



Prey preferences among the community of deep-diving odontocetes from the Bay of Biscay, Northeast Atlantic

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ABSTRACT

Long-finned pilot whales (*Globicephala melas*), Risso's dolphins (*Grampus griseus*), melon-headed whales (*Peponocephala electra*), Cuvier's beaked whales (*Ziphius cavirostris*), Sowerby's beaked whales (*Mesoplodon bidens*), northern bottlenose whales (*Hyperoodon ampullatus*), sperm whales (*Physeter macrocephalus*), dwarf sperm whales (*Kogia sima*) and pygmy sperm whales (*Kogia breviceps*) make up the large community of deep-diving odontocetes occurring off the Bay of Biscay, northeast Atlantic. The ecology of these toothed cetaceans is poorly documented worldwide. The present study described their prey preferences from stomach content analysis and showed resource partitioning within the assemblage. The majority of the species appeared to be mostly teutophageous. Fish was an important food source only for the Sowerby's beaked whale and, to a lesser extent, for the long-finned pilot whale. In terms of foraging habitats inferred from prey composition, either pelagic oceanic or demersal neritic habitats were exploited by toothed whales in the Bay of Biscay, with only the long-finned pilot whale foraging in the two habitats. Finally, with more than 14,000 identified cephalopods from 39 species, the present study highlighted also the poorly known deep-sea cephalopod community off the Bay of Biscay using top predators as biological samplers.

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1. Introduction

The diet of a given predator is a combination of resource availability and foraging strategies. Foraging strategies are constrained by energy requirements and are associated to foraging costs and benefits. The success of foraging strategies for a predator is linked to limitation in the predator's physiological, morphological or social functioning. Hence, prey composition in the diet of a given predator results from different evolutionary processes, which shaped predator's characteristics. Since resource partitioning allows co-existence of predators, inter-specific competition for food is probably a major process in the establishment of different foraging strategies among predators (Roughgarden, 1976).

Description of the different dimensions of the ecological niche allows estimating the degree of overlap versus segregation between species (Pianka, 1974). The foraging niche has three

major dimensions: the trophic (prey characteristics), spatial (both on horizontally and vertically) and temporal dimensions (from diel activity patterns to yearly migratory cycles). In marine top predator ecology, the study of these dimensions would provide important advances in the understanding of ecosystem functioning. For example, in the southwest Indian Ocean, the oceanic island Mayotte is characterized by a high odontocete diversity (Kiszka et al., 2007a). The existence of resource partitioning among co-occurring tropical dolphins around this island was revealed by analyzing ecological tracers (carbon and nitrogen stable isotopes) from skin and blubber biopsies. Results suggest some fine-scale mechanisms of segregation in the species foraging habitats and trophic levels (Gross et al., 2009). In the northeast Atlantic, a broad community of large fish and delphinids exploits oceanic pelagic ecosystems. Dietary investigations highlighted segregating mechanisms along several dimensions of the foraging niche, prey composition, prey size and diurnal activity, and suggested that energy requirements would shape predator foraging strategies (Pusineri et al., 2008).

The Bay of Biscay in the eastern North Atlantic is a contrasted marine area with an oceanic domain, a continental slope indented

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by numerous canyons and a continental shelf, which extends more than 200 km offshore in the north of the Bay and only 10 km in the south. The Bay supports a rich cetacean fauna (Hammond et al., 2002; Kiszka et al., 2007b; Certain et al., 2008). The slope and oceanic areas seem to be an important foraging area especially for medium to large odontocetes such as the sperm whale (*Physeter macrocephalus*), long-finned pilot whale (*Globicephala melas*) and a variety of beaked whales (Kiszka et al., 2007b). These toothed whales are often referred to as squid-eating deep-divers but, in general, their ecology is poorly documented around the world. All these species co-occur in the oceanic part of the Bay of Biscay, suggesting some segregation processes within the community. We hypothesized that each species occupies its own foraging niche and that overlap is limited. Therefore, the first aim of this work is the description of prey composition from stomach content analysis of 5 species of medium to large odontocetes: long-finned pilot whale, Cuvier's beaked whale (*Ziphius cavirostris*), Sowerby's beaked whale (*Mesoplodon bidens*), sperm whale and pygmy sperm whale (*Kogia breviceps*). Dietary results are also given for 4 additional species for which sample size is low: Risso's dolphin (*Grampus griseus*), melon-headed whale (*Peponocephala electra*), northern bottlenose whale (*Hyperoodon ampullatus*) and dwarf sperm

whale (*Kogia sima*). Secondly, dietary segregation among this community of deep-diving odontocetes is investigated using prey characteristics rather than prey taxonomy as descriptors. Finally, this study uses cetaceans as biological samplers for a baseline description of the poorly known deep-sea cephalopod fauna in the oceanic Bay of Biscay.

2. Materials and methods

2.1. Sampling

Strandings were examined by members of the French stranding scheme established since 1972, this monitoring effort depends substantially on volunteer involvement. Stranded animals were measured, sexed and, after necropsy, stomach contents were stored deep-frozen ($-20\text{ }^{\circ}\text{C}$) in polythene bags until further analyses.

A total of 42 stomach contents of adult deep-diving odontocetes were collected between 1993 and 2010 (Table 1), including 9 species from 4 families (Delphinidae, Ziphiidae, Physeteridae and Kogiidae): 11 long-finned pilot whales (*G. melas*), 2 Risso's

Table 1
Summary of deep-diving odontocetes stranding data in the Bay of Biscay available for dietary analysis.

