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Diet of the bottlenose dolphin (*Tursiops truncatus*) in the western Mediterranean Sea

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The stomach contents of 16 bottlenose dolphins *Tursiops truncatus* (Cetacea: Odontoceti) stranded in the Spanish Mediterranean coast were examined. Remains and size of prey were analysed and correlated with the ecological characteristics and behavioural patterns of this dolphin. Fish and cephalopods represented the main diet components, and hake *Merluccius merluccius* was the most important prey. The food habits were considered as mainly demersal according to the characteristics of the prey. The study suggested ontogenic and sexual differences in feeding behaviour based on diet composition and hake size. The potential causative factors, particularly as they relate to dolphin social structure, are discussed.

INTRODUCTION

The bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), is a cosmopolitan species fairly common in the Mediterranean Sea (McBrearty et al., 1986; Marini et al., 1996). The conservation of Mediterranean populations of bottlenose dolphins has received considerable attention in the last decades. These animals are protected by national and international laws and agreements (European Union, Convention for the protection of the Mediterranean Sea against Pollution and its protocols, Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic area). This species is primarily coastal and is frequent over the continental shelf, especially along the shelf break (Wells & Scott, 1999).

A large amount of dietary data (Walker, 1981; Clarke, 1996; Santos et al., 1996; Wells & Scott, 1999), as well as information on feeding behaviour (Hanson & Defran, 1993; Bearzi et al., 1999), has been assembled in many regions. However, data of intraspecific differences in the diet of cetaceans and particularly in wild bottlenose dolphin are very scarce (Wells & Scott, 1999; Bowen & Siniff, 1999). Some evidence of ontogenic and sexual differences in the diet relative to prey composition and size of prey has been previously reported for bottlenose dolphins (Barros & Odell, 1990; Cockcroft & Ross, 1990; Mead & Potter, 1990). Information from the Mediterranean Sea is also very scarce, concerning only seven specimens (Voliani & Volpi, 1990; Orsi Relini et al., 1994; Miokovic et al., 1997). An opportunistic character of the diet of the bottlenose dolphin has been inferred from the variability of prey according to local availability (Wells & Scott, 1999) and the diversity of feeding techniques used (Shane et al., 1986; Rossbach & Hertzing, 1997; Randall et al., 1999). The various interactions with fisheries reported from many areas (Wells & Scott, 1999) may favour this opportunistic diet.

In this paper the diet of the bottlenose dolphin in the western Mediterranean was analysed to cast some light on intraspecific dietary differences. It is unknown how long the prey items remained in the digestive tract of dolphins preventing the estimation of feeding rates. Therefore, as in previous studies of cetaceans, we will restrict the analysis to the diet composition only.

MATERIALS AND METHODS

The stomachs of 16 bottlenose dolphins, seven males, eight females and one specimen of undetermined sex were studied. According to data from the Atlantic (Mead & Potter, 1990), adult sexually mature specimens were considered to be those larger than 2.5 m in length, and as juveniles those under that body size. The latter category includes both juveniles *sensu stricto* and calves. The animals studied were found stranded along the Spanish Mediterranean coast, between 40°25′N 00°32′W and 37°35′N 00°45′E, from August 1983 to October 1997. In most cases, cause of death could not be determined. Stomachs were stored deep-frozen (−20°C) and the contents were subsequently flushed through 0.2-mm mesh sieves and preserved in 70% ethanol. Fish otoliths were stored dry.

The items found in the stomach contents were ascribed to species using taxonomic keys for fish sagitta otoliths (Härkönen, 1986), cephalopod lower beaks (Clarke, 1986; Pérez-Gándaras, 1986) and crustaceans (Zariquiey, 1968). The sagitta otoliths and lower cephalopod beaks were also compared with a local reference collection. The total number of fish was estimated as the number of complete and incomplete otolith pairs plus half the number of those that could not be allocated to either side. The total number of cephalopods was estimated as the highest number of either upper or lower beaks. Fish otoliths and cephalopod lower beaks were measured using a digital calliper with a thumb roller (SE ±0.02 mm). The length of individual hake, *Merluccius merluccius*, was estimated according to a morphometric relationship derived from Mediterranean specimens (Figueras, 1955), whereas the length and weight of cephalopods was inferred from the morphometric relationships given by Clarke (1986) and Pérez-Gándaras (1986).

A Friedman test with multiple comparisons (Conover, 1980) was used to establish whether there were significant differences in the prey composition among dolphins. The test could not be applied to the cephalopod prey species due to their low occurrence.

