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FOOD AND FEEDING ECOLOGY OF THE COMMON DOLPHIN (*DELPHINUS DELPHIS*) IN THE OCEANIC NORTHEAST ATLANTIC AND COMPARISON WITH ITS DIET IN NERITIC AREAS

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ABSTRACT

The short-beaked common dolphin, *Delphinus delphis*, is abundant in both neritic and oceanic habitats. These two domains differ largely in terms of the nature of forage organisms and their availability to surface-bound top predators, which suggests that the common dolphin should show extensive variability in foraging strategies as a response to these different habitats. However, although its diet is well known over continental shelves, so far, mostly because of sampling issues, nothing has been published on its diet in oceanic habitats. In this study, the diet of sixty-three common dolphins bycaught in the French albacore tuna driftnet fishery in the summers of 1992–1993 in the oceanic Bay of Biscay was determined from their stomach contents and compared to neritic studies. The diet was dominated by fish (90% by number [N] and 53% by mass of total diet [M]). Cephalopods were also important in the total diet (9%N, 46%M) but were a prey of secondary importance in the

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fresh fraction (3%N, 10%M), presumably due to longer retention of cephalopod remains in the stomach. Crustaceans were of minor importance. At the species level, the myctophid fish (*Notoscopelus kroeyeri*) largely dominated the diet. Prey size ranged from 1 to 68 cm, but the majority of preys were from 2 to 30 cm. The prey characteristics and their state of digestion suggest that the common dolphin forages preferentially on small schooling, vertically migrating mesopelagic fauna in the surface layer at dusk and early night. The diet is taxonomically distinct from results obtained in neritic studies but is similar in terms of prey type and the corresponding feeding behavior.

Key words: Bay of Biscay, short-beaked common dolphin, *Delphinus delphis*, diet, feeding ecology, Northeast Atlantic, oceanic domain.

The short-beaked common dolphin (*Delphinus delphis*) occurs in all temperate, subtropical, and tropical oceans (Evans 1994). It is the most abundant delphinid in offshore warm-temperate waters in the Atlantic and the Pacific oceans (Perrin 2002). It lives and forages in herds of a few tens of individuals that can aggregate into groups of several hundred individuals. Common dolphins may forage to depths of 260 m but most dives are less than 100 m depth (Evans 1994; Perrin 2002). The diet of the common dolphin is well known in neritic areas from stomach content analysis of stranded individuals (*e.g.*, Ross 1984; Sekiguchi *et al.* 1992; Gonzales *et al.* 1994; Young and Cockcroft 1994; Dos Santos and Haimovici 2001; Meynier 2004; Santos *et al.* 2004). These studies show that, over continental shelves, the bulk of the diet consists of a combination of the locally most abundant species of small pelagic shoaling fish or, rarely, cephalopods. In contrast, nothing has been published on the diet and foraging behavior of the species in fully oceanic areas.

The Bay of Biscay may be divided into three habitats: the neritic area (continental shelf, depth < 200 m), the slope (200–2,000 m depth), and oceanic waters (>2,000-m depth) (Fig. 1). The continental shelf in this region extends more than 300 km from shore in the north and more than 50 km in the south and shows a species composition very different from the oceanic area. Indeed, in the neritic area, the top predator community is dominated by the short-beaked common dolphin, the common bottlenose dolphin (*Tursiops truncatus*), and some large demersal fish such as the hake (*Merluccius merluccius*) and the sea-bass (*Dicentrarchus labrax*). The intermediate trophic levels are dominated by various gadids, the horse mackerel (*Trachurus trachurus*), the sardine (*Sardina pilchardus*), the Atlantic mackerel (*Scomber scombrus*), and cephalopods such as sepiolids and loliginids (Quéro *et al.* 1989; Velasco *et al.* 2001). Because depths are limited, all these potential prey organisms are within the reach of dolphin predators day and night. Conversely, the oceanic top predator community is dominated by the albacore tuna (*Thunnus alalunga*), the swordfish (*Xiphias gladius*), the blue shark (*Prionace glauca*), the striped dolphin (*Stenella coeruleoalba*), and the common dolphin (Goujon 1996). The intermediate trophic levels are mainly composed of the small vertically migrating mesopelagic fish and cephalopod species that are concentrated at depth during the day, constituting the deep scattering layer, which moves to the surface layer at night for feeding (Roe *et al.* 1984). From stomach content analysis, the diet of common dolphins stranded along the French coasts of the Bay of Biscay has been found to consist only of neritic species, in particular sardine, anchovy (*Engraulis encrasicolus*), horse mackerel, and *Trisopterus spp* (Meynier 2004). Cadmium concentration in the kidney of bycaught oceanic dolphins has been found