Species	Sexe	Length (cm)	Date	Observers	
Long-finned pilot whale	Male	258	28 December 1994	CRMM	
	Male	490	18 April 1998	CRMM	
	Male	578	18 April 1999	CRMM	
	Female	295	17 December 1999	CRMM	
	Female	469	13 April 2001	CRMM/J. Vimperc/O. Dian	
	Male	200	4 March 2003	GEFMA	
	Male	371	1 May 2005	CRMM/J. Vimperc	
	Male	540	27 June 2007	CRMM/J. Cloutour	
	Male	596	11 February 2009	ONCFS	
	Male	376	11 March 2009	CRMM	
	Male	211	3 July 1993	GERDAU	
	Risso's dolphins	Female	170	17 June 1993	GERDAU
		Female	320	6 May 2009	AL LARK
Melon headed whale	Male	243	29 August 2003	CRMM/G. Anselme/J.R. Meslin	
	Male	244	15 October 2008	CRMM/LPO	
Cuvier's beaked whale	Male	333	30 November 1998	GEFMA	
	Male	465	30 January 1999	CRMM	
	Female	590	26 November 2002	CRMM/J. Pourreau	
	Male	460	10 January 2007	CRMM/J.J. Boubert/R. Mirtain	
	Male	600	1 March 2007	CRMM/J.R. Meslin/G. Zieback	
	Male	590	31 March 2007	CRMM/GEFMA/G. Gautier	
	Male	540	18 January 2008	CRMM/C. Anselme	
	Female	420	21 January 2008	CRMM/C. Anselme	
	Male	554	7 March 2008	CRMM/ONCFS/J.J. Boubert	
Female	600	20 April 2008	CRMM/C. Anselme		
Sowerby's beaked whale	Male	316	29 May 2007	GEFMA/CRMM	
	Male	370	19 September 2008	CRMM/J.R. Meslin	
	Male	395	20 September 2008	CRMM/O. Dian/J. Cloutour	
Northern bottlenose beaked whale	Female	610	2 August 2009	G. Gautier/G. Cabassut	
Sperm whale	Male	1095	23 December 2001	CRMM/GEFMA/MARIN	
	Male	1045	23 December 2001	CRMM/GEFMA/MARIN	
	Male	1050	23 December 2001	CRMM/GEFMA/MARIN	
Pygmy sperm whale	Female	185	3 February 1984	CRMM	
	Male	225	29 August 1986	CRMM	
	Female	213	30 December 1989	CRMM	
	Male	160	11 December 1990	CRMM	
	Male	275	8 March 1993	CRMM	
	Male	200	7 December 1999	CRMM/J.J. Boubert	
	Male	211	28 December 2001	CRMM	
	Male	167	17 January 2008	CRMM/ONF/ONCFS	
	Male	212	26 August 2010	CRMM/ONF	
Dwarf sperm whale	Female	175	15 November 1999	CRMM	

dolphins (*G. griseus*), 2 melon-headed whales (*P. electra*), 10 Cuvier's beaked whales (*Z. cavirostris*), 3 Sowerby's beaked whales (*M. bidens*), 1 northern bottlenose whale (*H. ampullatus*), 3 sperm whales (*P. macrocephalus*), 1 dwarf sperm whale (*K. sima*) and 9 pygmy sperm whales (*K. breviceps*). For the pygmy sperm-whale, the present work compiles at species-level dietary analyses from 7 specimens that were individually published in a review paper (Santos et al., 2006), plus data from two recently stranded individuals.

2.2. Sample analysis

Sample analysis followed a general procedure that is now standard for marine top predators (e.g. Chérel et al., 2000; Ridoux, 1994; Spitz et al., 2006). Food remains found in stomachs of stranded odontocetes were constituted mainly of accumulated undigested materials. Diagnostic hard parts – fish otoliths and cephalopod beaks – were sorted from the samples and stored either dry (fish bones and otoliths) or in 70% ethanol (cephalopod beaks). Food items were identified to the lowest taxonomic level by using published guides (Clarke, 1986; Härkönen, 1986; Xavier and Chérel, 2009) and our reference collection. The number of individuals for each species was estimated from the maximum number of lower or upper beaks identified for each cephalopod species, and from the maximum number of either right or left otoliths for each fish species. Standard measurements of lower beaks and otoliths were taken using a digital vernier calliper (± 0.02 mm). A random sub-sample of up to 200 diagnostic hard parts per prey species per stomach sample was measured. Cephalopod dorsal mantle length (DML), fish standard length (SL) and prey body mass were back-calculated by using allometric equations (Clarke, 1986; Lu and Ickeringill, 2002; Santos et al., 2002; authors' unpublished data).

The dietary importance of each prey taxon was described by its percentages by number (%N) and by reconstructed biomass (%M). In this study, the stomach (i.e. the individual predator) was considered as the sample unit. For each individual, percentage by number and percentage by mass were calculated for each prey taxon, and then averaged at predator species-level. Ninety-five per cent confidence intervals (95% CI) around the percentages by number and mass were generated for each prey taxon by bootstrap simulations of sampling errors (Santos et al., 2001a). The bootstrapping routine was written using the R software (R Development Core Team, 2010). Random samples were drawn with replacement and the procedure was repeated 1000 times. The lower and upper bounds of 95% CI were the 25th and 975th values previously ranked in increasing order.

For cetacean species represented by one or two individuals, only individual dietary compositions were calculated.

2.3. Niche segregation

Niche segregation was only investigated only for 5 species, the long-finned pilot whale, Cuvier's beaked whale, Sowerby's beaked whale, sperm whale and pygmy sperm whale. Cetacean species represented by one or two individuals were excluded of the analyses.

Dietary overlaps by number and by mass (O_n and O_m , respectively) within the odontocete assemblage were calculated using the Pianka index, which varies from 0 (no overlap) to 1 (complete overlap)

$$O = \frac{\sum p_{iA} p_{iB}}{\sqrt{\sum p_{iA}^2 \sum p_{iB}^2}},$$

where p_{iA} is the percentage by number or by mass of prey i found in the diet of predator A and p_{iB} is the percentage by number or by mass

of prey i found in the diet of predator B . Segregation was considered substantial when overlap values were < 0.4 (Ross, 1986).

The non-parametric Mann–Whitney test was used to compare prey size distributions (significance level of $p=0.05$). Calculations were computed using R software (R Development Core Team, 2010). Prey characteristics, such as habitat or quality, used to describe species foraging strategies were derived from the literature (e.g. Guerra, 1992; Quéro et al., 2003; Spitz et al., 2010b).

3. Results

3.1. Long-finned pilot whale

The diet was mostly composed of small cephalopods (Table 2). A total of 2986 individual prey were found, which accounted for a total reconstructed biomass of about 33 kg. The diet was dominated by benthic octopods (% reconstructed biomass 21.1%M, estimated mean mantle length 114 ± 16 mm) and the oceanic squids *Todarodes sagittatus* (17.2%M; 255 ± 78 mm), *Histioteuthis reversa* (10.7%M; 22 ± 11 mm), *Histioteuthis bonnellii bonnellii* (10.6%M; 203 ± 29 mm) and *Galiteuthis armata* (9.2%M; 111 ± 25 mm). Two fish species accounted for a significant part of the diet in terms of ingested biomass, the conger eel (*Conger conger*: 8.3%M) and scad (*Trachurus trachurus*: 3.9%M). Finally, salps were occasionally fed in large quantities (8.1%M).

