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Antarctic jaws: cephalopod prey of sharks in Kerguelen waters

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Abstract

Only five species of sharks have been recorded in the Southern Ocean, where their biology is essentially unknown. We investigated the feeding habits of the three commonest species from stomach content analysis of specimens taken as bycatches of the fishery targeting the Patagonian toothfish (*Dissostichus eleginoides*) in upper slope waters of the Kerguelen Archipelago. The three species prey upon a diversity of fishes and cephalopods. They segregate by feeding on different species of squids of different sizes. The small lanternsharks (*Etmopterus* cf. *granulosus*; 0.3 m on average) feed on small-sized *Mastigoteuthis psychrophila*, while the large porbeagles (*Lamna nasus*; 1.9 m) feed on small-sized histioteuthids (*Histioteuthis atlantica* and *H. eltaninae*) and on medium-sized juvenile ommastrephids of the genus *Todarodes*. Finally, the huge sleeper sharks (*Somniosus* cf. *microcephalus*; 3.9 m) prey upon large-sized cephalopods (*Kondakovia longimana* and *Taningia danae*) and giant squids (*Mesonychoteuthis hamiltoni* and *Architeuthis dux*). Thus sleeper shark is a fish with sperm whale-like feeding habits and, hence, the second top predator known to science to rely significantly on giant squids. Prey species and biology indicate that porbeagles are pelagic predators in the entire water column, while sleeper sharks are mainly benthic top predators and scavengers. The present study also underlines the diversity and biomass of the poorly known cephalopod fauna, including giant squids, occurring in outer shelf and upper slope waters surrounding subantarctic islands.

Keywords: Giant squids; *Kondakovia longimana*; Lanternsharks; *Mesonychoteuthis hamiltoni*; Porbeagles; Sleeper sharks; Southern Ocean; *Taningia danae*

1. Introduction

Sharks are not frequent in the Southern Ocean, where only five species have been recorded so far (Compagno, 1990; authors' unpublished data). They include two rare species, the white-spotted spurdog (*Squalus acanthias*) and a dogfish (*Centroscymnus* sp.) plus three relatively common species that include the porbeagle (*Lamna nasus*) and two species of still uncertain taxonomic status, one sleeper shark (*Somniosus* cf. *microcephalus*) and one lanternshark (*Etmopterus* cf. *granulosus*). In northern waters, the porbeagle is known as a large shark, with a maximum total length of more than 3.0 m. It is a coastal and oceanic species with an amphitemperate distribution in epipelagic

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waters. Porbeagles are active and strong swimmers and are considered as voracious feeders on small pelagic schooling fishes and squids (Compagno, 1984; Joyce et al., 2002). Sleeper sharks are amongst the largest fish, attaining lengths of up to 7.3 m and body masses of up to 775 kg. In the Northern Hemisphere, they are sluggish epibenthic sharks of cold waters, which regularly occur inshore in the high Arctic but seem confined to deeper waters at lower latitudes. They have been described as voracious and indiscrimate predators and scavengers that feed mainly on fishes and marine mammals (Compagno, 1984; Fisk et al., 2002). Finally, lanternsharks belong to a large, complex and poorly known genus. They are small epibenthic sharks (<1 m) living on the outer shelves and upper slopes, where they prey upon squids, small mesopelagic fishes and shrimps (Compagno, 1990).

In the Southern Ocean almost nothing is known about the biology of sharks. Specimens have been recorded in Kerguelen waters, which is, to our knowledge, the only place where all five species are encountered (Compagno, 1990; Duhamel, 1997, unpublished data). The Kerguelen Islands are a large archipelago that is located in the vicinity of the Antarctic Polar Front in the Indian sector of the Southern Ocean (Park and Gamberoni, 1997). It is one of the most productive areas in the Southern Ocean with high chlorophyll concentrations occurring consistently during the summer months in the north and east of its extensive shelf (the so-called "island mass effect") (Blain et al., 2001; Moore and Abbott, 2002). Consequently, secondary production sustains high populations of top predators, including seabirds, marine mammals and fishes (Duhamel, 1987; Guinet et al., 1996). Since the mid-1980s, a commercial fishery targeting the Patagonian toothfish (*Dissostichus eleginoides*) has developed from upper slope to deeper waters surrounding the archipelago (Duhamel, 1992; Cherel et al., 1996). Sharks are taken as uncommon but regular bycatches of the fishery (Duhamel et al., 1997; authors' unpublished data), thus giving an unique opportunity to collect stomach contents to investigate their diet and feeding habits.

2. Material and methods

The three commonest species of sharks (lanternsharks, porbeagles and sleeper sharks) were caught during fishery operations aboard commercial trawlers and longliners from 1997 to 2001 in Kerguelen waters (mean position 49°30′S–69°00′E) (Table 1). Fishes were measured, sexed and then dissected to investigate their feeding habits. Fishery observers noted the main items, especially the fish species found in the shark stomachs and they discarded them thereafter. They collected cephalopod beaks and whole buccal masses and kept them in 70% ethanol and at −20°C, respectively, until analysis in the laboratory in France.