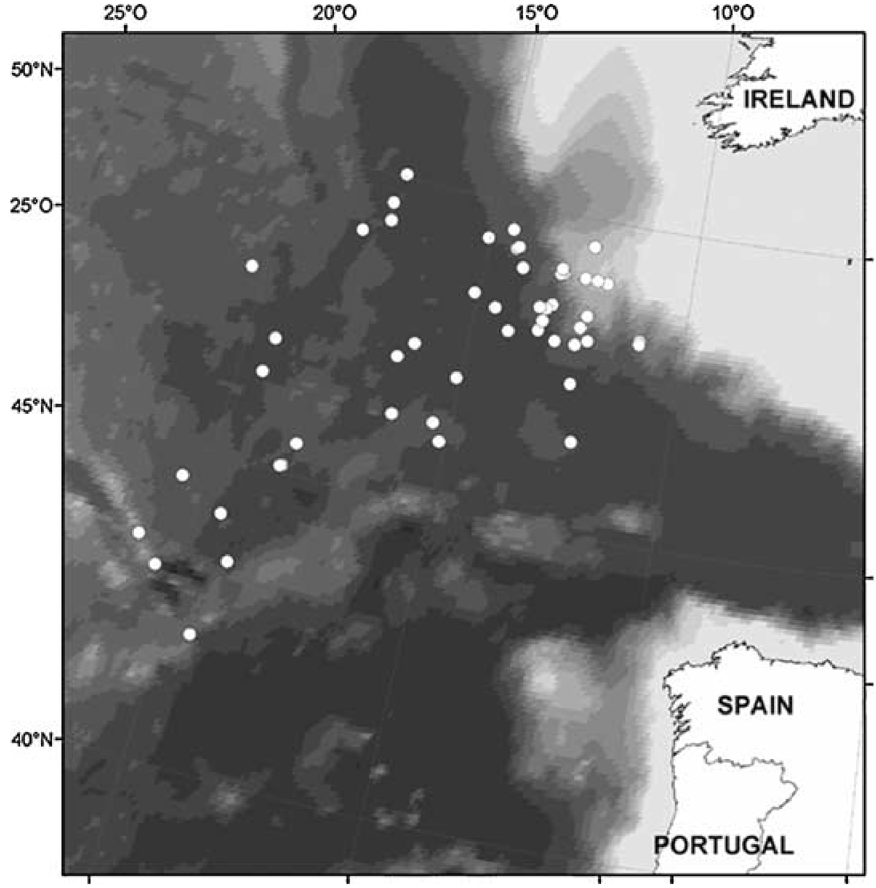

Figure 1. Sampling locations.

to be about four times higher than in stranded individuals partly because of diet differences (Lahaye *et al.* 2005). Hence, it is hypothesized that neritic and oceanic stocks of common dolphins are separated to some degree.

This study was based on the analysis of stomach contents of common dolphins bycaught in the French albacore tuna driftnet fishery in the oceanic Bay of Biscay. The purpose of the work was to describe the diet of common dolphins in the oceanic Bay of Biscay and to compare these between oceanic and neritic habitats in order to assess the species' variability in foraging strategy.

MATERIAL AND METHODS

Sampling

Stomachs were collected from sixty-three common dolphins bycaught in driftnets. Sampling was done by fishery observers from June–August 1992 and 1993, off the Bay of Biscay, from 39°N to 50°N and 10°W to 21°W (Fig. 1). Dolphins were caught at night in driftnets 2.5-km long with a vertical spread of 20 m. Body size of the sampled individuals ranged from 101 to 221 cm. The available material constituted 28 females, of which 3 were considered adults (body length > 190 cm, Collet 1981), 29 males, 7 of which were adults (body length > 200 cm, Collet 1981), and 6 individuals whose gender was not noted.

Stomachs were dissected onboard, ligatured, and stored deep-frozen (−20°C) in polythene bags awaiting further analysis.

Sample Analysis

Sample analysis was aimed at describing the diet in terms of prey occurrence, relative abundance, reconstituted 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 into a tray, and its wall weighed again to determine by difference the mass of the stomach content. The defrosted stomach contents were washed through a sieve of 0.2-mm mesh size. 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 remains with flesh attached. The items found were identified to the lowest taxonomic level using published guides (Lagardère 1971; Clarke 1986; Härkönen 1986) and our reference collection (ULR/CRMM).

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 and eyes for crustaceans) or odd structures (parasphenoïd for fishes, upper and lower beak and gladii for cephalopods, and carapace and telson for crustaceans). Diagnostic hard parts such as beaks, otoliths, and carapaces were measured with a digital vernier caliper (±0.02 mm) following established standards (Clarke 1986; Härkönen 1986). A random subsample of up to thirty diagnostic hard parts per prey species per stomach was measured.

Data Analysis

We first determined the prey individual body length and mass using relationships either from the literature (*e.g.*, Clarke 1986; Härkönen 1986) or from measurements performed on specimens in our reference collection. For cephalopods, the standard dorsal mantle length (DML) was used in the general description of the diet (Table 1); however, a total body length including arm length was derived from total length to mantle length ratios obtained from published illustrations of the corresponding species (Nesis 1987) and used in the figure representing overall prey size distributions, as it qualifies the prey size targeted by the dolphin (Fig. 2) better than DML. Prey size distributions were constructed both as the percentage by number and the percentage by mass contributed by each size class, because these two variables convey different information about the importance to the diet of prey of varying body lengths.

We then described the diet of the common dolphin computing the following index for each observed prey taxa: percent occurrence (%O; equation 1), relative abundance by number (%N; equation 2), and relative abundance by reconstituted biomass (%M; equation 3). We defined the occurrence of a given prey taxon as the number of stomachs in which the taxon was observed and the relative abundance by number as the number of items of the same taxon found in the sample set. The

Table 1. Diet composition of the common dolphin in the oceanic Bay of Biscay. %N is the percentage by number of the prey, %M the percentage reconstituted biomass. Length stands for standard length for fish, total length for cephalopods and total length without rostrum for crustaceans.