3.2. Cuvier's beaked whale

The diet of Cuvier's beaked whale was composed of small to medium cephalopods, but a few fish and salps remains were also found (Table 2). A total of 5092 individual prey were recovered, which accounted for a total reconstructed biomass of about 408 kg. Cranchiid squids accounted for a third of the reconstructed biomass, with include mainly *Teuthowenia megalops* (22.7%M; 212 ± 33 mm) and *G. armata* (8.0%M; 242 ± 24 mm). Another third of reconstituted biomass was composed by histioteuthids, with *H. reversa* (26.6%M; 44 ± 4 mm) and *H. bonnellii bonnellii* (4.4%M; 88 ± 44 mm). Finally, the giant octopod *Haliphron atlanticus* (10%M) and salps (10%M) could occasionally represent significant exploited resources.

3.3. Sowerby's beaked whale

Small fish dominated the 294 prey found in the stomach contents of Sowerby's beaked whales (Table 2). The total reconstructed biomass was estimated at about 1.6 kg. Four species of gadids were identified, with *Micromesistius poutassou* (24.7%M; 155 ± 60 mm) and *Trisopterus luscus/minus* (13.4%M; 71 ± 14 mm) being the most important items. The hake *Merluccius merluccius* was another major fish prey (11.8%M; 111 ± 57 mm). The swimming crabs *Polybius* spp. (33.0%M) and the cuttlefish species *Sepia* spp. (8.0%M; 57 ± 23 mm) held significant parts of the diet.

3.4. Sperm whale

Only cephalopod remains were recovered from the stomachs of sperm whales (Table 2). A total of 6978 individuals were found. They accounted for a total reconstructed biomass of more than 5 tons. With 26 different cephalopod species, the diet of sperm whales was highly diversified. However, one species, *H. bonnellii bonnellii*, dominated the diet, with about 50% of total reconstructed biomass (178 ± 37 mm). Another histioteuthid squid, *Histioteuthis arcturii* was also a significant prey (11.2%M; 136 ± 18 mm). The giant octopod *H. atlanticus* ranked second (18.2%M). Finally, large and giant squids represented a significant part of the diet, with

Table 2

Diet composition in frequency by number (%N) and reconstructed biomass (%M) of major deep-diving odontocetes in the Bay of Biscay. Confidence intervals at 95% (CI 95%) are given in brackets.

