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Cephalopod fauna of subantarctic islands: new information from predators

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ABSTRACT: Using top predators as biological samplers, we collected information on the poorly known—but ecologically important—cephalopod fauna of the Southern Ocean. A total of 4527 cephalopod beaks were identified from stomach contents of Patagonian toothfish caught in slope waters at Crozet and Kerguelen Islands (Indian Ocean). Main prey were the squid *Gonatus antarcticus* and *Kondakovia longimana* at both localities, *Taonius* sp. B (Voss) and *Slosarczykovia circumantarctica* at Crozet, and *Chiroteuthis veranyi* and *Mastigoteuthis psychrophila* at Kerguelen. Fish diet together with the feeding habits of sharks and seabirds show that at least 36 and 38 different cephalopod species inhabit Crozet and Kerguelen waters, respectively. Oegopsid squid dominate the assemblages (29 and 32 taxa at Crozet and Kerguelen, respectively) over octopods (7 and 5 taxa), 1 species of sepiolid occurring at Kerguelen. These rich communities include pelagic squid, benthopelagic cirrate octopods and a few endemic benthic octopodids. The results emphasize the importance of onychoteuthids and gonatids in the nutrition of top consumers in the Southern Ocean and they shed new light on the role of chiroteuthids, mastigoteuthids and cirrate octopods in the trophic web of the marine ecosystems.

KEY WORDS: Crozet · Kerguelen · Octopus · Patagonian toothfish · Slope · Southern Ocean · Squid

INTRODUCTION

The status of cephalopod systematics and biogeography worldwide is decades behind that of other marine taxa (Roeleveld 1998). In the Southern Ocean, the cephalopod fauna is poorly known, despite growing evidence that squid constitute a key group in the marine food webs (Kock 1987, Rodhouse & White 1995). The main limitations are the small number of research cruises targeting squid and octopuses, together with the difficulties in collecting cephalopods by nets. There is substantial potential, however, for using data on teuthophagous predators to gather unique information on the biology of their prey. For example, cephalopod eaters catch larger specimens and a greater diversity of species than sampling gear (Rodhouse 1990). Moreover, the increasing knowledge on the morphology of cephalopod beaks (chitinous hard structures that resist digestion) allows the identification to the species level of most of the accumulated items found in predators' stomach (Clarke 1986, Imber 1992). Description of dietary habits is the first step for a better understanding of trophic interactions and the determination of key species in the marine ecosystems. In turn, it can provide useful information on species composition, distribution, abundance and ecology of cephalopods occurring within the predator foraging range.

To our knowledge, no research cruise has been specifically devoted to targeting cephalopods in waters surrounding subantarctic archipelagoes (but see Rodhouse et al. 1992 and Rodhouse & Piatkowski 1995 for cephalopod paralarvae and juveniles occurring in the vicinity of the Falkland Islands and South Georgia, respectively). In the southern Indian Ocean, only 1 preliminary study based on specimens opportunistically

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collected listed a total of 11 species of cephalopods (5 squid, 1 sepiolid and 5 octopuses) caught in the vicinity of Prince Edwards, Crozet, Kerguelen and Heard Islands (Lu & Mangold 1978). Other information is sparse and adds only a few species in the area (Nesis 1987, Piatkowski et al. 1991, Duhamel & Piatkowski 1993, Piatkowski 1993, Xavier et al. 1999). The paucity of cephalopods collected by oceanographic cruises contrasts with their importance in the diet of top predators there, namely toothed whales (Mikhalev et al. 1981, Slip et al. 1995), seals (Slip 1995) and seabirds, including penguins, albatrosses and petrels (Ridoux 1994, Cherel et al. 1996, 2002d). At Crozet and Kerguelen Islands, it has been estimated that the communities of breeding seabirds and seals consume more than 400 000 tons of cephalopods, mainly squid, each year (Guinet et al 1996).

Our main goal was to collect information on the cephalopod communities inhabiting waters surrounding Crozet and Kerguelen archipelagoes by using top consumers as biological samplers. The study focused on the cephalopod diet of the Patagonian toothfish *Dissostichus eleginoides*, a species with subadults and adults living mainly in slope waters in the 400 to 1500 m depth range (Duhamel 1992). Patagonian toothfish is potentially an efficient biological sampler because first it is a large opportunistic predator feeding on a wide range of taxa (Garcia de la Rosa et al. 1997, Pilling et al. 2001, Goldsworthy et al. 2002). Second, subadults and adults are mainly resident (Williams et al. 2002), thus indicating that both fresh and accumulated food items come from the area where the fish are collected. Finally, Patagonian toothfish were caught in the depth range (>300 m) where the largest diversity of cephalopod taxa occurs in its food (Xavier et al. 2002). Additional information were collected from published and unpublished feeding habits of other apex predators from the areas, namely seabirds, marine mammals and sharks, to give a broad overview of the cephalopod assemblages and their importance in the southern Indian Ocean.

MATERIALS AND METHODS

Fieldwork was carried out at Crozet Islands by fishery observers during 3 cruises on longliners, including 1 exploratory research cruise on the Japanese vessel 'Anyo Maru 22', and at Kerguelen Islands during 6 commercial cruises, including both longliners and trawlers (Table 1). The fishery targeted subadults and adults of the Patagonian toothfish that were caught in upper slope waters surrounding the 2 archipelagoes (Duhamel 1992). Additional cephalopod records were obtained from miscellaneous observations from stomach contents of Patagonian toothfish caught during various commercial cruises at Kerguelen.

Fishery observers dissected fish and kept both accumulated beaks and fresh cephalopod remains found in their stomach in 70 % ethanol and at –20°C, respectively, until analysis in the laboratory. Fish remains and other food items were not quantified. Cephalopod beaks (both lower and upper beaks) were identified by reference to features given by Clarke (1986) and Imber (1992), and by comparison with material held in our own reference collection. Lower rostral length (LRL) of squid beaks and lower hood length (LHL) of octopus beaks were measured to 0.1 mm with a vernier caliper. Allometric equations given by Clarke (1962, 1980, 1986), Adams & Klages (1987), Rodhouse & Yeatman (1990), Rodhouse et al. (1990), Smale et al. (1993), Lu & Williams (1994), Jackson (1995), dos Santos & Haimovici (2000), Gröger et al. (2000) and Piatkowski et al. (2001) were used to estimate dorsal mantle length (ML) and whole wet mass (M) from LRL or LHL. For the few species where no relationships were available, ML and M were extrapolated from equations for closely related species or for species with a similar morphology. Dietary data are presented using 2 calculation techniques, namely the percentages by number and by reconstituted mass of each prey type. Cephalopod systematic order follows Clarke (1986).

Data were statistically analysed using Systat 9 for Windows (Wilkinson 1999). Values are means ± SD.

