J. Mar. Biol. Ass. U.K. (1999), **79**, 531–540
Printed in the United Kingdom

Diet of common dolphins, *Delphinus delphis*, off the Portuguese continental coast

M.A. Silva

Instituto da Conservação da Natureza, Rua Ferreira Lapa 29,4°, 1150 Lisboa, Portugal. E-mail: mop32660@mail.telepac.pt

Diet of common dolphins off the Portuguese coast was studied based on the examination of stomach contents of 50 stranded and incidentally caught animals. The relative importance of each prey species was assessed through occurrence, numerical and biomass indices. Common dolphins preyed on a large variety of items but four fish and two cephalopod species appeared to form the basis of their diet. Overall, sardine *(Sardina pilchardus)* was the most important prey, as given by all the indices used to measure prey relative importance. Although common dolphins preyed mostly on pelagic spccics, they seemed able to explore habitats with distinct features and employ various foraging strategies. A comparison between the diet of dolphins of different sex and size groups was not indicative of major differences. Common dolphins incidentally caught in fishing nets had taken a higher proportion of sardines, the target species of the fishery.

INTRODUCTION

The common dolphin (*Delphinus delphis* L.) is one of the most widely distributed cetaceans, inhabiting all temperate, subtropical and tropical seas (Evans, 1982). It is a pelagic species that occurs mainly over the continental shelf; approximately around the 100-200 m depth contour, or over areas with prominent bottom topographic features (Evans, 1982). Along the Portuguese coast, the common dolphin occurs in high numbers (Sequeira et al., 1997), particularly in the northern and central regions.

Common dolphins are known to feed mainly on small epipelagic fishes, although cephalopods are also important food items (Collet, 1981; Desportes, 1985; Pascoe, 1986; Young & Cockcroft, 1994). Their diet seems to change with geographical areas and according to seasonal fluctuations in prey abundance and distribution. Common dolphins off Natal (South Africa) appear to rely on a variety of fish and cephalopod species, although five major prey items have been identified. Overall, South African pilchard *(Sardinops ocellatus* L.) and *Loligo uulgaris reynaudii* (Orbigny), were the most important fish and squid prey species, respectively (Young & Cockcroft, 1994). In British waters, movements of common dolphins have been related to Atlantic mackerel *(Scomber scombrus* L.) and herring (*Clupea harengus* L.) concentrations (Evans, 1980) and Pascoe (1986) found remains of mackerel, clupeids (probably *Sprattus sprattus* L.) and one ommasrrephid squid *(Todaropsis eblanae* Ball) in the stomach contents of two common dolphins caught off Plymouth. Common dolphins off the French coast prey mostly on gadids, with a preponderance of *Trispterus* spp. and blue whiting *(Micromesistius poutassou* Risso) (Collet, 1981; Desportes, 1985).

According to Clarke (1986a), studies on the feeding habits of cetaceans can be used to improve knowledge on both predator and prey biology; information on prey distribution and habitat can provide some insight on cetacean distribution, movements, feeding behaviour and trophic relationships. Furthermore, the opportunistic feeding behaviour exhibited by common dolphins in different geographic regions (Collet, 1981; Young & Cockcroft, 1994) imply that their diet is likely to reflect the fish and cephalopod composition of the area. Hence, dietary studies can also be used to monitor the distribution and seasonal fluctuations in the relative abundance of dolphin prey.

In spite of being one of the most common cetacean species found off rhc Iberian and French Atlantic coasts, There is a remarkable lack of information on the diet of common dolphins in this area of the Atlantic, and most of the information comes from unpublished reports. This paper provides data on the feeding habits of common dolphins, stranded or incidentally caught in fishing nets, off the Portuguese continental coast. In addition to presenting a qualitative description of the diet, the relative importance of prey species is assessed through frequency of occurrence and numerical and biomass indices. Differences in the diet of stranded and incidentally captured common dolphins and between dolphins from distinct sex and six-classes are also examined. Foraging behaviour of common dolphins off the Portuguese coast is discussed based on prey habitat and behaviour.

MATERIALS AND METHODS

Between January 1987 and September 1997, the stomach contents of SO common dolphins were examined. Figure 1 shows the approximate location of the strandings and the position where dolphins became entrapped in fishing nets. Some of the results presented in this study were retrieved from Silva & Sequeira (1997) and re-analysed together with more recent data. Dolphins were necropsied according to the European Cetacean Society dissection protocol (Kuiken & Garcia Hartmann, 1993) and carcasses of stranded animals were checked for signs of net entanglement.

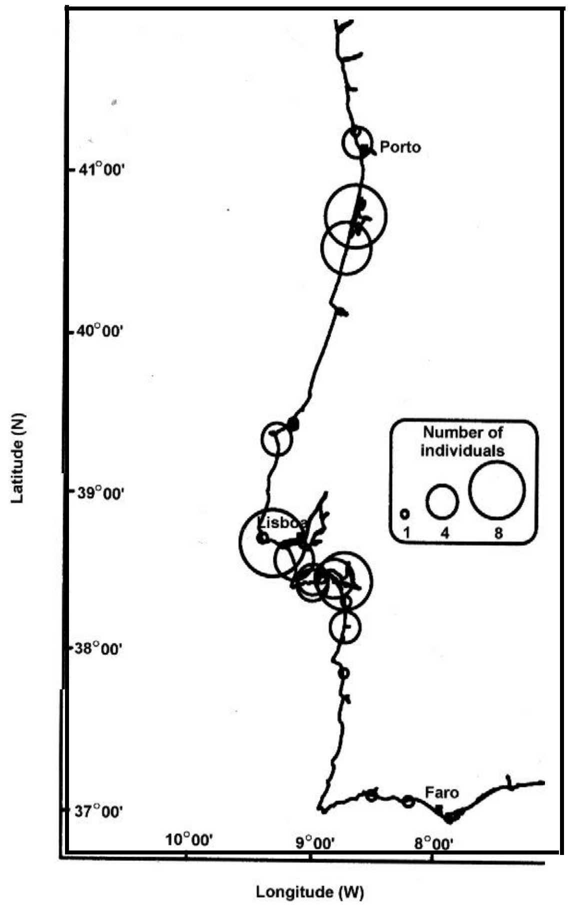

Figure 1. Map showing the approximate location of thr strandings and incidental catches of 50 common dolphins examined in this study. The number of individuals occurring in each location is proportional to the area of the circle.

