and reconstituted mass to the diet, respectively (Table 1).

The fish diet was dominated by myctophids, which accounted for 68.0% of the total number of identified fish taxons, 92.6% of the fish prey, and 89.8% of fish reconstituted mass. The commonest fish prey was *Protomyctophum tenisoni* (42.4% of fish prey), followed by *Krefftichthys anderssoni* (19.1%) and *Lampichthys procerus* (10.7%). Due to their small sizes, however, these three species only contributed 12.9, 4.1 and 6.7% of the fish mass, respectively. On the other hand, larger individuals of *Gymnoscopelus piabilis* contributed only 6.9% by fish number, but this was the main species by fish reconstituted-mass (50.5%).

The most important squids in the winter diet of king penguin chicks were onychoteuthids with three species (*Moroteuthis ingens*, *M. knipovitchi* and *Kondakovia longimana*) contributing 70.5% of squid numbers and 95.8% of squid reconstituted mass. While accounting for only 16.5% of the total number of cephalopods, large specimens of *M. ingens* contributed 88.0% of squid biomass, and this species was therefore by far the most important squid prey in winter, the second most important species being *M. knipovitchi* (5.9% of squid mass).

Index of diversity

The Shannon diversity index of individuals and biomass was calculated (using ln transformation; Begon et al. 1986) for each year separately and all three years combined (Fig. 4). It was calculated by determining for each species the proportion of individuals (or biomass) it contributed to the total in the sample. The value of the index depends on both the number of species (the richness) and the distribution of the individuals among species (equitability) (Begon et al. 1986). The values for 1990, 1991 and 1992 were 1.8 to 2.5 (equitability = 0.5 to 0.7) and 1.2 to 1.8 (0.4 to 0.5) for numbers and biomass, respectively. For the three years combined, it was 2.1 (equitability = 0.6) for individuals and 1.7 (0.5) for biomass. These values are higher than those calculated from data obtained in summer (Cherel and Ridoux 1992), i.e. 1.2 (equitability = 0.5) and 0.9 (0.3) for numbers and biomass, respectively (Fig. 4).

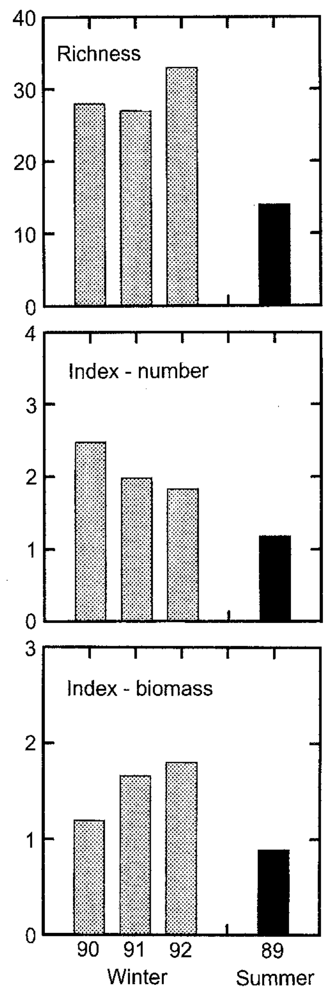

Fig. 4 *Aptenodytes patagonicus*. Richness (number of taxons) and Shannon diversity index for number of individuals and biomass calculated for king penguin diet in winters 1990, 1991 and 1992. For comparison, richness and indices were also calculated for summer 1989 from data published in Cherel and Ridoux (1992)

Discussion

Composition of chick diet in winter

This study shows that there are quantitative and qualitative changes in the diet of *Aptenodytes patagonicus* in winter compared to the other seasons (summer period). The same species of myctophid fishes (*Electrona carlsbergi*, *Krefftichthys anderssoni* and *Protomyctophum* spp.) have formed the bulk of the food during every summer season investigated in all the localities studied so far (Adams and Klages 1987; Hindell 1988; Adams and Brown 1989; Klages et al. 1990; Olsson and North 1996), including the Crozet Archipelago during the austral summers 1980/1981, 1988/1989, 1989/1990 and 1990/1991 (Cherel and Ridoux 1992; Cherel et al. 1993c; Ridoux 1994). In winter, squid is a main component of the diet at the Crozet Islands, accounting for 34% of the wet mass and 64% of the reconstituted mass over the three years studied. The difference between percentages of wet and reconstituted mass is due to the overestimation of the large squid prey *Moroteuthis ingens* in the reconstituted mass (57%; Table 1). This main squid prey-species was found either intact or semi-digested in the samples and, in the latter case, each lower beak was still enclosed in the buccal mass that weighs only a few grams. This gave an estimate of more than 300 g per buccal mass in the reconstituted mass.

