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Dietary plasticity of the oceanic striped dolphin, *Stenella coeruleoalba*, in the neritic waters of the Bay of Biscay

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Abstract

The striped dolphin, *Stenella coeruleoalba*, is an oceanic species that occasionally occurs in neritic habitats; in the Bay of Biscay it is abundant offshore and erratic in occurrence over the shelf. Given that prey assemblages differ widely among these habitats both in terms of taxonomic composition and of ecology, this would suggest that striped dolphins are able to shift from vertically migrating meso-pelagic prey to neritic or coastal prey types. We investigated the striped dolphin's dietary plasticity by examining the stomach contents of individuals stranded along the French Atlantic coast. 1109 prey items were identified belonging to 30 distinct taxa and their biomass was calculated. Fish accounted for 91% of the diet by number and 61% by mass; the rest was mostly cephalopods, crustaceans being present as trace. Specific composition included both oceanic (myctophid and sternoptychid fish; histioteuthid, gonatid and brachioteuthid cephalopods), neritic (gadids and anchovy; loliginid, sepiolid and sepiid cephalopods) and even coastal (atherinid fish) prey types, showing that these animals had changed their diet as they moved over the shelf.
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Keywords: Dietary plasticity; *Stenella coeruleoalba*; Continental shelf; Bay of Biscay

1. Introduction

The Bay of Biscay and the adjacent northeast Atlantic Ocean are subject to numerous fisheries and support a diverse cetacean fauna, with delphinids being by far the most abundant (Goujon, 1996; Hammond et al., 2002). Nonetheless, the relationships between fisheries, resources and top predators in the Bay of Biscay and the adjacent north-east Atlantic are little known. Central to this understanding are the assessment of cetacean population size and the quantification of their diet.

Resource availability, which combines with the predator's foraging strategies to shape the diet, is determined by a combination of spatially-defined characteristics of the environment such as depth and slope and more variable features such as a wide variety of meso- to small-scale hydrological processes. Within the limits of the Bay of Biscay, two contrasting

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compartments can be defined: the oceanic and the neritic domains, separated by a continental slope which runs from more than 200 km offshore in the north of the Bay to less than 10 km offshore in the south. Prey availability in these two compartments differs greatly, being dominated by myctophid and sternoptychid fish and oegopsid squid in the oceanic domain and by clupeiform and gadid fish in the neritic domain. In contrast, the small cetacean species assemblages do not differ to such an extent, since several species are known from both habitats and only the striped dolphin, *Stenella coeruleoalba*, shows a clear preference for the oceanic domain (see Goujon, 1996 and Hammond et al., 2002 for cetacean assemblages in two adjacent areas representative of each domain). Because the nature of food resources and their pattern of availability to air-breathing predators (depth range, accessibility to demersal resources, patterns of nycthemeral vertical migration, etc.) differ widely between the two main ecological domains of the Bay of Biscay, dolphin species which can utilise both domains must have some ecological plasticity, in terms of foraging strategies. It is not known whether this foraging plasticity can be expressed at the individual level, at the population level, or corresponds to distinct populations or even ecotypes.

Among the delphinid species assemblage of this area, only the striped dolphin does not seem to have permanent neritic groups. Nonetheless, sighting and stranding data show that the species occasionally wanders over the continental shelf. Examining the diet of striped dolphins found stranded should provide an opportunity to examine the foraging plasticity of oceanic individuals temporarily placed in a neritic context. Several scenarios could be expected. If striped dolphins associated with the abundant common dolphin over the shelf or at least adopted a similar foraging tactic, they might be expected to have a similar diet. If striped dolphins were unsuccessful in foraging over the shelf, their stomachs should contain few remnants of neritic prey species. In between these options, striped dolphins could have developed a distinct foraging tactic allowing them to prey upon a different prey species assemblage.

