Top predators and stable isotopes document the cephalopod fauna and its trophic relationships in Kerguelen waters

by

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ABSTRACT. - Information on the poorly known but ecologically important cephalopod fauna of Subantarctic islands was collected using fishery bycatches, together with published data from oceanographic cruises and top predators (fishes and seabirds) as biological samplers. Overall, the cephalopod fauna from Kerguelen Islands includes at least 38 different species. Oegopsid squids dominate the assemblage over octopods (31 and 6 taxa, respectively), with one species of sepiolid occurring over the shelf. This rich community includes a large diversity of pelagic squids, four benthopelagic cirrate octopods and two endemic benthic octopodids. The results emphasize the importance of ommastrephids, onychoteuthids, cranchiids and a few other squid species in the nutrition of top consumers in the Southern Ocean. The trophic structure of the community of cephalopods (n = 18 representative species) was subsequently investigated by using the stable isotopic signature of their chitinized beaks. $\delta^{13}C$ values demonstrated that cephalopods grew in three different marine ecosystems, with 16 species living and developing in Kerguelen waters and two species migrating from either Antarctica (*Slosarczykovia circumantarctica* Lipinski, 2001) or the Subtropics (the giant squid *Architeuthis dux* Steenstrup, 1857). Values of $\delta^{15}N$ indicate that species living in Kerguelen slope waters encompass almost three distinct trophic levels with a continuum of two levels between crustacean- and fish-eaters, and a distinct higher trophic level occupied by the colossal squid *Mesonychoteuthis hamiltoni* Robson, 1925. The stable isotopic signature of beaks therefore revealed new trophic relationships and migration patterns and is a powerful tool to investigate the role of the poorly known cephalopods in the marine environment.

RÉSUMÉ. - Utilisation des prédateurs supérieurs et de la méthode isotopique pour l'étude des céphalopodes de Kerguelen.

L'utilisation conjointe des rares données de campagnes océanographiques, des captures accessoires des pêcheries ainsi que des prédateurs supérieurs comme bio-échantillonneurs nous a permis de collecter des informations sur un groupe méconnu d'organismes marins, les céphalopodes subantarctiques. A Kerguelen, ce groupe est constitué d'au moins 38 espèces différentes, incluant 31 calmars oegopsidés, six poulpes et une sépiole. Cette riche communauté comprend une grande diversité de calmars pélagiques, quatre cirroctopodes bentho-pélagiques et deux octopodes endémiques benthiques. Les résultats soulignent l'importance des ommastrephidés, onychoteuthidés, cranchiidés et de quelques autres espèces de calmars dans le régime alimentaire des prédateurs supérieurs de l'océan Austral. La structure trophique de la communauté de céphalopodes (n = 18 espèces représentatives) a ensuite été étudiée en appliquant la méthode des isotopes stables à leurs becs chitinisés. Les valeurs en $\delta^{13}C$ ont montré que la grande majorité de ces céphalopodes (16 espèces) avaient effectué leur croissance dans les eaux de Kerguelen, mais également que deux espèces avaient récemment migré, une de l'Antarctique (*Slosarczykovia circumantarctica* Lipinski, 2001) et l'autre des eaux subtropicales (le calmar géant *Architeuthis dux* Steenstrup, 1857). Les valeurs en $\delta^{15}N$ ont indiqué que la communauté est structurée autour de trois niveaux trophiques, avec d'abord un continuum d'espèces entre deux niveaux, des consommateurs de crustacés à ceux se nourrissant essentiellement de poissons. Le troisième niveau, bien distinct, est occupé par une seule espèce, le calmar colossal *Mesonychoteuthis hamiltoni* Robson, 1925, qui domine l'écosystème pélagique. La méthode isotopique sur les becs a révélé de nouvelles interactions trophiques et voies migratoires, s'avérant être ainsi un outil puissant pour étudier le rôle méconnu des céphalopodes dans l'environnement marin.

Key words. - Beaks - Octopus - Southern Ocean - Seabirds - Squid - Stable isotopes - Toothfish.

The cephalopod fauna of the Southern Ocean (south the Subtropical Front) is poorly known, despite growing evidence that squid constitute a key group in the marine food webs (Rodhouse and White, 1995; Collins and Rodhouse, 2006). The main limitations are the small number of research cruises targeting squids and octopuses, together with the difficulties in collecting cephalopods by nets. In the southern Indian Ocean, only one preliminary study exists, based on specimens opportunistically collected, listing a total of 11 species of cephalopods caught in the vicinity of Prince Edwards, Crozet, Kerguelen and Heard Islands (Lu and Mangold, 1978). 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 (e.g., Ridoux, 1994). At Kerguelen Islands, it has been esti-

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mated that the communities of breeding seabirds and seals consume more than 200,000 tons of cephalopods, mainly squid, each year (Guinet *et al*., 1996). Thus, there is substantial potential for using data on teuthophagous predators to gather unique information on the biology of their prey (Rodhouse, 1990). Moreover, the increasing knowledge on the morphology of cephalopod beaks – chitinous hard structures that are resistant to digestion – allows the identification to the species level of most of the accumulated items found in predators' stomach (Clarke, 1986; Xavier and Cherel, 2009).