Cephalopod beaks (both lower and upper beaks) were identified from their morphological features by comparison with material held in our own collection and by reference to the available literature (Clarke, 1986a). Lower rostral lengths (LRL) of squids and lower hood lengths of octopuses were measured with a vernier caliper, and the size of cephalopods was estimated from allometric equations between LRL and dorsal

Table 1
Biological characteristics of sharks caught as bycatches of the Patagonian toothfish fisheries in Kerguelen waters from 1997 to 2001

Species	Fishing methods	Fishing depths (m)	*n*	Total length (m)	Sex (*n*)		
					Males	Females	Undetermined
Lanternsharks	Bottom trawl	687	12	0.30±0.02 (0.26–0.33)	9	3	0
Porbeagles	Bottom trawl (*n* = 18)	459±90 (200–582)	20	1.95±0.24 (1.24–2.25)	9	8	3
	Bottom longline (*n* = 2)	1320–1410					
Sleeper sharks	Bottom trawl	602±117 (350–763)	36	3.91±1.07 (1.50–5.00)	11	20	5

Values are means±SD with ranges in parentheses.

mantle length (ML) and wet mass (M) (Clarke, 1962, 1980, 1986a; Adams and Klages, 1987; Rodhouse and Yeatman, 1990; Rodhouse et al., 1990; Lu and Williams, 1994; Jackson, 1995; Roeleveld, 2000; Piatkowski et al., 2001; authors' unpublished data). For the few species where no relationships were available, ML and M were estimated from equations for closely related species or for species with a similar morphology. Dietary data were obtained by three calculation techniques, namely, the frequency of occurrence and percentages by number and by reconstituted mass of each prey type, as usually done in food analysis for seabirds (see, for example, Cherel et al., 2000). The minimum number of individuals for a given cephalopod species was determined in each shark stomach content as the maximum number of lower or upper beaks of that species. These minimum numbers were subsequently added to calculate the minimum number of individuals for a given cephalopod species in all the samples.

Data were statistically analysed with SYSTAT 9 for WINDOWS (Wilkinson, 1999). Values are means ± SD.

3. Results

3.1. General comments

Overall 68 sharks contained cephalopod remains in their stomachs, including 12 of 32 lanternsharks, 20 of 26 porbeagles and 36 of 36 sleeper sharks (Table 1). There were highly significant differences in size among the three species in the increasing order lanternsharks, porbeagles and sleeper sharks (ANOVA, $F_{2,64} = 104.84$, $p < 0.0001$; all post-hoc Tukey HSD multiple comparison tests, $p < 0.001$). Sex ratio was close to 1 for porbeagles, but more males and more females were caught for lanternsharks and sleeper sharks, respectively (Table 1).

All the lanternsharks were collected in the same bottom trawl, which contained 105 specimens of that species (Fig. 1). The trawl was conducted in the eastern fishing ground at about 700-m depth. Unlike lanternsharks, most of the porbeagles and sleeper sharks occurred singly in nets. All the

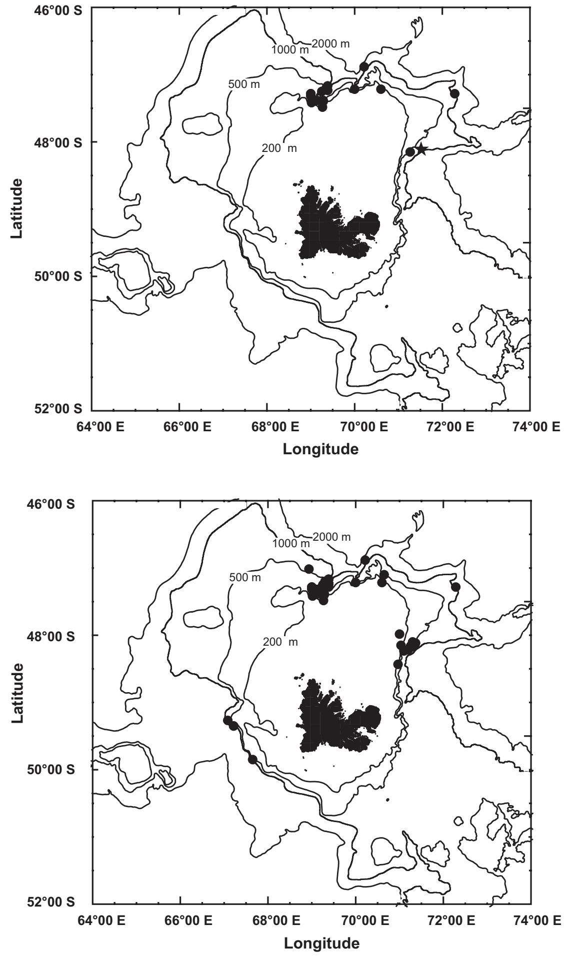

Fig. 1. Geographical positions of bycatches of porbeagles (upper panel) and sleeper sharks (lower panel) in Kerguelen waters. The star in the upper panel shows the location of the trawl that caught lanternsharks.

sleeper sharks and most of the porbeagles were caught in bottom trawls. Two porbeagles were hooked on bottom longlines, but could have been caught pelagically during setting or hauling operations. All porbeagles but one were taken in the northern fishing ground, while sleeper sharks were caught in the northern ($n = 15$), eastern ($n = 17$) and western ($n = 4$) areas (Fig. 1). Sleeper sharks were collected in trawls fished at deeper depths than those in which porbeagles were found, either when all trawling depths were considered (two-sample t-test, $t = 4.54$, $p < 0.001$) (Table 1), or when the trawling depths in the northern fishing ground only were considered (575 ± 70 m, $n = 15$, and 456 ± 91 m, $n = 17$, respectively; two-sample *t*-test, $t = 4.09$, $p < 0.001$).

3.2. Lanternsharks

Thirty-two lanternsharks were dissected. Only 14 stomachs contained prey items, including 12 samples with cephalopod remains. Other items were skin and eye lenses of fishes in one stomach, and one large lanternfish (Family Myctophidae; *Gymnoscopelus microlampas*) in another sample.

Four species of squids (30 beaks) were identified from the stomach contents of lanternsharks. By far, the main species was *Mastigoteuthis psychrophila*, which accounted for 73% of the total number of beaks and 85% by mass of the cephalopod diet (Table 2). The recently described brachioteuthid squid, *Slosarczykovia circumantarctica* (Lipinski, 2001) ranked second, while two other species were found only once. Overall, the estimated size of cephalopods eaten by lanternsharks is small, the largest prey being an individual of *M. psychrophila* with a 121-mm ML and weighing 67 g (Table 3).

