Diet of dusky dolphins, *Lagenorhynchus obscurus*, in waters off Patagonia, Argentina

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The dusky dolphin, *Lagenorhynchus obscurus*, is probably the best known species of the genus *Lagenorhynchus* in the Southern Hemisphere. It is common in temperate waters of New Zealand, South Africa, Peru, northern Chile, and Argentina (Crespo, 1991; Van Waerebeek, 1992; Crespo et al., in press). Incidental catches have been recorded in coastal and offshore fisheries of Argentina (Corcuera et al., 1994; Crespo et al., 1994a, 1994b; Dans et al., in press), whereas directed captures have occurred off Peru (Read et al., 1988; Van Waerebeek and Reyes, 1990; Reyes, 1992).

The biology of dusky dolphins has been studied in Argentina since the 1970's (Würsig and Würsig, 1980; Würsig and Bastida, 1986; Dans et al., 1993). A detailed behavioral study was carried out at Península Valdés (Würsig and Würsig, 1980), and preliminary information about the reproductive biology of females was obtained by Dans et al. (1993, 1997).

Feeding habits have been briefly described for dusky dolphins from New Zealand (Gaskin, 1972), Patagonia (Dans et al., 1993; Crespo et al., 1994c), and Antarctic and sub-Antarctic waters (Goodall and Galeazzi, 1985). In Patagonia, the behavior of dusky dolphins feeding on Argentine anchovy, *Engraulis anchoita*, schools has been described by Würsig and Würsig (1980). A more recent and detailed study of their feeding habits by stomach content analysis was carried out in coastal waters of central Peru (McKinnon, 1994). The Peruvian sample consisted of animals caught mostly in gill nets (McKinnon, 1994). Peruvian anchoveta, *Engraulis ringens*, was the most important prey species for Peruvian dusky dolphins, accounting for 92.5% in number and 83.8% in weight of the total sample, and 97.8% frequency of occurrence (McKinnon, 1994). Differences in diet between lactating and nonlactating mature females were not found, and the anchoveta was almost the exclusive prey species in both sexes (McKinnon, 1994).

The objective of the present study is to describe the diet of the dusky dolphin in Patagonia in terms of both species composition and prey size. Seasonal and annual composition were not investigated because the sample size was small when subdivided along these lines.

Materials and methods

The sample consisted of 25 dolphins (6 males and 19 females) caught incidentally between November 1989 and April 1994 by the trawling fishery that operates over the Patagonian Continental Shelf. All dolphins were caught in the area between 43°S and 46°30'S and between the coastline and the 100-m isobath. Most individuals were frozen onboard to –20°C when they were caught.

The total weight, standard length, and other body measurements (Norris, 1961) were recorded for each dolphin before dissections were made. Stomach contents were collected and then stored, either frozen or in 70% alcohol. They were separated with several sieves with a mesh size between 25 mm and 0.5 mm. Flesh material from the sieved contents was placed in a deep, water-filled plastic tray, enabling removal of the remaining flesh material. Otoliths, fish bones, and cephalopod beaks were identified with the aid of published catalogues (Clarke, 1962, 1980, 1986; Torno, 1976; Menni et al., 1984; Roper et al., 1984; Boschi et al., 1992; Gosztonyi and Kuba[1]) and a reference collection of otoliths, cephalopod beaks, and crustaceans belonging to the Marine Mammals Laboratory, Centro Nacional Patagónico, CONICET.

The number of individuals of a particular fish species (NF) found in a stomach was calculated as

[1] Gosztonyi, A., and L. Kuba. 1996. Atlas de huesos craneales y de la cintura escapular de peces costeros patagónicos. Plan de Manejo Integrado de la Zona Costera Patagonica (PMIZCP), Global Environmental Facility (GEF), Programa de las Naciones Unidas para el Desarrollo (PNUD), Wildlife Conservation Soc. (WCS), and Fundación Patagonia Natural (FPN) Informe Técnico 4, 29 p.

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Fishery Bulletin 96:366–374 (1998).

$$NF = LO + 0.5NO, \quad \text{if } LO > RO,$$

or as

$$NF = RO + 0.5NO, \quad \text{if } RO > LO,$$

where LO, RO, and NO = the number of left, right, and not assigned otoliths respectively.