	Total composition (N = 32588, M = 138189.9)										Fresh fraction (N = 24703, M = 54308.1)		
		Composition by number		Length (mm)			Mass (g)		Composition by mass				
	% Occurrence	%N	95% CI	*n*	Mean ± SD	Range	Mean ± SD	Range	%M reconstituted	95% CI	% Occurrence	%N	%M reconstituted
Sternoptychidae													
Maurolicus muelleri	43.8	7.2	1.8–14	415	45.9 ± 9.3	8.4–62.7	0.8 ± 0.3	<0.1–1.7	1.3	0.3–3.8	43.8	9.4	3.3
Platytroctidae													
Platytroctidae und	3.1	<0.1	<0.1	4	186.0 ± 5.7	19.3–192.9	77.9 ± 8.8	67.8–88.8	0.3	0.0–0.9	3.1	<0.1	0.7
Chauliodontidae													
Chauliodus sloani	10.9	0.1	0.0–0.2	30	107.3 ± 19.1	85.9–156.6	15.2 ± 2.7	12.2–22.4	0.3	0.0–0.4	10.9	0.1	0.6
Stomiidae													
Stomias boa ferox	42.2	0.2	0.1–0.3	111	133.6 ± 26.5	90.1–278.1	13.1 ± 10.4	1.2–49.7	0.8	0.6–1.5	6.3	<0.1	0.1
Bathylagidae													
Bathylagus greyae	1.6	<0.1	<0.1	6	146.0 ± 10.8	132.9–158.7	21.2 ± 1.6	19.3–23.0	<0.1	0.0–0.2	1.6	<0.1	0.1
Bathylagidae und	3.1	0.1	0.0–0.1	26	82.6 ± 8.3	67.5–110.0	10.7 ± 1.1	8.7–14.2	0.2	0.0–0.6	3.1	0.1	0.3
Myctophidae													
Benthosema glaciale	51.6	4.4	2.6–26	603	33.4 ± 7.8	15.6–99.7	0.5 ± 0.5	0.1–8.1	1.5	0.7–4.2	51.6	11.3	2.7
Ceratoscopelus maderensis	34.4	0.3	0.2–0.6	142	56.3 ± 10.6	24.9–83.2	2.2 ± 1.3	0.1–7.2	0.2	0.1–0.3	34.4	0.4	0.4
Electrona risso	3.1	0.1	0.0–0.3	36	49.7 ± 9.3	35.7–75.7	3.7 ± 0.7	2.6–5.6	0.1	0.0–0.3	3.1	0.1	0.1
Lampanyctus spp	37.5	2.2	0.6–5	309	46.1 ± 18.3	24.6–134.8	1.2 ± 3.5	<0.1–22.8	0.7	0.2–2.7	37.5	2.3	1.2
Lobianchia gemellarii	18.8	0.2	0.1–0.6	116	36.0 ± 23.1	4.8–90.5	2.0 ± 3.1	<0.1–12.6	0.1	0.0–0.5	18.8	0.3	0.3
Myctophum puntatum	68.8	5.5	3.2–8.4	718	53.3 ± 16.9	18.3–89.4	2.6 ± 2.5	10.1–10.4	3.5	1.9–7.4	65.6	5.3	6.3
Notoscopelus kroeyeri	84.4	65.1	47.2–70.4	1412	45.5 ± 20.1	9.9–132.0	1.9 ± 3.9	<0.1–30.5	31.1	22.8–53.7	81.3	62.4	54.9
Symbolophorus veranyi	34.4	0.7	0.3–1.2	350	73.8 ± 18.1	32.9–126.8	7.0 ± 5.2	1.4–34.8	1.3	0.6–2.6	34.4	0.7	2.2
Myctophidae und	15.9	0.5	0.1–1.3	0			1.9		0.3	0.0–0.8	15.9	0.5	0.5
Paralepididae													
Macroparalepis affinis	10.9	0.1	0.0–0.2	40	214.2 ± 49.7	140.6–206.6	6.0 ± 2.2	3.5–10.1	0.1	0.0–0.3	10.9	0.1	0.3
Arctozenus risso	28.1	0.9	0.3–1.8	159	130.2 ± 27.1	43.3–215.3	3.0 ± 1.9	0.2–15.7	0.6	0.2–1.4	28.1	1.1	1.5
Paralepis coregonoides	4.7	0.5	0.0–1.3	79	153.3 ± 26.2	104.56–355.0	5.5 ± 9.8	1.3–128.6	0.7	0.0–1.9	4.7	0.7	1.5