3.3. Porbeagles

Twenty-six porbeagles were dissected; 25 stomachs contained prey items, including 23 samples with cephalopod remains (cephalopod prey were identified from 20 of the samples) and 16 containing fish items. Fishes included a few specimens of shelf species in the families Channichthyidae (*Channichthys rhinoceratus* and *Champsocephalus gunnari*) and Congiopodidae (*Zanclorhynchus spinifer*) together with a greater number of mesopelagic fishes. Most of the latter were lanternfishes (Myctophidae) with the giant of the family *Gymnoscopelus bolini* (standard length up to 28 cm; Hulley, 1990) ranking first and the large *G. piabilis* second. Other mesopelagic fishes were specimens of dragonfish (*Stomias* sp., Stomiidae) and snake mackerels (*Paradiplospinus gracilis*, Gempylidae).

Fifteen species of squids (689 beaks) were identified from the stomach contents of porbeagles (Table 4). Two cephalopod species were important in the diet, the histioteuthid, *Histioteuthis atlantica*, which dominated by number (46% by number and 9% by mass), and the ommastrephid, *Todarodes* sp., which dominated by reconstituted mass (33% by number and 56% by mass). The latter species is identical or closely related to *T. angolensis* (Cherel and Weimerskirch, 1995), but its taxonomic status merits further investigation. Other significant prey were another histioteuthid *H. eltaninae*, the chiroteuthid *Chiroteuthis veranyi*, the onychoteuthid *Moroteuthis knipovitchi*, and another ommastrephid *Martialia hyadesi*. Finally, owing to its large size (Table 5), the onychoteuthid *Kondakovia longimana* accounted for a significant

Table 2
Lanternsharks: frequency of occurrence, numbers of cephalopod beaks (both lower and upper beaks), and reconstituted mass of the cephalopod diet at Kerguelen (total for all 12 samples pooled)

Species	Occurrence		Number		Minimum number of individuals	Reconstituted mass	
	(*n*)	(%)	(*n*)	(%)		(g)	(%)
Brachioteuthidae							
Slosarczykovia circumantarctica	4	33.3	5	16.7	4	18.49	3.2
Histioteuthidae							
Histioteuthis atlantica	1	8.3	1	3.3	1	20.29	3.5
Mastigoteuthidae							
Mastigoteuthis psychrophila	8	66.7	22	73.3	12	485.31	84.8
Batoteuthidae							
Batoteuthis skolops	1	8.3	2	6.7	1	48.48	8.5
Total			30	100.0	18	572.57	100.0

Table 3
Lanternsharks: measured lower rostral length (LRL), and estimated mantle length (ML) and body mass (*M*) of cephalopod prey identified from stomach contents at Kerguelen

Species	*n*	LRL (mm)	ML (mm)	*M* (g)
Slosarczykovia circumantarctica	3	2.0±0.3 (1.8–2.3)	57±5 (53–63)	4.6±0.9 (4.0–5.6)
Histioteuthis atlantica	1	1.9	27	20
Mastigoteuthis psychrophila	11	3.3±0.7 (2.0–4.3)	93±21 (56–123)	40±22 (9–80)
Batoteuthis skolops	1	3.6	[a]	[a]

Values are means±SD with ranges in parentheses.
[a] No allometric equations available.

Table 4
Porbeagles: frequency of occurrence, numbers of cephalopod beaks (both lower and upper beaks), and reconstituted mass of the cephalopod diet at Kerguelen (total for all 20 samples pooled)

Species	Occurrence		Number		Minimum number of individuals	Reconstituted mass	
	(*n*)	(%)	(*n*)	(%)		(g)	(%)
Ommastrephidae							
Martialia hyadesi	5	25.0	17	2.5	11	2890	4.9
Todarodes cf. *angolensis*	11	55.0	224	32.5	120	33321	56.5
Onychoteuthidae							
Moroteuthis ingens	4	20.0	8	1.2	5	1050	1.8
Moroteuthis knipovitchi	4	20.0	19	2.8	13	1856	3.1
Kondakovia longimana	4	20.0	12	1.7	7	11504	19.5
Brachioteuthidae							
Brachioteuthis linkovskyi	2	10.0	4	0.6	3	41	<0.1
Gonatidae							
Gonatus antarcticus	2	10.0	7	1.0	4	312	0.5
Histioteuthidae							
Histioteuthis atlantica	12	60.0	317	46.0	167	5484	9.3
Histioteuthis eltaninae	5	25.0	41	6.0	24	839	1.4
Neoteuthidae							
Alluroteuthis antarcticus	1	5.0	2	0.3	1	244	0.4
Nototeuthis dimegacotyle	1	5.0	1	0.1	1	138	0.2
Mastigoteuthidae							
Mastigoteuthis psychrophila	1	5.0	1	0.1	1	40	<0.1
?*Mastigoteuthis* A (Clarke)	1	5.0	2	0.3	1	120	0.2
Chiroteuthidae							
Chiroteuthis veranyi	6	30.0	33	4.8	17	1174	2.0
Cranchiidae							
Galiteuthis glacialis	1	5.0	1	0.1	1	6	<0.1
Total			689	100.0	376	59019	100.0

percentage of the diet by reconstituted mass (2% by number and 19% by mass).