Minimal number of cephalopods was obtained with maximum count of upper and lower beaks for each species.

All complete and nondigested elements (otoliths and beaks) were measured with digital calipers. Some otoliths or beaks were digested, or broken, and could not be measured. Any otolith was considered too digested to be measured if it presented rounded borders and rostrum, and an ill-defined sulcus. Around 42% of the prey items were represented by broken or digested elements. Size values for these pieces were randomly assigned from sizes of items taken from the stomach and measured. When only broken or digested elements were found in the stomach, the average individual weight of the prey species in the whole sample was used to estimate the individual weight of the items.

The length of prey items was estimated by using regressions between total length (TL) and otolith length (OL) for fishes, and between dorsal mantle length (DML) and lower rostral length (LRL), or lower hood length (LHL), for squids. Wet weight (W) was estimated from regression-estimated length of prey by using regressions between W and TL for fishes, and between W and DML for squids. Regressions for most prey species were developed during this study on the basis of materials collected from commercial hauls. All regressions were calculated as simple linear regressions. Those variables that did not have linear relationships were made linear with natural logarithms (Table 1). The TL and W of *Notothenia* sp. was estimated with *Notothenia angustifrons* regressions (Table 1). The W of *Octopus tehuelchus* was estimated with *Octopus vulgaris* regression between W and LHL (Table 1). The W of each *Semirossia tenera* was assumed to be 3 g, as was the average individual weight recorded for this species in a sample taken onboard a commercial trawler by one of the authors (N.A.G.). In one stomach (that of LO22 dolphin), only fish eye lenses and a few beaks were found. In this case, eye lenses were similar in size to those of anchovy; therefore the an-

Table 1

Equation, sample size (n), and determination coefficient (r^2) of the regressions used to estimate size and weight of prey of dusky dolphins in Patagonia. The variables used in the regressions were otolith length (OL), lower hood length (LHL), lower rostral length (LRL), total length (TL), dorsal mantle length (DML) and wet weight (W). OL, LHL, and LRL are in mm, TL and DML are in cm, and W is in g.

Scientific name	Common name	Equation	n	r^2	Source
Engraulis anchoita	Argentine anchovy	$TL = 2.368 + 3.56\ LO$	79	0.70	This study
		$W = 2.5\ 10^{-3}\ TL^{3.353}$	81	0.93	
Merluccius hubbsi	Argentine hake	$TL = 1.823\ LO^{1.072}$ if $OL<15$	447	0.93	
		$W = 4.76\ 10^{-3}\ TL^{3.061}$ if $OL<15$	469	0.92	This study
		$TL = 1.984\ LO^{1.05}$ if $OL>15$	693	0.91	
		$W = 9.72\ 10^{-3}\ TL^{2.886}$ if $OL>15$	742	0.96	
Stromateus brasiliensis	"pampanito"	$TL = 3.042\ LO^{1.159}$	51	0.98	This study
		$W = 6.418\ 10^{-4}\ TL^{3.917}$	63	0.98	
Notothenia angustifrons	Southern cod	$TL = 4.142\ LO^{0.768}$	22	0.91	Hecht, 1987
		$W = 3.73\ 10^{-6}\ (10\ TL)^{3.16}$	24	0.98	
Illex argentinus	Argentine shortfin squid	$DML = -3.178 + 5.617\ LHL$	27	0.93	This study
		$DML = 8.257\ 10^{-2} + 6.009\ LRL$	63	0.87	
		$W = 9.82\ 10^{-3}\ LDM^{3.238}$	66	0.98	
Loligo gahi	Patagonian squid	$DML = -0.712 + 4.622\ LHL$	98	0.76	This study
		$W = 2.6\ 10^{-2}\ LDM^{2.753}$	102	0.93	
Octopus vulgaris	octopus	$W = e^{1.82 + 3.03\ \mathrm{Ln}(LHL)}$	108	[1]	Clarke, 1986

[1] The determination coefficient of this regression was not available in the original source.

chovy average individual weight was used to estimate the W of these unidentified fishes. This last estimation was made to evaluate the relative contribution by weight of these unidentified fishes.