	Long-finned pilot whale		Cuvier's beaked whale		Sowerby's beaked whale		Pygmy sperm whale		Sperm whale	
	%N (CI 95%)	%W (CI 95%)	%N (CI 95%)	%W (CI 95%)	%N (CI 95%)	%W (CI 95%)	%N (CI 95%)	%W (CI 95%)	%N (CI 95%)	%W (CI 95%)
Cephalopods										
<i>Sepia</i> spp.	2.9 (0–7.7)	0.6 (0–1.9)			2.8 (0–8.4)	8.0 (0–24.1)				
<i>Loligo</i> spp.	2.3 (0–5.7)	3.2 (0.2–7.8)					0.3 (0–0.8)	0.5 (0–1.4)		
<i>Chtenopteryx sicula</i>							0.1 (0–0.1)	0.0 (0–0.1)		
<i>Ancistrocheirus lesueuri</i>	3.0 (0–9.1)	2.6 (0–7.9)							0.6 (0.1–1.6)	0.4 (0.1–0.9)
<i>Octopoteuthis</i> sp.									1.4 (0.8–2)	0.7 (0.3–1)
"Giant" <i>Octopoteuthis</i>									0.1 (0–0.2)	0.2 (0–0.3)
<i>Taningia danae</i>									0.3 (0.1–0.7)	5.4 (3.8–8.1)
<i>Ancistroteuthis lichtensteini</i>			0.0 (0–0.1)	0.1 (0–0.2)					0.4 (0.1–0.9)	0.2 (0.1–0.5)
<i>Moroteuthis/Onykia</i>									0.1 (0–0.1)	0.1 (0–0.1)
<i>Cycloteuthis akimushkini</i>									0.2 (0–0.3)	0.3 (0–0.5)
<i>Gonatus steenstrupi</i>	0.8 (0–2.3)	1.8 (0–5.4)	2.6 (0.7–4.9)	7.6 (2.3–14.5)			0.6 (0–1.9)	1.5 (0–4.4)	9.4 (0–28)	2.1 (0–6.2)
<i>Lepidoteuthis grimaldii</i>									0.7 (0.1–1.2)	3.3 (0.6–5.2)
<i>Pholidoteuthis bochmai</i>									0.1 (0–0.2)	0.3 (0.1–0.5)
<i>Architeuthis dux</i>									0.3 (0.2–0.3)	6.9 (0.9–16.2)
<i>Histioteuthis bonnellii</i>	4.0 (0–10.1)	10.6 (0–25.5)	2.1 (0.5–4.5)	4.4 (0.6–10)			1.5 (0–3.4)	5.5 (0–11.8)	48.5 (42.3–51.7)	48.1 (39.7–63.5)
<i>Histioteuthis arcturii</i>									22.6 (0.1–36.4)	11.2 (0–18.6)
<i>Histioteuthis corona</i>							0.3 (0–0.9)	0.7 (0–2.2)		
<i>Histioteuthis meleagroteuthis</i>							1.5 (0–3.4)	0.9 (0–2)	0.1 (0–0.2)	0.0 (0–0.1)
<i>Histioteuthis reversa</i>	12.7 (0.1–34.5)	10.7 (0.4–29.7)	32.6 (13.9–54.6)	26.6 (7.2–50.7)			69.3 (46.5–89)	59.7 (39.9–80.6)	4.7 (4–6.1)	0.4 (0.3–0.5)
<i>Brachioteuthis rissei</i>	0.1 (0–0.2)		1.2 (0.5–2.2)	0.1 (0–0.3)			0.6 (0–1.9)	0.1 (0–0.4)		
<i>Todarodes sagittatus</i>	22.3 (4.5–40.9)	17.2 (4.1–35.8)	2.2 (0.1–5.5)	7.8 (0.2–19.8)			3.5 (0.6–7.7)	9.2 (1.5–18.5)	0.6 (0.4–0.7)	0.4 (0.3–0.5)
Und. Ommastrephidae							2.3 (0–5.8)	3.8 (0–10.3)		
<i>Chiroteuthis veranyi</i>							0.1 (0–0.3)	0.1 (0–0.2)	0.2 (0–0.3)	0.0 (0–0.1)
<i>Chiroteuthis</i> sp.1							0.2 (0–0.5)	0.4 (0–1.1)	0.3 (0.1–0.5)	0.0 (0–0.1)
<i>Chiroteuthis</i> sp.2							0.2 (0–0.7)	0.9 (0–2.8)		
<i>Mastigoteuthis A (Imbert)</i>	1.0 (0–3)	0.7 (0–2)	0.0 (0–0.1)	0.0 (0–0.1)					0.3 (0–0.8)	0.1 (0–0.2)
<i>Mastigoteuthis schmidtii</i>							0.2 (0–0.5)	0.2 (0–0.5)		
<i>Teutowenia megalops</i>	0.1 (0–0.1)	0.0 (0–0.1)	26.6 (10.9–45.3)	22.7 (9.7–36.3)			0.3 (0–0.8)	0.3 (0–0.7)	2.3 (0.3–5.7)	0.3 (0.1–0.8)
<i>Galiteuthis armata</i>	13.7 (0–33.4)	9.2 (0–23)	9.5 (1.4–18.9)	8.0 (1.1–16.5)			0.1 (0–0.1)	0.2 (0–0.6)	4.0 (1.2–8.1)	0.9 (0.2–1.8)
<i>Taonius pavo</i>			1.4 (0.2–3.3)	1.2 (0.2–2.6)			0.2 (0–0.7)	0.2 (0–0.5)	0.5 (0–0.9)	0.1 (0–0.1)
<i>Megalocranchia</i> sp. 1			1.6 (0.6–2.9)	1.4 (0.4–2.6)					0.6 (0.3–0.7)	0.2 (0.1–0.3)
<i>Megalocranchia</i> sp. 2									0.1 (0–0.1)	0.1 (0–0.1)
<i>Vampyroteuthis infernalis</i>			0.0 (0–0.1)	0.0 (0–0.1)					0.3 (0–0.8)	0.3 (0–0.8)
Und. Octopodidae	14.5 (0.6–32.1)	21.1 (5.3–42)								
<i>Haliphron atlanticus</i>			10.0 (0–30)	10.0 (0–30)					1.5 (1.4–1.6)	18.2 (12.6–25.5)
Fish										
<i>Chauliodus sloani</i>			0.1 (0–0.3)	0.1 (0–0.2)						
<i>Notoscopelus kroeyeri</i>					1.9 (0–5.6)	1.4 (0–4.3)	0.2 (0–0.7)	0.2 (0–0.5)		
<i>Conger conger</i>	4.5 (0–13.6)	8.3 (0–24.9)								
<i>Sardina pilchardus</i>	0.6 (0–1.7)	0.6 (0–1.9)								
<i>Scomber scombrus</i>	0.6 (0–1.7)	0.4 (0–1.2)								
<i>Micromesistius poutassou</i>	0.6 (0–1.7)	0.5 (0–1.5)	0.1 (0–0.2)	0.1 (0–0.1)	20.4 (0–61.1)	24.7 (0–74.1)	3.5 (0–10.6)	2.8 (0–8.3)		
<i>Merlangius merlangus</i>					3.7 (0–11.1)	7.2 (0–21.7)	0.9 (0–2.8)	1.1 (0–3.3)		
<i>Trisopterus</i> spp	2.3 (0–6.8)	0.2 (0–0.6)			27.4 (0–82.1)	13.4 (0–40.3)				
<i>Gadiculus argenteus</i>					0.1 (0–0.4)	0.1 (0–0.3)				
<i>Trachurus trachurus</i>	4.5 (0–13.6)	3.9 (0–11.6)								
<i>Merluccius merluccius</i>	0.6 (0–1.7)	0.3 (0–0.8)			2.8 (0–8.4)	11.8 (0–35.3)	0.5 (0–1.4)	0.2 (0–0.7)		
Fish I	0.1 (0–0.1)	–								
Und. fish					7.7 (0–22.2)	–				
Others invertebrates										
Mysids							0.7 (0–2.2)	0.1 (0–0.1)		
Unid. shrimp							3.8 (0–11.4)	1.0 (0–3.1)		
<i>Polybius</i> spp.					33.3 (0–100)	33.3 (0–100)	9.0 (0–23.6)	10.5 (0–30.6)		
Salps	9.1 (0–27.2)	8.1 (0–24.2)	10 (0–30)	10 (0–30)						

three important species: *Architeuthis dux* (6.9%M), *Taningia danae* (5.4%M) and *Lepidoteuthis grimaldii* (3.3%M). The largest prey belonged to the first species, the giant squid, with an estimated dorsal mantle length of 1.5 m for a 46 kg body mass. All other cephalopod species accounted for a much lower fraction of the diet by mass.

3.5. Pygmy sperm whale

The diet was mostly composed of small cephalopods, added with crustaceans and limited amount of fish (Table 2). A total of 743 individual preys were found, which accounted for a total reconstructed biomass of about 27 kg. Despite a large prey diversity (18 cephalopods species, 4 fishes and 3 crustaceans), one species, *H. reversa*, accounted for 59.7%M (36 ± 10 mm) of the diet. Another histioteuthid squid, *H. bonnelli bonnelli*, made up a significant proportion of the diet (5.5%M). The ommastrephid squid *T. sagittatus* ranked second in term of cephalopods biomass with 9.2%M. Finally, the swimming crabs *Polybius* spp. (33.3%M) was occasionally exploited.

3.6. Others cetacean species

The two stomachs of melon-headed whales were both composed by cephalopods and fish remains (Table 3). Cuttlefish and neritic squid species were the dominant cephalopods species. Gadiform fish, mainly *T. luscus/minutus*, *M. poutassou* and *M. merluccius* were identified as important prey for the two melon-headed whales.

The first stomach of Risso's dolphin contained the remains of six cuttlefish (mainly large *Sepia officinalis*) and one large benthic octopod. A small quantity of salps was recovered from the second stomach content (Table 3).

The single stomach of dwarf sperm whale contained 44 individuals of *H. reversa* and remains of one swimming crab *Polybius* spp. (Table 3).