Porbeagles prey mainly upon one size class of *Todarodes* cf. *angolensis*, with a mode at 4.5–5.0 mm LRL (Fig. 2), which corresponds to estimated ML and *M* of 175–196 mm and 154–208 g, respectively. The mode corresponds to juvenile squids, as indicated by the undarkened wings of the lower beaks, thus contrasting with the wholly darkened beaks of two adult specimens

Table 5
Porbeagles: measured lower rostral length (LRL), and estimated mantle length (ML) and body mass (M) of cephalopod prey identified from stomach contents at Kerguelen

Species	n	LRL (mm)	ML (mm)	M (g)
Martialia hyadesi	9	4.7±1.3 (3.5–7.3)	241±37 (205–316)	268±156 (137–600)
Todarodes cf. *angolensis*	105	5.1±1.0 (4.2–11.2)	198±40 (163–452)	239±226 (128–2033)
Moroteuthis ingens	3	4.4±0.6 (3.8–4.9)	187±20 (165–203)	210±63 (141–265)
Moroteuthis knipovitchi	10	4.7±0.6 (4.0–6.1)	186±36 (141–277)	156±92 (77–406)
Kondakovia longimana	5	11.4±3.1 (6.0–13.6)	404±115 (200–484)	1805±938 (197–2642)
Brachioteuthis linkovskyi	2	4.0–4.4	97–106	12–14
Gonatus antarcticus	2	3.2–6.6	93–240	24–281
Histioteuthis atlantica	155	2.1±0.8 (1.0–4.9)	33±17 (9–95)	33±28 (5–192)
Histioteuthis eltaninae	20	2.4±0.3 (1.8–2.9)	39±8 (25–51)	37±12 (18–59)
Alluroteuthis antarcticus	1	4.3	145	244
Nototeuthis dimegacotyle	1	3.5	[a]	[a]
?*Mastigoteuthis* A (Clarke)	1	5.0	[a]	[a]
Chiroteuthis veranyi	16	5.2±0.6 (4.0–6.1)	138±15 (110–161)	69±21 (34–105)

Values are means±SD with ranges in parentheses.
[a] No allometric equations available.

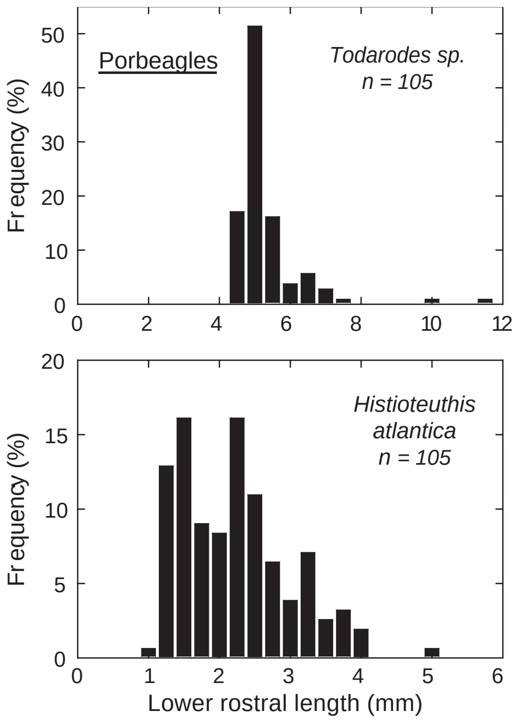

Fig. 2. Porbeagles: frequency distribution of LRL of *Todarodes* cf. *angolensis* and *H. atlantica* eaten in Kerguelen waters.

(9.7 and 11.2 mm LRL). Most histioteuthids were juveniles (undarkened wings) and subadults (darkening wings), with no well defined modes (Fig. 2), indicating that sharks fed on different size classes. Overall, histioteuthids (both *H. atlantica* and *H. eltaninae*) were small with an estimated ML and M of 30–40 mm and 30–40 g, respectively (Table 5). The largest cephalopod prey was an adult of *K. longimana* with a 48 cm ML and weighing 2.6 kg.

3.4. Sleeper sharks

Thirty-six sleeper sharks were dissected; all the stomachs contained cephalopod flesh and/or accumulated cephalopod beaks of large size. Stomach contents regularly contained whole specimens of Patagonian toothfish, and discarded fish heads of that species (fishery waste), which were most likely eaten directly in trawls and scavenged at the bottom, respectively. Other prey items were demersal fishes (mainly the skates *Bathyraja irrasa* and *B. eatonii*, and the nototheniids *Notothenia rossii* and *Lepidonotothen squamifrons*), benthic invertebrates (e.g. sea stars, ophiurids) and carrion. The stomach of nine sharks contained big chunks of flesh (up to 30 kg), which, in 2 cases, were identified as belonging to fur seals (probably the Antarctic fur seal *Arctocephalus gazella*).

Nineteen species of cephalopods (553 beaks) were identified from the stomach contents of sleeper sharks; they include 18 species of squids and one species of an unknown large cirrate

Table 6
Sleeper sharks: frequency of occurrence, numbers of cephalopod beaks (both lower and upper beaks), and reconstituted mass of the cephalopod diet at Kerguelen (total for all 36 samples pooled)