Table 1. Continued

	Total composition (N = 32588, M = 138189.9)										Fresh fraction (N = 24703, M = 54308.1)		
		Composition by number		Length (mm)			Mass (g)		Composition by mass				
	% Occurrence	%N	95% CI	*n*	Mean ± SD	Range	Mean ± SD	Range	%M reconstituted	95% CI	% Occurrence	%N	%M reconstituted
Scomberesocidae													
Scomberesox saurus	29.7	1	0.4–1.5	252	185.8 ± 21.4	103.1–233.8	23.0 ± 4.7	9.7–36.7	5.5	3.4–10.8	9.4	0.1	1.2
Gadidae													
Micromesistius poutassou	1.6	<0.1	<0.1	1	14.7		18.4		<0.1	0.0–0.1	<0.1	<0.1	<0.1
Bramidae													
Brama brama	4.7	<0.1	0.0–0.1	7	235.3 ± 16.8	213.0–255.0	289.8 ± 20.5	262.3–314.0	1.5	0.0–4.9	4.7	<0.1	3.7
Chiasmodontidae													
Chiasmodontidae nid	4.7	<0.1	0.0–0.1	19	101.6 ± 10.8	81.6–118.4	8.8 ± 0.9	6.9–10.1	0.1	0.0–0.2	3.1	<0.1	0.1
Gempylidae													
Nesiarchus nasutus	6.3	<0.1	0.0–0.1	11	364.2 ± 90.3	185.0–437.5	32.9 ± 8.2	16.7–42.8	0.3	0.0–0.6	3.1	<0.1	0.2
Nomeidae													
Cubiceps gracilis	17.2	0.4	0.0–1.0	80	141.5 ± 5.7	125.6–154.5	46.4 ± 1.9	41.2–51.0	4.3	0.6–14	12.5	0.2	4.3
Und fish	20.6	0.4	0.1–0.9				6.5		0.7	0.1–2.3	20.6	0.2	0.5
Total fish	93.4	90.0							53.0		95.6	95.3	86.8
Ocythoidae													
Ocythoe tuberculata	1.6	<0.1	<0.1	5	14.8 ± 1.6	12.3–17.1	13.4 ± 3.5	8.1–18.7	0.1	0.0–0.2	1.6	<0.1	0.1
Octopoteuthidae													
Octopoteuthis sp	12.5	0.1	0.0–0.1	20	10.8 ± 3.8	6.0–21.0	24.8 ± 9.3	21.0–51.5	0.4	0.1–0.9	3.1	<0.1	0.1
Onychoteuthidae													
Onychoteuthis banksii	1.6	<0.1	<0.1	4	110.2 ± 6.4	102.0–120.0	48.2 ± 15.6	30.3–48.2	0.1	0.0–0.6	1.6	<0.1	0.2
Ancistroteuthis lichtensteini	50.0	0.5	0.2–0.7	147	58.5 ± 16.5	32.3–155.1	31.3 ± 65.5	1.0–726.7	3.6	2.4–6.8	10.9	<0.1	1.3
Gonatidae													
Gonatus steenstrupi	62.5	0.9	0.6–1.2	293	110.3 ± 39.2	29.0–351.9	50.7 ± 67.7	15.6–847.4	11.7	9.6–19.5	9.4	<0.1	0.8
Pholidoteuthidae													
Pholidoteuthis sp	3.1	<0.1	<0.1	2	89.5 ± 8.9	81.0–98.0	104.2 ± 10.3	93.9–114.6	0.2	0.0–0.5	<0.1	<0.1	<0.1
Histioteuthidae													
Histioteuthis reversa	37.5	0.5	0.2–0.8	160	22.5 ± 8.1	114.0–86.0	32.4 ± 13.5	16.3–158.9	3.9	2.2–7.4	18.8	0.3	<0.1
Histioteuthis corona	14.1	0.3	0.1–0.5	90	22.5 ± 7.2	11.8–61.0	39.3 ± 12.5	20.6–106.1	2.8	1.3–6.2	9.4	0.1	1.5

Table 1. Continued

	Total composition (N = 32588, M = 138189.9)												
		Composition by number			Length (mm)		Mass (g)		Composition by mass		Fresh fraction (N = 24703, M = 54308.1)		
	% Occurrence	%N	95% CI	*n*	Mean ± SD	Range	Mean ± SD	Range	%M reconstituted	95% CI	% Occurrence	%N	%M reconstituted
Brachioteuthidae													
Brachioteuthis riisei	70.3	2.9	1.6–4.4	45	43.3 ± 11.5	11.2–78.9	3.2 ± 1.1	0.8–8.5	2.1	1.5–3.9	53.1	2.3	3.1
Ommastrephidae													
Ommastrephidae und	1.6	<0.1	<0.1	1	143.4		212.6		0.2	0.0–0.6	<0.1	<0.1	<0.1
Chiroteuthidae													
Chiroteuthis sp	7.8	<0.1	0.0–0.1	10	63.8 ± 21.6	39.7–113.3	8.8 ± 10.3	1.2–37.1	0.1	0.0–0.2	<0.1	<0.1	<0.1
Cranchiidae													
Teuthowenia megalops	68.8	3.4	2.1–5.1	670	115.8 ± 26.6	51.0–253.0	20.2 ± 12.7	1.8–131.8	17.9	0.0–20.1	23.4	0.2	1.9
Und cephalopods	3.1	<0.1	0.0–0.1	0			29.7		0.3	0.0–0.9	<0.1	<0.1	<0.1
Total cephalopods	93.4	8.6							46.2		22.8	2.9	10.1
Hyperiidae													
Hyperiidae und	4.7	<0.1	0.0–0.1	1	8.7		<0.1		<0.1	<0.1	4.7	0.1	<0.1
Euphausiidae													
Meganyctyphanes norvegica	14.1	0.3	0.0–0.6	22	25.1 ± 3	18.0–32.3	0.2 ± <0.1	0.1–0.3	<0.1	<0.1	14.1	0.4	<0.1
Penaeidae													
Funchalia woodwardii	10.9	0.1	0.0–0.1	7	84.7 ± 14.5	43.4–96.7	4.8 ± 3.1	0.1–9.2	0.1	0.0–0.2	6.3	<0.1	0.1
Sergestidae													
Sergestes arcticus	31.3	0.6	0.2–1.2	99	44.5 ± 5.7	31.6–65.4	6 ± 2.2	2.9–17.4	0.9	0.5–2.0	31.3	0.8	2.0
Sergia robusta	3.1	0.1	0.0–0.2	13	59 ± 11.2	47.9–84.4	1.4 ± 0.7	0.9–3.3	<0.1	0.0–0.1	3.1	0.1	<0.1
Pasiphaeidae													
Pasiphaea multidentata	9.4	0.2	0.0–0.4	30	99 ± 7.5	85.5–114.7	6.9 ± 0.7	5.7–8.6	0.3	0.1–0.7	7.8	0.2	0.4
Oplophoridae													
Acanthephyra purpurea	7.8	0.2	0.0–0.5	46	66.7 ± 10	48.5–95.3	2.8 ± 1.6	1.0–10.1	0.1	0.0–0.5	7.8	0.3	0.3
Systellapsis debilis	1.6	<0.1	<0.1	1	30.3		0.5		<0.1	<0.1	1.6	<0.1	<0.1
Total crustaceans	45.9	1.4							0.8		46.5	1.7	3.2