Our first goal was to collect information on the cephalopod community inhabiting waters surrounding Kerguelen Islands by using top consumers as biological samplers (Cherel *et al*., 2004). The study focused on the cephalopod diet of the Patagonian toothfish (*Dissostichus eleginoides* Smitt, 1898), a species that is targeted commercially in the 400-1500 m-depth range in slope waters surrounding the archipelago (Duhamel, 1992). Additional information were collected from published and unpublished feeding habits of other apex predators from the areas, namely sharks, seabirds and marine mammals, to give a broad overview of the cephalopod assemblage and their importance in the southern Indian Ocean. Within this objective, we looked at two major issues: the description of the cephalopod fauna in Kerguelen waters by reviewing all the available information and updating the only previous investigation (Cherel *et al*., 2004), and the importance of cephalopods in the diet of top predators foraging in the area to point out which squid families and species have a key role in the marine ecosystems surrounding the archipelago.

Knowledge of the diets of squid and octopuses in the Southern Ocean remains rather limited (Collins and Rodhouse, 2006). In the southern Indian Ocean, the conventional method of studying the food of cephalopods from stomach content analysis is restricted to one species [*Moroteuthis ingens* (Smith, 1881)] at Kerguelen Islands (Cherel and Duhamel, 2003) and a few individuals in the Prydz Bay region in Antarctica (Lu and Williams, 1994). The indirect method of lipids as trophic markers was used only once in the area, on *M. ingens* at Heard Island (Phillips *et al*., 2001). Again, our poor understanding of cephalopods as predators comes mainly from a paucity of scientific surveys devoted to the group and to our inadequacy in catching oceanic species in representative numbers. We consequently utilised a new tool to investigate the food and feeding ecology of cephalopods by combining the use of their predators as biological samplers together with measurements of the stable isotopic signature of their beaks (Cherel and Hobson, 2005). Since the stable isotopic signature of a consumer reflects that of its diet, stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been used extensively to trace pathways of organic matter among organisms (Kelly, 2000). Consumers are enriched in ^{15}N relative to their food and consequently $\delta^{15}N$ measurements serve as indicators of a consumer trophic position (Vanderklift and Ponsard, 2003). By contrast, $\delta^{13}C$ values vary little along the food chain and are mainly used to determine primary sources in a trophic network. In the marine environment, $\delta^{13}C$ values indicate the lower- versus higher-latitude plankton, and inshore versus offshore, or pelagic versus benthic contribution to food intake (Hobson *et al*., 1994; Cherel and Hobson, 2007). Hence, the second goal of the study was thus to investigate the trophic structure of the assemblage of cephalopods living in Kerguelen waters by measuring the isotopic signature of their beaks that accumulated in predators' stomachs.

MATERIALS AND METHODS

Fieldwork at sea on the Patagonian toothfish was carried out by fishery observers during commercial cruises on longliners and trawlers in Kerguelen waters (details in Cherel *et al*., 2004). The fishery operated in upper slope waters surrounding the archipelago. Additional cephalopod records were obtained from miscellaneous observations from stomach contents of by-catch sharks (lanternsharks *Etmopterus* cf. *granulosus* (Günther, 1880), porbeagles *Lamna nasus* (Bonnaterre, 1788) and sleeper sharks *Somniosus antarcticus* Whitley, 1939) caught during various commercial cruises (details in Cherel and Duhamel, 2004). Fishery observers dissected toothfish and sharks onboard, and they 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.

Fieldwork on land included the collection of seabird dietary samples during the chick-rearing period, when parent birds bring back food to their offspring at the nest sites. Each sample was thawed, drained and accumulated cephalopod beaks subsequently sorted. Accumulated beaks (beaks without flesh attached) were analysed separately from fresh items. Fresh remains were divided into broad prey classes (including cephalopods), which were weighed to calculate their proportion by fresh mass in the diet (Cherel *et al*., 2000).

Cephalopod beaks (both lower and upper beaks) were identified by reference to features given by Xavier and Cherel (2009), and by comparison with material held in our own reference collection. Undarkened or darkening beaks were considered as belonging to juvenile and subadult squids, respectively, while wholly darkened beaks indicated adult cephalopods (Clarke, 1986). Cephalopod systematic order follows Clarke (1986).