RESULTS

Biological data, season of stranding and stomach contents of the bottlenose dolphins studied are shown in Table 1. The stomach of the smallest dolphin (a 1.45 m long male) contained only milk. The remaining 15 dolphins had food matter in their stomachs. Remains of fish and cephalopods occurred in 31.25% of dolphins.

The prey species from the stomach contents identified are listed in Table 2. Nine fish species belonging to nine families, seven cephalopod species belonging to five families and three crustacean families, represented by a specimen each, were detected. Fish were the most important prey, both in terms of number (96.6% of total individual prey), and frequency (found in 86.7% of dolphins). According to the total number of individual prey, the stomach with the highest number of fish belonged to an adult male (2.94 m long) with 262 fish and one cephalopod. The stomach with the highest number of cephalopods corresponded to an adult female (3.05 m long) with nine cephalopod items only. Fish and cephalopods co-occurred in 40% of dolphins, whereas 66.6% of males and 25% of females had only fish items, and the stomachs of 25% of females contained only cephalopods.

There were significant differences in fish abundance between dolphins (Friedman test: $T=4.07$, $P<0.05$). The multiple comparison test between prey species showed that hake was the main prey for dolphins. The test also showed that *Cepola rubescens*, *Conger conger*, *Ophidion* sp. and *Pagellus erythrinus* could be considered as second in importance in the diet, whereas *Sardina pilchardus*, *Engraulis encrasicholus*, *Phycis blennoides* and *Trachurus trachurus* were ranked in third position.

Benthic cephalopods, *Octopus vulgaris* and *Eledone moschata* (Guerra, 1992), were the most abundant (63.6% of the total cephalopod prey). The range of cephalopod size from stomach content is shown in Table 3. *Octopus vulgaris* was the most important cephalopod prey according to its frequency (Table 2) and estimated total weight (Table 3).

The otoliths of hake prey ranged from 2.9 mm to 28.5 mm long, corresponding to a mean hake length of 23.3 cm (modal class 25.0–27.5 cm). The estimated size of hake preyed upon by dolphins is shown in Figure 1A.

Differences were found in hake size between adult and juvenile bottlenose dolphins (nested analysis of variance (ANOVA), $P<0.001$). Figure 1B shows the distribution of otolith length of hake in the stomachs of three juvenile ($N=49$ hake specimens) and six mature dolphins ($N=249$ hake specimens). Adult dolphins showed a wider range of hake size (3.7–28.5 mm in otolith length) and a higher modal class (12.5–15 mm) than juveniles (3.1–16.8 mm and 5–7.5 mm, respectively).

In this study no gender differences in the size of hake prey were found between dolphins (nested ANOVA, $P>0.15$). The distribution of hake length (Figure 1C) available from four males and four females, showed the

Table 1. *Collection data for bottlenose dolphins used in this study.*

Dolphin	L (m)	Date	N	N sp.	Taxa	H n	OL (mm)	HL (cm)	OL mean	HL mean
♂										
TT 43	1.45	95.10.12	0	0	–	–	–	–	–	–
TT 30	2.19	92.08.22	36	4	F	30	2,9–12,2	6,6–25,2	5.5	11.9
TT 20	2.36	89.04.23	2	2	F					
TT 42	2.54	95.10.11	48	5	F	5	7,5–13,2	15,9–27,2	9.9	20.6
TT 36	2.94	94.05.10	262	10	F,C	115	4,8–28,5	10,4–57,7	11.8	24.5
TT 12	3.06	84.04.18	2	2	F,Cr					
TT 37	–	94.06.01	2	1	F	2	11,8–12,9	24,3–26,6	12.3	25.5
♀										
TT 24	2.03	90.11.08	11	6	F,C	4	8,3–14,5	17,4–29,8	11.7	24.2
TT 39	2.19	95.04.06	53	3	F	44	3,1–16,8	6,9–34,3	8.3	17.3
TT 9	2.56	83.08.03	1	1	C					
TT 29	2.59	92.06.12	76	8	F,C,Cr	66	5,6–16,4	12,1–39,6	13.1	26.9
TT 25	2.89	91.01.26	8	4	F,C	3	10,9–14,6	22,5–30.2	13.3	27.5
TT 40	2.96	95.08.31	191	15	F,C	23	3,7–12,1	8,2–25,0	6.5	13.9
TT 46	2.98	97.01.15	64	7	F	45	5,9–22,3	12,5–45,4	13.8	28.5
TT 11	3.05	84.02.84	9	3	C	–	–	–	–	–
undetermined										
TT 19bis	–	89.04.09	20	5	F,C	6	3,5–19,7	7,8–40,3	10.5	21.9

L, length; N, number of individual prey; Nsp, number of species; taxa: F, fish, C, cephalopod, Cr, crustacean; Hn, number of individual hakes; OL, otolith length range; HL, estimated hake length range.