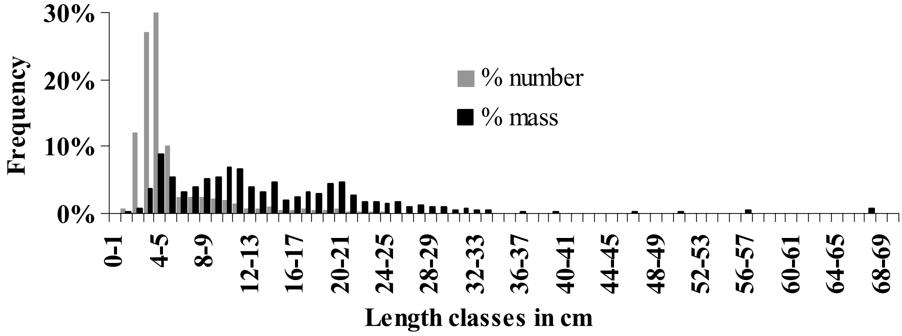

Figure 2. Prey length distribution, all species combined. Lengths are standard length for fish, total length for cephalopods, and total length without rostrum for crustaceans.

reconstituted biomass of a taxon was the product of the number of individuals in each stomach and its average reconstituted body mass, summed throughout the sample set.

$$\%O_i = (n_i/N)*100, \tag{1}$$

where n_i is the number of stomachs in which prey taxon i was found and N is the total number of stomachs.

$$\%N_i = (x_i/X)*100, \tag{2}$$

where x_i is the number of prey i found in the whole sample set and X is the total number of prey.

$$\%M_i = \left(\sum_j x_{i,j} * \bar{Y}_{i,j} \middle/ \sum_i \sum_j x_{i,j} * \bar{Y}_{i,j}\right)*100, \tag{3}$$

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

To minimize overestimation of prey resistant to digestion (*e.g.*, cephalopod beaks, Bigg and Fawcett 1985), each prey item was scored on a scale specific to the main prey type (fish, cephalopods, crustaceans), according to their state of decomposition. This allowed us to determine a "fresh fraction" that would provide a better representation of the composition of the ingested prey than the total stomach content. The diet descriptive indices (occurrence, relative abundance, and reconstituted mass) were calculated separately for the total content and the fresh fraction.

To account for uncertainty due to sampling, nonparametric 95% confidence intervals (95% CI) for the compositions by number (%N) and by reconstituted biomass (%M) were generated by bootstrapping (Reynolds and Aebischer 1991). The bootstrapping routine was written using the *R* software (Ihaka and Gentleman 1996). Random samples were drawn with replacement, and the procedure was repeated 300 times.

An explanatory diagram, the modified Costello diagram (Costello 1990, modified by Amundsen *et al.* 1996), was built. This tool is used to characterize graphically the diet variability of a predator by plotting prey-specific importance for each prey taxa (%P; equation 4) against frequency of occurrence (%O) on a two-dimensional graph. In the upper left corner of the diagram, each prey species occurs rarely but accounts for a large proportion of the diet when present; hence, if most prey species concentrate here, the predator is characterized by high between-individual variability. In the upper right corner of the diagram, a single prey is present in all individuals and accounts for the total diet. In this case, all predator individuals rely on the same resource. In the lower right corner, prey species occur at high frequency but each only accounts for a small proportion of the food when present. This suggests high within-individual variability in prey preference and low between-individual variability because all individual predators prey upon the same species assemblage. Finally, in the lower left corner of the diagram, individual prey species display both low occurrence and low relative importance when present. If most prey species concentrate here, the predator shows both within- and between-individual variability.

$$\%P_i = \left(\sum\nolimits_i M_i \Big/ \sum\nolimits_{ti} M_{ti}\right) \times 100, \tag{4}$$

where M_i is the contribution (by mass in this study) of prey taxa i (at species level, in this study) to stomach content, and M_{ti} is the total stomach content weight in only those individual dolphins where prey i was present.

RESULTS

General

The analysis was conducted on the 61 nonempty stomachs. The total mass of food remains was 33,196 g, which represented an average of 535 g per sample. In general, food remains were in fairly digested condition, being mostly composed of hard parts (beaks, bones, and exoskeletons) with little flesh attached.

Total Diet Composition

As many as 32,588 prey items were identified and accounted for a total reconstituted biomass of 138,190 g (Table 1). A total of 29,329 fishes were found, belonging to 36 species and amounting to 73,241 g of reconstituted mass. Cephalopods were represented by 2,803 individuals of twelve different species for a total reconstituted mass of 63,844 g. Crustaceans comprised a tiny share of the diet with only 456 individuals belonging to eight species and accounting for only 1,106 g of the reconstituted biomass.

Fish occurred in 93% of the stomachs. They represented 90% of the diet by number and 53% by mass (Table 1). They were largely dominated by the myctophid *Notoscopelus kroeyeri*, which occurred in 84% of the stomachs and accounted for 65%N and 31%M of the diet. Four other species of fish were significant: *Maurolicus muelleri* (44%O, 7%N, 1%M), *Benthosema glaciale* (52%O, 4%N, 2%M), *Myctophum punctatum* (69%O, 6%N, 4%M), and *Scomberesox saurus* (30%O, 1%N, 6%M).

Cephalopods were found in 93% of the samples (Table 1); their contribution to the diet was of 9%N and 46%M. They were mostly represented by four major species:

Ancistroteuthis lichtensteini (50%O, 1%N, 4%M), *Gonatus steentrupi* (63%O, 1%N, 12%M), *Brachioteuthis riisei* (70%O, 3%N, 2%M), and *Teuthowenia megalops* (69%O, 3%N, 18%M).