Beaks for isotopic analyses were collected either from cephalopods taken as bycatches from the Patagonian toothfish fishery, or from stomach contents of various Southern Ocean predators foraging in Kerguelen waters. Predators included Patagonian toothfish, sleeper sharks and albatrosses (Cherel *et al*., 2002c; Cherel and Duhamel, 2004; Cherel *et al*., 2004; unpubl. data). Stable isotopes were measured on lower and/or upper beaks from the commonest and representative species (n = 18) of the cephalopod community from Kerguelen Islands. Beaks from avian predators were fresh items, not accumulated items, thus indicating that squids were caught in Kerguelen waters, as were fish prey. Prior to analysis, cleaned whole beaks were dried and cut into small pieces. Relative abundance of stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) were determined by continuous-flow isotope-ratio mass spectrometry (CFIRMS). Results are presented in the usual δ notation relative to PDB belemnite and atmospheric N_2 (AIR) for $\delta^{13}C$ and $\delta^{15}N$, respectively.

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

RESULTS AND DISCUSSION

Cephalopod fauna in Kerguelen waters

A total of ~4100 cephalopod beaks were identified from stomach contents of fish, including the Patagonian toothfish (~2800 beaks) and the three shark species (~1300 beaks). Additionally, several hundreds of beaks were removed from fur seal scats and from food samples of birds, including penguins, petrels and albatrosses (fresh items only). The present work adds two new cephalopod prey for the Patagonian toothfish (Cherel *et al*., 2004), the colossal squid *Mesonychoteuthis hamiltoni* Robson, 1925 and the cirrate octopod *Opisthoteuthis* sp., and two new fresh squid prey for Kerguelen seabirds, namely *Histioteuthis atlantica* (Hoyle, 1885) and *Taonius* sp. B (Voss), whose buccal masses were found in food samples of wandering albatrosses (unpubl. data).

Top consumers as biological samplers together with the few available oceanographic data underline the large diversity of cephalopods living in slope and adjacent oceanic waters surrounding the Kerguelen archipelago. Excluding a few items with taxonomical problems (e.g., *Todarodes* sp., some brachioteuthids and Oegopsida sp. C), 38 taxa of cephalopods with well-recognized beaks were identified from the area. The assemblage includes 31 squids, one sepiolid and six octopuses (Tab. I). A first notable characteristic of the Kerguelen cephalopod fauna is the presence of two endemic species living over the shelf and in upper slope waters, the common benthic octopods *Benthoctopus thielei* Robson, 1932 and *Graneledone gonzalezi* Guerra *et al*., 2000 (Nesis, 1987; Guerra *et al*., 2000; Strugnell *et al*., 2011). A second characteristic of the fauna is the paucity of neritic species, with no cuttlefishes or myopsids (loliginids) and only one and two species of sepiolid and octopodids, respectively. The absence of shelf species is probably related to the remoteness of the islands within the Southern Ocean, thus precluding close relationships with other land masses. A third characteristic of the assemblage is the large diversity of oegopsid squids, at both the family (17) and species (31) levels, including five sympatric onychoteuthids and four cranchiids (Tab. I). The most likely explanation for that squid richness is the location of Kerguelen Islands within the Polar Frontal Zone (the zone delineated by the Polar and the Subantarctic Fronts), between the cold Antarctic waters in the South (~50°S) and the warmer Subantarctic and Subtropical waters in the North (~44°S) (Park and Gambéroni, 1997). Consequently, the Kerguelen squid fauna includes species that have primarily Antarctic (e.g., *Kondakovia longimana* Filippova, 1972*; Alluroteuthis antarcticus* Odhner, 1923*; Galiteuthis glacialis* (Chun, 1906)*; M. hamiltoni*), Subantarctic (e.g., *Martialia hyadesi* Rochebrune and Mabille, 1887*; M. ingens; Gonatus antarcticus* Lönnberg, 1898*; Histioteuthis eltaninae* Voss, 1969) and Subtropical (e.g., *Pholidoteuthis boschmai* Adam, 1950*; Taningia danae* Joubin, 1931*; Cycloteuthis akimushkini* Filippova, 1968) distributions (Nesis, 1987). By contrast, only 14 squid species were collected from waters surrounding South Georgia (Xavier *et al*., 2002; Collins *et al*., 2004), and only 22 species in all Antarctic waters, i.e., the marine area located south the Polar Front (Collins and Rodhouse, 2006).

This study emphasizes the abundance and diversity of oceanic squids living within the Southern Ocean, which includes the two gigantic species, the giant (*Architeuthis dux* Steenstrup, 1857) and colossal squids. It also highlights the need for more taxonomic work, including a detailed description of the beaks, on many cephalopod groups (i.e., *Moroteuthis* sp. B (Imber), mastigoteuthids/chiroteuthids, *Taonius* sp. B (Voss), cirrate octopods). 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 and ecology. The study also underlines the usefulness of teuthophagous predators to gain valuable information on the distribution and diversity of their prey (e.g., Cherel and Weimerskirch, 1995).

