Feeding habits of two sympatric dolphin species off North Patagonia, Argentina

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Among marine mammals, small cetaceans have received more attention due to operational interactions with fisheries and the subsequent incidental catch of many species around the world. Even though marine mammals can be considered top predators, their role as consumers and the effects of this consumption on species

interactions and community structure are little known. Since small cetaceans can feed at lower trophic levels or take smaller sizes of prey than fisheries, competitive effects have been considered less important. However many species, and especially those with pelagic habits, can be consuming "forage fish" species, and then interactions with fisheries and their effects may be indirect but important, instead of negligible (Crespo and Hall 2001).

In the western South Atlantic, short-beaked common dolphins, *Delphinus delphis*, and dusky dolphins, *Lagenorhynchus obscurus*, are the most abundant small cetaceans (Crespo and Dans 2008). The common dolphin is a widely distributed species that inhabits temperate, subtropical, and tropical habitats (Evans 1994, Perrin 2002), while dusky dolphins are restricted to cold temperate waters in the southern hemisphere (Van Waerebeek 1992, Crespo *et al.* 1997). However, in North Patagonian waters (35°–43°S) both species occur together. In this area of sympatry, aggregations of two dolphin species are frequently observed together with sea lions, *Otaria byronia*, and several species of seabirds, such as shearwaters (*Puffinus griseus, Puffinus gravis*), penguins (*Spheniscus magellanicus*), gulls (*Larus dominicanus, Larus atlanticus*), and terns (*Sterna hirundinacea*), composing an assemblage feeding on pelagic schooling fishes (Crespo and Dans 2008).

Information about common dolphins feeding ecology in the southwest Atlantic is lacking. On the other hand, dusky dolphins cooperative foraging behavior was well studied in a closed bay off the Patagonian coast (Würsig and Würsig 1980), and more detailed studies of feeding habits were done through the analysis of stomach contents of animals incidentally caught in fishing nets (Koen Alonso *et al.* 1998). Both species feed in herds from few tens to several hundred individuals mainly on schooling fish and squid (Koen Alonso *et al.* 1998, Perrin 2002). Although sympatric associations between these dolphin species have been reported, feeding habits of these interacting species have not been studied in great detail.

The marine community of North Patagonia has undergone an increase in fishing effort since the 1970s, with the development of several high-sea fisheries that target hake, *Merluccius hubbsi*, and squid, *Ilex argentinus*. When the first signs of overexploitation appeared at the end of the 1990s alternative target species like the Argentine anchovy, *Engraulis anchoita*, started to be explored. Even though the effort was low, the use of mid-water trawls on this target led to the highest probability of dolphin entanglement among all the types of fishing gear. Both common and dusky dolphins were affected suggesting an overlap in time and space of these delphinids, their prey, and the fishery (Crespo *et al.* 2000).

This paper provides an appraisal of the diet and feeding habits of common and dusky dolphins, two sympatric species inhabiting North Patagonia, in order to analyze how these species are using the available food resources.

For the diet analysis, 30 stomachs of common dolphins were collected in 1999 and in 2003–2009 along the northern area off Patagonia (Table 1). The animals were obtained from two sources: strandings (6 females and 3 males) and fisheries bycatch (7 females and 14 males). The bycatch was mostly by mid-water trawlers targeting Argentine anchovy, but one dolphin was caught by a hake mid-water longline vessel. Eighteen were caught in January 1999, between 40°30′–41°30′S and 61°00′–61°40′W (shown with a box in Fig. 1).

Diet composition of dusky dolphins was based on the analysis of contents of 31 stomachs. Information was available from the study of feeding habits of dusky dolphins by Koen Alonso *et al.* (1998), as well as additional individuals collected more recently (Table 1). For comparison purposes, the sample was split in two subsets,

Table 1. Summary of stomach contents analysis from common dolphins, *D. delphis*, off North Patagonia. For comparison purposes, information from dusky dolphins, *L. obscurus*, by region is also summarized.