The whole stomach was collected and frozen for later examination in the laboratory. Samples were thawed and washed through a l-mm sieve in order to separate hard parts from the remaining flesh. Although rarely found, intact prey were immediately identified, measured and weighed, and preserved in 5% formalin after removal of their otoliths or beaks for comparative studies. Otoliths, vertebrae and other skeletal elements were stored dry and cephalopod mandibles (beaks) were kept in 70% ethanol. All prey remains were identified to the lowest possible taxonomic level. Otoliths and fish bones were identified using published guides (Härkönen, 1986; Watt et al., 1997) and a reference collection prepared using specimens caught off the Portuguese coast, either sampled during research fishing operations or bought in a local market. Cephalopod beaks were identified using reference collections and according to Clarke (1986b). The minimum number of a fish species in a stomach was determined by the maximum number of either left or right otoliths added to half of the otoliths for which side could not be determined, or the maximum number of each vertebral or bone type. Similarly, the maximum number of upper or lower beaks was used to estimate the minimum number of cephalopods ingested.

Reconstruction of the original dimensions and weight of fish and cephalopod prey species was based on measurement of hard remains. Otoliths, vertebrae and cephalopod beaks were measured to the nearest 0.02 mm under a binocular microscope fitted with an eye-piece graticule. To avoid errors associated with reduction in otolith size due to erosion by stomach gastric acids only undamaged otoliths were used. When more than 30 otoliths, vertebrae or beaks were present in a sample a random subsample of 30 was measured. In order to assess the relative importance by weight of fish prey species, regressions relating fish length and wet weight to otolith or vertebral dimensions were used. For those fish species which could not be distinguished on the basis of otolith or bone structure, regressions established for the genus or family (with data from several species pooled) were used. The contribution in weight of those fish species for which no regression equations could be found was calculated using a mean estimated weight value available in the literature. For Atlantic anchovy *(Engraulis encrasicolus* L.) data were derived from Wiirtz & Marrale (1993) and for seabreams and black sea. mullet (*Liza ramada* Riso) from Cockcroft & Ross (1990). This procedure is unlikely to introduce any significant bias in the overall estimated weight, since the contribution of these species is almost negligible (taken together they only made up 0.73% of the total number of prey). Regression equations for sardine (*Sardina pilchardus* Walbaum), blue whiting, pouting (*Trisopterus luscus* L.), European hake *(Merluccius mcrluccius* L.), snipefish (*Macroramphosus* spp.), Atlantic mackerel, chub mackerel (*S. japonicus* Houttuyn), Atlantic mackerel/chub mackerel *(Scombcr* sp.) and *Trachurus* spp. are given by J.P. Granadeiro & M.A. Silva (unpublished data). Fish weight-otolith length relationships for the remaining species are given in Härkönen (1986). When available, regression equations calculated for the cephalopods of the Iberian coast were chosen. Dorsal mantle length and wet weight were estimated from hood lenqth of sepiid and sepiolid lower beaks. For the remaining cephalopods rostra1 length of lower beaks was measured (Clarke, 1986b; Pérez-Gándaras, 1986). When identification to species level was not possible, cephalopod weight and length were estimated by using regressions available for the genus or family. In stomachs where prey hard remains were too eroded to allow reliable measurements or when there were not any measurable structures available, a mean individual weight (MIW) (McKinnon, 1994) was computed for each species. The MIW corresponds to the mean of the estimated weights of the individuals of a given prey species found in all the stomachs examined. The total weight of a prey species in a dolphin stomach was determined as the number of prey individuals identified in that stomach multiplied by the MIW value calculated for the species. The relative importance of each food item in the diet was expressed as the percentage number (%N) and percentage weight (%W) of that prey in relation to the total estimated number and weight of prey and the percentage number of stomachs in which it occurred (%F).

Diet composition, prey diversity (measured as the number of different prey species) and size of prey consumed were used to investigate whether there were differences in the diet of stranded and incidentally caught dolphins and in the diet of dolphins of different sex and size-classes. Only data on sardine length was used to assess differences in the size of prey consumed, since using several prey species with very distinct size ranges would fail to provide a precise indication of the variation of prey size between groups of dolphins. Sardine was chosen because it was found in numbers large enough to allow for statistical comparisons.

Dolphins were assigned to one of two classes-mature or immature--according to their size. Males and females were classified as mature when they were at least 200 and 190 cm length, respectively, which corresponds approximately to the length at the onset of sexual maturity determined for common dolphins of the Portuguese coast [personal observations). Fish nomenclature and classification of fish behaviour and habitat followed Whitehead et al. (1984, 1986a,b). Classification of cephalopod behaviour and habitat followed Guerra (1992).

Nonparametric statistical procedures were used after rejecting the hypothesis of normality and homogeneity of variances of the data (Kolmogorov-Smirnov and Levene tests, respectively). Spearman rank correlation (r_s) was used to test for relationships between dolphin size and prey diversity, number of prey individuals ingested and prey size. Frequencies of occurrence of prey species in the diet of common dolphins were compared through contingency tables, using either the Fisher exact test, in the case of two-dimensional contingency tables, or the χ^2-test for the three-dimensional tables. Mann-Whitney U-tests (MWU) and two-way analyses of variance (ANOVA) were used to test for differences in the diet of dolphins from different sex and size-classes. Statistical procedures followed Zar (1996).

RESULTS

Homogeneity in the dirt of dolphins sampled in different areas (northern, central and southern) and seasons (winter and summer) was investigated using MWU and Krusk-Wallis analyses of variance (ANOVA). No significant differences were found in any of the studied variables: prey diversity (areas: ANOVA, $H_{(2,42)}=0.47$, *P>O.5; seasons:* MWU, Z=O.39, N=42, P>O.5), length of sardines consumed (areas: MWU, Z=l.88, N=30, *P>O.O5; seasons:* MWU, Z=O.35, N=30, *P>O.5);* percentage weight of sardines (areas: ANOVA, $H_{(2,42)}=5.15$, *P>O.O5; seasons:* MWU, Z=O.29, N=42, *P>O.5)* and relative proportion of fish and cephalopods in the diet (areas: ANOVA, $H_{(2,42)}$ = 1.39, *P>O.l; seasons:* MWU, Z= -0.32, N=42, P>O.5). Consequently, pooling data from different locations and seasons was considered appropriate since it should not introduce any significant bias.