Table 1. Sampling of cephalopod beaks in stomach contents of Patagonian toothfish in Crozet and Kerguelen waters

Locality	Date	Fishing method	Fishing vessel	Depth range (m)	No. of beaks
Crozet	01 Jan to 12 Apr 1997	Bottom longline	'Anyo Maru 22'	547–1463	761
	18 Sep to 19 Oct 1998	Bottom longline	'Saint-Jean'	520–1820	900
	20 Sep to 06 Oct 1999	Bottom longline	'Cap Kersaint'	733–1930	78
Kerguelen	03 to 14 Nov 1998	Bottom trawl	'Kerguelen de Tremarec'	475–920	348
	10 Feb to 03 Mar 1999	Bottom trawl	'Kerguelen de Tremarec'	505–910	756
	06 Mar to 14 Apr 1999	Bottom longline	'Northern Pride'	510–1000	180
	10 to 31 Oct 1999	Bottom longline	'Cap Kersaint'	557–1990	75
	16 Nov 1999 to 05 Jan 2000	Bottom trawl	'Kerguelen de Tremarec'	347–960	1188
	19 Feb to 08 Mar 2000	Bottom trawl	'Kerguelen de Tremarec'	370–770	255

RESULTS

Cephalopod diet of Patagonian toothfish at Crozet and Kerguelen

A total of 4527 cephalopod beaks were identified from stomach contents of Patagonian toothfish, including 1725 beaks from Crozet and 2802 beaks from Kerguelen Islands. One beak was too much eroded to be determined and 14 beaks of the ommastrephid squid *Illex argentinus* were identified at Crozet during 1 cruise, the species being the bait used on longlines. Thirty-four taxa of cephalopods were identified (29 and 25 at Crozet and Kerguelen Islands, respectively), including 30 squid and 4 octopuses (Table 2).

At Crozet, the cephalopod diet was primarily represented by number (>10%) and by mass (>10%) by 4 and 3 species, respectively, which contributed together to 65% by number and 64% by reconstituted mass. They were *Gonatus antarcticus* (21% by number and 13% by mass), *Taonius* sp. B (Voss) (19 and 10%, respectively), *Moroteuthis ingens* (8 and 17%) and *Kondakovia longimana* (6 and 34%). The brachioteuthid *Slosarczykovia circumantarctica* was a numerous prey (14%), but, owing to its small size, it accounted for an insignificant percentage by mass (<1%). At the family level, onychoteuthids and cranchids are equally important with 5 and 4 species, 16 and 21% by number, and 54 and 14% by mass, respectively. Noticeable also was the importance of cirrate octopods in the diet of Patagonian toothfish at Crozet, because 3 species accounted together for 6 and 8% of the diet by number and by mass, respectively (Table 2).

At Kerguelen, the cephalopod diet was dominated by number and by mass by 3 and 4 species, respectively, which contributed together to 60% by number and 58% by reconstituted mass. The main prey were *Chiroteuthis veranyi* (29% by number and 15% by mass) and *G. antarcticus* (11 and 13%, respectively). Owing to their small or large size, the others were either important by number (*Mastigoteuthis psychrophila*: 20%) or important by mass (*K. longimana*: 18% and *Todarodes* sp.: 12%), respectively. The closely related families Mastigoteuthidae and Chiroteuthidae accounted together for 49 and 20% of the cephalopod diet by number and mass, respectively, while onychoteuthids (5 species) totalized 8% by number and 32% by reconstituted mass. Other significant items included *Taningia danae*, histioteuthids, *Nototeuthis dimegacotyle* and octopodids (Table 2).

Large temporal variations in the cephalopod diet of Patagonian toothfish were observed at both localities. At Crozet, *Taonius* sp. B (Voss) was a minor prey in summer 1997 (3% by number) and the most abundant item in late winter 1998 (32%). Conversely, *Histioteuthis eltaninae* was much more numerous in 1997 (25%) than in 1998 (<1%), while *G. antarcticus* was a main fish prey during both cruises (14 and 26% in 1997 and 1998, respectively). At Kerguelen, some inter- and intra-seasonal changes occurred. When comparing to springs 1998 and 1999, the following summers 1999 and 2000 were marked by the high abundance of *C. veranyi* (57% versus 6–13% by number) and the low occurrence of *G. antarcticus* (<1–1% versus 19%) and *M. psychrophila* (<1–6% versus 30–49%). Intraseasonally, the fish diet included less *N. dimegacotyle* in spring 1998 (2%) than in 1999 (10%), and *Histioteuthis atlantica* was a major item in summer 1999 (24%) while none was found in 2000. Fishery observers noted the sudden abundance of squid in the diet of Patagonian toothfish at Kerguelen, for example *H. atlantica* in summer 1999, during which almost all fish stomachs were full of histioteutids during a few consecutive days.

Prey size

Depending on the species, both LRL and the level of darkening of the beaks showed that Patagonian toothfish preyed upon juvenile, subadult and adult cephalopods. For a given species, fish preyed upon 1 size-class, either juveniles (*Histioteuthis atlantica* at Kerguelen, Fig. 1) or adults (*Nototeuthis dimegacotyle* at Kerguelen, Fig. 1), or upon different size-classes (*Slosarczykovia circumantarctica* and *Taonius* sp. B (Voss) from Crozet, Fig. 2; *Gonatus antarcticus* at both localities, Fig. 3). We statistically analysed the differences in LRL of the same cephalopod species eaten by Patagonian toothfish at Crozet and Kerguelen (Table 3). Differences were significant ($p < 0.05$) for

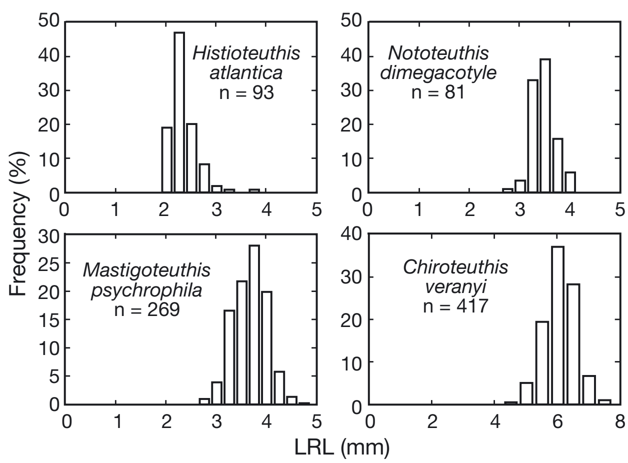

Fig. 1. *Dissostichus eleginoides.* Frequency distribution of lower rostral lengths (LRL) of cephalopods eaten by Patagonian toothfish in Kerguelen waters

Table 2. Number of cephalopod beaks (both upper and lower beaks) found in Patagonian toothfish stomach contents and (reconstituted) wet biomass represented by these beaks at Crozet and Kerguelen Islands