Cephalopods as prey

The food of 18 species of seabirds from Kerguelen Islands was investigated during the chick-rearing period over the last 15 years (Tab. II). The importance of cephalopods in their diet varies greatly in relation to their foraging strategies and sizes. Cephalopods do not account for a large mass proportion in the diet of diving birds (penguins, diving petrels, the cormorant) and fur seals (Cherel *et al*., 1997; Lea *et al*., 2002), but large specimens can be occasionally found (e.g., ommastrephids in the diet of rockhopper and king penguins). On the other hand, the importance of cephalopods in the food of surface feeding seabirds (procellariiforms) is related to their size, the larger the species the higher the pro-

Table I. - Cephalopod taxa from Kerguelen waters recorded in the diet of top predators and those listed in oceanographic literature. [a], Cherel *et al*. (2004) and unpubl. data; [b], Cherel and Duhamel (2004); [c], Only fresh items; [d], Cherel and Weimerskirch (1995), Cherel *et al*. (2000, 2002a, 2002b, 2002c), Lea *et al*. (2002), Delord *et al*. (2010) and unpubl. data; [e], Lu and Mangold (1978), Nesis (1987), Piatkowski *et al*. (1991), Duhamel and Piatkowski (1993), Piatkowski (1993), Guerra *et al*. (2000), Rodhouse and Lu (1998), Xavier *et al*. (1999); [f], Described from the morphology of the beaks.

Species	Patagonian toothfish[a]	Sharks[b]	Birds[c] and fur seals[d]	Oceanographic literature[e]
Decapoda				
Architeuthidae				
Architeuthis dux Steenstrup, 1857		+		
Ommastrephidae				
Martialia hyadesi Rochebrune and Mabille, 1887	+	+	+	+
Todarodes cf. *angolensis* Adam, 1962	+			
Todarodes filippovae Adam, 1975				+
Todarodes sp.	+	+	+	
Onychoteuthidae				
Moroteuthis ingens (Smith, 1881)	+	+	+	+
Moroteuthis knipovitchi Filippova, 1972	+	+	+	+
Moroteuthis robsoni Adam, 1962	+	+		
Moroteuthis sp. B (Imber) (= *Moroteuthopsis* sp. B)[f]	+			
Kondakovia longimana Filippova, 1972	+	+	+	
Pholidoteuthidae				
Pholidoteuthis boschmai Adam, 1950	+			
Psychroteuthidae				
Psychroteuthis glacialis Thiele, 1920 (small form)	+			
Brachioteuthidae				
Brachioteuthis linkovskyi Lipinski, 2001	+	+		
Brachioteuthis picta, *Brachioteuthis* sp.				+
Slosarczykovia circumantarctica Lipinski, 2001 (= *Brachioteuthis riisei*)	+	+	+	+
Gonatidae				
Gonatus antarcticus Lönnberg, 1898	+	+	+	+
Enoploteuthidae				
Abraliopsis gilchristi (Robson, 1924)				+
Octopoteuthidae				
Taningia danae Joubin, 1931	+	+		
Histioteuthidae				
Histioteuthis atlantica (Hoyle, 1885)	+	+	+	+
Histioteuthis eltaninae Voss, 1969	+	+		+
Neoteuthidae				
Alluroteuthis antarcticus Odhner, 1923	+	+		
Nototeuthis dimegacotyle Nesis and Nikitina, 1986	+	+		
Bathyteuthidae				
Bathyteuthis abyssicola Hoyle, 1885				+
Cycloteuthidae				
Cycloteuthis akimushkini Filippova, 1968		+		
Mastigoteuthidae				
Mastigoteuthis psychrophila Nesis, 1977	+	+	+	
?*Mastigoteuthis* A (Clarke)[f]	+	+	+	
?*Mastigoteuthis* B (Clarke)[f]		+		
Chiroteuthidae				
Chiroteuthis veranyi (Férussac, 1835)	+	+		+

Table I. - Continued.