Prey species and their relative importance in the diet

Of the 50 stomachs examined 84% (N=42) contained traces of food items. Table 1 presents the absolute and relative number, frequency of occurrence and weight, of each prey species identified in the stomachs of common dolphins. A total of 3015 prey were retrieved from the 42 stomach contents analysed with a maximum of 341 individuals found in a single stomach. Twenty-seven different fish species belonging to 18 families and eight cephalopod species from seven families, were identified. The maximum number of different fish or cephalopod species found in a single stomach varied from one to 12 but only 26% of the dolphins had rakcn more than seven different prey items.

Fish was the most important prey group, accounting for 83% of the total number of prey items taken and occurring in 97.6% of the stomachs examined (Table 1). Cephalopods were only found in 22 of the 42 stomach contents that contained food remains and comprised 17% in number of prey ingested. Fish was also the most important prey group on a weight basis, representing over 92% of the total weight. Six different fish items (sardine, blue whiting, sand smelts *(Atherina* sp.), *Trachurus* and scomhrid species) made up almost 84% of the total estimated weight. Overall, sardine was the most important prey species, occurring in 81% of the stomachs and representing 27.4% of the total number of prey taken and 43.4% of the estimated weight. Loliginids were the dominant cephalopod group both in number and on a weight basis. Eleven prey species occurred just once in all the stomachs examined and together represented 1.4% of all the individuals ingested and 1.3% of the total weight.

Figure 2 shows the relative importance (in number, frequency of occurrence and weight) of prey families. The Clupcidae, represented by a single species-sardine, dominated the diet of common dolphins, illustrating once more the preponderance of this prey species. Gadids and loliginids were also important items in the diet, accounting for 15.8 and 6.3%, respectively, of the estimated weight.

Prey size

Average length and weight of prey species of common dolphins are represented in Table 2. This table only includes species for which dimensions were computed directly from the available regression equations. The size range of prey consumed by common dolphins off the Portuguese coast was highly variable. Overall, average length of fish taken was 146 ± 39.5 mm (N=912) and their mean estimated weight was 27.5 ± 21.2 g (N=912), with 90% of the individuals ingested weighing less than 50g. Average mantle length of cephalopods was 43 ± 35.8 mm (N=315) and over 80% of the cephalopods ingested weighed less than 8 g (mean weight=9.7 f26.9 g, N=315).

Prey habitat and behaviour

Table 3 presents the classification of common dolphin prey species according to their behaviour and habitat characteristics. Pelagic species were present in most of the stomachs examined (90.5%) and accounted for 69.9%, in weight, of all the items taken. However, the importance of pelagic prey in the diet is strongly influenced by the contribution of sardine to this group. Frequency of occurrence of henthic, mesopelagic and bentho-pelagic species was very similar, although mesopelagic items were more important in terms of weight (18.1%).

Differences in the diet according to dolphin sex and size

The same group of fish and squid species made up the bulk of the diet of all sex and size groups, yet some variation was observed in the relative contribution of each

Table 1. *Number (N), frequency of occurrence (F) and weight (W) of the prey items identified in the stomach contents of common dolphins stranded and incidental & caught off the Portuguese coast.*

Prey species		Number		Occurrence		Weight	
		N	%N	F	%F	W	%W
Fish							
Clupeidae	*Sardina pilchardus* (Walbaum)	826	27.4	34	81."	27709.6	43.4
Engraulidae	*Engraulis encrasicolus* (L.)	12	0.4	6	14.3	75.5	0.1
Myctophidae	*Myctophum* sp.	15	0.5	I	2.4		
Macroramposidae	*Macroramphosus* sp.	256	8.5	10	23.8	2151.6	3.4
Merluccidae	*Merluccius merluccius* (L.)	42	1.4	5	11.9	1307.9	2.1
Gadidae	*Gadiculus argenteus* (Guichenot)	7	0.2	2	4.8	0.4	<o.o
	Micromesistius poutassou (Risso)	726	24.1	13	31.0	9898. 1	15.5
	Trisopterus sp.	26	0.9	4	9.5	168.0	0.3
Caproidae	*Capros aper* (L.)	1.0	0.3	I	2.4		
Cepolidae	*Cepola macrophthalma (I,.)*	5	0.2	3	7.1		
Carangidae	*Trachurus* sp.	148	4.9	19	45.2	4431.7	6.9
Sparidae	*Boops boops* (L.)	3	0.1	2	4.8	169.5	0.3
	Diplodus vulgaris (Saint-Hillaire)	1	<0.0	1	2.4	84.8	0.1
	Unidentified Sparidae	3	0.1	2	4.8	255.3	0.4
Ammodytidae	*Hyperoplus lanceolatus* (Le Sauvage)	1	<0.0	1	2.4	7.9	<0.0
Scombridae	*Scomber japonicus* (Hauttuyn)	28	0.9	14	33.3	1439.8	2.3
	Scomber scombrus (L.)	2	0.1	2	4.8	158.2	0.3
	Scomber spp.	33	1.1	6	14.3	2595.9	4.1
Gabiidae	*Deltentostheus quadrimaculatus* (Valenciennes)	173	5.7	2	4.8	572.7	0.9
	Gobius niger (L.)	6	0.2	3	7.1	lG.G	<o.o
	Unidentified Gobiidae	2	0.1	2	4.8	2.6	< 0.0
Callionymidae	*Callionymus lyra* (L.)	1	<0.0	1	2.4		
Mugilidae	*Liza ramada* (Risso)	3	0.1	1	2.4	486.0	0.8
Atherinidac	*Atherina* sp.	141	4.8	5	11.9	7044.2	11.0
Bothidae	*Arnoglossus imperialis* (Rafinesque)	6	0.2	1	2.4	170.8	0.3
	Arnoglossus laterna (Walbaum)	1	< 0.0	I	2.4	28.5	<
	Unidentified Bothidae	I	<0.0	1	2.4	76.1	0.1
Soleidae	*Microchirus variegatus* (Donovan)	2	0.1	2	4.8	125.5	0.2
Unidentified fish		22	0.7	8	19.1		
Total (fish group)		2502	83.0	41	97.6	58977.2	92.4
Cephalopods							
Sepiidac	*Sepia* sp.	0.0	3.1	5	11.9	176.5	0.3
	Unidentified Sepiidae	23	0.8	3	7.1	43.7	0.1
Sepiolidae	*Sepiola atlantica* (Orbigny)	1	<0.0	1	2.4	1.4	<0.0
	Unidentified Sepiolinae	69	2.3	6	14.3	299.8	0.5
Loliginidae	*Loligo sp.*	111	3.7	10	23.8	2113.6	3.3
	Alloteuthis sp.	164	5.4	14	33.3	937.6	1.5
	Unidentified Loliginidae	39	1.3	5	11.9	969.0	1.5
Octopoteuthidae	*Octopoteuthis sicula* (Rüppell)	4	0.1	2	4.8	133.2	0.2
Ommastrcphidae	*Illex coindetii* (Vèrany)	4	0.1	2	4.8	178.1	0.3
Brachioteuthidae	*Brachioteulhis* sp.	2	0.1	l	2.4	6.0	<0.0
Chirotruthidac	*Chiroteuthis* sp.	1	<0.0	1	2.4	10.1	<0.0
Unidentified cephalopods		2	0.1	2	4.8		
Total (cephalopod group)		513	17.0	22	52.4	4869	7.7
'Total		3015	100	42	100	65846.1	100