The "percent frequency of occurrence" (%FO), the "percent total number" (%N), and the "percent total wet weight" (%W) were calculated (Hyslop, 1980; Castley et al., 1991; McKinnon, 1994). The relative importance of each prey species was evaluated with the index of relative importance (IRI) (Pinkas et al., 1971), where the volumetric percentage was replaced by the %W ($IRI=(\%N+\%W)\%FO$) (Castley et al., 1991).

Results

Dolphins used in this study (Table 2) were caught mostly at night in midwater hauls for the shrimp *Pleoticus muelleri*, with the exception of LO10 and LO23 dolphins that were caught in diurnal bottom hauls for shrimp, LO22 dolphin that was captured in a diurnal bottom haul for hake, and LO26 dolphin that was caught by an unknown fishing vessel. The locations of the catches were principally in the Golfo San Jorge (approximately between 45 and 46°30'S), except LO22 dolphin that was captured in the vicinity of Isla Escondida (43°S). There is no information

Table 2

Biological information (sex, size, age, and reproductive status), number of prey species eaten, and most important prey species by weight in the stomach of each dusky dolphin considered in this study. The biological information of females (F) were taken from Dans et al. (1997) and those of males (M) were provided by S.L. Dans.[1] The date of death is approximate and indicates which dolphins were caught in the same fishing trip.

Field number	Date of death	Sex	Length (cm)	Age (years)	Reproductive status	No. of prey eaten	Important prey species in the stomach
LO01	19 Nov 89	F	158	5	immature	3	Argentine anchovy and Argentine shortfin squid
LO02	19 Nov 89	F	157	4	immature	4	Argentine shortfin squid and Argentine anchovy
LO04	27 Apr 90	F	159	6	immature	3	Argentine shortfin squid and Argentine anchovy
LO05	01 Jun 90	F	166.5	6	mature (lactating)	1	Argentine anchovy
LO06	01 Jun 90	F	174	8	mature (resting)	4	Argentine anchovy
LO07	Jul 90	M	169	6	immature	5	Argentine anchovy
LO08	Apr 92	F	161	7	mature (pregnant)	2	Argentine anchovy
LO09	Apr 92	F	174	11	mature (pregnant)	4	Argentine anchovy
LO10	08 Sep 92	F	172	3+	immature	4	Argentine shortfin squid and Argentine hake
LO11	Sep 92	F	172	7+	mature (resting)	4	Argentine anchovy
LO12	Sep 92	F	162	7+	mature (pregnant)	6	Argentine hake
LO13	Sep 92	F	170	8+	mature (resting)	5	Argentine anchovy and hake
LO14	Sep 92	F	167	7+	immature	3	Argentine hake
LO15	11 Mar 93	F	166	5	immature	2	Argentine anchovy
LO16	11 Mar 93	F	174	6	mature (pregnant)	3	Argentine anchovy
LO17	16 Mar 93	F	164	4	immature	2	Argentine anchovy
LO18	06 Apr 94	F	171	5	immature	4	Argentine anchovy
LO19	11 May 93	M	164	8	mature	3	Argentine anchovy
LO20	Sep 93	M	161	9	mature	2	Argentine hake
LO21	02 Sep 93	F	158	3	immature	4	Argentine hake
LO22	30 Oct 93	F	164	3	immature	2	Unidentified fishes
LO23	15 Oct 93	M	169	9	mature	3	Argentine shortfin squid
LO24	Mar 94	M	173	10	mature	4	Argentine anchovy
LO25	Mar 94	M	162	8+	unknown	3	Argentine anchovy
LO26	94	F	161	8	mature	5	Argentine anchovy and hake

[1] Dans, S. L. Laboratorio de Mamíferos Marinos, CENPAT (CONICET), Boulevard 3600, (9120) Puerto Madryn, Chubut, Argentina

about the location of collection of two dolphins (LO07 and LO26). The entire sample was biased toward females and it was composed of immature and mature dolphins (Table 2) (Dans et al., 1997).

Some dolphins in the sample may have been caught in the same haul because fishermen reported that occasionally more than one dolphin are caught. However, when fishermen capture several dolphins in a fishing trip (between 30 and 60 days), they may discard some of them. In these cases it is uncertain whether those dolphins caught during the same fishing trip (same date of death, see Table 2) were caught together in the same haul.