Species	Patagonian toothfish[a]	Sharks[b]	Birds[c] and fur seals[d]	Oceanographic literature[e]
Batotheutidae				
Batoteuthis skolops Young and Roper, 1968	+	+		
Cranchiidae				
Taonius sp. B (Voss)	+	+	+	
Teuthowenia pellucida (Chun, 1910)	+			
Galiteuthis glacialis (Chun, 1906)	+	+		+
Mesonychoteuthis hamiltoni Robson, 1925	+	+		
Oegopsida sp. C (Cherel) [f]		+		
Sepiolidae				
cf. *Stoloteuthis leucoptera* (Verrill, 1878)	+			+
Octopoda				
Octopodidae				
Benthoctopus thielei Robson, 1932	+		+	+
Graneledone gonzalezi Guerra *et al*., 2000 (= *G*. sp. & *G*. cf. *antarctica*)	+			+
Stauroteuthidae				
Stauroteuthis gilchristi (Robson, 1924)	+			
Grimpoteuthis sp.				+
Opisthoteuthidae				
Opisthoteuthis sp.	+			+
Cirrata sp. A (Cherel) [f]		+		
Total	31	26	12	18

portion of cephalopods in their food (albatrosses > *Procellaria* petrels > *Pterodroma* petrels > blue petrel and prions; Tab. II). Squids account for a major part of the diet of two albatross species, namely the wandering and grey-headed albatrosses, thus confirming previous dietary investigations conducted elsewhere in the Southern Ocean (review in Cherel and Klages, 1998). The two species occupy different trophic niches, with the wandering albatross targeting mainly adult squids, while the grey-headed albatross focuses on juvenile specimens. Cephalopod remains also occur commonly in stomach contents of large predatory fishes (sharks and the Patagonian toothfish) living in Kerguelen waters, but their proportion by mass was not quantified (Cherel and Duhamel, 2004; Cherel *et al*., 2004).

Predators' diet underlines the key role of at least 14 species of cephalopods in Kerguelen waters, including 13 squids and one benthic octopod (Tab. III). Noticeable is the importance of ommastrephids and onychoteuthids. Juvenile ommastrephids are the main cephalopod prey of the porbeagle and of black-browed and grey-headed albatrosses. Interestingly, while *M. hyadesi* is the main ommastrephid species elsewhere in the Southern Ocean, it is replaced at Kerguelen Islands by *Todarodes* sp., a species related to *T. angolensis* Adam, 1962 that is not known to occur in waters surrounding other Subantarctic islands (Cherel and Weimerskirch, 1995; Cherel *et al*., 2004). Among onychoteuthids, owing to their large size, adults of *K. longimana* are key prey for sleeper sharks (Tab. III), wandering albatrosses (unpubl. data), and possibly some marine mammals (Slip, 1995; Slip *et al*., 1995). Among other squid families, cranchiids, mainly *G. glacialis*, are important in the food of sleeper sharks, albatrosses and marine mammals (Slip *et al*., 1995; Cherel *et al*., 2000, 2002c). The endemic octopod *B. thielei* is a significant prey of the black-browed albatross (Tab. III) and possibly of the gentoo penguin (Lescroël *et al*., 2004), which reflects the two seabird species foraging in neritic and slope waters (Cherel *et al*., 2000; Lescroël and Bost, 2005). More unexpected findings were the abundance of *Slosarczykovia circumantarctica* Lipinski, 2001 in the diet of white-chinned petrels, and of *Mastigoteuthis psychrophila* Nesis, 1977 and *Chiroteuthis veranyi* (Férussac, 1835) in the diet of Patagonian toothfish (Tab. III). To our knowledge, those species were not previously found to be key items in the nutrition of any squid predator (Clarke, 1996), except may be the brachioteuthid in the diet of southern elephant seals [*Mirounga leonina* (Linnaeus, 1758)] from South Georgia (Rodhouse *et al*., 1992). This result emphasizes how poorly the trophic interactions of many cephalopod taxa in the Southern Ocean are known.

Investigation of the feeding habits of top predators from Kerguelen Islands is ongoing. Thus, it is likely that new findings will highlight the importance of cephalopods in their diet in the near future. In the same way, further beak identifications (e.g., the squid prey of wandering albatrosses) will

Table II. - Importance of cephalopods (% wet mass) in the diet of seabirds during the chick-rearing period at Kerguelen Islands.