prey type (Table 4). Sardine was the dominant prey species in the diet of all the groups, with the exception of immature males, where it was outnumbered by blue whiting.

Although fish was the major prey group in the diet of all classes, the relative proportion of fish and squid varied according to dolphin sex and size. Immature females consumed the highest percentage of cephalopods by weight (13.5%), followed by mature females (9.1%). Cephalopods contributed only with 1.3% in weight to the diet of mature males. There was a significant effect of sex (but not of size) in the weight contribution of cephalopods to the diet of common dolphins (two-way ANOVA, sex: $F_{1,38}=4.23$, $P<$ 0.05, size: $F_{1,38}=0.28$, $P>$ 0.5; interaction: $F_{1,38}=2.34$, $P>$ 0.1). Furthermore, among mature dolphins, squid were taken more often by females (67%) than by

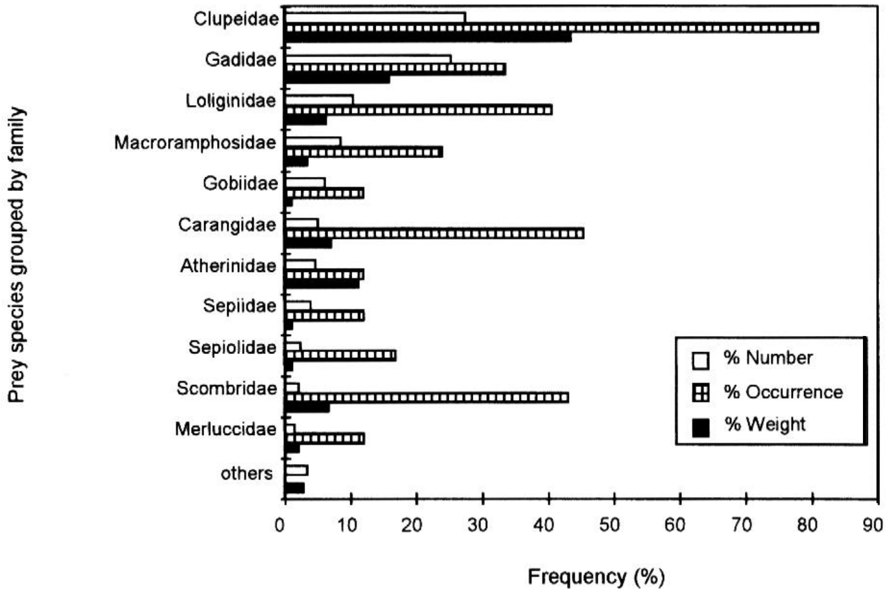

Figure 2. Percentage number (%N), occurrence (%F) and weight (%W) of prey species found in the stomach contents of common dolphins grouped by family.

Table 2. *Estimates of average length (mm) and wet weight (g) of prey species taken by common dolphins off the Portuguese coast. Prey species for which no regression equations were, found are not included in this table. Range values and sample sizes are indicated. With the exception of snipefish for which standard length was measured, total body length of fish and total mantle length of cephalopod species is presented.*

Prey species	Average total length (mm)	Range of length [mm)	Average wet weight (g)	Range of weight (g)	N
Fish					
Sardina pilchardus	159.1	81.9-210.3	33.9	4.3-75.6	471
Macroramphosus sp.	122.5’	104.1-150.0	8.5	5.4-14.4	36
Merluccius merluccius	147.8	70.8-303.1	31.3	1.7-179.2	41
Micromesistius poutassou	125.0	61.CG226.7	12.9	1.1-64.5	214
Trisopterus sp.	66.6	25.9-157.4	6.9	0.1-44.2	16
Trachurus sp.	144.3	75.1-277.8	30.2	3.2-170.7	68
Hyperoplus lanceolatus	146.9		7.9		1
Scomber japonicus	213.1	204.4-227.0	57.6	48.5-73.0	4
Scomber scombrus	227.2		79.1		1
Gobius niger	63.5	53.3-78.3	2.8	1.2-4.8	3
Arnoglossus imperialis	128.2	111.3-143.1	28.5	18.5-38.7	7
Microchirus variegatus	192.2	182.1-202.3	62.8	52.2-73.3	2
Cephalopods					
Sepia sp.	24.1	16.7-39.0	1.8	0.6-6.4	76
Sepiola atlantica	15.6		1.4		I
Loligo sp.	44.6	1.0-244.6	25.2	1.4-325.4	69
Alloteuthis sp.	59.5	10.0-281.3	5.7	0.5-118.1	116
Octopoteuthis sicula	71.1	59.9-100.5	33.3	20.3-68.8	4
Brachioteuthis sp.	46.2	43.8-48.6	3.0	2.7 3.4	2
Illex coindetii	110.1	84.8-161.2	44.5	12.2-124.1	4
Chiroteuthis sp.	74.3		10.1		1

*, average standard length

males (20%), although this difference was not statistically significant (Fisher exact test, N =14, $P>0.1$). In fact, the relative frequencies of cephalopods in the diet were independent of sex and size of dolphins ($\chi^2=4.07$, df=3, $P>0.25$).