	D. delphis	*L. obscurus*	
Region	North Patagonia	North Patagonia	Central Patagonia
Sampling interval	1999–2009	1998–2009	1989–1994
Sample size	13 females	2 female	19 females
	17 males	3 males	7 males
Standard Length range (cm)	170–220	164–175	157–174
Age range (GLGs)	2—18	5–12	3–11
Sample sources	Incidental catch 21	Incidental catch 3	Incidental catch 25
	Dead ashore 7	Dead ashore 2	Unknown 1
Number of stomachs containing prey items	27	5	25
Total number of individual prey	1,946	618	3,702
Number of prey species	15 (+3 unidentified)	9	8 (+1 unidentified)
Most frequent prey species %FO	*E. anchoita*	*E. anchoita*	*Loligo gahi*
Most important prey species %W	*E. anchoita*	*E. anchoita*	*E. anchoita*
Most important prey species %N	*E. anchoita*	*E. anchoita*	*E. anchoita*

GLGs: growth layer groups; %FO: percent frequency of occurrence; %N: percentage by number; %W: percentage by estimated wet weight.

those individuals from the area where common and dusky dolphins distributions overlap (North Patagonia, analyzed in the present study) and those from farther south than $43°$S, where only dusky dolphins occur (analyzed by Koen Alonso *et al.* 1998). The samples from the overlap area came from strandings (2 males) as well as fishery bycatch (2 females and 1 male), while the more southerly sample came from bycatch (19 females and 7 males), with the exception of one individual from unknown origin.

Standard length (SL, cm) was recorded before necropsy. Whole stomachs were removed and stored deep-frozen ($-20°$C) in polyethylene bags. Age of each individual was determined from growth layer groups (GLG) in teeth (on the assumption of one GLG/yr).

The stomach contents were thawed and sorted using sieves of different mesh size (from 0.5 to 10 mm). The rarely found intact prey were immediately identified, measured with Vernier calipers (± 0.01 mm) and weighed with an Ohaus electric balance (± 0.01 g). Diagnostic hard parts (otoliths, bones, and cephalopod beaks) were retrieved and stored in 70% ethanol. All prey remains were identified to the lowest possible taxonomic level using the reference collection of the Marine Mammals Laboratory (CENPAT-CONICET, Puerto Madryn, Argentina) and published catalogs (Clarke 1986, Gosztonyi and Kuba 1996, Volpedo and Echevarría 2000).

The total number of consumed fish was determined from counts of left, right and unassigned otoliths. The minimal number per species was obtained as the sum of
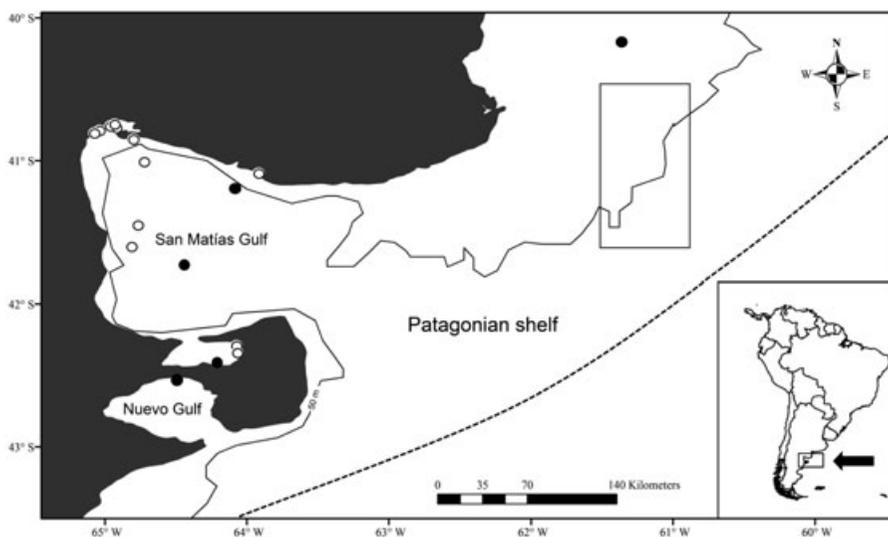
Figure 1. Study area. The empty circles and the box indicate common dolphin, *D. delphis*, sampling sites and the filled circles indicates northern dusky dolphin, *L. obscurus*, sampling sites. The broken line shows the boundary between Argentine (northern) and Magallanic (southern) zoogeographic provinces (Balech and Ehrlich 2008).

half the number of otoliths rounded up to the nearest whole number. The number of cephalopods was estimated as the maximum number of lower or upper beaks (Pierce and Boyle 1991). The size (total length [TL] of fish and dorsal mantle length [DML] of squid in cm) and wet weight (g) of prey was estimated from hard parts with allometric regression (Pineda *et al.* 1996, Koen Alonso *et al.* 2000).