Predator species	Location	Food samples (n)	Cephalopods (% fresh mass)	References
King penguin *Aptenodytes patagonicus* Miller, 1778	Ratmanoff	10	7.4	Unpubl. data
Gentoo penguin *Pygoscelis papua* (Forster, 1781)	Ile Longue	9	0.0	Unpubl. data
	Estacade	10	2.7	Unpubl. data
Macaroni penguin *Eudyptes chrysolophus* (Brandt, 1837)	Cap Cotter	10	0.6	Unpubl. data
Rockhopper penguin *Eudyptes chrysocome* (Forster, 1781)	Ile Mayes	11	0.1	Unpubl. data
	Rivière des Macaronis	10	18.9	Unpubl. data
Wandering albatross *Diomedea exulans* Linnaeus, 1758	Péninsule Courbet	28	46.8	Unpubl. data
Black-browed albatross *Thalassarche melanophrys* (Temminck, 1828)	Canyon	114	9.7	Cherel *et al.*, 2000
	Iles Nuageuses	35	38.5	Cherel *et al.*, 2002c
Grey-headed albatross *Thalassarche chrysostoma* (Forster, 1785)	Iles Nuageuses	38	52.4	Cherel *et al.*, 2002c
Indian yellow-nosed albatross *Thalassarche carteri* (Rothschild, 1903)	Iles Nuageuses	6	12.8	Cherel *et al.*, 2002c
White-chinned petrel *Procellaria aequinoctialis* Linnaeus, 1758	Canyon	55	17.4	Delord *et al.*, 2010
Grey petrel *Procellaria cinerea* Gmelin, 1789	Ile Mayes	80	26.9	Unpubl. data
White-headed petrel *Pterodroma lessoni* (Garnot, 1826)	Ile Mayes	55	26.6	Unpubl. data
Soft-plumaged petrel *Pterodroma mollis* (Gould, 1844)	Ile Foch	31	6.7	Unpubl. data
Blue petrel *Halobaena caerulea* (Gmelin, 1789)	Ile Mayes	103	2.5	Cherel *et al.*, 2002b
Thin-billed prion *Pachyptila belcheri* (Mathews, 1912)	Ile Mayes	85	2.9	Cherel *et al.*, 2002a
Antarctic prion *Pachyptila desolata* (Gmelin, 1789)	Ile Verte	104	2.9	Cherel *et al.*, 2002a
South Georgian diving petrel *Pelecanoides georgicus* Murphy and Harper, 1916	Ile Verte	83	0.0	Bocher *et al.*, 2000
Common diving petrel *Pelecanoides urinatrix* (Gmelin, 1789)	Ile Mayes	81	0.0	Bocher *et al.*, 2000
Kerguelen shag *Phalacrocorax verrucosus* (Cabanis, 1875)	Ile Mayes	26	0.0	Unpubl. data

Table III. - Main cephalopod species in the diet of top predators at Kerguelen Islands. Numbers refer to the percentages by number (> 5%, +: present).

Species	Porbeagle	Sleeper shark	Patagonian toothfish	Black-browed albatross		Grey-headed albatross	White-chinned petrel
				Canyon	Nuageuses		
Number of beaks	689	553	2802	573	510	1358	248
Todarodes sp.	32.5	+	+	9.1	13.9	13.5	11.3
Martialia hyadesi	+		+	5.6	+	+	
Ommastrephidae sp.				31.9	59.8	54.2	
Kondakovia longimana	+	49.5	+	+	+	9.1	+
Slosarczykovia circumantarctica		+	+		+		51.2
Gonatus antarcticus	+	+	10.8	+		+	9.7
Taningia danae		12.5	+	+			
Histioteuthis atlantica	46.0	+	6.6	+		+	
Histioteuthis eltaninae	6.0		6.2		+	+	6.0
Nototeuthis dimegacotyle	+		5.4	+		+	
Mastigoteuthis psychrophila	+	+	19.7	+		+	+
Chiroteuthis veranyi	+		29.5	+	+	+	
Galiteuthis glacialis	+	+	+	20.2	5.3	17.9	+
Mesonychoteuthis hamiltoni		16.1	+				
Benthoctopus thielei			+	23.4	15.3		+
References	Cherel and Duhamel, 2004	Cherel and Duhamel, 2004	Cherel *et al.*, 2004; unpubl. data	Cherel *et al.*, 2000	Cherel *et al.*, 2002c	Cherel *et al.*, 2002c	Delord *et al.*, 2010

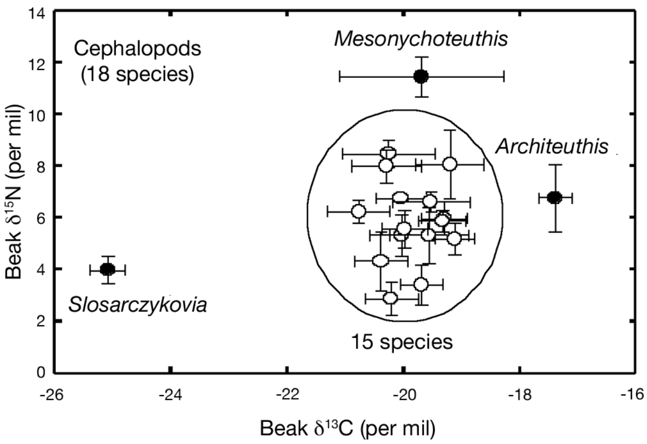

Figure 1. - Stable carbon and nitrogen isotope values of beaks from 18 representative cephalopod species from Kerguelen waters. Values are means ± SD.

help us to disentangle the trophic relationships of the poorly known Southern Ocean cephalopods within the pelagic ecosystem.