	Crozet				Kerguelen			
	Number	(%)	(Mass)	(%)	Number	(%)	Mass	(%)
Decapoda								
Ommastrephidae								
Martialia hyadesi	20	1.2	7680	2.3	14	0.5	3014	1.1
Todarodes sp.	6	0.3	4249	1.3	107	3.8	33399	12.4
(*Illex argentinus*)[a]	(14)	–	(1514)	–				
Onychoteuthidae								
Onychoteuthis sp. C (Imber)	2	0.1	445	0.1				
Moroteuthis ingens	132	7.7	55409	16.9	76	2.7	21305	7.9
Moroteuthis knipovitchi	37	2.1	7269	2.2	33	1.2	5236	1.9
Moroteuthis robsoni					4	0.1	3505	1.3
Moroteuthis sp. B (Imber)	2	0.1	368	0.1	59	2.1	9498	3.5
Kondakovia longimana	108	6.3	113153	34.5	39	1.4	47916	17.8
Pholidoteuthidae								
Pholidoteuthis boschmai	5	0.3	3474	1.1	4	0.1	1826	0.7
Psychroteuthidae								
Psychroteuthis glacialis					1	<0.1	112	<0.1
Brachioteuthidae								
Brachioteuthis linkovskyi	19	1.1	131	<0.1	49	1.7	310	0.1
Slosarczykovia circumantarctica	245	14.2	1126	0.3	60	2.1	287	0.1
Gonatidae								
Gonatus antarcticus	355	20.6	42647	13.0	304	10.8	35942	13.4
Octopoteuthidae								
Taningia danae	3	0.2	5472	1.7	13	0.5	21142	7.9
Histioteuthidae								
Histioteuthis atlantica	2	0.1	41	<0.1	186	6.6	2973	1.1
Histioteuthis eltaninae	192	11.1	7681	2.3	174	6.2	5377	2.0
Neoteuthidae								
Alluroteuthis antarcticus	9	0.5	2112	0.6	7	0.2	1116	0.4
Nototeuthis dimegacotyle	11	0.6	898	0.3	152	5.4	9807	3.6
Mastigoteuthidae								
Mastigoteuthis psychrophila	63	3.7	1968	0.6	551	19.7	13338	5.0
?*Mastigoteuthis* A (Clarke)					7	0.2	658	0.2
?*Mastigoteuthis* B (Clarke)	1	<0.1	183	<0.1				
Chiroteuthidae								
Chiroteuthis veranyi	3	0.2	184	<0.1	826	29.5	39649	14.7
Chiroteuthis sp. F (Imber)	2	0.1	365	0.1				
Batoteuthidae								
Batoteuthis skolops	29	1.7	929	0.3	15	0.5	408	0.2
Cranchiidae								
Taonius sp. B (Voss)	321	18.6	32414	9.9				
Teuthowenia pellucida					2	<0.1	70	<0.1
Galiteuthis glacialis	27	1.6	1037	0.3	8	0.3	400	0.1
Galiteuthis stC sp. (Imber)	5	0.3	160	<0.1				
Mesonychoteuthis hamiltoni	13	0.8	12830	3.9				
Oegopsida sp. A	4	0.2	1116	0.3				
Octopoda								
Octopodidae								
Graneledone gonzalezi/Benthoctopus thielei					108	3.9	11555	4.3
Stauroteuthidae								
Stauroteuthis gilchristi	53	3.1	9760	3.0	3	0.1	329	0.1
Opisthoteuthidae								
Opisthoteuthis sp.	50	2.9	10488	3.2				
Cirrata sp. A	6	0.3	4425	1.3				
Total	**1725**	**100.0**	**328018**	**100.0**	**2802**	**100.0**	**269172**	**100.0**

[a]Bait

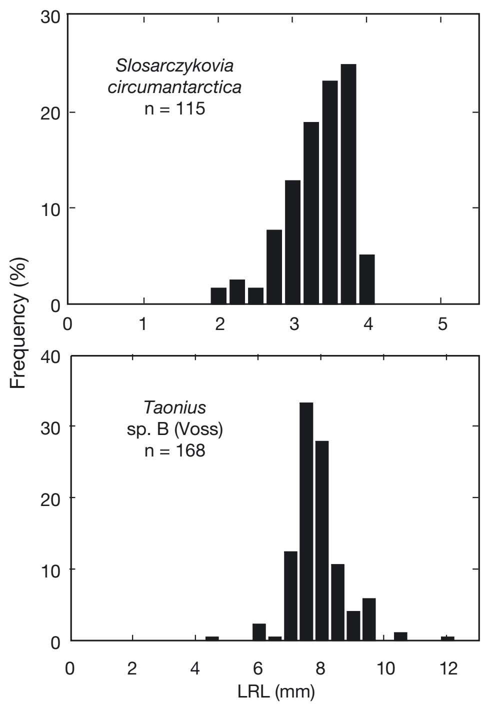

Fig. 2. *Dissostichus eleginoides*. Frequency distribution of lower rostral lengths (LRL) of cephalopods eaten by Patagonian toothfish in Crozet waters

6 species and non-significant for the remaining 8 species. For example, the mean size of *G. antarcticus* was identical at both localities, but the mean size of *Histioteuthis eltaninae* was not (Fig. 3). The largest prey

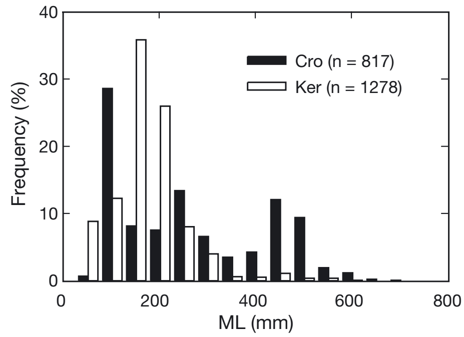

Fig. 4. *Dissostichus eleginoides*. Frequency distribution of dorsal mantle lengths (ML) of cephalopods eaten by Patagonian toothfish in Crozet (Cro) and Kerguelen (Ker) waters

were 1 specimen of *Taningia danae* at Crozet (15.8 mm LRL, 63 cm ML, 5.3 kg M) and 1 specimen of *Kondakovia longimana* at Kerguelen (15.7 mm LRL, 56 cm ML, 4.2 kg M).

To compare the overall size of cephalopods eaten by Patagonian toothfish at Crozet and Kerguelen Islands, we estimated ML from LRL and, for each locality, we pooled and plotted together the estimated ML from all the specimens of the different species of cephalopods (Fig. 4). Fish from Crozet included more large cephalopods in their diet than those from Kerguelen, thus inducing significant differences in mean sizes of cephalopods (ML = 244 ± 159 mm, n = 817 and 148 ± 82 mm, n = 1278, respectively; Mann-Whitney *U*-test, $U = 686165$, $p < 0.0001$) and in their ML distribution (Kolmogorov-Smirnov, $p < 0.0001$).