To minimize the underestimation of length or weight, only undamaged otoliths and beaks were measured. When digested or broken pieces were found in a stomach, the measurements for these elements were assigned from a random sample of undigested and whole parts from the same stomach (Koen Alonso *et al.* 1998).

The importance of prey was determined using the percent frequency of occurrence (*%FO*), the percentage by number (*%n*), the percentage by estimated wet weight (*%W*) and the Index of Relative Importance (*%IRI*; Cortés 1997). The *%FO* was defined as 100 multiplied by the number of stomachs in which a prey species was present, divided by the total number of full stomachs in the sample. The *%n* was calculated as 100 multiplied by the quotient between the number of individuals of a species of prey and the sum of individuals for all prey species. The *%W* was obtained in a similar way as the *%n* but replacing the numbers by the regression-estimated weights (Hyslop 1980). *IRI* ((*%W* + *%n*) × *%FO*) is a commonly used index that provides a summary of dietary composition (Koen Alonso *et al.* 2000).

These indices were calculated by species, major taxonomic groups (fish, mollusks and annelids) and ecological groups. The ecological groups considered were *pelagic*, *benthic*, and *demersal*. The latter group was divided into demersal-pelagic (with a daily vertical migration pattern, dispersing in the water column during the night and remaining close to the bottom during daylight hours) and demersal-benthic (no vertical migration).

To account for uncertainty due to sampling, nonparametric 95% confidence intervals (95% CI) for *%n* and *%W* were generated by bootstrapping (Efron 1979) using Microsoft QBasic. Random samples were drawn with replacement 1,000 times.

Spearman rank correlation (r_s) was used to evaluate the relationship between predator and prey sizes (Conover 1999). The variables considered in this analysis were predator SL and estimated length of prey, excluding the highly digested ones. The sample size was too small to allow examination of some factors that can influence diet, *e.g.*, sex, maturity, season, and year.

Feeding strategy was assessed by the Costello graphical method (Costello 1990) as modified by Amundsen *et al.* (1996). This method is based on a two-dimensional representation, where each point relates the *%FO* of a prey taxon to its prey-specific abundance (*%P*; Eq. 1).

$$\%P_i = (\Sigma_i S_i / \Sigma_{ti} S_{ti}) \times 100 \tag{1}$$

where $\Sigma_i S_i$ = total of prey i (expressed in number in this study), and $\Sigma_{ti} S_{ti}$ = total of prey (expressed in number) in the stomachs with prey i.

The interpretation of Amundsen's diagram can be obtained by examining the distribution of points along the diagonals and axes of the graph. The diagonal from the lower left to the upper right corner provides a measure of prey importance, with dominant prey at the top and rare or unimportant prey at the lower end. The vertical axis represents the feeding strategy of the predator in terms of specialization or generalization. In general, predators have specialized on prey positioned in the upper part of the graph, whereas prey positioned in the lower part have been eaten only occasionally. Prey points located at the upper left of the diagram would be indicative of specialization by individual predators, and those in the upper right would represent specialization by the predator population.

Common dolphin body size ranged from 170 to 220 cm, and estimated age ranged from 2 to 18 yr. With the exception of three stomachs (Del.del. 024, 025, and 040) which were empty, all others contained food remains. In general, stomach contents were in an advanced state of digestion, being mostly composed of hard parts (beaks, bones, and otoliths). A total of 1,946 individual prey were retrieved, and the total estimated biomass was 41.5 kg with a mean ± SE of 1.5 ± 0.2 kg per stomach. The mean number of prey items per stomach was 72.1 ± 23.1. The mean number of individual prey per stomach was 90.2 ± 28.5 for bycaught animals and 7.3 ± 3.8 for stranded animals.