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Table 2. *Prey found in stomach contents of 15* Tursiops truncatus *from the western Mediterranean.*

				% N*			% F			
		N	F	total	♂	♀	total	♂	♀	%N**
Teleosts										
Merluccidae	*Merluccius merluccius*	348	11	43.9	45.5	43.5	73.3	66.7	75.0	45.5
Congridae	*Conger conger*	87	6	11.0	11.6	9.4	40.0	33.3	37.5	11.4
Cepolidae	*Cepola rubescens*	61	7	7.7	11.3	4.5	46.7	33.3	50.0	8.0
Ophiidae	*Ophidion* sp.	62	6	7.8	10.1	6.4	40.0	33.3	50.0	8.1
Sparidae	*Pagellus erythrinus*	27	7	3.4	2.3	4.5	46.7	50.0	50.0	3.5
Carangidae	*Trachurus* sp.	20	3	2.5	0.3	4.5	20.0	16.7	25.0	2.6
Gadidae	*Phycis blennoides*	4	3	0.5	0.3	0.7	20.0	16.7	25.0	0.5
	undetermined	35	2	4.4	9.3	0.7	13.3	16.7	12.5	4.6
Clupeidae	*Sardina pilchardus*	19	4	2.4	4.1	1.2	26.7	33.3	25.0	2.5
Engraulidae	*Engraulis encrasicholus*	53	2	6.7	1.7	11.1	13.3	16.7	12.5	6.9
undetermined		48	8	6.1	3.5	7.8	53.3	66.7	37.5	6.3
	total fish	**764**	**13**	**96.5**	**99.4**	**94.1**	**86.7**	**100.0**	**75.0**	**100.0**
Cephalopods										
Octopodidae	*Octopus vulgaris*	10	4	1.3		2.4	26.7		50.0	40.0
	Eledone moschata	3	2	0.4		0.7	13.3		25.0	12.0
Loliginidae	*Loligo vulgaris*	4	2	0.5		0.9	13.3		25.0	16.0
Ommastrephidae	*Todarodes sagittatus*	4	3	0.5	0.3	0.5	20.0	16.7	12.5	16.0
	Todaropsis eblanae	1	1	0.1		0.2	6.7		12.5	4.0
Sepiolidae	*Rondeletiola minor*	1	1	0.1		0.2	6.7		12.5	4.0
Sepiidae	*Sepia elegans*	1	1	0.1		0.2	6.7		12.5	4.0
undetermined		1	1	0.1		0.2	6.7		12.5	4.0
	total cephalopods	**25**	**8**	**3.2**	**0.3**	**5.4**	**53.3**	**16.7**	**75.0**	**100.0**
Crustaceans										
Alphaeidae	*Alphaeus glaber*	1	1	0.1		0.2	6.7		12.5	33.3
Penaeidae	*Solenocera membranacea*	1	1	0.1		0.2	6.7		12.5	33.3
Grapsidae	undetermined	1	1	0.1	0.3		6.7	16.7		33.3
	total crustaceans	**3**	**2**	**0.4**	**0.3**	**0.5**	**13.3**	**16.7**	**12.5**	**100.0**

N, total number; F, frequency; N*, per cent of total number of prey individuals; and N**, per cent of individuals within each taxa.

Table 3. *Cephalopod size from stomach contents of bottlenose dolphin.*

	*HL/LRL (mm)	ML (mm)	W (g)
Octopus vulgaris	*2.54–7.24	185	8505.5
Eledone moschata	*1.82–2.2	48	120.2
Loligo vulgaris	1.09–4.07	300	1299.2
Todarodes sagittatus	3.39–4.47	173	453.3
Todaropsis eblanae	4.09	133	156.8
Rondeletiola minor	*1.7	20	3.1

*HL, hood; LRL, lower rostral beak length; ML, estimated mantle length; W, estimated total weight.

same modal length-class for both sexes: 12.5–15.0 mm in otolith length corresponding to 25–30 cm estimated body length.

Table 2 shows the abundance of cephalopods in the female bottlenose diet. A Mann–Whitney *U*-test ($U=9.5$, $N=15$, $P=0.0089$) showed that the difference between dolphin of different sexes in cephalopod abundance is statistically significant. However, there were no differences between seasons (Kruskal–Wallis test, $H=2.486$, $P=0.477$).