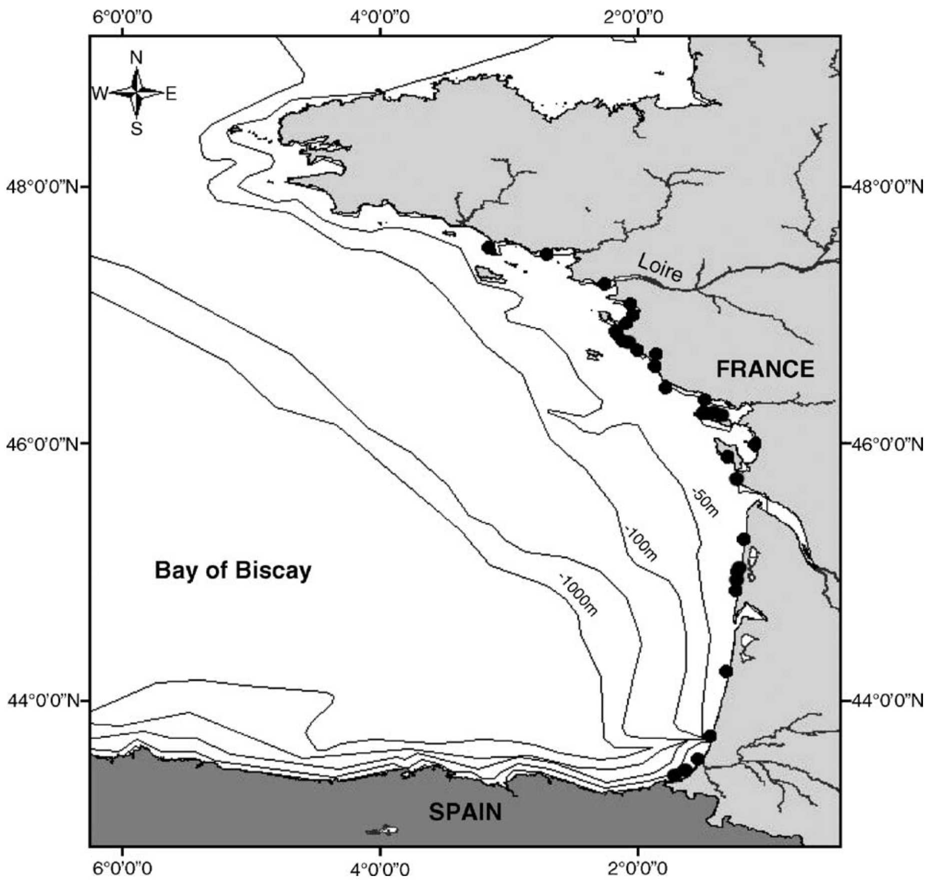

Fig. 1. Locations of striped dolphin strandings.

Table 1
Summary of stranding data

Date	Sex	Length (cm)	Weight (kg)	Age (years)
14 May 1999	♂	210	N/A	6
30 May 1999	♂	231	N/A	12
12 August 1999	♂	206	107	11
9 December 1999	♀	155	N/A	2
19 December 1999	♀	205	N/A	9
17 March 2000	♀	183	N/A	2
6 July 2000	♀	202	N/A	11
10 November 2000	♂	234	147	22
25 November 2000	♂	183	N/A	1
9 January 2001	♂	227	N/A	23
26 January 2001	♂	153	N/A	1
31 January 2001	♂	228	117	17
20 March 2001	♂	173	N/A	2
15 September 2001	♀	137	31	1
26 July 2001	♂	212	N/A	N/A
23 January 2002	♀	171	55	2
15 February 2002	♂	185	64	4
9 May 2002	♂	152	40	2
10 April 2002	♀	147	N/A	2
13 April 2002	♂	227	N/A	19
11 July 2002	♀	198	72	6
30 October 2002	♀	165	N/A	18
4 November 2002	♂	209	95	10
31 July 2002	♀	198	N/A	N/A
7 February 2003	♂	164	50	N/A
9 February 2003	♂	208	74	N/A
13 April 2003	♂	231	60	N/A
1 December 2003	♂	144	29	N/A
26 January 2004	♀	199	80	N/A
15 June 2004	♂	225	101	N/A
29 June 2004	♂	218	N/A	N/A
22 October 2004	♀	198	N/A	N/A

♂ male; ♀ female; Age: counts of growth-layer groups; N/A: non-available.

In this study we have examined the diet of the striped dolphin in the neritic Bay of Biscay from stomach content analyses of stranded animals and discuss the results in the light of the known oceanic diet of the species and the neritic diet of the other small cetaceans dwelling over the shelf, notably the common dolphin.

2. Materials and methods

2.1. Sampling

In this study, 32 stomachs of striped dolphins stranded along the French Atlantic coast, mostly south of the river Loire, were analysed (Fig. 1). The animals studied were recovered and examined by members of the French stranding network from May 1999 to October 2004. The sample set includes individuals of both sexes, and immatures and adults are represented fairly equally (Table 1). After necropsy, the stomachs were ligatured and stored deep-frozen (−20°C) in polythene bags until further analysis.

2.2. Sample analysis

Sample analysis was aimed at describing the diet in terms of prey occurrence, relative abundance, calculated mass and size distribution and followed a general procedure which is now standard for marine top predators (Pierce and Boyle, 1991; Croxall, 1993; Ridoux, 1994). Each stomach was weighed, emptied in a tray and its wall weighed again to obtain the mass of stomach content by subtraction. The stomach content was washed through a 0.2 mm mesh sieve. The diagnostic parts were recovered and stored dry for fish bones and otoliths or in 70% ethanol for cephalopod beaks, crustacean remains as well as any remain with flesh attached. The items found were identified to the lowest taxonomic level by using published guides (Lagardère, 1971; Clarke, 1986; Härkönen, 1986) and our reference collection of specimens caught by commercial or scientific trawlers in the Bay of Biscay and adjacent Atlantic areas. The total number of food items was estimated as the highest number given either by paired structures (otoliths, operculum, hyomandibular, dentary and premaxillary for fishes, upper and lower beaks for cephalopods and eyes for crustaceans) or impaired structures (parasphenoid for fishes, gladii for cephalopods and carapace and telson for crustaceans). Diagnostic hard parts such as beaks, otoliths and carapaces were measured with a digital vernier calliper (±0.02 mm) following standards (Clarke, 1986; Härkönen, 1986). A random sub-sample of up to 30 diagnostic hard parts per prey species per stomach sample was measured.