Cephalopods as predators: a stable isotope investigation

Figure 1 illustrates the isotopic (trophic) structure of the cephalopod assemblage from Kerguelen Islands, with a cluster of 15 taxons and three distinct species that differed either by their $\delta^{13}C$ (*S. circumantarctica* and the giant squid) or their $\delta^{15}N$ (the colossal squid) values. Cephalopods were segregated by the $\delta^{13}C$ (a proxy of their habitats) and $\delta^{15}N$ (a proxy of their trophic levels) values of their beaks (Kruskal-Wallis test, $U = 84$ and 130, both $p < 0.0001$) (Tab. IV). They had a restricted range in $\delta^{13}C$ values, with 16 out of 18 species showing a gradual enrichment in ^{13}C from -20.8 to -19.1‰. Those values are close to those previously found in other marine organisms from the area (Cherel *et al*., 2008; unpubl. data), thus indicating that the 16 species grew in Kerguelen waters, where some of them – the two octopods – are moreover known to be endemic. On the other hand, *S. circumantarctica* and giant squids showed very low (-25.1‰) and high (-17.4‰) $\delta^{13}C$ values, respectively. In the Southern Ocean, lower-latitude plankton food bases have higher $\delta^{13}C$ values relative to higher-latitude waters and this well-defined isotopic gradient allows estimating the latitudes at which consumers forage (Cherel and Hobson, 2007; Jaeger *et al*., 2010). Accordingly, the very negative $\delta^{13}C$ value of *S. circumantarctica* is identical to that of the endemic Antarctic squid *Psychroteuthis glacialis* Thiele, 1920, while the isotopic value of the ^{13}C enriched giant squid is close to that of the Subtropical *Octopus vulgaris* Cuvier, 1797 (Guerra *et al*., 2010) from Amsterdam Island (Cherel and Hobson, 2005). Hence, our data strongly suggest that *S. circumantarctica* and giant squids fed in different water masses before migrating into the Kerguelen area. In summary, the large range in $\delta^{13}C$ values demonstrates that Kerguelen cephalopods grew in three different marine ecosystems, from the Subtropics to Antarctica.

The $\delta^{15}N$ values of the co-exist-

Table IV. - Cephalopod species, predator species and the isotopic signature of cephalopod beaks from Kerguelen Islands. Values are means ± SD.

Species	Provenance (predator or bycatch)	Isotopic signature		
		n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Decapoda				
Architeuthidae				
Architeuthis dux	Sleeper shark	4	-17.4 ± 0.3	6.7 ± 1.3
Ommastrephidae				
Martialia hyadesi	King penguin	10	-20.2 ± 0.5	2.8 ± 0.6
Todarodes sp.	Grey-headed albatross	10	-19.7 ± 0.4	3.4 ± 0.8
Onychoteuthidae				
Moroteuthis ingens	Patagonian toothfish	5	-19.5 ± 0.7	5.3 ± 1.1
Moroteuthis knipovitchi	Patagonian toothfish	5	-20.8 ± 0.5	6.2 ± 0.4
Moroteuthis sp. B (Imber)	Patagonian toothfish	10	-19.3 ± 0.4	6.0 ± 0.6
Kondakovia longimana	Patagonian toothfish	3	-20.4 ± 0.5	4.3 ± 1.1
Brachioteuthidae				
Brachioteuthis linkovskyi	Patagonian toothfish	10	-20.0 ± 0.5	5.3 ± 0.8
Slosarczykovia circumantarctica	Patagonian toothfish	10	-25.1 ± 0.3	4.0 ± 0.5
Gonatidae				
Gonatus antarcticus	Patagonian toothfish	10	-20.2 ± 0.8	8.4 ± 0.5
Octopoteuthidae				
Taningia danae	Patagonian toothfish	3	-20.0 ± 0.4	6.7 ± 0.1
Histioteuthidae				
Histioteuthis eltaninae	Patagonian toothfish	10	-20.0 ± 0.4	5.5 ± 0.7
Neoteuthidae				
Nototeuthis dimegacotyle	Patagonian toothfish	10	-19.5 ± 0.7	6.6 ± 0.4
Mastigoteuthidae				
Mastigoteuthis psychrophila	Patagonian toothfish	10	-20.3 ± 0.6	8.0 ± 0.6
Chiroteuthidae				
Chiroteuthis veranyi	Patagonian toothfish	10	-19.2 ± 0.6	8.0 ± 1.3
Cranchiidae				
Mesonychoteuthis hamiltoni	Sleeper shark	10	-19.7 ± 1.4	11.4 ± 0.8
Octopoda				
Octopodidae				
Benthoctopus thielei	Fishery bycatch	10	-19.1 ± 0.4	5.2 ± 0.6
Graneledone gonzalezi	Fishery bycatch	10	-19.3 ± 0.4	5.9 ± 0.4