Crustaceans were found in 46% of the stomachs. They made 1%N of the diet and 1%M. None of the species constituted a significant part of the diet.

Fresh Diet Composition

The fresh fraction differed significantly from the total diet. Indeed, the proportion of fish increased to 95%N and 87%M, while the proportion of cephalopods decreased to 3%N and 10%M presumably due to longer retention of their remains in the stomach. The proportion of crustaceans remained stable: 2%N, 3%M. At the species level, the fish *N. kroeyeri* was even more prevalent than in the total diet (62%N, 55%M). *M. muelleri* (9%N, 3%M), *B. glaciale* (11%N, 3%M), and *M. punctatum* (5%N, 6%M) remained important, but the proportion of *S. saurus* decreased (<1%N and 1%M). As for the cephalopods, only *B. riisei* was found to remain a noticeable prey (2%N, 3%M).

Length Distribution

The overall prey size range was between 1 cm and 68 cm (Fig. 2). The prey size distribution by number showed a mode at 4–5 cm. Eighty percent of the individuals were concentrated in classes ranging between 2 cm and 6 cm and the frequency of individuals in classes larger than 20 cm was almost nil. The distribution by mass was more evenly spread, with 95% of the mass corresponding to sizes between 3 cm and 30 cm.

At prey species level (Fig. 3), the length distribution of the myctophid *N. kroeyeri* ranged from 0 cm to 14 cm. It showed a mode at 4–5 cm and 89% of the individuals ranged from 2 cm to 6 cm. The cephalopod *T. megalops* ranged from 7–40 cm, but 99% of the individuals ranged from 9 cm to 30 cm with a mode at 20–21 cm. *G. steenstrupi* ranged from 5 cm to 68 cm, but 98% ranged from 5 cm to 34 cm with a mode at 19–20 cm.

Diet Variability

The Costello diagram splits the different prey species into three groups (Fig. 4). Forty-five species were seldom observed in the stomachs (Occ $< 30\%$) and always in small proportions when present ($P < 20\%$). Fourteen species were categorized as being common as they were observed fairly often ($30\% <$ Occ $< 75\%$) but in small proportions ($P < 20\%$). A single dominant prey species was found, *N. kroeyeri*, which was almost always observed (Occ $= 84\%$) and comprised a high percent mass when present ($P = 38\%$).

DISCUSSION

Limitations of the Study

This work provided the first quantitative analysis of the food of the common dolphin in a fully oceanic habitat. Limitations of the study arose both from the sampling

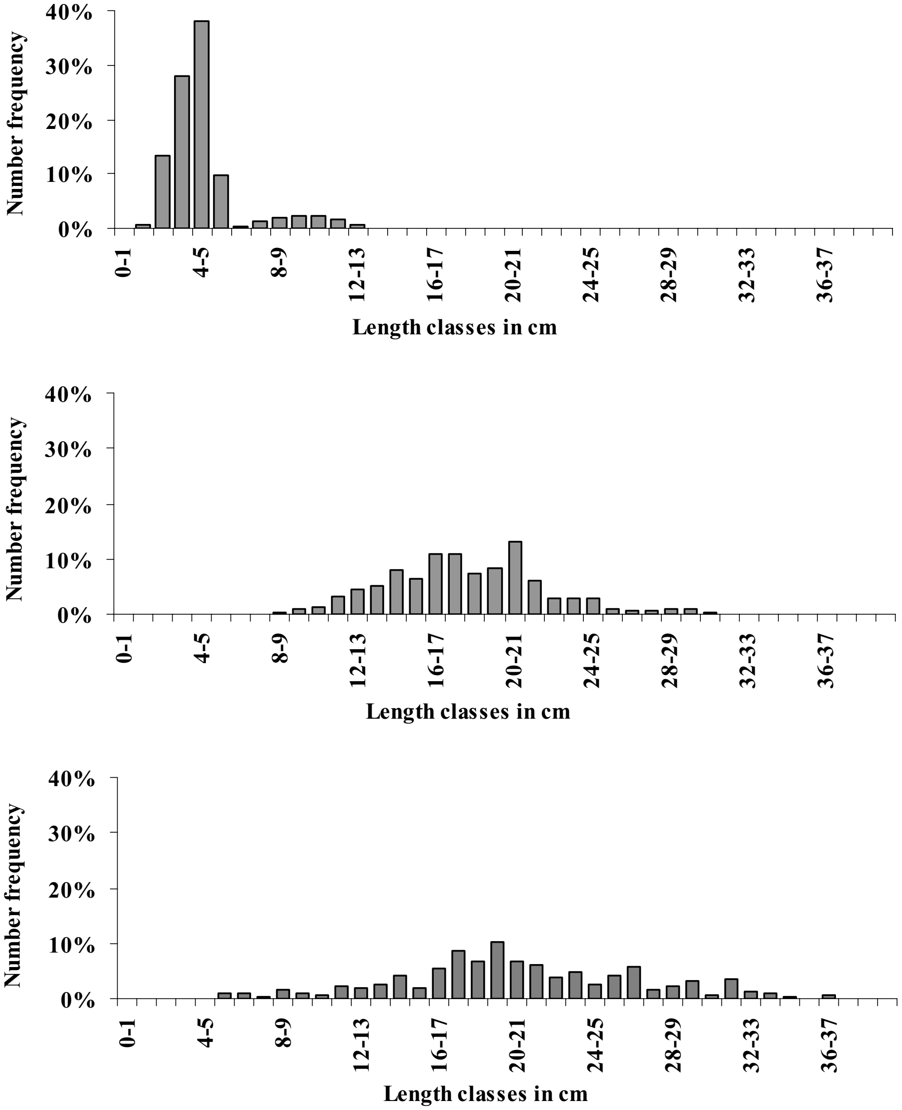

Figure 3. Length distribution of main prey: (A) *Notoscopelus kroeyeri*, (B) *Teuthowenia megalops*, (C) *Gonatus steenstrupi*. Lengths are standard length for fish and dorsal mantle length for cephalopods.