2.3. Data analysis

The occurrence of a given prey taxon was the number of stomachs in which this taxon was observed. The

Table 2
General composition of the diet of *Stenella coeruleoalba* stranded on the French Atlantic coast

	Occurrence	Abundance		Calculated mass		Diversity
	%	N	%	M	%	I
Fish	71	1009	91	8020	61	18
Cephalopods	52	95	9	5117	39	9
Crustaceans	24	5	0	3	0	2
All prey	100	1109	100	13,140	100	30

N: total number of each prey type in the stomachs; M: total mass of each prey type in the stomachs in g; I: total number of species.

Table 3
Prey found in stomach contents of *Stenella coeruleoalba* stranded on the French Atlantic coast

Species	Occurrence	Number		Body length (mm)			Body mass (g)		Reconstituted biomass	
	%O	N	%N	n	x±σ	Range	x±σ	Range	M	%M
FISH										
Sternoptychidae										
Maurolicus muelleri	4.4	6	0.5	11	30.0	–	0.5	–	3.0	0.0
Alepocephalidae										
Xenodermychthys copei	4.4	1	0.1	1	58.0	–	1.0	–	1.0	0.0
Myctophidae										
Benthosema glaciale	4.4	1	0.1	1	48.0	–	0.5	–	0.5	0.0
Ceratoscopelus maderensis	8.7	3	0.3	3	54±5.5	49.6–63.1	2.3±0.7	2.0–3.1	6.9	0.1
Myctophum punctatum	8.7	4	0.4	4	37±8	24.9–45.4	0.6±0.4	0.2–1.1	2.5	0.0
Nannobranchium atrum	4.4	1	0.1	1	70.0	–	1.8	–	Z1.8	0.0
Notoscopelus kroeyeri	13.0	12	1.1	10	67.6±11.6	46.7–83.8	3.7±2.1	1.1–6.8	44.9	0.3
Lobianchia gemellari	4.4	1	0.1	1	68.0	–	5.2	–	5.2	0.0
Engraulidae										
Engraulis encrasicolus	8.7	2	0.2	1	124.9		11.4		22.7	0.2
Gadidae										
Merlangius merlangus	4.4	15	1.4	29	161±37	86.4–236.3	33.2±25.2	3.73–98.48	498.6	3.8
Micromesistius poutassou	21.7	363	32.7	74	129.3±32.9	85.8–213.3	12.4±16.3	3.5–52.7	4498.4	34.2
Trisopterus spp.	26.1	93	8.4	58	67.6±34.8	10.3–144.8	6.4±8.9	0.1–35.6	595.0	4.5
Rockling [a]	8.7	29	2.6	49	82.3±20.3	47.5–127.4	4.9±4.9	0.8–16.0	141.7	1.1
Unidentified Gadidae	4.4	1	0.1							
Merluccidae										
Merluccius merluccius	4.4	5	0.5	1	202.4	–	45.5	–	227.4	1.7
Atherinidae										
Atherina presbyter	26.1	184	16.6	137	84.7±19.4	21 – 111	8.8±40	0.1–21.3	1610.3	12.3
Sparidae										
Spondylosoma cantharus	8.7	6	0.5	11	75.4±75.6	68.3–84.5	5.5±5.7	4–7.8	33.2	0.3
Mugilidae										
Unidentified Mugilidae	4.4	1	0.1	2	293.7		232.5		232.5	1.8
Gobiidae										
Unidentified Gobiidae	17.4	269	24.3	97	37.1±8.5	16.9–53.3	0.3±0.3	0.02–1.03	94.1	0.7
Other fish										
Unidentified fish	21.7	12	1.1							
CEPHALOPODS										
Loliginidae										
Alloteuthis spp.	13.0	10	0.9	10	73.8±16.8	37.4–94.4	6.2±2.4	1.8–9.6	62.2	0.5
Loligo spp.	8.7	4	0.4	4	166.8±10.7	160–185.3	118±71	106.4–150	471.9	3.6
Ommastrephidae										
Unidentified Ommastrephidae	13.0	7	0.6	7	149.4–51.5	96.2–232.9	304.6±285.2	61.2–838.2	2131.9	16.2
Brachioteuthidae										
Brachioteuthis riisei	4.4	2	0.2	2	51.6±1	50.6–52.6	3.8±0.2	3.7–4	7.6	0.1
Histioteuthidae										
Histioteuthis reversa	4.4	1	0.1	1	34.4		29		29.0	0.2
Gonatidae										
Gonatus steenstrupi	4.4	15	1.4	5	172.3±69.8	47.5–227.1	153±420.7	6.3–239.7	2294.4	17.5
Cranchiidae										
Teutowenia megalops	4.4	1	0.1	1	165.1	–	45.6	–	45.6	0.3
Sepiolidae										
Undeterminatided Sepiolidae	13.0	43	3.9	30	15.7±0.1	15.6–16.2	1.5±1.1	1.3–1.5	63.0	0.5
Sepiidae										
Sepia officinalis	13.0	3	0.3	3	59.5±16.7	40.8–81.4	3.9±0.1	3.8–4.1	11.8	0.1
Other cephalopods										
Unidentified cephalopods	17.4	9	0.8							
CRUSTACEANS										
Oplophoridae										