ing cephalopods show that most fed along a continuum of about two trophic levels (5.6‰) from 2.8‰ (*M. hyadesi*) to 8.4‰ (*G. antarcticus*). This gradual enrichment in ^{15}N then stopped and there was a jump of 3.0‰ along the food chain to the colossal squid, which reached the highest $\delta^{15}N$ value of the community (11.4‰; Tab. IV). At Kerguelen Islands, juveniles of *M. ingens* feed on both euphausiids and mesopelagic fish (Cherel and Duhamel, 2003), while juveniles of the ommastrephids *M. hyadesi* and *Todarodes* sp. prey upon hyperiid amphipods and euphausiids (unpubl. data). Accordingly, the medium $\delta^{15}N$ value of *M. ingens* is higher (5.3‰) than that of ommastrephids (2.8-3.4‰), which had the lowest $\delta^{15}N$ values of the community. This strongly suggests that Subantarctic cephalopods spread out in a continuum between crustacean- and fish-eating species. On the other hand, the high $\delta^{15}N$ value of colossal squid indicates that the species is a top predator, probably feeding on large fish and squids, and in turn being the prey of apex predators like sperm whales and sleeper sharks (Clarke, 1980; Cherel and Duhamel, 2004).

Stable isotope measurements also revealed interesting features among closely related cephalopods by underlining segregative mechanisms allowing co-existence. For example, the two benthic octopods have identical carbon signatures (Kruskal-Wallis test: $U = 60.5$, $p = 0.427$), but they segregated by their $\delta^{15}N$ values ($U = 18.5$, $p = 0.017$), indicating different diets within the same habitat. By contrast, juveniles of the two ommastrephids had almost identical $\delta^{15}N$ values ($U = 25.0$, $p = 0.059$), but differed in their $\delta^{13}C$ values ($U = 20.0$, $p = 0.023$), showing that both species fed on the same trophic level but that *M. hyadesi* lives in more offshore waters than *Todarodes* sp. Even larger isotopic differences were found between the two brachioteuthids that segregated by their $\delta^{13}C$ values ($U = 100.0$, $p < 0.0001$), with *S. circumantarctica* being an Antarctic species and *Brachioteuthis linkovskyi* Lipinski, 2001 a Subantarctic one. In the same way, four co-existing onychoteuthids segregated by both their habitat and trophic position ($U = 94.0$ and 8.1, $p = 0.001$ and 0.045, respectively). Their $\delta^{13}C$ values illustrate the inshore/offshore isotopic gradient (Cherel and Hobson, 2007) with *M. ingens* (the most abundant squid in fishery bycatches) and *Moroteuthis* sp. B (Imber) living in more inshore waters than *K. longimana* and *Moroteuthis knipovitchi* Filippova, 1972 (Fig. 2). It is also notable that the largest species (*K. longimana*) has the lowest trophic position, suggesting that it feeds on both crustaceans and fish.

In brief, the stable isotopic signature of cephalopod beaks is a powerful tool to investigate the trophic position and migration patterns among poorly known cephalopods. Importantly however, as chitin induces an impoverishment of beaks in ^{15}N (but not in ^{13}C) when compared to muscle tissues, correction factors must be applied before comparing the beak $\delta^{15}N$ values with those from other tissues and organisms to better depict trophic relationships of cephalopods (Cherel and Hobson, 2005; Hobson and Cherel, 2006, Cherel *et al.*, 2009).

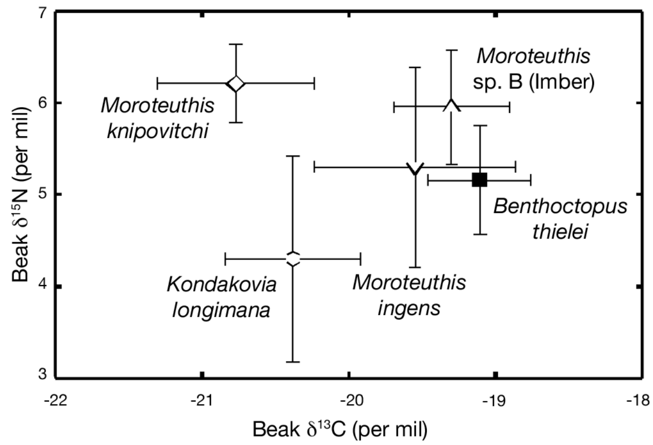

Figure 2. - Stable carbon and nitrogen isotope values of beaks from four onychoteuthid squids that co-exist in Kerguelen waters. The octopod *Benthoctopus thielei* illustrates the isotopic niche of a species living over the shelf and in upper slope waters. Values are means ± SD.

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