Species	Occurrence		Number		Minimum number of individuals	Reconstituted mass	
	(*n*)	(%)	(*n*)	(%)		(g)	(%)
Architeuthidae							
Architeuthis dux	7	19.4	14	2.5	8	324644	14.9
Ommastrephidae							
Todarodes cf. *angolensis*	2	5.6	4	0.7	2	2801	0.1
Onychoteuthidae							
Moroteuthis ingens	1	2.8	2	0.4	1	1021	<0.1
Moroteuthis robsoni	3	8.3	5	0.9	3	7213	0.3
Moroteuthis knipovitchi	1	2.8	1	0.2	1	804	<0.1
Kondakovia longimana	24	66.7	274	49.5	154	458519	21.0
Brachioteuthidae							
Slosarczykovia circumantarctica	1	2.8	11	2.0	11	128	<0.1
Gonatidae							
Gonatus antarcticus	2	5.6	8	1.4	7	1251	<0.1
Octopoteuthidae							
Taningia danae	16	44.4	69	12.5	40	235678	10.8
Histioteuthidae							
Histioteuthis atlantica	1	2.8	6	1.1	4	1583	<0.1
Neoteuthidae							
Alluroteuthis antarcticus	1	2.8	3	0.5	2	467	<0.1
Cycloteuthidae							
Cycloteuthis akimushkini	5	13.9	11	2.0	6	6800	0.3
Mastigoteuthidae							
Mastigoteuthis psychrophila	1	2.8	24	4.3	24	1249	<0.1
Mastigoteuthis B	1	2.8	1	0.2	1	234	<0.1
Cranchiidae							
Taonius sp. B (Voss)	1	2.8	6	1.1	6	1147	<0.1
Galiteuthis glacialis	2	5.6	22	4.0	17	903	<0.1
Mesonychoteuthis hamiltoni	22	61.1	89	16.1	49	1133621	52.0
Oegopsida sp. C	1	2.8	1	0.2	1	234	<0.1
Cirrata sp. A	1	2.8	2	0.4	1	2237	0.1
Total			553	100.0	338	2180535	100.0

octopod (Table 6). Four species dominated the cephalopod diet, accounting together for 81% of the total number of beaks and 99% of the reconstituted mass. They were *K. longimana*, which was the main prey by number (50% by number and 21% by mass), the cranchiid *Mesonychoteuthis hamiltoni*, which was the main prey by mass (16% by number and 52% by mass), plus the octopoteuthid *Taningia danae* (12% by number and 11% by mass) and the architeuthid *Architeuthis dux* (3% by number and 15% by mass).

Sleeper sharks fed on adult *K. longimana*, as indicated by the large size and level of darkening of the beaks. Fig. 3 shows a mode at 14–15 mm LRL, which corresponds to estimated ML and M of 50–54 cm and 2.9–3.6 kg, respectively. On the other hand, sharks prey upon juveniles, subadults and adult *M. hamiltoni*, *T. danae* and *A. dux*, as indicated by the large range in size in LRL and in the level of darkening of the beaks (Fig. 3, Table 7). The mean ML and *M* of *T. danae* were 65 cm and 6.1 kg, respectively, while both *M. hamiltoni* and *A. dux* were much larger on average

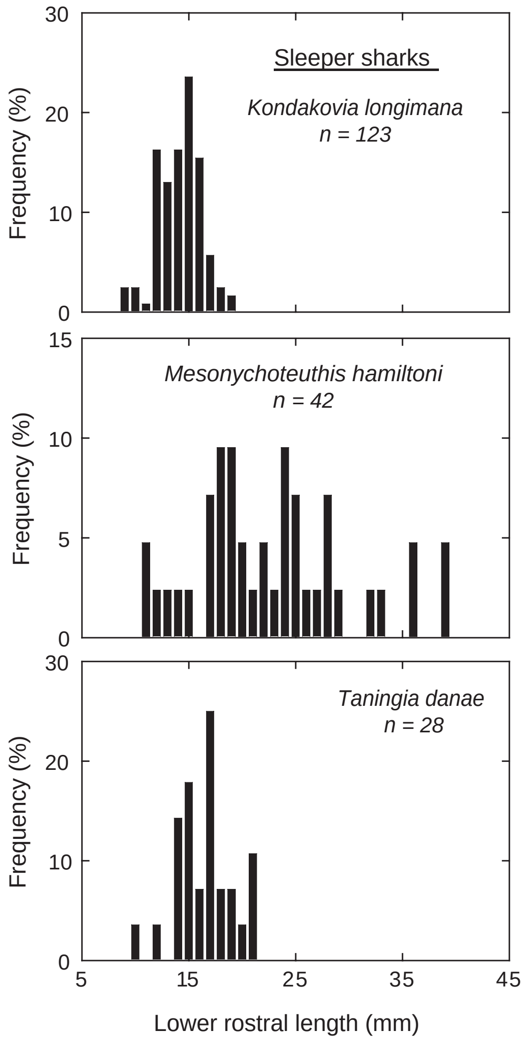

Fig. 3. Sleeper sharks: frequency distribution of LRL of *K. longimana*, *M. hamiltoni* and *T. danae* eaten in Kerguelen waters.

(136 cm and 24 kg, and 110 cm and 39 kg, respectively). The largest cephalopod prey was an adult of *A. dux* with a 220 cm ML and weighing 96 kg.

3.5. Relationship between predator size and prey size

To compare the size of cephalopods eaten by the three species of sharks, we estimated ML from LRL and, for a given shark species, we pooled and plotted together the estimated ML from all the specimens of the different species of cephalopods (Fig. 4). The two modes in ML of cephalopods eaten by porbeagles correspond to histioteuthids (<50 mm ML) and *Todarodes* cf. *angolensis* (175–200 mm ML), while the marked mode (400–600 mm) observed in the size of cephalopods caught by sleeper sharks corresponds to *K. longimana*, and, to a lesser extent, *T. danae* (Fig. 4).

Overall, sharks fed on cephalopods of different sizes (ML = 98 ± 30 mm, $n = 16$, 110 ± 93 mm, $n = 330$, and 681 ± 425 mm, $n = 219$, for lanternsharks, porbeagles and sleeper sharks, respectively; Kruskal-Wallis test statistic = 379, $p < 0.0001$). However, sleeper sharks preyed upon larger items than the two other fishes, but no significant difference was found between the size of cephalopods eaten by lanternsharks and porbeagles (Mann-Whitney U test statistic = 2680, $p = 0.918$). When related to predator size, again, the huge sleeper sharks fed on large to giant prey, but the large porbeagles, on average, caught relatively small prey, and the small lanternsharks preyed upon small cephalopods only (Fig. 5).