Table 3 (*continued*)

Species	Occurrence	Number		Body length (mm)			Body mass (g)		Reconstituted biomass	
	%O	N	%N	n	x±σ	Range	x±σ	Range	M	%M
Acanthephyra sp.	4.4	1	0.1	1	46.2	–	2		2	0.0
Crangonidae										
Crangon crangon	4.4	1	0.1	1	20	–	0.5		0.5	0.0
Other crustaceans										
Unidentified crustaceans	13.0	3	0.3							

N: number of each prey; n: number of measurements; M: total mass of each prey in g; x: mean value; σ: standard deviation; ∗ several genera are present in the area and cannot be distinguished from their otoliths.

[a] Several genera are present in the area and cannot be distinguished from their otoliths.

relative abundance was given by the number of individuals of the same taxon found throughout the sample set. The calculated biomass was given by the product of the average calculated body mass and the number of individuals of the same taxon in each sample, summed throughout the sample set. These three indices can be expressed by their percentage frequency with, respectively, percentage of occurrence (%O), percentage by number (%N) and percentage by biomass (%M):

$$\%O_i = n_i/N*100$$

where n_i is the number of stomachs where the prey i was found and N the total number of stomachs;

$$\%N_i = x_i/X*100$$

where x_i is the number of prey i found and X the total number of prey;

$$\%M_i = \left(\sum_j x^*_{i,j}\,\overline{Y}_{i,j} \Big/ \sum_i \sum_j x^*_{i,j}\,\overline{Y}_{i,j}\right)*100$$

where x_{ij} is the number of prey i found in the sample j and $\overline{Y}_{i,j}$ average individual body mass of prey i in sample j.

Individual prey body length and body mass were back-calculated by using relationships that came either from the literature (Perez-Ganderas, 1983; Clarke, 1986; Härkönen, 1986) or were fitted from measurements performed on specimens of our reference collection (unpubl. data). When diagnostic hard parts in stomach contents were well below the lower limit of the size range on which the relationship was fitted, we supposed that the growth was isometric between the origin (diagnostic part size = 0; body length = 0; body mass = 0) and this lower limit of the hard part's size range; by doing so, aberrant results such as negative lengths were avoided. Body size distribution was established on the basis of the whole series of individuals of each prey i. Therefore, size distributions were established at sample j level from the 30 measured individuals or prey i, level-headed to total number of prey i individuals in sample j and summed throughout the sample series. These prey size distributions were constructed both as the percentage by number and the percentage by mass contributed by each size class, since these two variables convey quite different information on the importance to the diet of prey of varying body lengths.

Thus, the diet of the striped dolphin in the neritic Bay of Biscay was described by the following indices: occurrence, number and reconstructed mass as well as body size distributions for each prey species. Intervals of confidence for the compositions by number and by mass were generated by bootstrap simulations allowing sampling error to be estimated (Reynolds and Aebischer, 1991). The bootstrapping routine was written by using the *R* software (Ihaka and Gentleman, 1996). Random samples were drawn with replacement and the procedure was repeated 1000 times. Possible biases related to subsampling for length measurements and to erosion of diagnostic parts were not estimated.

3. Results

3.1. General

Food remains were recovered from 23 out of 32 samples. The total mass of examined food material was 2423 g, which represented an average stomach content mass of 76±152 g (N=32; range 0–640). In general, food remains were composed of highly digested material and included few prey remains with flesh attached.

A total of 1109 prey individuals were found. They accounted for a total reconstructed biomass of 13 140 g (Table 2). Fish, cephalopods and crustaceans were identified and represented a diversity of 30 different species. Average prey diversity was 3.2±2.1 species per sample (N = 23 non-empty stomachs). Fish dominated the diet in relative abundance (91%), whereas both cephalopods and fish represented a more balanced share of the diet in reconstructed biomass (61% and 39%, respectively), as a result of the generally greater individual body mass of cephalopods relative to fish (Table 2). Crustaceans accounted for a negligible fraction of the diet, by number and by mass.