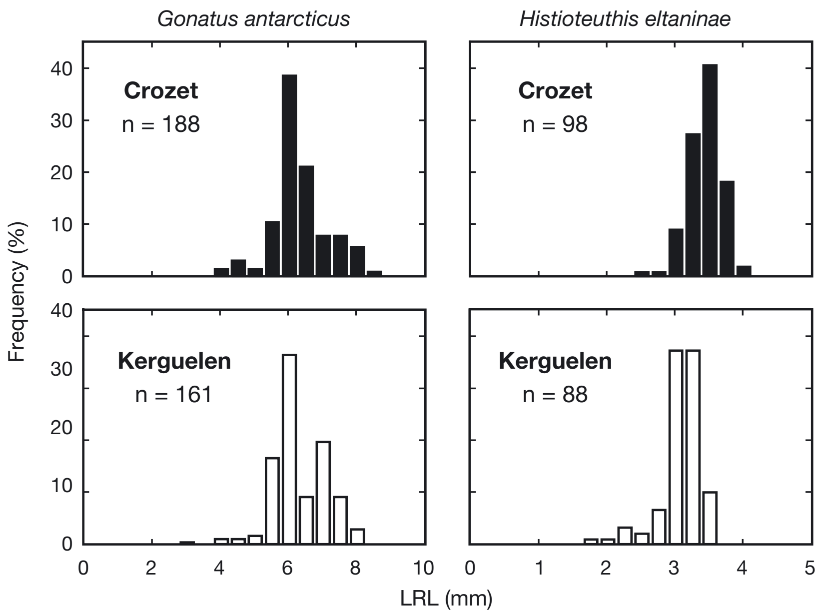

Fig. 3. *Dissostichus eleginoides*. Frequency distribution of lower rostral lengths (LRL) of cephalopods eaten by Patagonian toothfish in Crozet and Kerguelen waters

Additional records and further information on some taxa

Genus *Todarodes*. Two species or groups of species live in the Southern Ocean, *Todarodes angolensis* and *T. filippovae* (Dunning & Wormuth 1998, Rodhouse 1998). Since we cannot distinguish between their beaks, they were called *Todarodes* sp. One specimen of *T. filippovae* was previously caught in Kerguelen waters (Piatkowski et al. 1991, Rodhouse 1998). However, based on the number of teeth on the medial manus sucker rings, all the other known records (including some specimens eaten by Patagonian toothfish) refer to *T. angolensis* or a species closely related to it (Cherel & Weimerskirch 1995, authors' unpubl. data). Thus, 2 species occur at Kerguelen, *T.* cf. *angolensis* in outer-shelf and slope waters and *T. filippovae*

Table 3. Measured lower rostral length (LRL) of squids and lower hood length (LHL) of octopuses, and estimated dorsal mantle length (ML) of cephalopods identified from stomach contents of Patagonian toothfish at Crozet and Kerguelen. Values are means ± SD with ranges in parentheses. Mann-Whitney *U* tests were performed to compare LRL of squids between the 2 localities

Species	Location	n	LRL/LHL (mm)	Statistics	ML (mm)
Martialia hyadesi	Crozet	7	7.2 ± 0.7 (6.6–8.3)	$U = 32$, $p = 0.018$	314 ± 19 (295–346)
	Kerguelen	5	5.7 ± 0.8 (4.8–6.8)		271 ± 25 (244–303)
Todarodes sp.	Crozet	3	9.8 ± 0.1 (9.8–10.0)	$U = 126$, $p = 0.091$	396 ± 5 (392–401)
	Kerguelen	53	6.6 ± 2.4 (4.1–11.9)		260 ± 100 (160–479)
Illex argentinus[a]	Crozet	6	4.1 ± 0.3 (3.8–4.5)		214 ± 18 (195–236)
Onychoteuthis sp. C (Imber)	Crozet	2	3.7–3.7		–[b]
Moroteuthis ingens	Crozet	62	6.8 ± 2.5 (2.4–10.2)	$U = 1610$, $p = 0.023$	272 ± 86 (118–388)
	Kerguelen	41	5.9 ± 1.8 (2.9–10.2)		239 ± 62 (136–386)
Moroteuthis knipovitchi	Crozet	20	5.6 ± 1.1 (3.3–7.8)	$U = 190$, $p = 0.552$	244 ± 70 (97–382)
	Kerguelen	17	5.5 ± 0.8 (3.8–7.1)		234 ± 52 (134–337)
Moroteuthis robsoni	Kerguelen	2	8.4–8.9		512–564
Moroteuthis sp. B (Imber)	Crozet	1	5.6		–[b]
	Kerguelen	28	5.1 ± 0.5 (3.7–6.3)		–[b]
Kondakovia longimana	Crozet	56	11.7 ± 2.9 (2.3–16.4)	$U = 367$, $p = 0.084$	415 ± 106 (62–588)
	Kerguelen	18	12.7 ± 2.7 (3.4–15.7)		451 ± 101 (106–563)
Pholidoteuthis boschmai	Crozet	3	8.6 ± 0.5 (8.1–9.1)		363 ± 20 (344–383)
	Kerguelen	2	6.9–8.7		296–367
Psychroteuthis glacialis	Kerguelen	1	5.0		166
Brachioteuthis linkovskyi	Crozet	9	4.2 ± 0.3 (3.6–4.6)	$U = 156$, $p = 0.013$	101 ± 5 (88–108)
	Kerguelen	22	3.9 ± 0.3 (3.5–4.6)		95 ± 6 (87–108)
Slosarczykovia circumantarctica	Crozet	115	3.2 ± 0.4 (1.8–3.8)	$U = 1686$, $p = 0.701$	81 ± 8 (53–94)
	Kerguelen	28	3.2 ± 0.4 (2.1–3.9)		81 ± 8 (59–94)
Gonatus antarcticus	Crozet	188	6.1 ± 0.8 (3.5–8.4)	$U = 15502$, $p = 0.695$	216 ± 36 (107–318)
	Kerguelen	161	6.0 ± 0.8 (2.8–7.9)		216 ± 35 (75–293)
Taningia danae	Crozet	2	6.1–15.8		Small[b]–633
	Kerguelen	5	13.0 ± 2.6 (8.5–14.9)		422 ± 195 (82–564)
Histioteuthis atlantica	Crozet	1	2.5		42
	Kerguelen	93	2.2 ± 0.3 (1.8–3.6)		36 ± 6 (26–67)
Histioteuthis eltaninae	Crozet	98	3.3 ± 0.3 (2.3–3.8)	$U = 7200$, $p < 0.0001$	60 ± 6 (38–72)
	Kerguelen	88	3.0 ± 0.3 (1.7–3.5)		52 ± 7 (25–63)
Alluroteuthis antarcticus	Crozet	4	5.1 ± 0.2 (5.0–5.3)	$U = 15$, $p = 0.059$	175 ± 5 (169–182)
	Kerguelen	4	4.4 ± 0.7 (3.4–5.1)		149 ± 25 (116–175)
Nototeuthis dimegacotyle	Crozet	6	3.6 ± 0.3 (3.3–4.0)	$U = 370$, $p = 0.034$	–[b]
	Kerguelen	81	3.3 ± 0.2 (2.7–3.9)		–[b]
Mastigoteuthis psychrophila	Crozet	35	3.9 ± 0.2 (3.5–4.4)	$U = 7462$, $p < 0.0001$	119 ± 1 (116–122)
	Kerguelen	269	3.5 ± 0.3 (2.5–4.5)		116 ± 2 (110–123)
?*Mastigoteuthis* A (Clarke)	Kerguelen	5	5.1 ± 0.5 (4.5–5.7)		–[b]
Chiroteuthis veranyi	Crozet	2	5.8–5.9		153–156
	Kerguelen	417	5.8 ± 0.5 (4.2–7.5)		154 ± 13 (113–195)
Batoteuthis skolops	Crozet	15	4.1 ± 0.4 (3.4–4.6)	$U = 65$, $p = 0.119$	–[b]
	Kerguelen	6	3.6 ± 0.7 (2.5–4.5)		–[b]
Taonius sp. B (Voss)	Crozet	168	7.6 ± 0.9 (4.3–11.6)		455 ± 53 (254–701)
Teuthowenia pellucida	Kerguelen	1	4.5		196
Galiteuthis glacialis	Crozet	14	4.4 ± 1.2 (2.1–5.7)	$U = 23$, $p = 0.801$	376 ± 101 (184–486)
	Kerguelen	3	4.7 ± 0.4 (4.5–5.2)		404 ± 30 (384–438)
Galiteuthis stC sp. (Imber)	Crozet	2	3.8–5.5		–[b]
Mesonychoteuthis hamiltoni	Crozet	7	9.5 ± 1.3 (8.1–11.4)		571 ± 77 (482–685)
Oegopsida sp. A	Crozet	1	7.2		–[b]
Graneledone gonzalezi/ *Benthoctopus thielei*	Kerguelen	48	5.5 ± 1.1 (3.2–7.6)		77 ± 13 (47–104)
Stauroteuthis gilchristi	Crozet	21	3.8 ± 0.8 (1.2–5.4)		–[b]
	Kerguelen	1	3.4		–[b]
Opisthoteuthis sp.	Crozet	26	4.8 ± 0.8 (3.5–6.5)		73 ± 15 (49–107)
Cirrata sp. A	Crozet	3	7.5 ± 1.8 (6.4–9.5)		–[b]