With the exception of one stomach (LO22) which contained fish eye lenses and a few beaks, all others were half full or full. On average (± standard deviation), 3.40 ±1.19 prey species per stomach were found, but only one or two of them were important by weight in the stomach (Table 2). The mean number of prey items per stomach was 148.08 ±137.91, and the mean regression-estimated ingested biomass was 2,675.63 ±1,848.44 g per stomach.

A total of 3,702 prey items belonging to eight species were found in the 25 stomach contents analyzed, including four fish and four cephalopod species. The fish species were Argentine anchovy, *Engraulis anchoita;* Argentine hake, *Merluccius hubbsi;* "pampanito," *Stromateus brasiliensis*, and the southern cod *Notothenia* sp. The cephalopods were Argentine shortfin squid, *Illex argentinus;* Patagonian squid, *Loligo gahi*, the sepiolid *Semirossia tenera;* and common octopus, *Octopus tehuelchus*.

Argentine anchovy was the most important prey species, representing 39% of prey by number, 46% by weight (Table 3). However, the most frequent prey was the Patagonian squid which was present in 84% of stomachs (Table 3). According to the IRI, the second species in importance was the Argentine shortfin squid, followed by the Patagonian squid and the Argentine hake, whereas by weight the second species was hake, followed by Argentine shortfin and Patagonian squid (Table 3). The "pampanito," octopus, and southern cod were of little importance in dusky dolphin diet (Table 3).

The Argentine anchovy had a unimodal length-frequency distribution with a mode at 16 cm (Fig. 1). Individual anchovies eaten by dusky dolphins were mostly of mature sizes (Hansen, 1994).

Both Argentine shortfin and Patagonian squids were consumed at small sizes. Patagonian squids had a modal DML of 3 cm (Fig. 2), and most of them were smaller than 8 cm, a size that corresponded to that of immature squid (Hatfield et al., 1990). The DML frequency distribution of shortfin squid showed two important peaks at 1–2 cm, and 7–8 cm of DML (Fig. 3) which corresponded to juvenile sizes (Brunetti and Ivanovic, 1992).

Argentine hake showed the widest size range (Fig. 4). Its TL frequency distribution showed three peaks at 8 cm, 22–24 cm, and 36 cm in order of importance (Fig. 4). These sizes corresponded to age-0 group, age 1–2 group, and age 2–5 group, respectively (Gaggiotti and Renzi, 1990).

Average individual length of fish eaten by dusky dolphins ranged from 7.54 cm (southern cod) to 19.81 cm (Argentine hake). The DML range for cephalopod preys was estimated to be between 2 cm (observed DML of *S. tenera*) and 6.35 cm (shortfin squid).

Table 3

Relative importance of prey species of dusky dolphins in the Patagonian continental shelf.

	Percent total number (%N)	Percent total wet weight (%W)	Percent frequency of occurrence (%FO)	Index of relative importance (IRI)
Cephalopods				
Illex argentinus	30.71	21.05	68.00	3,520.11
Loligo gahi	20.64	4.58	84.00	2,118.09
Semirossia tenera	3.40	0.57	36.00	142.87
Octopus tehuelchus	0.05	0.00	4.00	0.22
Fishes				
Engraulis anchoita	39.25	46.36	80.00	6,848.60
Merluccius hubbsi	5.19	26.46	48.00	1,518.82
Stromateus brasiliensis	0.14	0.29	12.00	5.05
Notothenia sp.	0.03	0.00	4.00	0.11
Unidentified fishes	0.59	0.70	4.00	5.18
Total	100.00	100.01		

For all prey species, average individual length was smaller than 20 cm.

Average individual wet weights of Argentine shortfin squid, Patagonian squid, Argentine hake, and Argentine anchovy ranged from 4 to 92 g. The Argentine anchovy, Argentine hake, and Argentine shortfin squid had an average individual wet weight (± standard deviation) of 21.34 ±7.49, 92.17 ±121.62, and 12.39 ±33.62 g, respectively.