and the analytical procedures. Because samples came from dolphins bycaught in driftnets, they were biased toward younger animals, because this age category gets caught more often in driftnets than adults do (Goujon 1996). Furthermore, sampling took place in only two consecutive years and the sampling pattern was constrained by the operating scheme of the fishery (at night, from June to September), which obviously limits the potential for investigating temporal variations of the diet. Some other

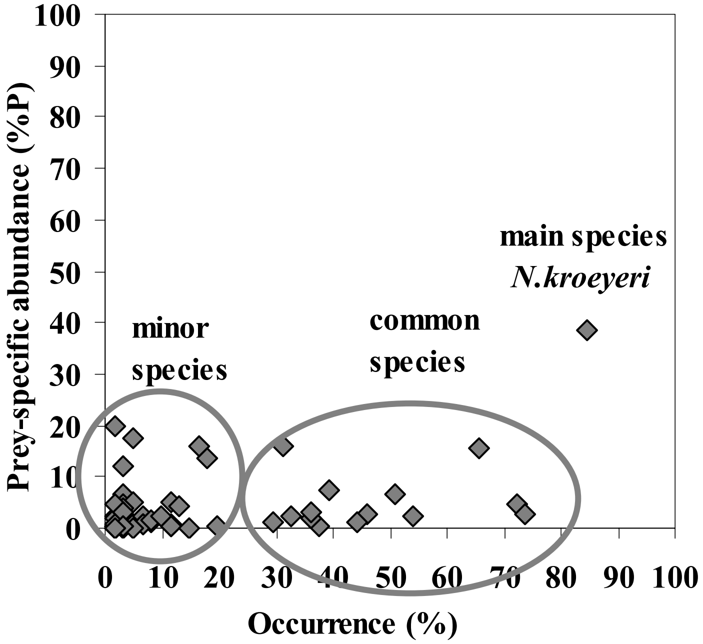

Figure 4. Costello diagram, a scatterplot of all prey species according to their occurrence and their importance by mass.

limitations are inherent to studying the diet of marine top predators by analyzing stomach contents and these are described in detail by several authors (*e.g.*, Bigg and Fawcett 1985; Jobling and Breiby 1986). These limitations include prey species-specific gut transit times and digestibility rates, which can lead to substantial biases in prey composition. To cope with this difficulty, in the present work the digestion condition of each prey remain was scored, which allowed a fresh, supposedly less biased, fraction to be separated from more digested material. We assumed here that the composition of the fresh fraction gave a better picture of the nocturnal feeding habits of the common dolphin. Finally, another difficulty in interpreting the observed diet is the paucity of contextual information on the ecology of the prey community, with only one significant work in the area (Roe *et al.* 1984), and the absence of *in situ* information on the common dolphin activity pattern and its preferred depth range.

Comparison with Neritic Areas

Many works have been published on the diet of the common dolphin in neritic areas, but only a few are based on a large sample size and attempt to quantify the diet both by number and by mass at the species level (Table 2). In all these studies, fish largely dominated the diet (>85% by number and by mass), but the most important prey families either by mass or by number differed largely among study areas and habitats. They were gadids, gobiids, and clupeids in Galicia; clupeids, scombrids, pomatomids, sparids, and loliginids in South Africa; and gadids, clupeids, engraulis, and carangids in the neritic Bay of Biscay (references in Table 2). The dominant species

Table 2. Diet composition in three neritic areas. %N is the percentage by number of the prey, %M the percentage reconstituted biomass. ND stands for no data. Only prey making more than 5% by mass or number are presented.

	Santos *et al*. 2004 – Galician coast (Spain) – N = 414 – strandings and accidental catches			Young and Cockcroft 1994 – Southeastern South Africa – N = 297 – accidental catches			Meynier 2004 – Neritic Bay of Biscay – N = 71 – strandings		
	%Occurence	%N	%M	%Occurence	%N	%M	%Occurence	%N	%M
Clupeidae	83.5	7.5	25.8	69.4	49	48.9	69.8	11.8	40.3
Engraulidae							56.3	16.9	11.7
Myctophidae				5.2	10.4	0.3			
Gadidae	71.2	30.6	40.4				71.8	19.8	13.9
Pomatomidae				14.5	2.1	8.7			
Carangidae	42.1	3.2	8.8				70.4	15.5	18.3
Sparidae				12.1	6.8	9.4			
Scombridae				13.1	1.8	13.5	23.9	0.6	6.2
Gobiidae	46.5	26.9	2.7				59.2	24.8	1
Atherinidae	21.5	8.0	8.8						
Total fishes	99	87.7	91.5	ND	86.3	89.8	98.6	91.5	95.2
Sepiolidae							46.5	6.3	1.3
Loliginidae				29.3	9.3	8.4			
Total cephalopods	72.9	10.8	8.5	ND	12.2	11.2	62	8.5	4.8
Total crustaceans	32.7	1.5	<0.1	ND	ND	ND	1.4	<0.1	<0.1

may belong to many different taxa depending on regions and habitats, but they share the characteristic of being abundant pelagic shoaling species. Hence, the diet of the common dolphin in the oceanic Bay of Biscay is taxonomically completely different from previous results obtained in neritic studies; however, it is very similar in terms of prey profile, which could be defined as small shoaling pelagic prey, most often fish and occasionally cephalopods, available in the epipelagic water layer. Furthermore, within the Bay of Biscay, the complete diet differentiation between the neritic and oceanic common dolphins is in line with what has been suggested from kidney cadmium accumulation rates (Lahaye *et al.* 2005).