Only two other studies (Adams and Klages 1987; Hindell 1988) have investigated the winter diet of king penguins. As in the present study, these investigators noted a change in the diet associated with the presumably declining food supply. At Macquarie Island, the myctophid *Krefftichthys anderssoni*, dominant in summer, is replaced by another myctophid, *Electrona carlsbergi*, in winter (Hindell 1988), while at Marion Island myctophids are partly replaced by the squid *K. longimana* (Adams and Klages 1987). Onychoteuthid squids, either *K. longimana* (Marion Island) or *Moroteuthis ingens* and *M. knipovitchi* (Crozet Islands) are therefore important to the nutrition of king penguins during the austral winter in the western Indian Ocean, where most of the world's population breeds. *M. ingens* is the largest prey eaten by king penguins, with some specimens reaching a mantle length of > 300 mm and a body mass of ~ 1000 g. Most of the specimens, however, were juvenile squids, as indicated by the wings of the lower beaks that were undarkened or just beginning to darken. The only other large squids eaten were two juveniles of the ommastrephid squid *M. hyadesi*, a species not previously recorded in Crozet waters.

As previously found at Marion and Macquarie Islands (Adams and Klages 1987; Hindell 1988), the winter fish diet is dominated by myctophids, which account for 90% of reconstituted fish mass at the Crozet Islands. However, king penguins from the Crozets had a more diverse myctophid diet in winter (15 species) than birds from Marion (6 species) and Macquarie (2 identified species) during both winter and summer seasons. Such differences probably result from the analysis of only small subsamples of the stomach contents inducing an underestimation of occasional and rare prey items (Hindell 1988), and because of problems in identifying highly digested prey from hard-part remains at a time when only limited information was available (Adams and Klages 1987). Consequently, dietary analyses from the Crozet Islands (Cherel and Ridoux 1992; and present study) add eight myctophid species as prey for king penguins, including *Electrona subaspera*, *Gymnoscopelus piabilis*, *Lampichthys procerus*, *Metelectrona ventralis* (formerly called Myctophid A in Adams and Klages 1987; N. Klages personal communication) and *Protomyctophum choriodon*. In addition to king penguins, antarctic fur seals and, to a lesser extent, gentoo penguins and white-chinned petrels, also prey upon a great number of species of myctophid fish (Sabourenkov 1992).

Even if less important than in summer, *Krefftichthys anderssoni* and *Protomyctophum tenisoni* are the most numerous myctophids eaten in winter, but together, due to their small size, they never accounted for $> 10\%$ of the reconstituted mass of the diet. The trend for the number of prey items to rise over the three years is related to an increase in the proportion of *K. anderssoni* and *P. tenisoni* in 1991 and 1992 compared to 1990. There was no interannual variation, however, in the size of the fishes. The size-frequency of *K. anderssoni* is bimodal (Fig. 1), as previously found during summer at Crozet Islands (Cherel and Ridoux 1992), and throughout the year at Marion Island (Adams and Klages 1987), the two size classes corresponding to juvenile and subadult fish.

Individuals of the genus *Gymnoscopelus* are important prey items in winter, with *G. nicholsi* and *G. piabilis* contributing 4 and 6%, respectively, by number. However, owing to its larger size, *G. piabilis* contributed more to the reconstituted mass than *G. nicholsi* (18 vs 1%). Since *G. piabilis* and *G. nicholsi* are sexually mature at ~ 9 and 160 mm, respectively (Hulley 1990), king penguins prey on adult fish of the former species and juveniles of the latter. No interannual variation in the size of *G. piabilis* was noted, whereas specimens of *G. nicholsi* were larger in 1990.

The present study is the first to record *Lampichthys procerus* as an important prey item for a sub-antarctic/antarctic marine predator (Sabourenkov 1992). One size-class of juvenile fish was found every year in the samples, and appears therefore to be a common food for king penguins in winter at the Crozet Islands. The paralepids *Magnisudis prionosa* and *Arctozenus risso*, the myctophid fishes *Metelectrona ventralis*, *Protomyctophum bolini*, *P. choriodon*, *P. normani*, and the gempylid *Paradiplospinus gracilis* have previously been recorded in the diet of fur seals and seabirds, including king penguins, but were not usually major food components (Hindell 1988; Adams and Brown 1989; Cherel and Ridoux 1992; Sabourenkov 1992; Olsson and North 1996).

Interannual variation in the diet of sub-Antarctic penguins is poorly documented. The few data available from Marion Island suggest that prey species of king penguins vary little from year to year (Brown et al. 1990). A complete analysis of the king penguin diet during three consecutive summers at South Georgia has shown that birds prey always upon the same fish species, but that the proportion of items by number and mass vary from year to year (Olsson and North 1996). Similar results were obtained for the food of birds at the Crozet Islands during winter (Table 3), suggesting that within either the summer or winter seasons no substantial change in prey species composition occurs, whereas there is a switch to different prey between the summer and winter months (Adams and Brown 1987; and present study).