Sex and size of dolphins did not have any obvious effect on prey diversity (two-way ANOVA, sex: $F_{1,38}=0.18$, $P>0.5$; size: $F_{1,38}=2.36$, $P>0.1$; interaction: $F_{1,38}=0.07$, $P>0.5$). Total number of prey items consumed was not correlated with dolphin size ($r_s=0.24$, N=42,

Table 3. Some *data on biology, behaviour and habitat characteristics of fish and cephalopod species identified in the stomach contents of common dolphins. Data on fish species are derived from Whitehead et al. (1984, 1986a, b). Data on cephalopods are derived from Clarke (1986a) and Guerra (1992).*

Prey species	Behaviour	Habitat	Depth (m)	Biology/Behaviour/Habitat characteristics
Fish				
Sardina pilchardus	P	N	15-35	Die1 vertical migrations
Engraulis encrasicolus	P	N	15-100	Euryhaline, enters estuaries
Myctophum sp.	M	O	100-750	Die1 vertical migrations
Macroramphosus sp.	B/P	N	50-500	Pelagicjuveniles and henthic adults, gregnrious
Merluccius merluccius	M	N/O	150~500	Die1 vertical migrations
Gadiculus argenteus	M	N/O	200-1000	
Micromesistius poutassou	M	N/O	100-750	Die1 vertical migrations
Trisopterus sp.	B	N	30-300	Juveniles close to shore, gregarious
Capros aper	B/P	N	100-400	Gregarious
Cepola macrophthalma	B	N	15-200	Lives singly or in small groups in burrows
Trachurus sp.	P	N	20-500	Forms mixed schools within the genus
Boops boops	B	N	15-300	Inshore waters, die1 vertical migrations, gregarious
Diplodus vulgaris	B	N	1 5-90	Littoral waters
Hyperoplus lanceolatus	B	N	15-60	Inshore waters, estuaries
Scomber japonicus	P	N	20-300	Large schools
Scomber scombrus	P	N	20-250	Large schools
Deltentosteus quadrimaculatus	B	N	20 90	On sandy or muddy sand bottoms
Gobius niger	B	N	25-75	Inshore waters, estuaries
Callionymus lyra	B	N	20-100	On sandy or muddy bottoms
Liza ramada	P	N	15-50	Inshore waters, estuaries
Atherina sp.	P	N	15-50	Littoral waters, estuaries, schooling
Arnoglossus imperialis	B	N	15-350	On sandy or muddy bottoms
Arnogloss us laterna	B	N	15-200	On mixed or muddy bottoms
Microchirus variegatus	B	N	80-400	On sandy or muddy bottoms of continental shelf and slope
Cephalopods				
Sepia sp.	B	N	50-450	Muscular body, neutral buoyancy (vacuum)
Sepiola atlantica	B	N	20-100	Luminous organs, neutral buoyancy (vacuum)
Loligo sp.	B/P	N	20-200	Die1 vertical migrations, negative buoyancy
Alloteuthis sp.	B	N	20-200	Negative buoyancy
Octopoteuthis sicula	M	0	50-2000	Die1 vertical migrations, luminous organs, gelatinous body, neutral buoyancy (ammoniacal)
Brachioteuthis sp.	M	O	50-3000	Die1 vertical migrations, luminous organs, muscular body, negative buoyancy
Illex coindetii	B/P	N/O	100-400	Die1 vertical migrations, muscular body, negative buoyancy
Chiroteuthis sp.	M	O	500-2000	Die1 vertical migrations, luminous organs, gelatinous body, neutral buoyancy (ammoniacal)

Behaviour: P, pelagic; M, mesopelagic; B/P, bentho-pelagic; B, benthic. Habitat: N, neritic; 0, oceanic

P> 0.1). However, dolphin size was positively correlated with the estimated weight of stomach contents (r_s=0.35, N=42, *P*<O.O5) and total length of sardines taken (r_s=0.52, N=30, *P*<O.O05). Sardines consumed hy mature females (mean=153±22.3 mm, N=7) were significantly smaller than those taken by mature males (mean=174±8.4 mm, N=4) (MWU, Z=2.27, *P*<O.O5); however, the same kind of difference was not detected in immature individuals (MWU, Z=O.68, N=19, *P*>O.l).

Prey species of different habitats occurred in similar proportions in the stomach contents of all sex and size groups; however, benthic species were more frequently found in the diet of mature common dolphins.

Differences in the diet of stranded and incidental& captured dolphins

Comparison of prey composition of stranded and incidentally caught dolphins did not indicate substantial differences, although the relative importance of each prey species varied (Table 5). Sardine dominated the diet of incidentally killed dolphins and although it was also the most frequent prey of stranded dolphins, blue whiting appeared as the dominant species both in number (40.7%) and weight (34.0%). Thirty different prey items were identified in the stomach contents of the 19 stranded common dolphins, whereas 31 different prey were found in the stomachs of the incidentally caught dolphins (N=23). Thus no significant differences were found in the number of different prey species consumed hy stranded and incidentally captured animals (MWU, Z=1.18, N=42, *P*>O.l). *No* significant difference was observed in the contribution (in number and weight) of cephalopods to the diet of the two groups (MWU, number: Z=-0.85, N=42, *P*>O.1; weight: Z=-0.82, N=42, *P*>O.l) nor in its frequency of occurrence (Fisher exact test, N=42, *P*>O.5). However, the proportion of sardines

Table 4. *Percentage number (%N), occurrence (%F) and weight (% W) of the main prey species identified in the stomach contents of common dolphins grouped according to different sex and size-classes.*