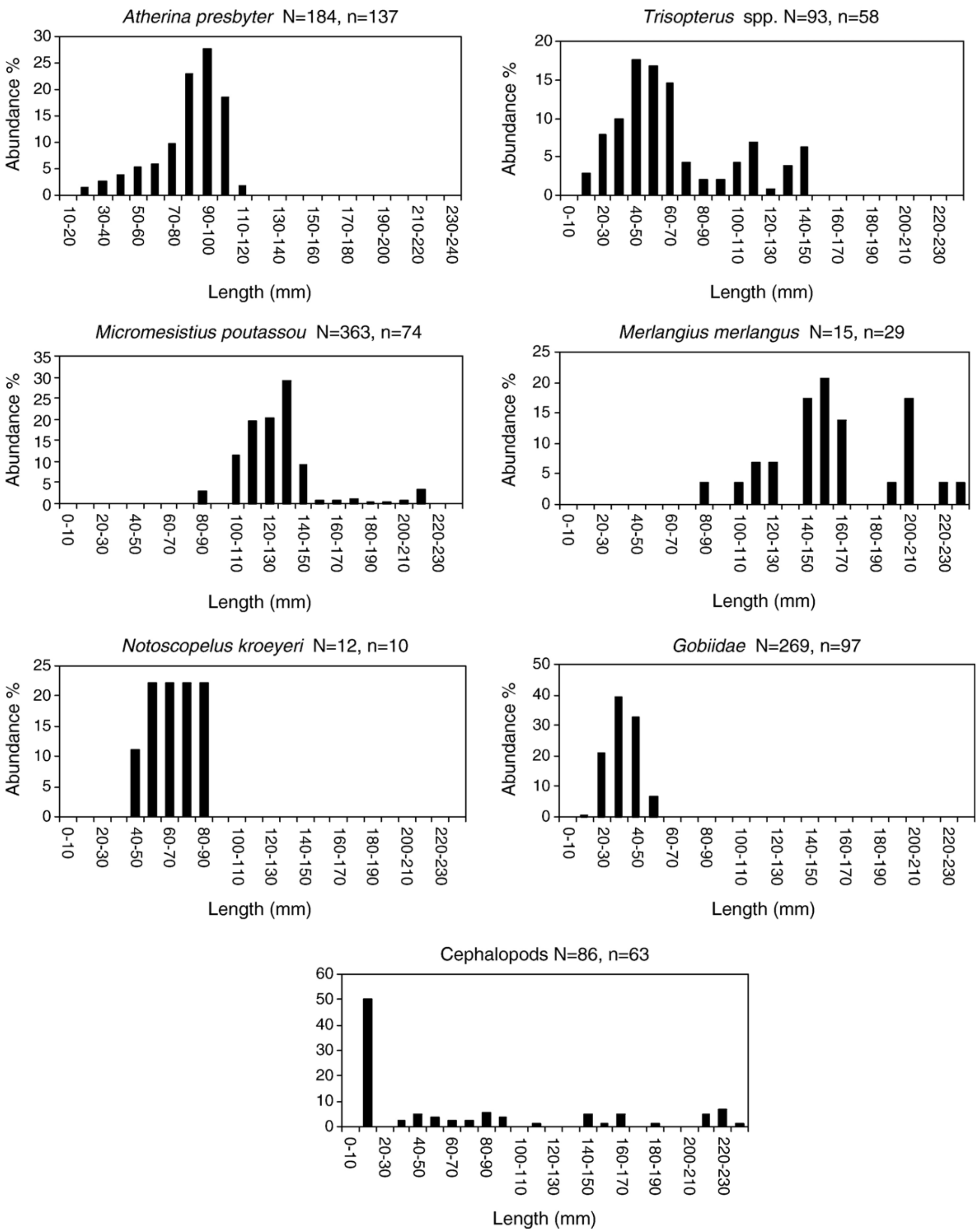

Fig. 2. Size distributions of the main prey species (n: number of measurements; N: number of prey individuals).

3.2. Specific composition

The fish part of the diet (Table 3) was composed of a combination of oceanic (families Myctophidae and Sternoptychidae), neritic (families Engraulidae, Gadidae, Merluccidae), and coastal species (families Atherinidae and Gobiidae). In terms of species diversity, 45% of the species encountered can be classified as oceanic. However, only neritic and coastal species actually accounted for proportions by number or mass higher than 10% (Table 2). Gobies represented 24% by number but, owing to their very small body size (37±9 mm standard length; see also Fig. 2 for complete distribution), less than 1% by mass. The same applies to *Trisopterus* spp. (67±4 mm), which accounted for 8% by number and only 4.5% by mass. By contrast, the sand smelt, *Atherina presbyter*, and the blue whiting, *Micromesistius poutassou*, accounted for high proportions of the diet both by number (17 and 33%, respectively) and by mass (12 and 34%, respectively) as a result of their larger body size (85±21 mm and 153±26 mm, respectively).

The squid diet of the striped dolphin (Table 3) also showed a combination of oceanic (families Ommastrephidae, Histioteuthidae, Gonatidae, Cranchiidae and Brachioteuthidae) and neritic species (families Ommastrephidae, Loliginidae, Sepiidae, Sepiolidae). Oceanic species represented 56% of the cephalopod species. Among them, *Gonatus steenstrupi* represented 1% by number and, because of its very large size (172±70 mm dorsal mantle length), as much as 17% by mass of the total prey. The ommastrephids, which can be regarded as a ubiquitous family dwelling both in oceanic and neritic habitats, amounted to less than 1% by number but 16% by mass, again because of their large body size (159±49 mm DML). Among coastal cephalopods, only the common squid, *Loligo* spp., accounted for non-trace amounts (4% by mass).