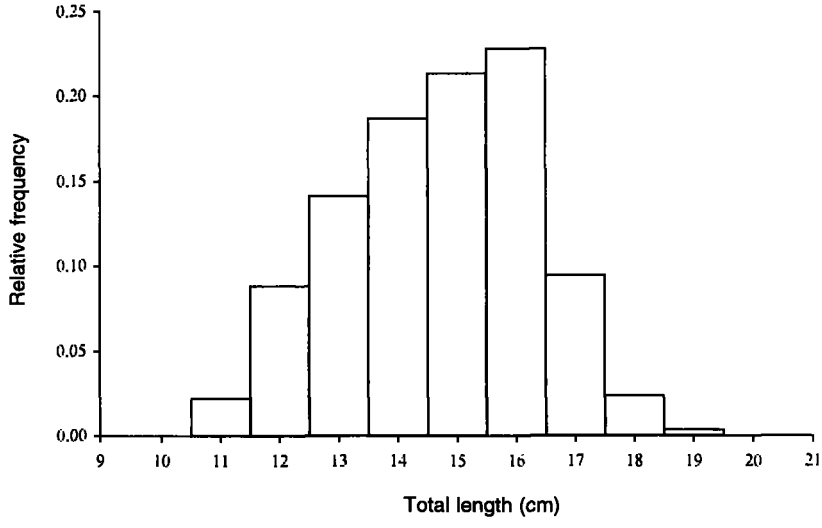

Figure 1

Length-frequency distribution of Argentine anchovy, *Engraulis anchoita*, eaten by dusky dolphins in Patagonia.

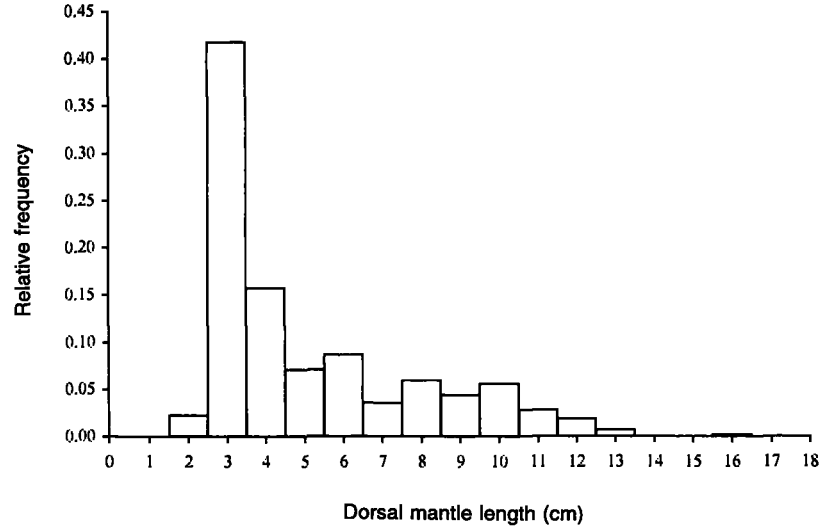

Figure 2

Length-frequency distribution of Patagonian squid, *Loligo gahi*, eaten by dusky dolphins in Patagonia.

Discussion

Patagonian dusky dolphins fed mostly on pelagic species or pelagic stages of demersal species. Argentine anchovy is typically a pelagic species (Brandhorst et al., 1974; Angelescu, 1982; Angelescu and Anganuzzi, 1986; UNESCO, 1990), and Argentine shortfin squid, Patagonian squid, Argentine hake, and "pampanito" are demersal-pelagic species (FAO, 1983; Angelescu and Prenski, 1987; Nigmatullin, 1989; Hatfield et al., 1990; Rodhouse and Hatfield, 1990; Brunetti and Ivanovic, 1992). The sepiolid and southern cod are demersal-benthic species, whereas common octopus is benthic (Roper et al., 1984; Angelescu and Prenski, 1987).

Anchovies are the main food item for dusky dolphins in Argentine and Peruvian waters. *Engraulis ringens* was found to be the principal prey species for dusky dolphins in waters off Peru (McKinnon, 1994), and this study shows that *E. anchoita* is the most important prey species in Argentine waters. Furthermore, squids were the second prey by numbers (*I. argentinus* and *L. gahi* in Argentine waters, and *L. gahi* and *Dosidicas gigas* in Peruvian waters) and hakes were rated second by weight (*M. hubbsi* and *Merluccius gayi* in Argentine and Peruvian waters respectively) (McKinnon, 1994). Moreover, the number of commonly eaten and important prey species (by weight) was quite similar between Argentine and Peruvian dusky dolphins (4 and 6 prey species respectively), considering the difference in the sample size in this work (n=25) and that in McKinnon's (1994) study (n=136). Both populations of the dusky

dolphin feed on ecologically similar species, mostly schooling fishes. However, whereas anchoveta represented 80% in weight of the diet of Peruvian dolphins, Argentine anchovy represented between 40% and 50% in weight of the diet of Argentine dolphins.