	Immature males (N =17)			Mature males (N=5)			Immature females (N =ll)			Mature females (N =9)		
Prey species	%N	%F	% w	%N	%F	%W	%N	%F	%W	%N	% F	%W
Fish												
Sardine	28.5	82.4	46.5	26.6	80.0	45.7	16.9	73.7	43.4	36.2	88.9	38.8
Snipefish	4.6	29.4	0.1	22.3	40.0	8.2	14.7	3.1	9.8	4.7	22.2	1.2
European hake	1.5	11.7	0.4	0.4	20.0	5.3	0	0	0	2.8	22.2	4.2
Blue whiting	46.6	29.4	34.7	26.6	40.0	3.6	3.1	45.5	4.R	1.7	11.1	2.5
Trachurus sp.	2.1	41.2	2.6	2.6	60.0	8.9	5.8	27.3	14.6	9.3	66.7	7.6
Scomber spp.	0.9	23.5	2.3	4.4	80.0	11.0	0.9	36.4	4.2	4.5	66.7	10.7
Toothed goby	**0**	**0**	**0**	**0**	0	**0**	22.6	9.1	6.1	0.1	11.1	0.0
Sand smelt	2.0	5.3	5.0	0.4	20.0	0.9	0	0	0	14.9	33.3	23.3
Cephalopods												
Sepiidae	0.2	5.3	0.0	0	0	0	3.8	18.2	1.5	4.9	22.2	0.3
Sepiolinae	0.9	17.7	0.1	4.8	20.0	1.0	4.6	18.2	1.6	1.7	11.1	0.3
Loliginidae	3.x	47.1	4.5	0.3	20.0	0.2	10.9	27.3	8.4	13.8	66.7	8.5
Total	97.1	34.1	36.8	89.0	100	82.8	95.3	90.3	94.4	94.6	100	97.6

Table 5. *Percentage number (%N), occurence (%F) and weight (% W) of the main prey species identified in the stomach contents of* ***stranded*** *and incidentally caught common dolphins.*

	Stranded (N=19)			Incidentally caught (N=23)		
Prey species	%N	%F	%W	%N	%F	%W
Fish						
Sardine	10.5	63.2	23.3	48.6	95.7	56.3
Snipefish	13.4	'36.8	7.1	2.4	13.0	0.8
European hake	1.7	10.5	3.2	1.0	13.0	1.2
Blue whiting	40.7	42.1	34.0	3.3	21.7	2.5
Trisopterus sp.	0.1	5.3	0.2	1.3	13.0	0.3
Trachurus sp.	4.8	31.6	9.6	5.0	56.5	4.9
Scomber spp.	1.7	42.1	8.6	2.5	43.5	5.4
Toothed goby	10.3	5.3	2.2	0.1	4.4	0.0
Sand smelt	0	0	0	10.5	21.7	18.6
Cephalopods						
Sepiidae	4.5	10.5	0.5	3.1	13.0	0.2
Sepiolinae	1.4	15.8	0.5	3.5	17.4	1.0
Loliginidae	7.1	26.3	7.2	14.6	52.2	5.6
Total	36.2	83.8	97.0	36.5	100	96.8

in the diet of common dolphins that had been incidentally killed in fishing operations was significantly higher (Fisher exact test, N=42, P<0.05). There was also a significant difference in the estimated weight of sardines identified in the stomach contents of stranded (mean=332.0±406.2 g, N=ll) and captured dolphins (mean=930.5±1135.4 g, N=19) (MWU, Z= -2.09, P<O.O5).

DISCUSSION

Diet composition

Common dolphins have often been described as mainly ichthyophagous predators (Collet, 1981; González et al., 1994; Berrow & Rogan, 1996). Although cephalopods are common in the diet and usually taken in large numbers, the majority of the individuals are very small and light and do not generally represent a significant amount of the overall ingested weight (Desportes, 1985; Young & Cockcroft, 1994). Data from the present study agrees with previous findings-cephalopods were found in more than half of the samples and comprised 17% of all prey taken but only represented less than 8% of total biomass.

Despite the high diversity of prey items identified, four fish and two cephalopod species appear to form the basis of the diet of common dolphins off the Portuguese coast. Sardine, blue whiting, snipefish, *Trachurus* and loliginids accounted for over 75%, in number and weight, of all prey taken. All these species have been reported in the diet of common dolphins elsewhere (Collet, 1981; Desportes, 1985; Pascoe, 1986, González et al., 1994; Berrow & Rogan, 1996), in spite of regional variations in the relative proportion of each one.

Sardine as the main prey item

One of the most striking results presented here relates to the obvious dominance of sardine in the diet of dolphins from Portuguese waters. However, this should not be interpreted as a clear evidence of feeding specialization; instead, considering the high local availability of sardine this could simply imply that dolphins are preying on the most abundant species. In fact, although relatively uncommon in northern Europe (Whitehead et al., 1984), sardine is one of the most abundant fish species off the Iberian coast (Anon., 1997).

Data on the dominance of sardine in the diet of dolphins from Portuguese waters are not entirely supported by studies in adjacent waters. Preliminary data from the Galician coast (Spain) indicates that common dolphins feed mainly on blue whiting and horse mackerel (Santos et al., 1995), whereas results from the French Atlantic coast suggest a predominance of gadids, namely blue whiting and *Trisopterus*, horse mackerel *(T. trachurus* L.) and European hake (Collet, 1981; Desportes, 1985). The variation observed in the importance of sardine in the Portuguse and French samples could be a consequence of differences in the availability and abundance of sardine. However, differences detected between estimates from Portugal and Galicia are probably the result of mcrhodological discrepancies. In fact, in the study conducted on the Galician coast, identification and size estimation of sardines were essentially based on the otoliths, whereas in this study both otoliths and vertebrae were used. It is now widely recognized that differences in the digestion rate of otolirhs of different species can significantly underestimate counts and measurements of fish ingested (da Silva & Neilson, 1985). Moreover, fish species with very small and fragile otoliths (like the clupcids and scombrids) will have lower recovery rates (da Silva & Neilson, 1985; Tollit et al., 1997; personal observations) and are thus more likely to be underestimated in terms of numerical importance (Tollit et al., 1997). Using additional hard remains (such as vertebrae and bones), which are less prone to acidic digestion by the gastric fluids, is currently assumed to be a suitable alternative to correctly estimate fish importance, specially in those fish species with more fragile otoliths (Pierce et al., 1991).

Care must be taken, however, as the inclusion in this study of animals incidentally caught appears to be contributing to an overestimate of the importance of sardine in the diet of common dolphins. Still, for the purpose of energetic requirement estimates or when dealing with cetacean-fishery interactions, data on food consumption of dolphins accidentally caught should also be assessed and taken into consideration. Furthermore, sardine was also the most frequent prey species of stranded dolphins and the second most important prey on a weight basis, suggesting that this fish species is in fact an important item in the diet of common dolphins foraging off the Portuguese continental coast.