3.3. Prey sizes

The overall prey size distributions ranged from 10 to 236 mm (Fig. 3). The distribution by number displayed a principal mode at 20–60 mm and a secondary one at 80–150 mm; these modes resulted from the high relative abundance of the smaller forms (gobies and, secondarily, the other fish species). In contrast, the distribution by mass showed a principal mode for the sizes >200 mm due to squids, and two secondary ones at 130–180 and 70–120 mm, mostly resulting from the importance by mass of blue whiting and sand smelt, respectively. Overall, 61% of all prey individuals were smaller than 70 mm and 3% were larger than 130 mm body length. Conversely, prey individuals smaller than 70 mm represented only 10% of the reconstructed biomass, whereas those over 130 mm accounted for 68% of the biomass.

3.4. Variation

Because of the generally low frequency of occurrence of most prey taxa, the number of species found increased with the number of stomachs examined but did not reach a plateau (Fig. 4). Additionally, the multiplying coefficient of the logarithmic model was high. Moreover, the intervals of confidence of the frequencies by number and by mass for each main species were wide (Table 4). Accordingly, no intraspecific difference in the diet could be demonstrated

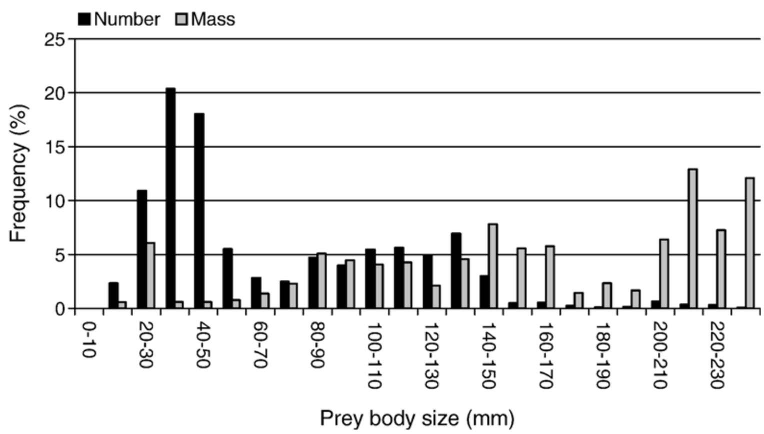

Fig. 3. Overall prey-size distribution in the diet of the striped dolphin in relative number and relative mass.

Table 4
Interval of confidence (IC) calculated by bootstrapping for main prey in diet of striped dolphin

Species	Number		Mass	
	%N	IC	%M	IC
Micromesistius poutassou	32.7	3–65	34.2	3–73
Merlangius merlangus	1.4	0–4	3.8	0–10
Trisopterus spp.	8.4	2–15	4.5	0–27
Rocklings [a]	2.6	0–10	1.1	0–6
Merluccius merluccius	0.5	0–1	1.7	0–4
Atherina presbyter	16.6	1–41	12.3	0–30
Gobiidae	24.3	0–53	0.7	0–2
Gonatus steenstrupi	1.4	0–6	17.5	0–47
Ommastrephidae	0.6	0–2	16.2	0–44
Loligo spp.	0.4	0–1	3.6	0–8

[a] Several genera are present in the area and cannot be distinguished from their otoliths.

either according to sex and age, or to stranding regions and seasons.

4. Discussion

4.1. General

The present work is the first quantitative study of the diet of the striped dolphin stranded in the neritic Bay of Biscay. The diet appeared to be a combination of oceanic and neritic species including fish and cephalopods at comparable amounts in terms of reconstructed biomass. However, several limitations are inherent to sampling small cetaceans from stranding schemes. Firstly, the sample size and composition (geographical range, demographic structure, etc.) cannot be set a priori. Here, only 32 individuals were collected because the striped dolphin does not belong to the permanent cetacean fauna of the continental shelf; nonetheless, samples are fairly evenly distributed along the Atlantic coast south of the river Loire and across sex and age classes. Secondly, a characteristic of stranded material is that the stomach contents often merely consist of digested material, which is clearly the case here. This is likely to cause some biases in the quantification of the importance by number and by mass of the different species as the diagnostic parts used in the analyses do not have the same retention times in the stomachs (abundant literature available on differential digestion rates in many different marine top predators; e.g. Murie, 1987; Pierce and Boyle, 1991; Santos et al., 2001). This effect is evidenced here by the fact that several oceanic species are known not to occur at all on the shelf, and therefore the remains of such species found here would correspond to feeding bouts that occurred prior to the dolphins' foraging over the shelf. Another effect of dealing with mostly digested material is that the numbers of prey individuals per sample and the frequencies of occurrence are generally lower than in studies based on samples which contain essentially fresh food material. This increases inter-individual variation and, combined with limited sample size, increases uncertainty around the estimated contribution of each prey species to the diet. In spite of these limitations, however, the present work provides new quantitative figures on the dietary composition of the striped dolphin in the neritic part of the Bay of Biscay.