[a]Bait; [b]no allometric equations available

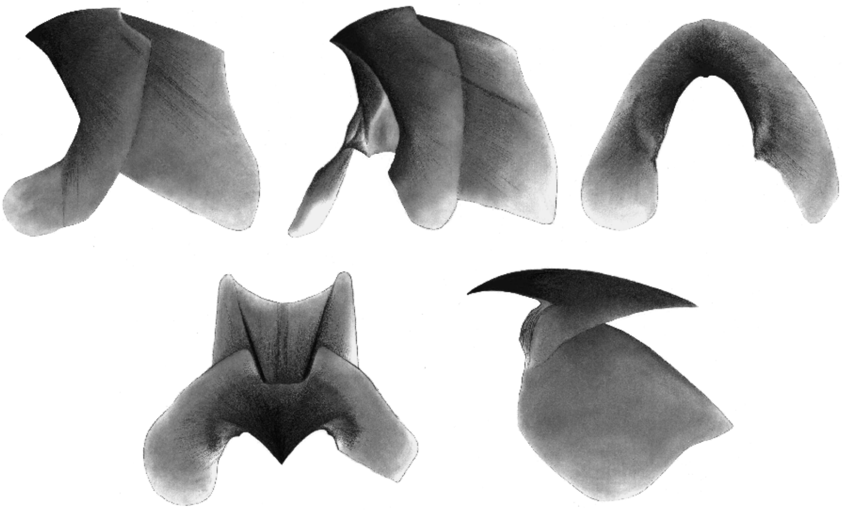

Fig. 5. *Moroteuthis* sp. B (Imber). Drawings of lower and upper beaks

ern Atlantic Ocean (Pilling et al. 2001, Xavier et al. 2002).

Nototeuthis dimegacotyle. One damaged squid eaten by Patagonian toothfish at Crozet had an intact tentacular club showing the 2 distinctive enormous manus suckers (Nesis & Nikitina 1986). This allowed us to identify and describe its beaks (Fig. 6) that were misidentified in previous works (see Imber 1999). *N. dimegacotyle* was a common prey of Patagonian toothfish at Kerguelen (5% by number), but a rare item at Crozet (Table 2).

***Taonius* sp. B (Voss).** This still undescribed species was one of the main prey of Patagonian toothfish at Crozet (see above). A few additional records indicate that *Taonius* sp. B (Voss) is a rare item in the fish diet in Kerguelen waters.

probably in more oceanic waters. We have no indication of *T.* cf. *angolensis* from Crozet.

***Moroteuthis* sp. B (Imber).** Imber (1992) identified a rare lower beak called *Moroteuthopsis* sp. B that shares features in common with those of *Moroteuthopsis* (= *Moroteuthis*) *ingens*. The species is a common prey in the diet of Patagonian toothfish from Kerguelen (2% by number) and a rare item at Crozet Islands (Table 2), thus allowing us to illustrate both its lower and upper beaks for the first time (Fig. 5).

Brachioteuthid squid. Two new species of brachioteuthids have been recently described from the Southern Ocean (Lipinski 2001). Examination of beaks from the holotype of *Brachioteuthis linkovskyi* and from 1 paratype of *Slosarczykovia circumantarctica* showed that the 2 species are common items in the diet of Patagonian toothfish at Crozet and Kerguelen Islands (Table 2). A distinctive feature is the presence of a strong thickened ridge on the lateral wall of the lower beak of *B. linkovskyi* that does not exist on the beak of *S. circumantarctica*. We previously identified beaks of *B. linkovskyi* and *S. circumantarctica* as *Brachioteuthis* sp. and *Brachioteuthis* ?*picta*, and *Brachioteuthis* ?*riisei*, respectively (Cherel et al. 1996, 2002a,c,d, Catard et al. 2000, Lea et al. 2002), and those beaks probably correspond to *Brachioteuthis* 'B' (Clarke) (ridge) and *Brachioteuthis* ?*picta* (Rodhouse) (no ridge), respectively, from the south-

Oegopsida sp. A. From a single lower beak found in the diet of sooty albatrosses collected at Marion Island (southern Indian Ocean), Imber (1978) described a new species, *Gonatus phoebetriae*. We called this squid Oegopsida sp. A, because a new species of cephalopods cannot be described from the beaks only and, in our opinion, the beaks cannot be assigned with confidence to *Gonatus* (Fig. 7). Oegopsida sp. A was a rare prey of Patagonian toothfish at Crozet and it was not found at Kerguelen Islands (Table 2).

cf. *Stoloteuthis leucoptera.* Two specimens of Heteroteuthinae (27 and 29 mm ML) were identified from the