In spite of the similarity in hake prey size between both sexes previously indicated, it is possible to distinguish two different female populations according to the cephalopods consumed. The two dolphin females with hake and octopodid remains in their stomachs preyed upon hakes of similar size as the juveniles. By contrast, the two females without octopodids had preyed upon hakes of similar size as the adult males (Figure 1D). However, this result should be interpreted with caution given the small sample size.

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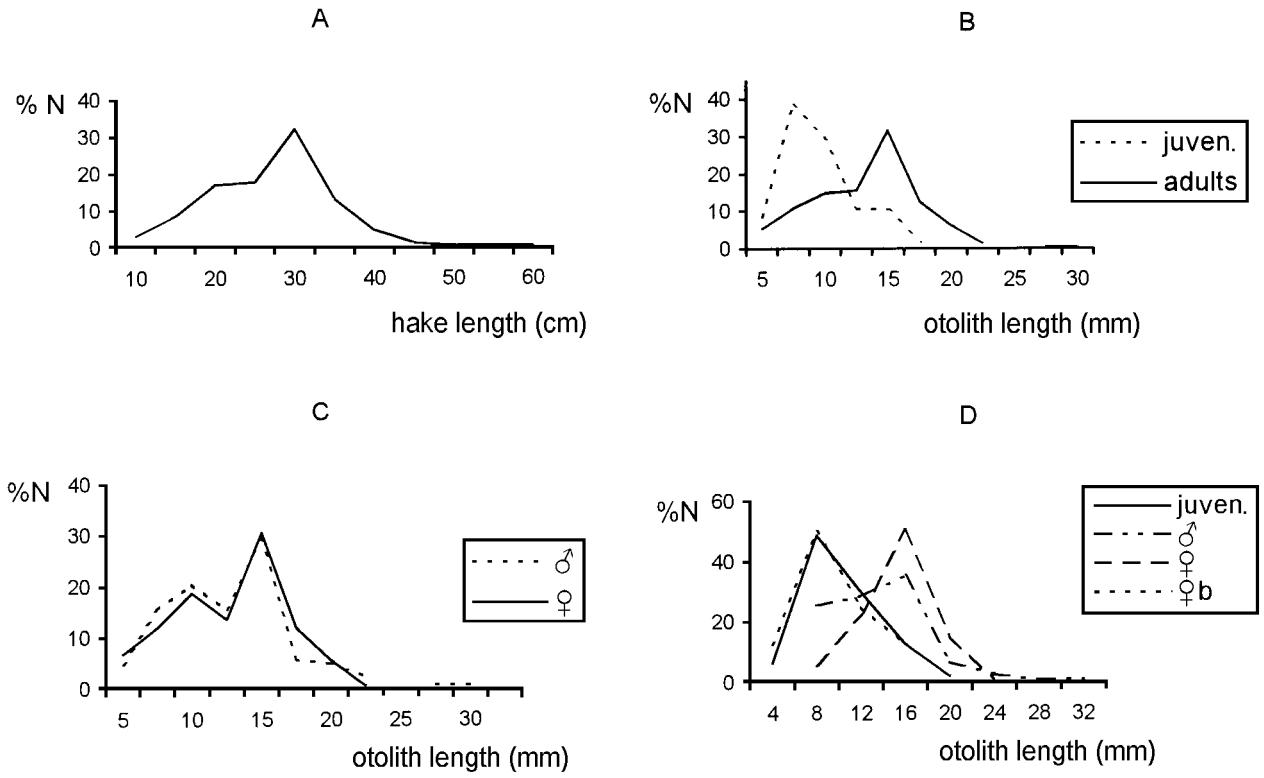

Figure 1. Distribution of hake size from stomach contents of 15 bottlenose dolphins from the western Mediterranean. (A) Data from all dolphins combined; (B) comparisons between juveniles and adults; (C) by sex; (D) of juveniles, adult males and adult females with (♀b) or without (♀) benthic cephalopods.

DISCUSSION

The diet of bottlenose dolphins in the western Mediterranean Sea seems mainly composed of fish, with *Merluccius merluccius* being the most frequent and numerically important prey. Cephalopod prey were less important and included mainly octopodids. All crustaceans found in the stomach of these dolphins are decapods, known to be the most common crustacean prey of Mediterranean hake (Bozzano et al., 1997). In fact, species of *Solenocera* and *Alphaeus* are particularly consumed by adult hakes (Karlovac, 1959; Macpherson, 1977). In addition, clupeids are the most important fish prey for Mediterranean and Atlantic *M. merluccius* (Larrañeta, 1970; Olaso, 1993; Bozzano et al., 1997). The low number of crustaceans and the associated presence of decapods and clupeids with hake suggest that these organisms were indirectly consumed by the dolphins, at least in part.