4.2. Comparisons with previous studies

The diet of the striped dolphin has been studied in various parts of the world (Table 5). The dominant prey species vary between study areas, but the significance of the observed differences is not always easy to assess as origin of samples, analytical procedures and metrics used

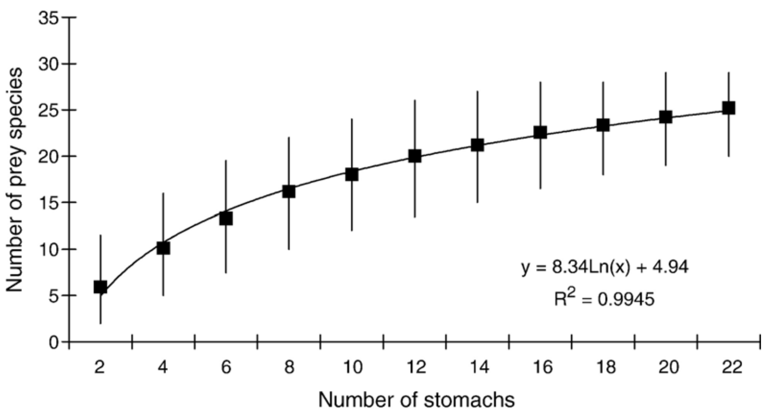

Fig. 4. Average total number of species simulated by randomisation versus number of stomachs considered.

Table 5
Previous studies of on the diet of the striped dolphin

Study area	French coast				West Mediterranean coast					South Africa		Japan
Source	1		2		3		4		5	6	7	8
	%N	%M	%N	%M	%N	%M	%N	%M	%N	%N	%M	%N
FISH	91	61	92	72			91	49	56	80	14	28
Acinaceidae												<1
Alepocephalidae	<1	<1										
Ammodytidae			2	<1								
Argentinidae			2	1					<1	1		<1
Atherinidae	17	12	9	4								
Belonidae								3				
Carangidae			3	3					3		4	
Chauliodontidae							0	1				2
Clupeidae			2	7					<1			
Emmelichthydae												2
Engraulidae	<1	<1					3	1	1			
Gadidae	45	44	67	50			31	19	1			
Gobiidae	24	1										
Gonostomatidae										3		<1
Lepidopidae										1		
Lutjanidae												<1
Merluccidae	1	2	1	1			1	4	4	9	9	
Mugilidae	<1	2	6	5								
Myctophidae	2	<1					16	2	33	66	1	18
Nemichthydae												4
Paralepididae												1
Pleuronectidae			1	1								
Priacanthidae												<1
Scombridae			<1	<1					<1			
Sparidae	1	<1					3	14	3			
Sternoptychidae	1	<1					24	1	4			<1
Stomiatidae							12	4				
Zeidae									<1			
CEPHALOPODS	9	39	8	28	100	100	7	50	40	19	86	35
Brachioteuthidae	<1	<1	1	<1	22	5						
Chiroteuthidae			<1	2	3	3						
Cranchiidae	<1	<1	<1	1					<1			
Enoploteuthidae					29	21			1			
Gonatidae	1	18	<1	5								
Histioteuthidae	<1	<1	0	<1	2	7	1	15	10	1	1	
Loliginidae	1	4	3	12	1	3				7	75	
Lycoteuthidae										10		
Octopodidae									<1		2	
Octopoteuthidae					7	7						
Ommastrephidae	1	16	2	8	10	30	3	27	4		8	1
Onychoteuthidae					19	25	1	6	11			
Sepiidae	<1	<1										1
Sepiolidae	4	1	<1	0	8	0	1	0	10			
CRUSTACEANS	<1	<1					2	1	4			37
Oplophoridae	<1	<1					<1	<1	<1			1
Crangonidae	<1	<1										
Pasiphaeidae							1	1	3			3
Sergestidae							<1	<1	<1			
Benthesicymidae												33
Penaeidae									<1			

1: this study; 2: Desportes, 1985; 3: Blanco et al., 1995; 4: Würtz and Marrale, 1993; 5: Meotti and Podestà, 1997; 6: Gess, 1984; 7: Sekiguchi et al., 1992; 8: Miyazaki et al., 1973.

differ between studies. Off the coast of Japan and South Africa, stomach contents collected from striped dolphins caught at sea contained mainly lanternfish (Myctophidae). In the Mediterranean Sea, the dominant prey species were oceanic cephalopods (e.g. Ommastrephidae, Histioteuthidae, Onychoteuthidae). In the oceanic northeast Atlantic, the diet consisted of a large variety of mesopelagic fish accounting for 39% by mass of the diet, dominated by the family Myctophidae (23%M), cephalopods for 56% by mass (e.g. Onychoteuthidae, Histioteuthidae, Cranchiidae), as well as a significant contribution of oceanic shrimps, 5% by mass (Ringelstein et al., in press). (CRMM/University of La Rochelle on 60 striped dolphins caught in the albacore drift-net fisheries during the summer of 1992 and 1993, unpubl. data). Overall, these studies carried out in oceanic habitats all show the prevalence of species assemblages that belong to the vertically migrating mesopelagic community. Only Desportes (1985) reports on the presence of some neritic prey from samples collected from stranded animals along the French Mediterranean and Atlantic coasts.