Since sharks fed on different species of cephalopods, a direct comparison of the size of a given species of squid eaten by different sharks was possible for *K. longimana* only (Tables 5 and 7). There was a tendency for porbeagles to prey upon *K. longimana* of smaller size than those eaten by sleeper sharks (Mann-Whitney U test statistic = 159.5, $p = 0.069$).

4. Discussion

4.1. General comments and resource partitioning

The three species of sharks segregate both by their food and feeding ecology in Kerguelen waters. All occur in upper slope waters, but porbeagles were caught on average in shallower waters than sleeper sharks. The three sharks prey upon different species of squids, which can be related to the size of the predators. The small lanternsharks feed on small-sized *M. psychrophila*, the large porbeagles on small-sized histioteuthids (*H. atlantica* and *H. eltaninae*) and medium-sized juveniles *Todarodes* cf. *angolensis*, while the

Table 7
Sleeper sharks: measured lower rostral length (LRL), and estimated mantle length (ML) and body mass (M) of cephalopod prey identified from stomach contents at Kerguelen

Species	n	LRL (mm)	ML (cm)	M (kg)
Architeuthis dux	6	13.9±3.1 (10.4–18.1)	110±69 (45–220)	39.0±34.9 (7.6–95.7)
Todarodes cf. *angolensis*	2	9.6–10.0	39–40	1.3–1.5
Moroteuthis robsoni	3	9.4±0.2 (9.3–9.7)	62±3 (61–65)	2.4±0.2 (2.3–2.7)
Kondakovia longimana	123	13.7±2.0 (8.4–18.9)	49±7 (29–68)	2.9±1.3 (0.6–7.6)
Gonatus antarcticus	2	5.6–5.8	20–21	0.2
Taningia danae	28	16.0±2.7 (9.4–20.9)	65±20 (15–101)	6.1±3.2 (0.9–13.6)
Histioteuthis atlantica	2	6.3–7.1	13–14	0.3–0.4
Alluroteuthis antarcticus	1	4.2	14	0.2
Cycloteuthis akimushkini	5	13.8±2.7 (10.3–16.1)	43±8 (32–50)	1.1±0.4 (0.6–1.5)
Galiteuthis glacialis	5	4.0±1.5 (1.6–5.1)	17±6 (8–22)	<0.1
Mesonychoteuthis hamiltoni	42	22.3±7.2 (10.1–38.8)	136±44 (61–237)	24.4±22.1 (2.1–91.2)
Cirrata sp. A	1	13.8[a]	[b]	[b]

Values are means±SD with ranges in parentheses.
[a] Lower hood length (mm).
[b] No allometric equations available.

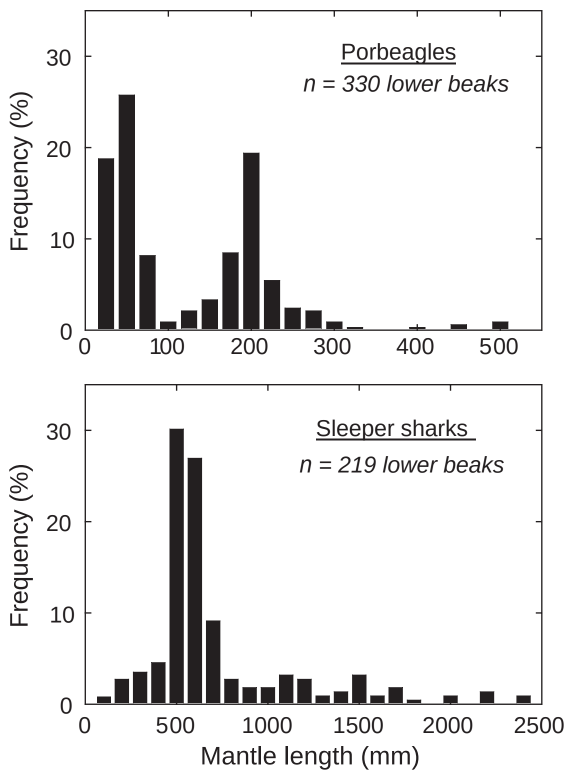

Fig. 4. Frequency distribution of dorsal MLs of squids eaten by porbeagles and sleeper sharks in Kerguelen waters. Note the different scales of the x-axis on upper and lower panels.

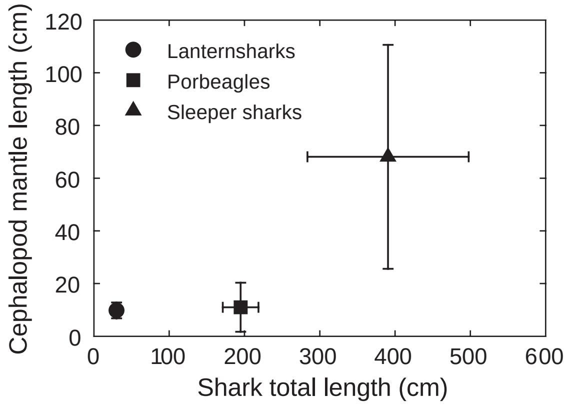

Fig. 5. Relationship between prey size (dorsal ML of squids) and predator size (total length of sharks) in Kerguelen waters.

gigantic sleeper sharks feed on large-sized and giant squids (see below). Little is known about the food of lanternsharks elsewhere. Specimens from Kerguelen prey upon squids, and, to a lesser extent upon mesopelagic lanternfishes (myctophids). This is in broad agreement with previous results obtained on various species of *Etmopterus* (Compagno, 1984; Ebert et al., 1992), including *E. lucifer* and *E. granulosus*, which are probably closely related to the species occurring in Kerguelen waters (Compagno, 1990; Duhamel, 1997).