Sample size in this study is relatively small and possibly biased by age and sex (Dans et al., 1997; in press). However, our sample included mature and immature dolphins of both sexes, and all the stomach contents were very similar in composition (Table 2). Moreover, dusky dolphins had never been reported to be feeding around fishing vessels on discards and disturbed fish, even when the dolphins in this sample were caught by shrimp trawlers. Furthermore, the diet composition of Peruvian dusky dolphins did not show any difference between sexes or reproductive status (McKinnon, 1994). At Península Valdés, dusky dolphin feeding groups consisted of individuals of both sexes and of almost all age classes (calves and small young could be excluded from the feeding group) (Würsig and Würsig, 1980). Therefore, considering the general similarities in diet composition between Argentine and Peruvian populations, the absence of differences in the diet between sexes and reproductive status in the Peruvian population, the lack of evidence to suggest that dolphins feed on discards and disturbed fishes, and the gregarious feeding behavior of patagonian dusky dolphins described by Würsig and Würsig (1980), we conclude that the sample analyzed in this study is a reasonable indicator of diet composition of dusky dolphins in Argentine waters.

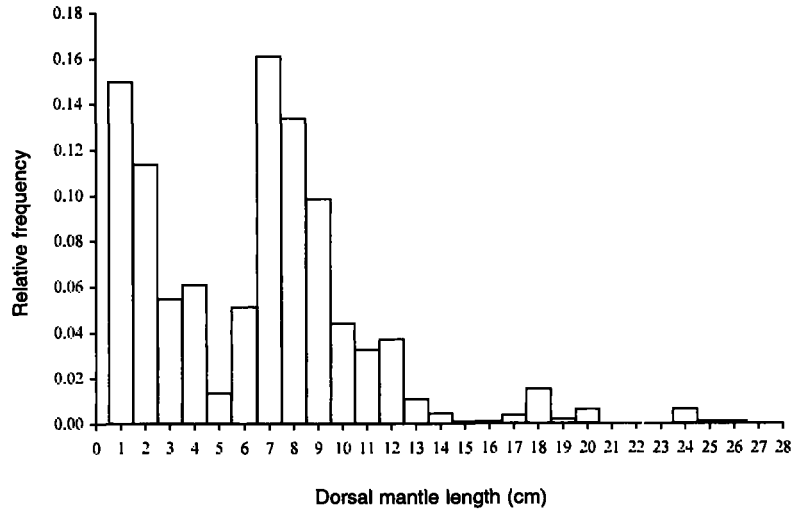

Figure 3

Length-frequency distribution of Argentine shortfin squid, *Illex argentinus*, eaten by dusky dolphins in Patagonia.

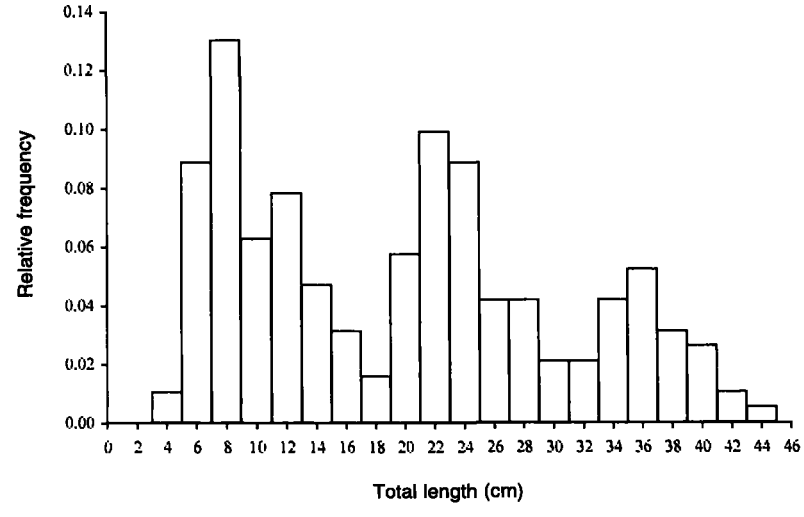

Figure 4

Length-frequency distribution of Argentine hake, *Merluccius hubbsi*, eaten by dusky dolphins in Patagonia.