Foraging behaviour

The reliance of common dolphins on pelagic shoaling prey species, has been widely reported (Collet, 1981; Pascoe, 1986; Young & Cockcroft, 1994). Feeding on species that form very large schools could be an advantageous strategy for pelagic cetaceans that forage in open waters (Wiirsig, 1986), as common dolphins usually do. In spite of this, the variety of prey species from different habitats and exhibiting distinct behaviours, suggests that common dolphins feeding in Portuguese waters have a largely versatile foraging behaviour. Various mesopelagic fish and cephalopod species have been retrieved from the stomach contents (Table 2). Although common dolphins could occasionally descend at greater depths in order to feed, this strategy, when applied systematically, could be relatively time and energy consuming. All these species exhibit die1 vertical migrations (Whitehead et al., 1984, 1986a; Clarke, 1986a; Guerra, 1992), becoming available nearer the surface at night, which could suggest a nocturnal feeding activity Alternatively, common dolphins could take advantage of prey schools brought to the surface or discarded during commercial fishing operations. Some true benthic species were also found in the diet (Table 2). In Portugal, common dolphins are often seen entering estuaries and coming close to shore to feed (personal observations). However, some of these species, of low commercial value, are frequently discarded (dead or alive) during fishery activities and could also be easily caught by dolphins feeding in association with fishing operations.

Prey dimensions

Young & Cockcroft (1994) reported a much larger size and weight range of prey taken by common dolphins off South Africa; the average estimated length and weight of fish and squid consumed suggests that common dolphins in Portuguese waters are feeding mainly on juvenile and immature forms. Generally, average length of prey taken is smaller than the minimum landing size for commercial fisheries (Pinho, 1994), indicating that dolphins arc not in direct competition with the fishermen. However, if there is a significant impact of dolphin predation on the younger classes this could affect the recruitment rate of those fish species, Although difficult to assess, ecological interactions between commercial fishcries and marine mammals are an important component of the ecosystem dynamics and should be carefully monitored to allow for a multi-species management of the marine resources.

Diet of dolphins from different sex and size groups

Differences in the diet between dolphins from distinct sex and size groups have often been used to make inferences on the composition of dolphin schools during foraging activities (e.g. Cockcroft & Ross, 1990; Young & Cockcroft, 1994). Young & Cockcroft (1994) showed that adult and adolescent males of common dolphins in South Africa employ the same feeding strategies, whereas female adolescents, calves and probably female subadults form ‘nursery groups’. Feeding studies have also been used to investigate the relation between reproductive condition and energetic requirements (Cockcroft & Ross, 1990; Young & Cockcroft, 1994). Compared to other individuals, lactating and pregnant females are expected to exhibit marked differences in their feeding habits, following higher energy demands of lactation.

In the present study, only one female was pregnant and differences in the diet could not be related to the reproductive condition of dolphins. Comparison of the prey composition between common dolphins from distinct sex and size groups did not reveal any significant differences, except in the contribution of cephalopods, where female dolphins showed a greater reliance on squid. However, without further data on the diet of lactating and pregnant females this result is difficult to interpret. Dolphin size was related to prey size and reconstituted weight of prey taken. These results could indicate that immature individuals prey on the same species hut choose smaller forms, which could illustrate diffcrcnccs either in physical features or foraging strategies and abilities. For example, the smaller specimens of several fish and squid species tend to concentrate in the upper layers of the water column, whereas larger individuals are mostly available at greater depths (Whitchcad et al., 1984, 1986a,b; Guerra, 1992). In this case, adult dolphins with greater diving capacities could forage on the same species but at greater depths, contributing to improve the allotment of the resources and, therefore, reducing the competition among individuals of the same population. In addition, variation in the size of sardines taken by mature males and females could also suggest the existence of distinct groups among adult common dolphins.

Diet of stranded and incidentally caught dolphins

Several authors have postulated that dietary studies based on the examination of stomach contents from stranded marine mammals, are not truly representative of the feeding habits of healthy animals; differences in prey composition and prey relative importance (Clarke, 1986a; Selzer et al., 1986) or unusually high percentages of empty stomachs (Selzer et al., 1986) are expected to occur. However, studies suggesting the opposite can also be found (e.g. Ross, 1979; Berrow & Rogan, 1996) and, presently, no strong evidence seems to point either way. In this study, the diet of 19 stranded common dolphins was compared to that of 23 animals incidentally caught in fishing nets. The latter include nine dolphins (39%) caught in beach seine nets, a type of purse seine that operates close to the shoreline and catches various pelagic fishes but mainly sardine. Consequently, it would he expected that the stomach contents of common dolphins incidentally caught in fishing operations exhibited less prey diversity and a bias towards pelagic fishes, specially sardine.

No differences were detected between the diet of the two groups (stranded and incidentally caught) hascd on prey composition and diversity. Howcvcr, the diffcrcncc in the contribution of sardines between the two groups, indicates that there is a bias towards the target species of the fishery in the diet of dolphins incidentally caught. Whether captured dolphins are taking advantage of fishing operations (by eating sardines trapped in the nets, discarded or gathered and brought up during the operation) or simply feeding on the same fishing grounds of the commercial fisheries is currently unknown and should be further investigated.

Descriptions of the feeding habits of marine mammals, based on samples from animals that have died in consequence of direct interaction with the commercial fisheries, could be deceptive, as they can involve a significant over representation of the target species of the fishery.

I gratefully acknowledge M.B. Santos (Univcrsiry of Abcrdccn), Dra. M.M. Cunha, A. Moreno and J. Pereira (IPIMAR, Lisbon) for their work in the identification of some of the cephalopod beaks. J.P. Granadeiro allowed me to use his bony fishes reference collection. I thank Dra. Margarida Reis (University of Lisbon) for permission to use the laboratory facilities M. Sequeira provided some of the material analysed in this study, for which I am indebted. I would also like to thank A. Silva for thr guidance on fish and cephalopod literature. Many thanks to A. Teixcira for the opportunities and encouragement. I am grateful to J.P. Granadeiro, A. Silva and two anonymous referees whose valuable comments greatly improved an early draft of the paper.

REFERENCES

Anon., 1997. Report of the ICES Advisory Committee on Fishery Management, 1996. *International Council for the Exploration of the Sea Cooperative Research Report, no. 221.*

Berrow, S.D. & Rogan, E., 1996. Stomach contents of harhour porpoises and dolphins in Irish waters. *European Research on Cetaceans 9,* 179-181.