The importance of fish in the diet of bottlenose dolphins agrees with data available from other areas, where in some cases the fish is the only component of the diet (Kenney et al., 1997; Barros & Wells, 1998). The importance of hake reported in the present study conforms with previous data of the diet of the bottlenose dolphin in the Mediterranean Sea (Voliani & Volpi, 1990; Orsi Relini et al., 1994; Miokovic et al., 1997), but contrasts with the greater importance of gadids in the East Atlantic (Santos et al., 1994, 1996) and sciaenids (Barros, 1992) or sparids (Barros & Wells, 1998) in the West Atlantic. This suggests that bottlenose dolphins are able to exploit different food resources in different geographical areas, likely in response to the local availability of potential prey.

Most fish (86.8%) were of demersal and/or benthic habits of soft bottoms. Only clupeids and *Trachurus* spp. could be considered as pelagic (Tortonese, 1970, 1975). The demersal character of most prey species found in this study, whose main concentration in the north-western Mediterranean Sea occurs between 50 and 200 m on the continental shelf (Merella et al., 1998), suggests that this area is the most frequently used by this dolphin. This is consistent with the sighting distribution of bottlenose dolphins in the western and central areas of the Mediterranean Sea (Notarbartolo di Sciara et al., 1993; Marini et al., 1996). Likewise, all cephalopods except *Todarodes sagittatus* were benthonic or nektobenthonic inhabiting from the coastal line to the outer edge of the continental shelf, mostly on dendritic or muddy bottom (Guerra, 1992; Belcari & Sartor, 1993). *Todarodes sagittatus* is an oceanic species of wider bathymetric and horizontal distribution with a well-documented daily and ontogenetic migration. Remains of this species (see Table 3) corresponded to immature specimens that normally occur in shallow waters (Quetglás et al., 1998).

Hake is of great economic value in the local fisheries. The estimated size of hake consumed by dolphins is much larger than that of hake caught by trawling nets, which is the most frequent gear used in the western Mediterranean (<20 cm in length most often), but lower than that of hake caught in longline fisheries (frequently >40 cm length)

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(Recasens et al., 1998). Therefore it seems that bottlenose dolphins and fisheries tend to exploit hake of different size-classes. However, the extent of the interaction between bottlenose dolphins and fisheries requires evaluating the effect of dolphin predation on the hake population.

The higher abundance of cephalopods especially octopodids in the females' diet found in this study disagrees with the importance of cephalopods consumed by males in South Africa (Cockroft & Ross, 1990). In spite of these contradictory results that may be due to ecological differences of the prey species, our results suggest a different exploitation of resources by both sexes.

Differences in fish size preyed by juveniles and adults of bottlenose dolphin have previously been reported in South Africa (Cockcroft & Ross, 1990). Despite the statistical similarity of hake size preyed upon by males and females, it is possible to speculate on the existence of two feeding behaviours in females according to ecological characteristics of the cephalopod ingested as previously indicated. Octopodids are exclusively benthic cephalopods, especially *Octopus vulgaris*, inhabits the shallowest waters in western Mediterranean (Sánchez, 1986; Belcari & Sartor, 1993). It seems that adult females have two different feeding behaviours according to their association with calves and juveniles. The social organization of this species with a dual firstly nutritional and later social bonding function of a long lactation (Randall et al., 1999) and its possible overlapping with the next gestation period (Wells & Scott, 1999) are well established. This long-term association between juveniles and lactating females may explain differences in the diet of females. This agrees with the different composition of the diet for lactating females found in South Africa (Cockroft & Ross, 1990).

According to Wells & Scott (1999) the area which calves, juveniles and some adult females inhabit may correspond to a more near-shore region, that agrees with the inhabiting zone deduced in this study from the ontogenic distribution of hakes which reach deeper levels along the slope (Orsi Relini et al., 1992; D'Onghia et al., 1995). The absence of benthic cephalopods in the juvenile diet may be attributed to the more limited physiological ability of the young to dive deep (Le Boeuf et al., 1996; Dearolf et al., 2000) and/or a greater difficulty in capturing benthic prey (Bowen & Siniff, 1999) as has been shown for other marine mammals.

It is concluded that there are ontogenic and sexual intraspecific differences in the diet of bottlenose dolphin in the western Mediterranean and it is possible to infer interdependence between feeding and social behaviour of this dolphin as in other marine mammals (Wells et al., 1999; Bowen & Siniff, 1999). More studies are required to establish the causes behind this intraspecific variability and to understand the differential habitat use according to reproductive status.

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