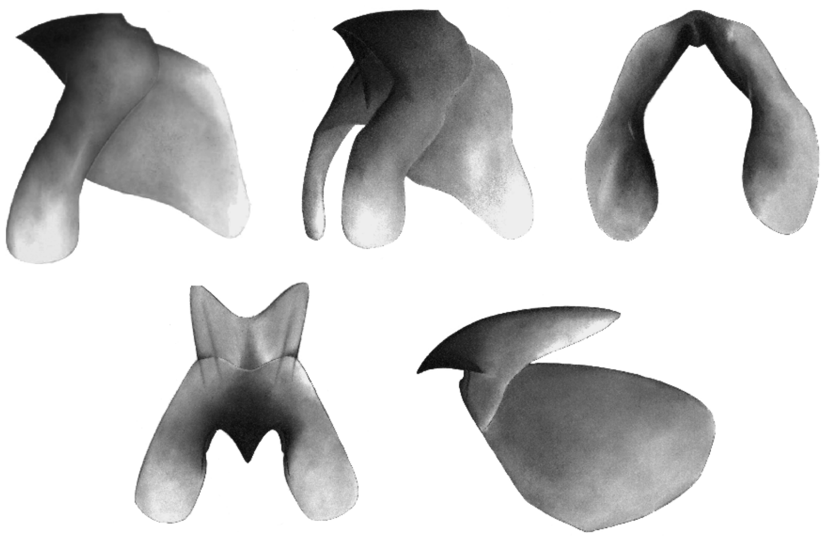

Fig. 6. *Nototeuthis dimegacotyle*. Drawings of lower and upper beaks

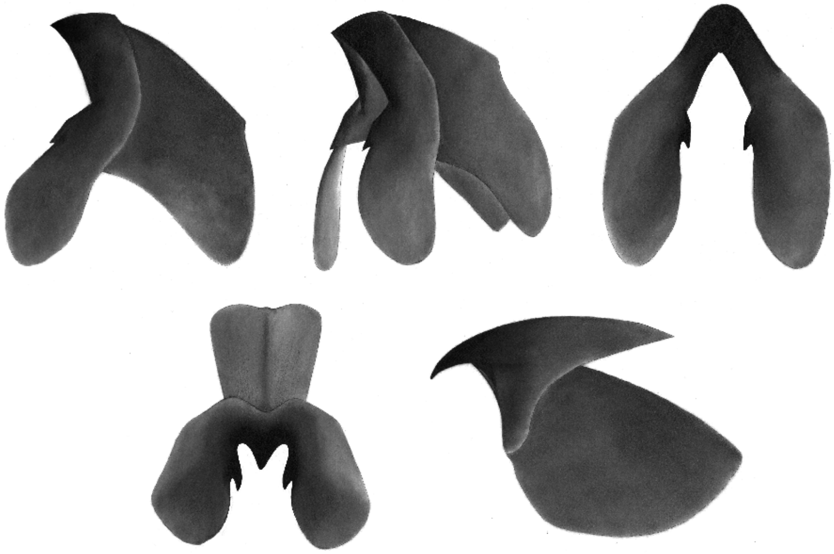

Fig. 7. Oegopsida sp. A. Drawings of lower and upper beaks

flesh in the diet of Patagonian toothfish and of the skate *Bathyraja irrasa* at Kerguelen Islands in February 1994. According to Nesis (1987), these sepiolids are closely related to *Stoloteuthis leucoptera*.

Octopods. Two endemic octopodids are common on the Kerguelen Plateau, *Benthoctopus thielei* and *Graneledone gonzalezi* (Lu & Mangold 1978, Nesis 1987, Guerra et al. 2000). Their beaks are almost identical, thus precluding identification to the species level. Patagonian toothfish prey upon the 2 species, as indicated by fresh remains that can be easily determined (*B. thielei* has 2 rows of suckers on arms and *G. gonzalezi* 1 row). The complex *B. thielei*/*G. gonzalezi* was a common dietary item of Patagonian toothfish at Kerguelen Islands (4% by number) (Table 2).

The recent revision of the cirrate-octopod family Stauroteuthidae includes the redescription of a species from the southern Atlantic Ocean, *Stauroteuthis gilchristi* (Collins & Henriques 2000). A close comparison of beaks from that species with those found in the fish diet at Crozet and Kerguelen Islands (Fig. 8) showed they are identical, thus extending the geographical range of *S. gilchristi* to the southern Indian Ocean. The species was a rare prey at Kerguelen Islands, but, together with beaks of the other cirrate *Opisthoteuthis* sp. (Fig. 9), it was a common item of Patagonian toothfish at Crozet (3% by number each) (Table 2).

DISCUSSION

Cephalopod diet of Patagonian toothfish

Patagonian toothfish is primarily ichthyophagous, preying secondarily on cephalopods and crustaceans with young fish feeding on macrozooplankton (Duhamel & Pletikosic 1983, Garcia de la Rosa et al. 1997). At Crozet and Kerguelen, cephalopods are more important in large fish caught at deep depths (Duhamel 1981, 1992, Duhamel & Pletikosic 1983). While the goal of the present study was not the determination of the main prey classes, our data nevertheless show that cephalopods are important dietary items in the deep sea at both localities, some squid (like *Histioteuthis atlantica* and *Chiroteuthis veranyi* at Kerguelen) even being the major prey during some cruises. The large diversity of cephalopods eaten by Patagonian toothfish underlines the opportunistic behaviour of this large predatory fish that is known to have a diverse diet throughout its whole geographic range (Garcia de la Rosa et al. 1997, Pilling et al. 2001, Goldsworthy et al. 2002).

Only a few previous studies have detailed the cephalopod component of the food of Patagonian toothfish. In Patagonian waters, 4 species were identified, all being endemic from the area (Garcia de la Rosa et al. 1997). A larger diversity of cephalopods was found at South Georgia and Macquarie Island with 16 taxa at each locality (Pilling et al. 2001, Goldsworthy et al. 2002, Xavier et al. 2002). Five taxa dominated the