At least two populations of Argentine anchovy have been reported over the Argentine Continental Shelf: the bonaerensis (northern) and the Patagonian (southern) stocks (Brandhorst et al., 1974; Angelescu, 1982; Angelescu and Anganuzzi, 1986; UNESCO, 1990; Hansen, 1994). Preadults and adults of the bonaerensis stock migrate northwest from coastal spawning areas to offshore feeding grounds; available information indicates that the Patagonian stock, however, does not show a seasonal migration (Brandhorst et al., 1974; Angelescu, 1982; Angelescu and Anganuzzi, 1986; UNESCO, 1990; Hansen,

1994). Dolphins in this study were caught off central Patagonia throughout the year between 43°S and 46°30'S; thus dusky dolphins appear to feed on Argentine anchovies from the Patagonian stock. The absence of a well-defined seasonal migration pattern in Argentine dusky dolphins (Würsig and Würsig, 1980) could be related to predation on the Patagonian stock of Argentine anchovy. However, long-distance movements of two dusky dolphins have been recorded after several years in Argentine waters (Würsig and Bastida, 1986).

The Argentine shortfin squid is a neritic-oceanic species, distributed from 30°S to 54°S (Rodhouse and Hatfield, 1990). At least three spawning stocks, 1) the bonaerensis to north Patagonian (early winter), 2) the south Patagonian (winter), and 3) the summer spawning stock (Nigmatullin, 1989; Brunetti et al., 1991; Brunetti and Ivanovic, 1992) have been described over the Argentine Continental Shelf. The latter spends its entire life cycle over the continental shelf, the former two have their spawning grounds on the shelf break and in oceanic waters. Their larvae and juveniles grow and mature over the continental shelf (Nigmatullin, 1989; Rodhouse and Hatfield, 1990; Brunetti and Ivanovic, 1992). The shortfin squids captured by dolphins could belong to any of the spawning stocks because their distributions overlap in the area where dolphins were caught. In addition, the size of squids eaten by dolphins corresponds with that for juvenile squids from all spawning stocks. These juvenile squids are pelagic (Brunetti and Ivanovic, 1992; Ivanovic and Brunetti,1994) and can be found mostly between the 50- and 100-m isobaths (Brunetti and Ivanovic, 1992).

The Patagonian squid is a neritic species and its life cycle is associated with the Malvinas Current over the continental shelf and slope (Hatfield et al., 1990). Its spawning grounds are in shallow and coastal waters, and it migrates to deeper waters to grow, reaching maturity at sizes larger than 10 cm of DML (Hatfield et al., 1990). Patagonian squids eaten by dusky dolphins were mostly of small size; thus feeding on this species could occur as juveniles migrate from the coastal area to deeper feeding grounds beyond the shelf break.

The main TL peak for Argentine hake eaten by dolphins corresponds to the age-0 group. This group exhibits pelagic schooling behavior (Angelescu and Prenski, 1987). Moreover, juveniles do not follow the adult hake migration pattern but remain in their nursery grounds (south of the Golfo San Jorge and Isla Escondida area) (Angelescu and Prenski, 1987).

In sum, these results indicate that dusky dolphins of Patagonia feed mostly on species whose stages exhibit pelagic and schooling behavior.

Finally, Argentine hake, Argentive anchovy, and squids are key species in the trophic web of the Patagonian Continental Shelf ecosystem and seem to present some degree of association (Angelescu and Prenski, 1987). Peneid crustaceans, like the shrimp, appear to be associated with these species in the study area even when their abundance is comparatively less (Angelescu and Prenski, 1987). Shrimp were not found in dolphins stomachs, even when they were caught incidentally in shrimp hauls. There are no data about the behavior of the dolphins at the moment of the catch, but the absence of shrimp in the diet suggests that dolphins avoid shrimp as a prey.

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