However, the small sample size of lanternsharks together with the fact that all specimens were caught in the same trawl preclude any definite conclusion about the feeding ecology of the species at Kerguelen.

Previous studies on the feeding ecology of the porbeagle were largely anecdotal, but a recent article details its food in the northwest Atlantic Ocean. Fishes dominated by far in its diet, fresh remains of cephalopods being much less important (Joyce et al., 2002). In contrast, stomach content analysis made onboard by fishery observers has shown that both fish and cephalopods were the main food items of porbeagles in Kerguelen waters. Interestingly, ommastrephids are the main squid prey both in the Atlantic (where the only identified cephalopod was *Illex argentinus*, Joyce et al., 2002) and at Kerguelen (*Todarodes* cf. *angolensis*). At the latter locality, the diet was dominated by species that are known to be primarily pelagic, i.e. myctophid fishes of the genus *Gymnoscopelus* (Hulley 1990), *Todarodes* squids (Dunning and Wormuth, 1998) and *Histioteuthis* squids (Voss et al., 1998). Other prey include a few specimens of the demersal shelf fishes *C. rhinoceratus* and *Z. spinifer* and the semi-pelagic icefish *C. gunnari* (Duhamel and Hureau, 1985; Heemstra and Duhamel, 1990). Hence, the porbeagle at Kerguelen is mainly a pelagic predator, thus contrasting with specimens from the northwest Atlantic where both pelagic and demersal fish are important components of their diet (Joyce et al., 2002).

The sleeper shark from Kerguelen belongs to the subgenus *Somniosus* and is therefore closely related to the two giant species *S. microcephalus* from the north Atlantic and *S. pacificus* from the north Pacific (Compagno, 1990). In the Northern Hemisphere, these sharks are voracious, indiscriminate predators and scavengers that feed mainly on the bottom on a wide variety of pelagic and demersal fishes, as well as on marine mammals and various invertebrates (Compagno, 1984, 1990; Yang and Page 1999; Fisk et al., 2002). Accordingly, stomach contents of specimens from Kerguelen contained large benthic fishes (skates, Patagonian toothfish), fishery offal and carrion, including fur seals. A consistent feature was the presence of cephalopod remains in all the samples, thus indicating that squids are of primary importance in the diet of sleeper sharks in Kerguelen. Elsewhere, cephalopods are minor prey, but the giant octopod *Enteroctopus dofleini* accounted for a small but significant percentage by mass (5%) of the diet of sleeper sharks in the north Pacific Ocean (Yang and Page, 1999).

In summary, sleeper sharks are benthic top predators and scavengers, while porbeagles are pelagic predators in upper slope waters of the Kerguelen archipelago. Moreover, sleeper sharks are sluggish fish at and near the bottom and porbeagles active swimmers throughout the water column (Compagno, 1984). Prey species and biology also suggest that, unlike a recent estimate in a review indicating an identical trophic level (4.1) for *Somniosus microcephalus*, *S. pacificus* and porbeagles (Cortes, 1999), the trophic position of sleeper sharks is higher than that of porbeagles in Kerguelen waters.

4.2. The sleeper shark: a fish with a sperm whale-like diet

The main food items of sleeper sharks were two large species of squids *K. longimana* (ML up to 0.9 m) (Nesis, 1987) and *T. danae* (ML up to 1.7 m) (Nesis, 1987), together with the largest invertebrates living on earth, the endemic Antarctic cranchiid *M. hamiltoni* (ML up to 2.3 m) (Klumov and Yukhov, 1975; Nesis, 1987) and the giant architeuthid *A. dux* (ML up to 5 m) (Nesis, 1987). *K. longimana* is an endemic squid from Antarctic and subantarctic waters (Nesis, 1987; Cherel and Weimerskirch, 1999) that is rarely caught by research trawls. It was found in stomach contents of many top predators in the Antarctic (Cherel and Weimerskirch, 1999; Santos et al., 2001a), including the largest flying bird the wandering albatross (*Diomedea exulans*) (Cherel and Klages, 1998) and the deepest diving odontocet, the sperm whale (*Physeter catodon*) (Clarke, 1980). Other large and giant squids were not previously reported to be important in the diet of marine predators, except the sperm whale. *M. hamiltoni* is a leading member of the Antarctic teuthofauna by biomass (Nesis, 1987) and is typically present in the diet of sperm whales in the Antarctic (Klumov and Yukhov, 1975; Clarke, 1980; Yukhov, 1982). *T. danae* and *A. dux* are cosmopolitan cephalopod species (Nesis, 1987; Roper and Vecchione, 1993; Förch, 1998) that were found to be important food items in sperm whales in various parts of the world (Clarke, 1986b). This makes the sleeper shark the only fish with feeding habits like sperm whale and, hence, the second top predator known to rely to a significant extent on giant squids. To our knowledge, no other shark species target giant squids (Smale, 1996), but *A. dux* was occasionally reported in the diet of sharks from the North Atlantic (Clarke and Merrett, 1972; Gonzalez et al., 2002), off South Africa (Smale and Cliff, 1998) and off eastern Australia (Dunning et al., 1993).

Comparison of the size of squids eaten by sleeper sharks and sperm whales (Clarke, 1980) shows that both species prey upon adult *K. longimana* and upon different size-classes (from juveniles to adults) of *T. danae*, *M. hamiltoni* and *A. dux*. The mean estimated size of cephalopods eaten by sleeper sharks was 68 cm ML and 8.2 kg, which is slightly larger than the average mass (7.2 kg) estimated for cephalopods eaten by sperm whales in the Antarctic (Clarke, 1980). The two predators thus target the same species of cephalopods with about the same size and also in the same location, since Kerguelen was a whaling ground for sperm whales in the last century (Yukhov, 1982). The mean size of squids eaten by sharks is, moreover, likely to be underestimated because the smallest individuals were probably secondary items ingested with primary prey. Indeed, the main food of sleeper sharks—large squids and the Patagonian toothfish—are known to feed on cephalopods (Rodhouse and Nigmatullin, 1996; Xavier et al., 2002). ML—the standard length for cephalopods—does not take into account the size of arms and tentacles. By doing so, the largest squids had a much bigger size than that of sharks. For example, a specimen of *A. dux* with a ML of 2.2 m reached a total length of more than 12 m. How sharks catch such giant squids remains unknown because they may either prey on live animals or scavenge on dead individuals.