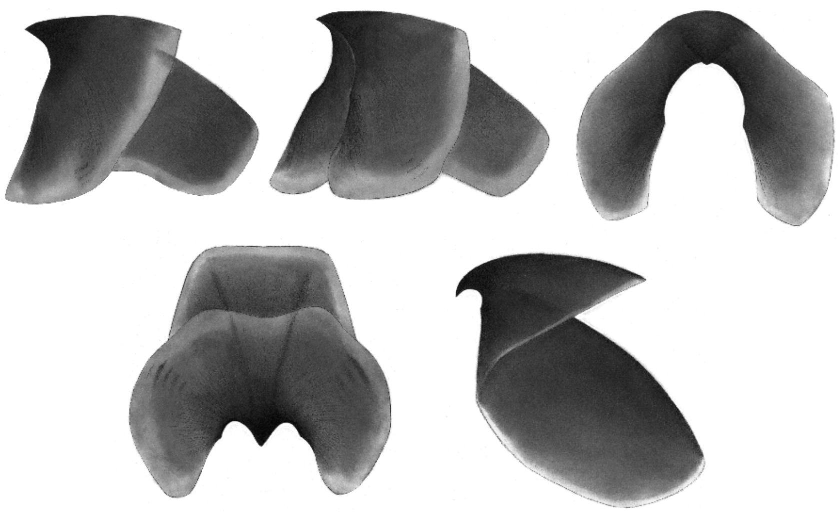

Fig. 8. *Stauroteuthis gilchristi*. Drawings of lower and upper beaks

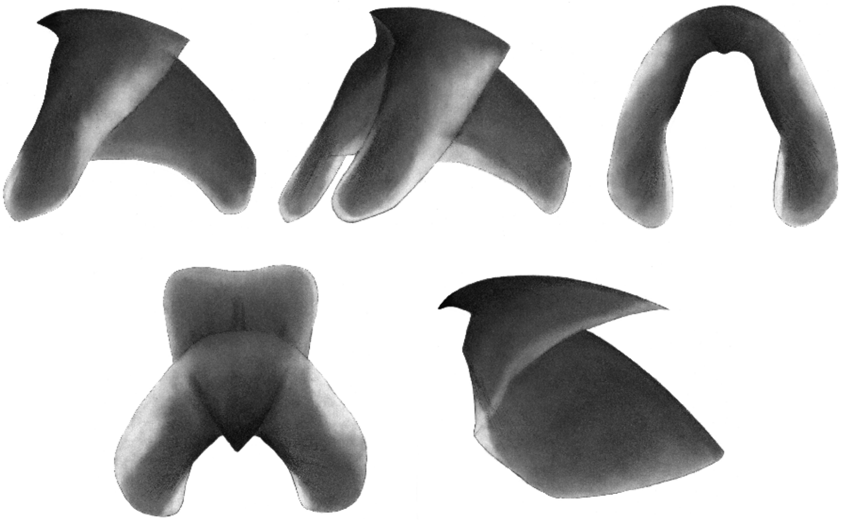

Fig. 9. *Opisthoteuthis* sp. Drawings of lower and upper beaks

cephalopod diet at South Georgia, including 1 endemic octopodid and 4 squid (*Gonatus antarcticus*, *Kondakovia longimana*, *Moroteuthis knipovitchi* and *Chiroteuthis veranyi*), with *K. longimana* being the main item by mass (Garcia de la Rosa et al. 1997, Xavier et al. 2002). At Macquarie Island, the major cephalopod prey were *G. antarcticus*, and, to a lesser extent, undetermined *Mastigoteuthis*, *Moroteuthis*, *Chiroteuthis* and cirrate octopods (Goldsworthy et al. 2002). All these taxa were also found at Crozet and Kerguelen Islands but in different proportions between localities. This, together with large temporal and spatial variations within localities (Goldsworthy et al. 2002, this study) and the well-known opportunistic fish predatory behaviour, strongly suggests the occurrence of large spatio-temporal changes in the abundance and availability of cephalopods in slope waters of subantarctic archipelagoes.

It is noticeable that *Gonatus antarcticus* was an important dietary item at the 4 subantarctic islands so far investigated. The species is abundant around the Falkland Islands and South Georgia (southern Atlantic Ocean) (Nesis 1999) and the dietary habits of Patagonian toothfish furthermore indicate that *G. antarcticus* is a common squid both in the southern Indian (Crozet, Kerguelen) and Pacific (Macquarie) Oceans. Fish preyed upon squid of the same size everywhere, the mean LRL of *G. antarcticus* being identical at Crozet, Kerguelen and South Georgia (Xavier et al. 2002, this study). They also targetted mainly adults of *Kondakovia longimana* whatever the locality, but they caught larger *Moroteuthis knipovitchi* and smaller *Chiroteuthis veranyi* at South Georgia than in the southern Indian Ocean (Xavier et al. 2002, this study). Overall, Patagonian toothfish ate larger cephalopods at Crozet than at Kerguelen. We cannot exclude a bias in sampling due to deeper fishing depths at Crozet than at Kerguelen. However, the most likely explanation is again differences in the availability and abundance of cephalopods between localities, some of the main prey species at Kerguelen (*C. veranyi*, *Mastigoteuthis psychrophila*) being much smaller than those from Crozet (e.g. *Taonius* sp. B (Voss)).

Trophic role of cephalopods as prey

This study points out the importance of some cephalopod taxa in the nutrition of Patagonian toothfish. This, together with other investigations on the diet of top predators allows the determination of cephalopods playing a key role in the trophic webs of the Southern Ocean. Squid of the family Onychoteuthidae are main items in the fish diet at both Crozet and Kerguelen Islands with 4 species involved, i.e. *Kondakovia longimana*, *Moroteuthis ingens*, and to a lesser extent *Moroteuthis knipovitchi* and *Moroteuthis* sp. B (Imber). The 3 former species are major dietary components of marine mammals, seabirds and fish (review in Cherel & Weimerskirch 1999, Jackson et al. 2000, Cherel & Duhamel 2004). The latter species, however, was not previously found as a significant food item for a predator. Another important family worldwide are Ommastrephidae (Clarke 1996). In the Southern Ocean, only 1 species (*Martialia hyadesi*) is targetted by predators (Rodhouse 1997) with *Todarodes* sp. being also a main prey in Kerguelen waters (Cherel et al. 2000, 2002d, Cherel & Duhamel 2004, this study). In the same way, large amounts of gonatids are consumed in the Northern Hemisphere (Clarke 1996), while the importance of the family in the Southern Ocean is restricted to 1 species, *Gonatus antarcticus* which is eaten by marine mammals (Clarke & Goodall 1994, Slip 1995), seabirds (Clarke 1996), and the Patagonian toothfish (see above).

This study also sheds new light on the trophic role as prey of some cephalopod taxa for which almost no information is available. For example, the Patagonian toothfish at Crozet is one of the few predators, together with bottlenose whale (Clarke & Goodall 1994), wandering albatross (Xavier et al. 2003) and to a lesser extent great-winged petrel (Ridoux 1994), to prey heavily upon *Taonius* squid in the Southern Ocean. Unexpected findings were the abundance of *Chiroteuthis veranyi* and *Mastigoteuthis psychrophila* in the fish diet at Kerguelen and that of cirrate octopods at

Table 4. Cephalopod taxa from Crozet and Kerguelen waters recorded in the diet of top predators and those listed in oceanographic literature

Species	Crozet (n = 37 taxa)			Kerguelen (n = 40 taxa)			
	Toothfish[a]	Birds[b,c]	Lit.[d]	Toothfish[a]	Sharks[e]	Birds[c], fur seals[f]	Lit.[d]
Architeuthis dux					+		
Martialia hyadesi	+	+		+	+	+	+
Todarodes cf. *angolensis*				+			
Todarodes filippovae							+
Todarodes sp.	+	+		+	+	+	
Onychoteuthis sp. C (Imber)	+						
Moroteuthis ingens	+	+	+	+	+	+	+
Moroteuthis knipovitchi	+	+	+	+	+	+	+
Moroteuthis robsoni			+	+	+		
Moroteuthis sp. B (Imber)	+	+		+			
Kondakovia longimana	+	+		+	+	+	
Pholidoteuthis boschmai	+			+			
Psychroteuthis glacialis				+			
Brachioteuthis linkovskyi	+	+		+	+		
Brachioteuthis picta, *Brachioteuthis* sp.			+				+
Slosarczykovia circumantarctica (= *Brachioteuthis* ?*riisei*)	+	+		+	+	+	+
Gonatus antarcticus	+	+		+	+	+	+
Abraliopsis gilchristi							+
Taningia danae	+			+	+		
Histioteuthis atlantica	+	+		+	+		+
Histioteuthis eltaninae	+		+	+	+		+
Histioteuthis macrohista		+					
Alluroteuthis antarcticus	+	+		+	+		
Nototeuthis dimegacotyle	+			+	+		
Bathyteuthis abyssicola			+				+
Cycloteuthis akimushkini					+		
Mastigoteuthis psychrophila	+			+	+	+	
?*Mastigoteuthis* A (Clarke)				+	+	+	
?*Mastigoteuthis* B (Clarke)	+				+		
Chiroteuthis veranyi	+			+	+		+
Chiroteuthis sp. F (Imber)	+						
Batoteuthis skolops	+			+	+		
Taonius sp. B (Voss)	+			+	+		
Teuthowenia pellucida				+			
Galiteuthis glacialis	+	+	+	+	+		+
Galiteuthis stC sp. (Imber)	+						
Mesonychoteuthis hamiltoni	+		+		+		
Oegopsida sp. A	+						
Oegopsida sp. C					+		
cf. *Stoloteuthis leucoptera*				+			+
Octopus dofleini (? = *O. magnificus*)			+				
Benthoctopus thielei (= *B. levis*)				+		+	+
Graneledone gonzalezi (= *G.* sp. & *G.* cf. *antarctica*)				+			+
Graneledone macrotyla			+				
Graneledone sp. A			+				
Stauroteuthis gilchristi	+			+			
Cirroteuthis magna			+				
Opisthoteuthis sp.	+		+				+
Grimpoteuthis sp.							+
Cirrata sp. A	+				+		
Total	**29**	**13**	**13**	**29**	**26**	**10**	**18**