Implications for chick nutrition

The king penguin has a unique reproductive cycle among birds, since the whole cycle, including molt, lasts 14 to 15 mo. The rearing period lasts about 11 mo, and can be divided into three parts: a first period of growth from hatching to mid-April, a prolonged period of undernutrition in winter until mid-September, and a second period of growth in spring (Stonehouse 1960; Barrat 1976; Weimerskirch et al. 1992). During the two phases of chick growth, the diet of king penguin chicks always consists of large meals provided at a high rate and containing a large number of myctophid fishes and only a few squids (Adams and Klages 1987; Hindell 1988; Cherel et al. 1993c). Consequently, the rate of energy flow between adult and chick has been estimated to be 25.7 and 16.2 W ($1 \mathrm{W} = 1 \mathrm{J\,s^{-1}}$), in the first and second periods of growth, respectively (Cherel and Ridoux 1992 and unpublished data). Such high rates of energy delivery explain why pre-winter and pre-molting chicks are able to grow and build up nutrient reserves simultaneously (Cherel et al. 1993a).

In winter, meal mass decreases, the proportion of squid in the diet increases, and feeding frequency is very low (Cherel et al. 1987, 1993c; and present). The calculated rate of energy flow between adults and chick therefore approximates 1.0 W, a value 16 to 26 times lower than that calculated during the two periods of growth. Because chick energy-expenditure amounts to 2.6 W kg^{-1} during the winter fasting (Cherel et al. 1993b), the rate of energy-delivery is insufficient to sustain chick metabolism. Consequently, growth of king penguin chicks ceases, body mass decreases, energy reserves are progressively exhausted; and mortality is high during the winter months (Stonehouse 1960; Barrat 1976; Cherel et al. 1987; Van Heezik et al. 1993).

Implications for adult foraging ecology

The duration of the foraging trip, mass of stomach contents, composition of the food and species of prey indicate that the foraging ecology of adult breeding king penguins is different in winter and summer. The three main species of lanternfish eaten in summer were either virtually absent (*Electrona carlsbergi*) or occurred less frequently and in smaller amounts (*Krefftichthys anderssoni* and *Protomyctophum tenisoni*) in the winter diet. The most probable explanation is that these three species of oceanic myctophids are not available, or are less readily available, to king penguins in winter. In the "polar frontal zone", *E. carlsbergi* occurs in smaller and less dense concentrations, which are localized at greater depths and which do not perform extensive daily vertical migration, in the winter months (Kozlov et al. 1991). The greater diversity of prey species and sizes (Fig. 4) suggests more opportunistic feeding behaviour in the winter period of food scarcity. Another difference between the prey eaten during summer and winter is the importance in winter of species inhabiting the outer shelf, shelf break and upper slope areas. The main prey item in winter, the onychoteuthid squid *Moroteuthis ingens*, lives primarily near the bottom in the lower sublittoral to bathyal zones (Nesis 1987; Jackson 1995), and small juveniles of notothenioid fish inhabit the shelf area (Loeb et al. 1993). The lanternfishes *E. subaspera*, *Gymnoscopelus nicholsi*, *G. piabilis*, *Metelectrona ventralis* and *P. choriodon*, which account for 23% of the diet by reconstituted mass, have an epibenthic distribution during the day and have been found in stomach contents of the channichthyid *Champsocephalus gunnari* and the nototheniid *Dissostichus eleginoides* caught in bottom trawls in the eastern shelf edge of Kerguelen Islands (Hulley et al. 1989).

In accordance with the known oceanic distribution of the prey, stomach contents containing numerous individuals of *Krefftichthys anderssoni* or *Protomyctophum tenisoni* were highly digested, indicating distant foraging areas. In summer, prey are also highly digested (authors' unpublished data) and the mean foraging range of adult king penguins is 320 to 670 km, depending on the breeding phase (Jouventin et al. 1994). However, the majority of food samples collected in winter contained less digested prey and, in some cases, almost intact individuals of *Gymnoscopelus piabilis*, *Lampichthys procerus*, *Metelectrona ventralis*, notothenioid juveniles and *Moroteuthis ingens*. Together with known prey distribution (see above), these data strongly suggest that breeding king penguins forage closer to the colony in the outer shelf and slope areas during the winter months.

In winter, chick feeding-frequency is very low (Cherel et al. 1987), and satellite fixes of one bird have shown a very long track, heading south of the "antarctic polar front" and reaching the limit of the pack ice (Jouventin et al. 1994). This is not consistent with the conclusion above that feeding takes place close to the breeding colony. A possible explanation for this discrepancy could be that in winter breeding adults hunt to feed themselves far from the island and forage for their chick close to the colony.