The single stomach of northern bottlenose whale contained 872 cephalopods from two different species that represented 86 kg of ingested biomass. The most abundant species by far was the cranchiid *T. megalops*. The other species was the oceanic octopod *Stauroteuthis syrtensis* (Table 3).

3.7. Niche segregation

Niche segregation was investigated only for the 5 most documented species (long-finned pilot whales, Cuvier's beaked whales, Sowerby's beaked whales, sperm whales and pygmy sperm whales). In general, dietary niches were well segregated, showing low values of Pianka's index in most cases both by number and by mass (Table 4). However, some cases of substantial overlaps were identified. The pygmy sperm whale and the Cuvier's beaked whale showed the highest overlap ($O_n=0.71$; $O_m=0.68$). The diet of long-finned pilot whale overlapped slightly in terms of ingested biomass composition with the pygmy sperm whale ($O_m=0.40$) and the Cuvier's beaked whale ($O_m=0.39$).

In term of general prey size selection (Fig. 1), the prey body mass distributions varied significantly between predator species (Mann-Whitney test, $p < 0.05$ for each pair-species). The Sowerby's beaked-whale fed almost exclusively on very small prey items (< 10 g body mass). The long-finned pilot whale, the pygmy sperm whale and the Cuvier's beaked whale fed mostly on small prey item (10–100 g body mass) with proportions of very small and medium prey that varied between the different cetaceans. Only sperm whale fed on medium to large preys, with 14% of ingested preys weighting more than 1 kg and the largest prey item being estimated at about 46 kg. When looking at several of the main prey targeted by odontocetes, *G. armata* (Fig. 2), *Gonatus steenstrupi* (Fig. 4) and *H. bonnelli bonnelli* (Fig. 5), length distributions varied significantly between predator species (Mann-Whitney test, $p < 0.05$). In contrast, size distributions of *T. megalops* and *H. reversa* were quite similar across all predators (Figs. 3 and 6).

4. Discussion

4.1. Representativeness of dietary results

Stomach content analysis is subject to some selectivity and biases which could affect our perception of top predator diets. The representativeness of diet was in this case subject to difficulty in controlling sampling design and to differential digestion of ingested prey

Table 3
Stomach composition in frequency by number (%N) and reconstructed biomass (%M) of additional deep-diving odontocetes in the Bay of Biscay.

	Risso's dolphin				Melon headed whale				Northern bottlenose beaked whale		Dwarf sperm whale	
	Ind. 1		Ind. 2		Ind. 1		Ind. 2		Ind. 1		Ind. 1	
	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M
Cephalopods												
<i>Sepia</i> spp.	85.7	94.6			35.7	85.6	2.2	24.7				
Und. Sepiolidae							19.7					
<i>Alloteuthis</i> spp.					7.1	0.6	0.6	0.2				
<i>Loligo</i> spp.					7.1	1.8	2.2	13.3				
<i>Histioteuthis reversa</i>											97.8	99.6
Und. Ommastrephidae							8.4	37.7				
<i>Teutowenia megalops</i>									13.5	93.6		
<i>Stauroteuthis syrtensis</i>									86.5	6.4		
Und. Octopodidae	14.3	5.4										
Fish												
<i>Micromesistius poutassou</i>					35.7	7.7						
<i>Trisopterus</i> spp							58.4	16.5				
<i>Merluccius merluccius</i>					14.3	4.3	6.2	5.6				
Und. Pleuronectidae							2.2	2.0				
Others invertebrates												
<i>Polybius</i> spp.											2.2	0.4
Salps			100.0	100.0								

Table 4

Niche overlaps (Pianka's index) in the trophic dimension by number (above diagonal) and by mass (below diagonal). Values in bold denoted substantial overlap (< 0.4).

	Long-finned pilot whale	Cuvier's beaked whale	Sowerby's beaked whale	Sperm whale	Pygmy sperm whale
Long-finned pilot whale		0.01	0.00	0.17	0.39
Cuvier's beaked whale	0.39		0.00	0.15	0.71
Sowerby's beaked whale	0.00	0.00		0.00	0.00
Sperm whale	0.28	0.12	0.00		0.11
Pygmy sperm whale	0.40	0.68	0.00	0.09	

(e.g. Tollit et al., 1997; Santos et al., 2001a; Pierce et al., 2007). Especially for large and/or oceanic species, dietary results are often limited by size, spatio-temporal coverage, or for instance, age, sex, reproductive and health status compositions of individuals providing the stomach content sample set. Thus, several limitations are inherent to small sets of individuals obtained from stranding schemes. Indeed, in our study prey remains were often highly digested and eroded. This was likely a source of biases in quantifying the importance by number and by mass of the different prey species. Species with large diagnostic hard parts were likely overestimated in the diet compared to species having small or no hard parts, because retention time in the stomach would not be the same for all types and sizes of diagnostic parts (e.g. Murie, 1987; Pierce and Boyle, 1991; Santos et al., 2001a). This is particularly relevant for cephalopod beaks which are relatively indigestible and would tend to accumulate in the predators' stomachs whereas fish bones and otoliths disappear more quickly from stomach contents (Bigg and Fawcett, 1985). Moreover, the number of prey species found in the diet of a top predator increases with the number of analyzed stomachs (Spitz et al., 2006). Hence, diversity of prey species is likely underestimated and confidence limits around the proportion by number and by mass of identified preys are often wide for odontocete species for which only a few stomach samples were analyzed. This study is fully subjected to these limitations and sources of heterogeneity as ontogenetic, temporal or geographic changes cannot be considered here. Nevertheless, published data on dietary preferences of deep-diving cetaceans are scarce and they rely on limited sample sets (see for example, the world review on the diet of beaked whales by MacLeod et al., 2003). Hence, the present work should be considered as providing representative general patterns on prey preferences for the most deep-diving odontocetes of the north-east Atlantic but not as a fine and exhaustive description of their diets.