[a] This study
[b] Ridoux (1994), Cherel et al. (1996), Weimerskirch et al. (1997), Cherel & Weimerskirch (1999) and unpubl. data
[c] Only fresh items
[d] Lu & Mangold (1978), Nesis (1987), Piatkowski et al. (1991), Villanueva et al. (1991), Duhamel & Piatkowski (1993), Piatkowski (1993), Kubodera & Okutani (1994), Guerra et al. (1998, 2000), Rodhouse & Lu (1998), Xavier et al. (1999)
[e] Cherel & Duhamel (2004)
[f] Cherel & Weimerskirch (1995), Cherel et al. (2000, 2002a,b,d), Lea et al. (2002)

Crozet Islands. *C. veranyi* is a squid with a wide geographical distribution (Nesis 1987). It was not reported to be an important component in the food of marine predators (but see dos Santos & Haimovici 2002), even if an unidentified chiroteuthid—possibly *C. veranyi*—is the main cephalopod prey of sooty albatrosses from Marion Island (Cooper & Klages 1995). In the same way, mastigoteuthids were not previously found to be key items in the nutrition of any squid predator (Clarke 1996). A recent work, however, suggests that *Mastigoteuthis schmidti* is a significant component of the food of Cuvier's beaked whales in the North Atlantic (Santos et al. 2001), and *M. psychrophila* is also the main prey of lanternsharks at Kerguelen (Cherel & Duhamel 2004). Lastly, one of the most poorly known groups of cephalopods are the Cirrata. The few data available on the trophic interactions of these deep-sea octopods indicate that they feed on benthic invertebrates (Villanueva & Guerra 1991), but their possible predators remain unknown (Villanueva et al. 1997). Our study is therefore the first to show cirrate octopods as prey of large carnivorous fish.

Cephalopod fauna of subantarctic islands

Using top consumers as biological samplers, the cephalopod communities in slope waters surrounding Crozet and Kerguelen archipelagoes show a large diversity. In addition to Patagonian toothfish food, seabirds diet contributes 1 more species for Crozet (*Histioteuthis macrohista*) and that of sharks 5 more species for Kerguelen (including *Cycloteuthis akimushkini* and the 2 gigantic squid *Architeuthis dux* and *Mesonychoteuthis hamiltoni*). This considerably increases the available information about cephalopod diversity and biogeography occurring in the area (Table 4). Oceanographic cruises recorded only a few other squid species: *Moroteuthis robsoni* at Crozet, *Todarodes filippovae* and *Abraliopsis gilchristi* at Kerguelen, and the small deep-sea *Bathyteuthis abyssicola* at both localities. The situation is more complex for octopods due to a chaotic taxonomy for some species. Elsewhere, Xavier et al. (2002) identified 16 cephalopods in the diet of Patagonian toothfish in South Georgia, including 13 squid and 3 endemic octopods. Interestingly, all these squid also occurred at Crozet and Kerguelen, with the exception of the high-Antarctic squid *Psychroteuthis glacialis* at Crozet. The more likely explanations for the lower squid diversity at South Georgia are first the small number of beaks collected there (178 lower beaks), and second its location. The island lies in Antarctic waters while Crozet and Kerguelen are located further north (Park & Gambéroni 1997). A less diverse community at South Georgia is in agreement with the cephalopod diet of elephant seals that suggests a decreasing number of squid with increasing latitudes in the Southern Ocean (van den Hoff et al. 2003).

Overall, the cephalopod fauna at Crozet and Kerguelen includes 36 and 38 different species, respectively, including squid (29 and 32 species, respectively), sepiolid (1 species at Kerguelen) and octopods (7 and 5 taxa) (Table 4). The 2 communities are closely related with most squid species living at both localities (n = 24). Taxa occurring in 1 area only are rare species, except *Todarodes* cf. *angolensis* and the 2 endemic octopodids *Benthoctopus thielei* and *Graneledone gonzalezi*, which are common at Kerguelen and absent from the Crozet Islands (Lu & Mangold 1978). Three studies investigated juvenile squid in cold waters off East Antarctica (Kubodera 1989, Lu & Williams 1994, Jackson et al. 2002). They collected only 8 species in the oceanic zone, all of them living also at Crozet and Kerguelen Islands. The most likely explanation for the richness of the assemblages at these 2 archipelagoes is their location in the Polar Frontal Zone (the zone delineated by the Polar and the Subantarctic Fronts), between the cold Antarctic waters in the South and the warmer subantarctic and subtropical waters in the North (Park & Gambéroni 1997). Consequently, their cephalopod fauna include squid that have primarily Antarctic (e.g. *Kondakovia longimana*, *Alluroteuthis antarcticus*, *Galiteuthis glacialis*, *Mesonychoteuthis hamiltoni*), subantarctic (e.g. *Martialia hyadesi*, *Moroteuthis ingens*, *Gonatus antarcticus*, *Histioteuthis eltaninae*) and subtropical (e.g. *Pholidoteuthis boschmai*, *Taningia danae*, *Cycloteuthis. akimushkini*) distributions (Nesis 1987).

Cephalopod diversity at the subantarctic islands of the southern Indian Ocean agrees well with that found in slope waters from various parts of the world oceans (Roeleveld et al. 1992, Collins et al. 2001, Gonzalez & Sanchez 2002). The main differences are the lack of cuttlefishes and loliginids, and the paucity of sepiolids and benthic octopodids in subantarctic waters. Since these cephalopods are organisms living mainly in continental shelf waters, their absence from Crozet and Kerguelen Islands is probably related to the remoteness of the archipelagoes of the Southern Ocean together with the relatively small extent of most of the peri-insular shelves.

This study is the first to describe in detail the deep-water cephalopods from islands of the Southern Ocean. The results emphasize their abundance and diversity and they add considerable knowledge on biogegraphy of squid and octopuses living there. The study also highlights the need for more taxonomic work—including a detailed description of the beaks—on many cephalopod groups. This, together with the need to quantify biomass merits further surveys using a variety of sampling gears to maximise catches of cephalopods with different sizes (from paralarvae to adults) and ecology (from epipelagic to benthic). The study also underlines the usefulness of teuthophagous predators to gain valuable information on the biology of their prey. Its diverse diet and large bathymetric distribution make the Patagonian toothfish a suitable and efficient cephalopod sampler. Since the species has a circumglobal distribution in the Southern Ocean, it has the potential to be used at various places to describe cephalopod assemblages and to compare them in relation to geography, bathymetry, physical oceanography and the size of the peri-insular shelves.

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