Foraging Behavior

The present results have highlighted three main features of common dolphin foraging behavior in the oceanic Bay of Biscay. First, most of the prey species consumed, and in particular the main ones—the myctophids *N. kroeyeri*, *B. glaciale*, and *M. punctatum*, the sternoptychid *M. muelleri*, and the cephalopods *A. lichtensteini*, *G. steentrupi*, *B. riisei*, and *T. megalops*—are small schooling species. This characteristic is consistent with the morphology and feeding behavior of this predator. Indeed, this small delphinid has a long narrow rostrum well adapted to swallowing entire prey by suction feeding combined with seizing of the prey with the teeth (Berta and Sumich 1999). Fresh prey remains, in particular crustaceans, were observed with clear teeth marks on the body. Furthermore, as the common dolphin forages in groups (*e.g.*, Clua and Grosvalet 2001), preying on shoaling species is probably the most energetically profitable foraging tactic (Götmark *et al.* 1986). Other top predators known to feed on pelagic shoaling resources are also cooperative hunters (*e.g.*, Götmark *et al.* 1986 in gulls; Similä and Ugarte 1993 in killer whales,' and Tremblay and Cherel 1999 in penguins).

Second, most of the species consumed by the common dolphin in the oceanic Bay of Biscay belong to the small mesopelagic fauna that migrates to the surface at night. For air-breathing top predators that forage on such prey, the challenge is either to repeatedly dive during the day deeply enough to reach the dense layer of mesopelagic prey, or to exploit the same assemblage at night at shallower depth where the shoals are less compacted because they are actively looking for their own food (Roe *et al.* 1984). Here, most prey remains were highly digested and the stomach content did not contain much fresh material. From digestion time of small prey organisms observed in various predators (Bigg and Fawcett 1985; Olson and Boggs 1986) and if one considered that postmortem digestion would be gradually stopped as a result of digestive enzymes, pectin, and others, not being renewed after death, it appears that the dominant digestion condition observed in our samples would have been reached about 6 h after ingestion; because the samples were all collected during the night, it would suggest that most of the foraging activity took place at dusk or early night, when deep sea organisms move up to the surface layer. Interestingly, prey items in fresh condition were rare, suggesting that the middle of the night might not be as favorable for foraging as dusk and early night are. This might result from prey organisms being less aggregated when they forage than when they migrate up to the surface layer. This result is supported by the limited telemetry data on the common dolphin indicating that the species forages essentially in the epipelagic water layer and preferentially in the 100-m depth (Perrin 2002). Furthermore, Evans (1994), based on radio-telemetric studies and analysis of stomach contents, has shown a similar behavior off California where common dolphin start feeding at dusk. However, many more telemetry studies would be necessary to fully understand the foraging behavior and the daily activity rhythm of the species; it would notably lift the uncertainties related to the interpretation of digestion condition of prey found in stomach contents.

The third characteristic of the common dolphin diet in the oceanic Bay of Biscay is its strong interindividual consistency, with the lantern fish *N. kroeyeri* as a widespread pivotal species complemented by a mixture of small species that occur slightly less frequently in the stomachs but, above all, represent a smaller share of the food by mass (Fig. 4). Small mesopelagic species migrate in mixed-species shoals to the surface at night, which seem to be dominated in the study area by the myctophid *N. kroeyeri* (Roe *et al.* 1984; Quéro *et al.* 2002; Fock *et al.* 2004). Hence, it seems that in this particular case, the common dolphin selects a particular prey type (*i.e.*, small shoaling migrating mesopelagic species) rather than a particular prey species, and that the proportion of the different prey species in its diet reflects their abundance in the mixed-species shoals. This is in contrast to what is observed in the neritic Bay of Biscay, where the common dolphin shows a high proportion in its diet of the high-energy sardine, which is not the dominant small shoaling pelagic species of the area, and is being dominated by the less energetic horse mackerel (Meynier 2004).

To conclude, short-beaked common dolphins in the Northeast Atlantic forage both in oceanic and neritic habitats, preying on taxonomically distinct prey assemblages, but with similar prey profiles: small aggregating species available in the epipelagic layer. Additionally, the complete absence of overlap in prey composition (this study and Meynier 2004), together with the distinct rates of cadmium accumulation (Lahaye *et al.* 2005), suggests that the groups of dolphins forage in only one of the two main habitats, oceanic or neritic, rather than regularly switching back and forth. Other delphinid species have been found to be able to forage both in neritic and in oceanic areas. In the Bay of Biscay, the striped dolphin is mainly observed in the oceanic area where it preys on the small migrating mesopelagic fauna (Ringelstein *et al.* 2006), as does the common dolphin. However, the species is sometimes found on the continental shelf of the Bay of Biscay where it consumes essentially small demersal fish. In this case, the individuals involved clearly moved between oceanic and demersal neritic habitats to forage (Spitz *et al.* 2006). In neritic areas, the bottlenose dolphin prefers large demersal fish (*e.g.*, Barros and Odell 1990; Barros *et al.* 2000; Santos *et al.* 2001), but in oceanic areas, it seems to also prey on the small migrating mesopelagic fauna (Mead and Potter 1990; Van Waerebeek *et al.* 1990). Hence the striped and the bottlenose dolphin switch prey types as they change foraging but the common dolphin seems to have a more stable prey preference and foraging strategy among geographic areas.

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