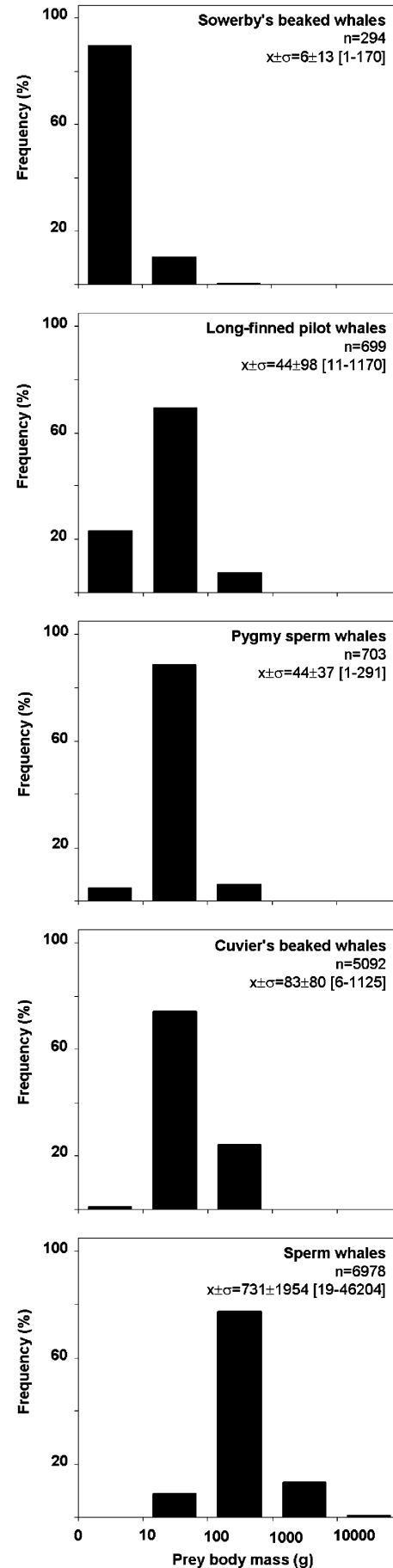


Fig. 1. Frequency distribution of prey body mass (g) eaten by deep-diving odontocetes in the Bay of Biscay with n =the number of prey, $\bar{x} \pm \sigma$ =mean value \pm standard deviation, and [min.–max. value].

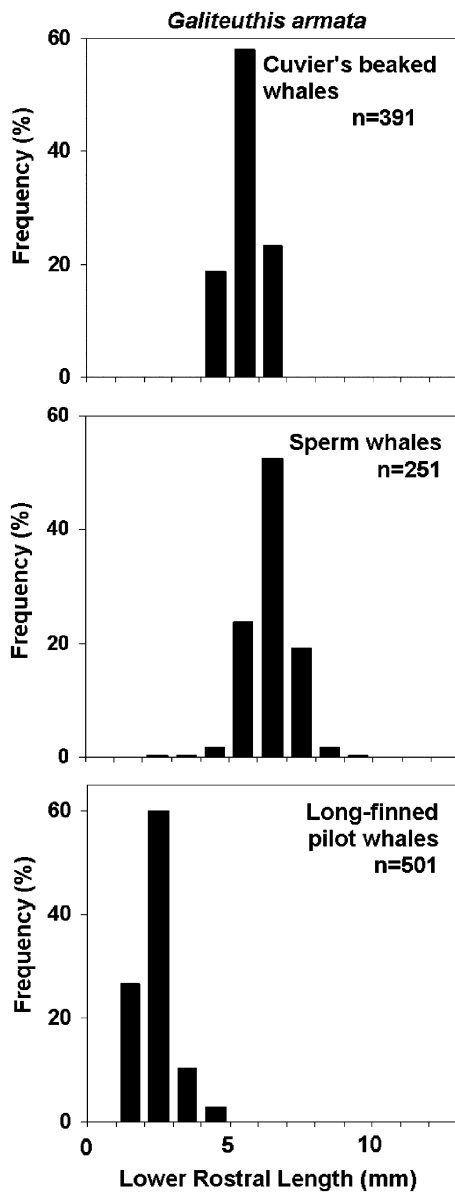


Fig. 2. Frequency distributions of LRL (mm) of *Galiteuthis armata* eaten by deep-diving odontocetes in the Bay of Biscay.

4.2. Prey preferences

Given the limitations discussed above, the present work is nevertheless the first quantitative study of prey preferences for a deep-diving assemblage of odontocetes (at least for 5 of the 9 studied species belonging to 4 families) collected in the same geographical zone. The key role of cephalopods, mainly oceanic species, was confirmed in the ecology of these deep-diving top predators. Indeed, the majority of studied species appeared to be mostly teutophageous. However, fish seemed to be a significant resource for some species, such as the Sowerby's beaked whale or the long-finned pilot whale. The overall results are consistent with previous studies and they strengthen the already available albeit scattered data on their feeding habits (e.g. Beatson and O'shea, 2009; Best, 2007; Blanco et al., 2006; Fernández et al., 2009; Gannon et al., 1997; Gonzalez et al., 1994; Jefferson and Barros, 1997; MacLeod et al., 2003; Santos et al., 1999, 2001b, c, 2002, 2006; see also references therein). However, the present study highlights some key features. Firstly, the main characteristic of the long-finned pilot whale diet was the unique

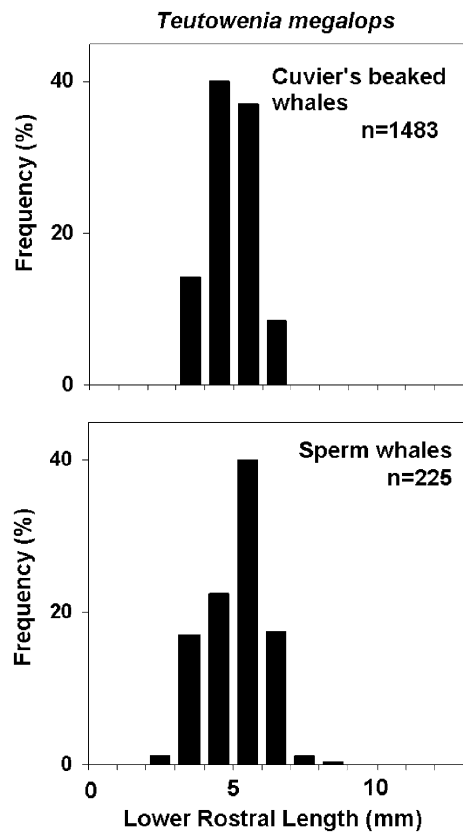


Fig. 3. Frequency distributions of LRL (mm) of *Teutowenia megalops* eaten by deep-diving odontocetes in the Bay of Biscay.