Three other small cetaceans permanently inhabit in the neritic Bay of Biscay: the common dolphin, *Delphinus delphis*, the bottlenose dolphin, *Tursiops truncatus*, and the harbour porpoise, *Phocoena phocoena*. Comparison with the common dolphin deserves particular attention because the two species are extremely similar in size and shape and therefore one could expect similar foraging abilities and diets. The common dolphin relies for as much as 65% by mass of its diet on small pelagic fish such as sardine, *Sardina pilchardus*, horse mackerel, *Trachurus trachurus*, and anchovy, *Engraulis encrasicolus*, in the neritic Bay of Biscay (Meynier, 2004), none of which was of any importance to the striped dolphin in the same area. Conversely, the sand smelt and the blue whiting are of secondary importance in the food of the common dolphin. The bottlenose dolphin relies on large-sized epibenthic prey composed of 91%M fish, (including 41%M hake, *Merluccius merluccius*, 13% horse mackerel and 12%M mullets, family Mugilidae) and 9%M cephalopods *Loligo* spp. (Spitz, 2004). In the same area, the harbour porpoise mainly feeds on fish (98%M) with 28%M horse mackerel, 21%M sardine, 21%M blue whiting and 20%M whiting, *Merlangius merlangus* (Spitz, 2004). Thus, the food of the striped dolphin in the neritic habitat appears to differ from that of all other small cetaceans in the area, including the most similarly shaped and sized common dolphin.

From these comparisons it appears that when striped dolphins wander over the continental shelf (present results), they forage upon neritic, mostly epibenthic, prey species and not on pelagic species. Therefore, their diet over the shelf differs widely from their diet in nearby oceanic habitats and from the diet of the morphologically similar common dolphin in neritic habitats.

4.3. Ecological significance of the diet

The presence of both neritic and oceanic prey species indicates that the striped dolphins examined here had successively exploited oceanic, neritic and even coastal habitats. The oceanic prey species are all from the vertically migrating mesopelagic community, and the neritic ones are mostly epibenthic. For example, species such as sand smelt or common shrimp, *Crangon crangon*, are littoral and live at depths from 0 to 50 m, whereas *Trisopterus* spp. are epibenthic fish of the 30–300 m depth range and blue whiting preferentially lives at 200–400 m, which corresponds to outer shelf and upper slope habitats. All these species tend to disperse vertically in the water column at night for feeding.

These details suggest that individual striped dolphins wandering over the shelf belong to the oceanic population and only make temporary incursions over the shelf. There, they do not behave in the same way as the neritic common dolphins, because they rely on bottom-dwelling rather than pelagic prey. It is not understood at this stage whether this habitat and resource utilisation is an integral part of the species' repertoire of foraging behaviours or whether it is an example of suboptimal use of neritic resources by displaced individuals; the actual success of striped dolphins in using demersal prey is unknown. However, it would not be the first evidence of a typically oceanic delphinid showing enough ecological and behavioural plasticity to exploit coastal habitats. The spinner dolphin, *Stenella longirostris*, a tropical congener of the striped dolphin, is known to be mainly distributed in open ocean oceanic waters, but in Hawaii some discrete groups use coastal habitats (Norris et al., 1994). Similarly, striped dolphins in the western Mediterranean Sea are primarily oceanic top predators, but they also routinely exploit coastal areas characterised by submarine canyons, which create spatially defined patterns in food availability (Gannier, 1999; Gannier, unpubl. data). In the Bahamas, Atlantic spotted dolphins *Stenella frontalis* are resident in shallow waters and forage on bottom-dwelling prey (Herzing, 1996; Herzing et al., 2003). Similarly, the same species was observed feeding in a coordinated manner in 40 m deep water in the Gulf of Mexico (Fertl and Würsig, 1995). This level of foraging plasticity, however, is far lower than that achieved by the bottlenose dolphin worldwide. This species is known from truly oceanic habitats where it often associates with various species of the genus *Stenella* (Balance and Pitman, 1998; Clua and Grosvalet, 2001; Herzing et al., 2003) and is also known to use slope and shelf habitats extensively, as is the case in the Bay of Biscay (CRMM/ULR unpubl. data), as well as in various coastal areas, including lagoons and estuaries, where it tends to form resident and stable social units which exploit discrete home ranges (e.g. Irvine et al., 1981; Liret, 2001; Gubbins, 2002).

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