King penguins as biological samplers of mesopelagic fauna

The pelagic fish fauna in the vicinity of sub-antarctic islands is poorly documented, most information being collected during dietary studies of seabirds and fur seals (Gon and Klages 1988; Williams 1988; Sabourenkov 1992). Hulley (1990) indicated the presence of ten myctophids in the Crozet area, with four additional species occurring south of the archipelago. The present study adds therefore new information on the mesopelagic fauna surrounding the Crozet Islands. Moreover, the analysis of king penguin food samples opportunistically collected in winter indicated the occurrence of three fish taxons not recorded in the present study: one individual of *Stomias* sp. (Stomiidae), two specimens of *Gymnoscopelus braueri* (Lönnberg, 1905) (OL = 2.40 and 2.73 mm), and one individual of *G. microlampas* Hulley, 1981 (OL = 4.40 mm). Thus, 17 myctophid fish have been identified to the species level in the king penguin diet, including poorly known species (*G. microlampas, Lampichthys procerus*) in the southern Indian Ocean (Hulley 1990). This study is also the first to report in this area the occurrence of the sternoptychid *Maurolicus muelleri*, a cosmopolitan sub-tropical species abundant in upper slope and shelf waters (Robertson and Roberts 1978; Armstrong and Prosch 1991).

Following the zoogeographical classification of Hulley (1981, 1990), the myctophids eaten by king penguins

Table 4 Distribution patterns for mesopelagic myctophids, as based on Hulley (1981), consumed by king penguin chicks during winter at Crozet Islands (*na* not applicable)

Distribution	No. of prey species	% No. of myctophid species in:		Identified myctophids	
		pattern	diet	No.	% No.
Sub-tropical	0	0.0	0.0	0	0.0
Sub-tropical convergence	3	20.0	17.7	583	12.7
Sub-antarctic[a]	9	64.3	52.9	531	11.6
Broadly antarctic[b]	5	100.0	29.4	3461	75.7
Antarctic	0	0.0	0.0	0	0.0
	17	*na*	100.0	4575	100.0

[a,b] *Gymnoscopelus microlampas* and *G. braueri*, respectively, were included because they were found in king penguin diet during study period, but not in study samples (see "Discussion-King penguins as biological samplers of mesopelagic fauna")

belong to three patterns of the cool-water group (Table 4). "Broadly antarctic" fishes comprise the bulk of the food by number (76%), whereas two distribution types are important in terms of number of species ("sub-antarctic" = 53%, "broadly antarctic" = 29%). "Sub-tropical" and "antarctic" species were not found, but three "sub-tropical convergence" species accounted for 13% of the number of specimens. The distribution of mesopelagic fishes and ichthyoplankton is influenced by hydrographic features (Hulley 1981; Koubbi 1993), and the diversity of myctophids found in the king penguin diet reflects the complexity of the hydrology of the Crozet basin. The Crozet Archipelago (46°S) lies in the "polar frontal zone", between the "antarctic polar front" (50°S) and the "transition frontal zone" (40 to 43°S), an unusual hydrological region resulting from the confluence of three fronts (the sub-antarctic, sub-tropical and Agulhas fronts) north of the islands (Park et al. 1991). Consequently, the sub-antarctic zone is absent from the Crozet basin and sub-antarctic species live within the "transition frontal zone" or close to it (Koubbi 1993); i.e. in waters surrounding the archipelago.

The present work emphasizes the usefulness of seabirds as sampling agents for otherwise unstudied marine fauna. Because king penguins are deep-diving and specialist-foraging birds (Kooyman et al. 1992), careful analysis of their food allows the description of the fishes and squid fauna in the upper 300 m of the water column. Additional data on prey biology can be also gathered. For example, the occurrence of small relatively undigested squids in the king penguin diet suggests that the spawning grounds of *Moroteuthis ?knipovitchi*, *Kondakovia longimana*, *Gonatus antarcticus* and *Brachioteuthis ?riisei* may be located near the Crozet Islands.

The next step in the investigation on both the king penguin feeding ecology and prey biology is to determine where and how king penguins feed in winter. Dietary analysis coupled with the recent development of satellite-tracking or position-determining devices (Jouventin et al. 1994; Wilson et al. 1994), time-depth recorders (Kooyman et al. 1992) and stomach temperature sensors (Pütz and Bost 1994) appears a fruitful way to locate previously undetected concentrations of marine animals, as recently demonstrated for squids eaten by albatrosses in the Southern Ocean (Cherel and Weimerskirch 1995; Rodhouse et al. 1996).

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