combination of mesopelagic prey living in oceanic waters and of prey living at or close to the bottom in neritic waters. This combination suggested some degree of dietary plasticity allowing long-finned pilot whales to exploit successively both the oceanic and neritic habitats, as previously shown in the Bay of Biscay for only one other cetacean species, the striped dolphin (*Stenella coeruleoalba*; Spitz et al., 2006). Secondly, the diet of sperm whales in the northeast Atlantic was dominated either by *Gonatus* species or by *H. bonnellii bonnellii*, and the prevalence of one of the two prey species was generally discussed according to migration patterns (Santos et al., 2002). *Gonatus*, a cold-temperate species, is associated to northern localities such as the North Sea (e.g. Santos et al., 1999, 2002; Simon et al., 2003), whereas *H. bonnellii bonnellii* was described from southern localities such as the Canary Islands (Fernández et al., 2009) or the Madeira Archipelago (Clarke, 1962). Hence, the vast numbers of *H. bonnellii bonnellii* and the small amount of gonatid squids found in the present work suggest that sperm whales were either foraging in the Bay of Biscay or traveling northwards. In the same way, gonatid squids were reported as the key prey in the diet of northern bottlenose whales across north Atlantic waters (Hooker et al., 2001; Santos et al., 2001b). We reported here for the first time the predominance of another squid species, *H. reversa*, in a stomach content of a northern bottlenose whale.

Finally, remains of fishing gears, like hooks were recovered from two stomach contents of long-finned pilot whales and two of Sowerby's beaked whales, suggesting that these two species may be involved in longline depredation in the Bay of Biscay.

4.3. Considerations on cetaceans foraging strategies

Beyond the taxonomic composition of the diets of these deep-diving odontocetes, prey biological characteristics can help

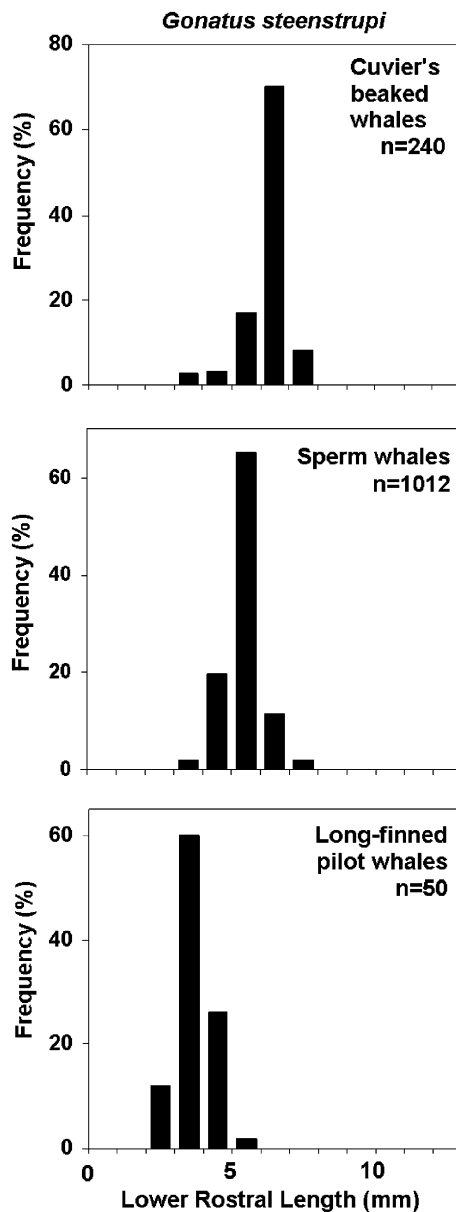


Fig. 4. Frequency distributions of LRL (mm) of *Gonatus steenstrupi* eaten by deep-diving odontocetes in the Bay of Biscay.

documenting indirectly several dimensions of the cetaceans foraging niche, and so, contribute to a better understanding of segregation mechanisms likely to take place among these predators in the Bay of Biscay.

Differences were observed along the spatial and trophic dimensions of the foraging niche. Indeed, on the axis of foraging habitats, diets revealed the presence of both neritic and oceanic prey assemblages. The continental shelf seabed seemed exclusively exploited by Risso's dolphins, melon-headed whales and Sowerby's beaked whales, while all other cetaceans exploited mesopelagic prey living in the oceanic habitat beyond the shelf break, except long-finned pilot whales that can forage in both habitats.

On the trophic dimension of the foraging niche, three main prey types, cephalopods, fish and crabs, were recovered in the present work. Sowerby's beaked whales was the only species primarily targeting fish, then melon-headed whales and long-finned pilot whales showed significant part of fish (>10%W). Crabs (*Polybius* spp.) represented a significant part of the diet for Sowerby's beaked whales and pygmy sperm whales. Others

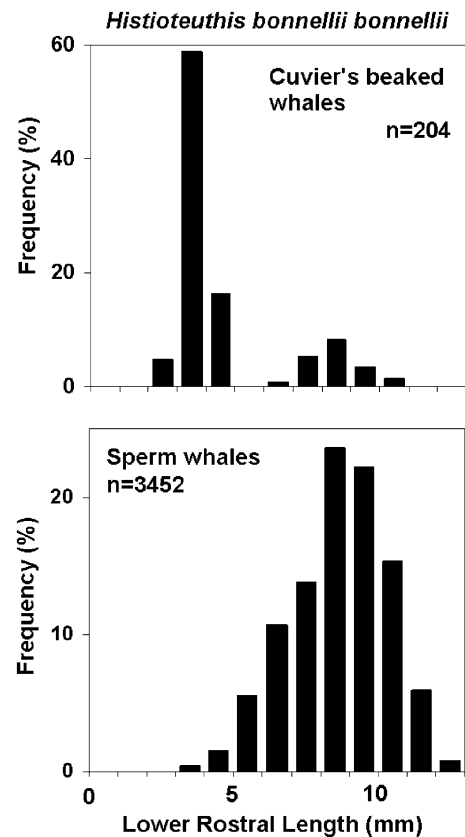


Fig. 5. Frequency distributions of LRL (mm) of *Histiotteuthis bonnellii bonnellii* eaten by deep-diving odontocetes in the Bay of Biscay.

cetaceans seemed to be almost exclusively teutophagous. As seabirds which exhibit different dive behaviors according to whether the prey was a fish, a squid or a crustacean (Elliott et al., 2008), these differences in prey types imply probably different diving strategies among these predators. Similarly, prey size was explored as a possible segregation mechanism within the trophic dimension of the foraging niche. Significant differences occurred between teutophagous predators regarding prey size with pygmy sperm whales feeding on small cephalopods, whereas large species were found in the diet of sperm whales. Differences in prey size distribution between toothed whales might reflect two alternative techniques of prey ingestion. The large prey would be captured using pincer-like movement of jaws, whereas small prey would be ingested by suction-feeding (MacLeod et al., 2006).