4.3. Predator indication of key cephalopod species on the Kerguelen Plateau

Almost nothing is known about the cephalopod fauna and its biomass on the Kerguelen Plateau (Lu and Mangold, 1978; Guerra et al., 2000). Recent works on the diet of top predators breeding at Kerguelen and at the closely related Heard Island point out the importance of cephalopods in the nutrition of some fishes, seabirds and marine mammals. Predators' diet underlines the key role of at least 17 species of cephalopods, including 16 squids and one benthic octopod in the area (Table 8). Noticeable is the importance of ommastrephids and onychoteuthids. *M. hyadesi* is the main prey by mass of king penguins during the austral winter (Moore et al., 1998), and juveniles of *Todarodes* cf. *angolensis* are important items for porbeagles (present study), and for the black-browed and grey-headed albatrosses (Cherel et al., 2000, 2002). Among onychoteuthids, owing to their large size, adults of *K. longimana* are key prey for sleeper sharks (present study), wandering albatrosses (Cherel and Weimerskirch, unpublished data), southern elephant seals (Slip, 1995) and southern bottlenose whales (Slip et al., 1995). *Moroteuthis ingens*, which is an abundant bycatch species on shelf and upper slope fishery grounds (Cherel and Duhamel, 2003), makes up a significant part of the diet of elephant seals (Green and Burton, 1993), and to a lesser extent of king penguins in winter (Moore et al., 1998).

Among other squid families, cranchiids, mainly *Galiteuthis glacialis*, are important in the food of sleeper sharks, albatrosses and marine mammals (Slip et al., 1995; Cherel et al., 2000, 2002; present study). An unexpected finding was the abundance of *M. psychrophila* in the diet of lanternsharks, elephant seals and bottlenose whales (Table 8). To our knowledge, mastigoteuthids were not previously found to be key items in the nutrition of any squid predator (Clarke, 1996), except probably the Cuvier's beaked whales in the North Atlantic (Santos et al. 2001b). This emphasizes how poorly known are trophic interactions of many cephalopod taxa in the Southern Ocean and elsewhere. The present study also underlines the diversity and biomass of cephalopods, including

Table 8
Main cephalopod species in the diet of top predators from the Kerguelen Plateau

Species	Sharks			Birds				Mammals		
	Etmopterus cf. *granulosus*	*Lamna nasus*	*Somniosus* cf. *microcephalus*	*Aptenodytes patagonicus*	*Diomedea melanophrys*		*Diomedea chrysostoma*	*Mirounga leonina*		*Hyperoodon planifrons*
	Kerguelen	Kerguelen	Kerguelen	Heard	Kerguelen	Nuageuses	Nuageuses	Heard	Heard	Heard
Ommastrephidae										
Martialia hyadesi		+		24	6	+	+		+	+
Todarodes cf. *angolensis*		33	+		9–32	14–60	14–54	+		+
Onychoteuthidae										
Moroteuthis ingens		+	+	20	+	+	+	19		5
Moroteuthis knipovitchi		+	+		+			18	+	15
Kondakovia longimana		+	50	54	+	+	9	10	+	14
Brachioteuthidae										
Slosarczykovia circumantarctica	17		+			+ [a]		4[b]	+ [b]	9[b]
Gonatidae										
Gonatus antarcticus		+	+	+	+		+	12	6	14
Octopoteuthidae										
Taningia danae			12		+					
Histioteuthidae										
Histioteuthis atlantica	+	46	+		+		+			
Histioteuthis eltaninae		6				+	+	6	+	+
Neoteuthidae										
Alluroteuthis antarcticus		+	+		+		+	12	+	7
Mastigoteuthidae										
Mastigoteuthis psychrophila	73		+		+		+	11[c]	50[c]	21[c]
Cranchiidae										
Liocranchia sp.									11	+
Taonius pavo/sp. B (Voss)			+				+	+	6	+
Galiteuthis glacialis		+	+	+	20	5	18	+	12	5
Mesonychoteuthis hamiltoni			16						+	
Octopodidae										
Benthoctopus thielei					23	15				
References	Present study	Present study	Present study	Moore et al. (1998)	Cherel et al. (2000)	Cherel et al. (2002)	Cherel et al. (2002)	Green and Burton (1993)	Slip et al. (1995)	Slip (1995)

Numbers refer to the percentages by number (>5%, +present) of the cephalopod diet.

[a] Formerly identified as *Brachioteuthis* ?*riisei*.

[b] Formerly identified as *Mastigoteuthis* sp.? In Slip (1995), and as ?*Mastigoteuthis* sp. in Slip et al. (1995), thus possibly also identified as *Mastigoteuthis*? In Green and Burton (1993).

[c] Formerly misidentified as *Psychroteuthis glacialis* in Slip et al. (1995), thus possibly also in Slip (1995) and in Green and Burton (1993). One of us (YC) examined 81 lower beaks labelled *P. glacialis* from the study of Slip et al. (1995) at ANARE in March 1997; it was a mixture of beaks from *Mastigoteuthis psychrophila* ($n = 76$) and from *Batoteuthis skolops* ($n = 5$).

giant squids, occurring in outer shelf and upper slope waters surrounding subantarctic islands.

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