Clarke, M.R., 1986a. Cephalopods in the diet of odontocetes In *Research on dolphins* (ed. M.M. Bryden and R. Harrison), pp. 281-321. Oxford: Oxford University Press.

Clark, M.R., 1986b. *A handbook for the identification of cephalopod beaks.* Oxford: Clarendon Press.

Cockcroft, VG. & Ross, G.J.B., 1990. Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. In *'The bottlenose dolphin* (ed. S. Leatherwood and R.R. Reeves), pp. 295- 308. San Diego: Academic Press.

Collet, A., 1981. *Biologie du dauphin commun* Delphinus delphis *L. en Atlantique Nord-Est* Thèse doctoral, Université de Poitiers, France.

Desportes, G., 1985. *La nutrition des Odontocetes en Atlantique Nord-Est (côtes Français—iles Feroë).* Thèse doctoral, Université de Poitiers, France.

Evans, P.GH., 1980. Cetaceans in British waters. *Mammal Review,* 10, 52pp.

Evans. W.E.. 1982. Distribution and differentiation of stocks of *Delphinus delphis* Linnaeus in the northeastern Pacific. *Food and Agriculture Organization, Fisheries Series, 5, 45-66.*

González A.F.,López A., Guerra, A. & Barreiro A., 1994. Diets of marine mammals stranded on the northwestern Spanish Atlantic coast with special reference to Cephalopoda. *Fisheries Research,* 21, 179-191.

Guerra, A., 1992. Mollusca, Cephalopoda. In *Fauna Ibérica vol.* 1 (ed. M.A. Ramos et al.), pp. 327. Madrid: Museo Nacional de Ciencias Naturales, CSIC.

Härkönen, T.J., 1986. *Guide to the otoliths of the bony fishes of the northeast Atlantic.* Hellerup: Danbiu ApS.

Kuikcn. T. & Garcia Hartmann, M., ed., 1993. Proceedings of the first European Cetacean Society workshop on cetacean pathology: dissection techniques and tissue sampling. *ECS Newsletter,* 17, special issue, 39pp.

McKinnon, J., 1994. Feeding habits of the dusky dolphin, *Lagenorhynchus obscurus, in* the coastal waters of central Peru. *Fishery Bulletin. National Oceanic and Atmospheric Administration, Washington, DC, 92, 569-578.*

Pascoe, PL., 1986. Size data and stomach contents of common dolphins, *Delphinus delphis, near* Plymouth. *Journal of the Marine Biological Association of the United Kingdom, 66,* 319-322.

Pérez-Gándaras, G., 1986. *Estudios sobre los cefalópodos ibéricos: sistemática y bionomia mediante el estudio morfométrico comparado de sus mandíbulas.* Tesis doctoral, Universidad Complutense de Madrid, Spain.

Pierce. G.J.. Boyle, P.R. & Diack. J.S.W.. 1991. Identification of fish otolihs and bones in faeces and digestive tracks of seals. *Journal of Zoology 224, 320-328.*

Pinho, R.M.A., 1994. *Caracterização das principais espécies de interesse comercial. Material de apoio ao curso de Inspecção e Controlo sanitário de produtos marinhos.* Lisboa: IPIMAR

Ross, G.J.B., 1979. *The smaller cetaceans of the south east coast of southern Africa.* PhD thesis, University of Port Elizabeth, South Africa.

Santos, M.B., Pierce, C.J., González, A.F., I.ópez, A. & Gucrra, A., 199.5. Diets of small cetaceans stranded an the Galician coast (NW Spain). International *Council for the Exploitation of the Sea (CM Papers and Reports), N:* 11.

Selzer, L.A., Early, G., Fiorelli, PM., Payne, P.M. & Prescott, R., 1986. Stranded animals as indicators of prey utilization by harbor seals, *Phoca vitulina concolor, in* southern New England. *Fishery Bulletin. National Oceanic and Atmospheric Administration Washington, DC, 84,* 217-220.

Sequeira, M., Inácio A. & Silva, M.A., 1997. Cetacean strandings in Portugal: 1993-95. *European Research on Cetaceans,* 10, 136-140.

Silva, J. da & Neilson, J.D., 1985. Limitations of using otoliths recovered in scats to estimate prey consumption in seals. *Canadian Journal of Fisheries and Aquatic Sciences, 42,* 1439-1442.

Silva, MA. & Sequeira, M., 1997. Preliminary results on the diet of common dolphins *(Delphinus delphis off* the Portuguese coast. *European Research on Cetaceans,* 10, 253-259.

Tollit, D.J., Steward, MJ., Thompson, P.M., Pierce, G.J., Santos, M.B. & Hughes, S., 1997. Species and size differences in the digestion of otoliths and beaks: implications for estimates of pinniped diet composition. *Canadian Journal of Fisheries and Aquatic Sciences, 54,* 105-119.

Watt, J., Pierce, G.J.& Boyle, P.R., 1997. Guide to the identification of North Sea fishes using premaxillae and vertebrae. *International Council for the Exploitation of the Sea Cooperative Research Report, no. 220.*

Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J, & Tortonese, E., ed., 1984. *Fishes of the north-eastern Atlantic and Mediterranean,* vol. I. Paris: UNESCO.

Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. & Tortonese, E., ed., 1986a. *Fishes of the north-eastern Atlantic and Mediterranean, vol. 2.* Paris: UNESCO.

Whitehead, P.J.P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. & Tortonese, E., ed., 1986b. *Fishes of the north-eastern Atlantic and Mediterranean,* vol. *3.* Paris: UNESCO.

Wiirsig, B., 1986. Delphinid foraging strategies. In *Dolphin cognition and behavior: a comparative approach* (ed. R.J. Schusterman et al.), pp.347-359. Hillsdale, NJ & London: Lawrence Erlbaum Associates.

Würtz, M. & Marrale, D., 1993. Food of striped dolphin, *Stenella coeruleoalba, in* the Ligurian Sea. *Journal of the Marine Biological Association of the* United Kingdom, 73, 571-578.

Young, D.D. & Cockcroft, VG., 1994. Diet of common dolphins *(Delphinus delphis) off* the south-east coast of southern Africa: opportunism or specialization? *Journal of zoology* 234,41-53.

Zar, J.H., 1996. *Biostatistical analysis,* 3rd ed. New Jersey: Prentice Hall.

Submitted 16 January 1998. Accepted 27 July 1998.