Finally, prey quality could be involved in prey selection and trophic segregations among top predators with contrasted energy requirements (Pusineri et al., 2008; Spitz et al., 2010a). In the present work, almost all prey species had low energy contents ($\leq 4 \text{ kJ g}^{-1}$; Clarke et al., 1985; Spitz et al., 2010b). Hence, predator-specific energy requirements per unit body mass are interpreted as broadly equivalent across all studied species. One possible exception could be the long-finned pilot whale whose diet includes several high-quality species (Spitz et al., 2010b) such as scad (*T. trachurus*), conger eel (*C. conger*) or mackerel (*Scomber scombrus*). Here, high-quality preys represented more than 10% of total ingested biomass and were likely underestimated as otoliths are less resistant to digestion than cephalopod beaks. This dietary characteristic of pilot whales would be consistent with recent telemetry observations of its diving behavior. Pilot whales undertake deep foraging sprints, and this costly foraging strategy would be sustainable only if the target species had a high energy density (Soto et al., 2008).

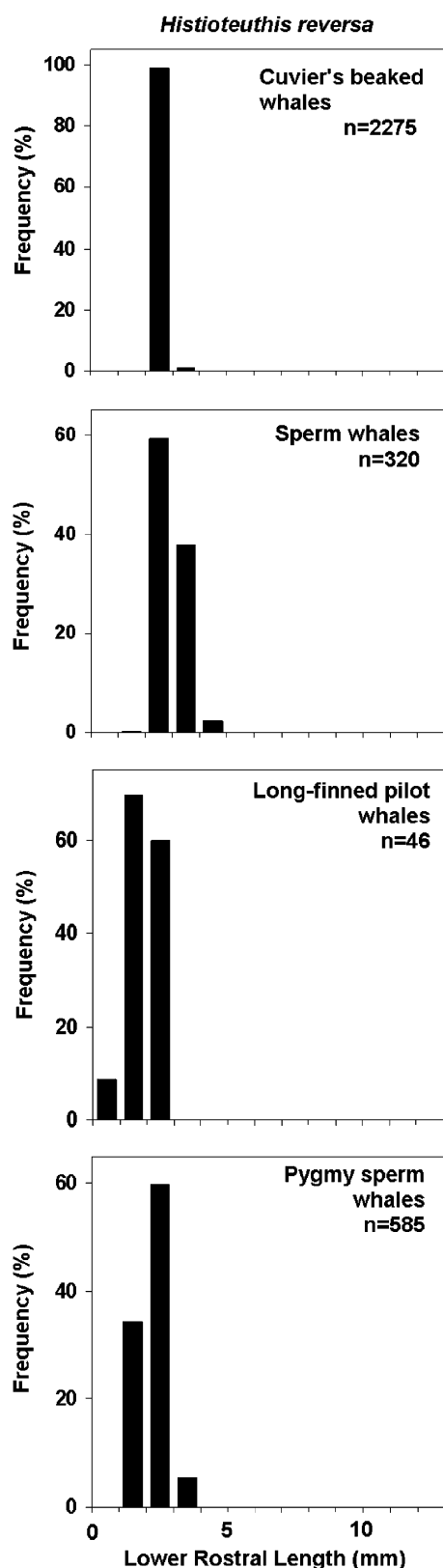


Fig. 6. Frequency distributions of LRL (mm) of *Histiototeuthis reversa* eaten by deep-diving odontocetes in the Bay of Biscay.

In brief, most toothed whales from the Bay of Biscay were segregated by different dimensions of their trophic niche, with only pygmy sperm whales showing substantial overlaps with both Cuvier's beaked whales and long-finned pilot whales. These

observed differences in foraging niche among these top marine predators explain their co-existence in the Bay of Biscay.

4.4. Considerations on the cephalopod community

Deep-sea cephalopods are often poorly known all around the world, mainly because of their low value for commercial fisheries and of the difficulties to catch them. Thus, research cruises specifically targeting cephalopods are seldom conducted, and no adapted fishing gears allow adequate sampling of most of species. Nonetheless, cephalopods play an important role in marine food webs, most particularly in deep-sea ecosystems (Rodhouse and Nigmatullin, 1996). In oceanic waters of the northeastern Atlantic, cephalopods constitute a major resource for top predators (e.g. Pusineri et al., 2008; this study). However, the composition of the cephalopod fauna was almost unknown in this area and especially in the oceanic part of the Bay of Biscay. The most detailed, and geographically closest, study described recently the cephalopod fauna along the northern mid-Atlantic ridge from 1295 specimens sampled by trawls (Vecchione et al., 2010).

For a better knowledge of cephalopod communities, an alternative to traditional fishing techniques is the use of top predators as biological samplers (Cherel et al., 2004). Indeed, the diet of top predators can be a good indicator of prey availability and it sometimes brings more data than experimental catches with fishing gears (e.g. Quérou et al., 2006). In the present study, more than 14,000 individual cephalopods were identified from stomachs of 9 cetacean species and they shed new insights on the oceanic cephalopod community off the Bay of Biscay. Overall, the cephalopod diversity is fairly high with a least 39 species from 22 families and the presence of charismatic species such as the giant and large squids *A. dux*, *T. danae*, *L. grimaldii* and the “giant” *Octopoteuthis*, together with the oceanic octopods *Vampiroteuthis infernalis* and *H. atlanticus*. Then, the community appears to be dominated by two families, the histiototeuthids with the large *H. bonnellii bonnellii* and the smaller *H. reversa*, and the cranchiids with mainly *T. megalops* and *G. armata*. Thus, the oceanic cephalopods community of the Bay of Biscay appears to be different from northern adjacent areas where *Gonatus* species dominated the cephalopod assemblages (Kristensen, 1984; Vecchione et al., 2010).

This study is the first description of the oceanic cephalopod community of the Bay of Biscay. The knowledge of cephalopod biogeography worldwide is decades behind that of other marine taxa (Roeleveld, 1998). Hence, this work brought a valuable new insight on the relative abundance and diversity of oceanic cephalopods living in the northern Atlantic and especially for large species that are almost always absent from trawling surveys.

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