Twelve species of fish and three species of cephalopods were identified from food remains (Table 2). The mean number of prey species per stomach was 3.6 ± 0.2. Both taxonomic groups were found in more than 92% of the stomach examined, although fish were more important (*IRI%* = 85.8%). Argentine anchovy, *Engraulis anchoita*, was the primary prey and represented 80.8% in number and 62.6% in weight of the total, with an overall occurrence of 81.5%. South American (SA) long-fin squid, *Loligo sanpaulensis*, ranked second in importance and made up 6.4% of the total number and 16.7% of the total weight of prey, with an overall occurrence of 74.1%. In *IRI%* the two species combined reached a value close to 95% (anchovy = 82.3% and squid = 12.1%). Of the remaining species, only the silver warehou, *Seriolella porosa*, had an *IRI%* greater than 1% in the pooled sample.

In terms of ecological groups, the pelagic species dominated the diet, mainly due to the large contribution of Argentine anchovy. The demersal-pelagic species ranked second in importance, due to the contribution of cephalopods and silver warehou.

Table 2. Diet composition of the common dolphin *Delphinus delphis* and the dusky dolphin *Lagenorhynchus obscurus* off North Patagonia. EG: ecological group of the prey (B: benthic, DB: demersal-benthic, DP: demersal-pelagic, P: pelagic, NA: not assigned), %FO: percent frequency of occurrence; %n: percentage by number; %W: percentage by regression-estimated wet weight; %IRI: percent of Index of Relative Importance; n: number of prey items; CI: confidence intervals.

		D. delphis							*L. obscurus*						
			Composition by number		Composition by mass					Composition by number		Composition by mass			
	EG	%FO	%n	CI	%W	CI	%IRI	n	%FO	%n	CI	%W	CI	%IRI	n
Fish		**92.59**	**92.24**		**80.34**		**85.82**		**100**	**91.26**		**84.51**		**93.57**	
E. anchoita	P	81.48	80.88	58.76–90.74	62.59	47.59–75.92	82.67	1,574	100	85.11	72.10–94.65	59.5	29.92–77.57	85.15	526
S. porosa	DP	33.33	4.62	1.06–12.90	7.04	2.06–14.88	2.75	90	60	0.97	0.32–5.10	8.37	1.23–43.37	3.3	6
C. guatucupa	DB	37.04	0.92	0.34–1.95	1.49	0.64–2.57	0.63	18							
M. hubbsi	DP	18.52	1.75	0.25–5.47	3.03	0.42–6.88	0.63	34	40	4.05	0.00–9.85	9.61	0.00–34.69	3.22	25
R. brasiliensis	DB	14.81	2.31	0.07–7.65	0.56	0.02–1.80	0.3	45							
P. brasiliensis	DB	7.41	0.31	0.00–1.45	3.13	0.00–9.12	0.18	6							
S. brasiliensis	DP	14.81	0.26	0.04–0.62	1.1	0.00–3.55	0.14	5	40	0.97	0.00–1.71	7.01	0.00–8.95	1.88	6
S. incisa	P	7.41	0.41	0.00–1.50	0.29	0.00–0.80	0.04	8							
P. pagrus	DP	3.7	0.15	0.00–0.64	0.58	0.00–1.92	0.02	3							
T. picturatus	P	7.41	0.1	0.00–0.38	0.24	0.00–0.74	0.02	2							
B. albescens	DB	3.7	0.15	0.00–0.65	0.27	0.00–1.13	0.01	3							
M. magellanicus	P								20	0.16	0.00–0.41	0.02	0.00–0.07	0.02	1
Flounder sp.	B	3.7	0.05	0.00–0.21	0.02	0.00–0.09	0	1							
Unknown fish sp. 1	NA	11.11	0.15	0.00–0.44				3							
Unknown fish sp. 2	NA	3.7	0.15	0.00–0.66				3							
Cephalopods		**96.3**	**7.76**		**19.66**		**14.18**		**100**	**6.8**		**15.49**		**6.43**	
L. sanpaulensis	DP	74.07	6.37	2.55–15.26	16.72	8.91–28.70	12.1	124	60	5.99	0.14–14.74	4.07	0.10–13.94	3.55	37
L. gahi	DP	18.52	1.03	0.17–3.35	1.33	0.09–3.48	0.31	20							
I. argentinus	DP	14.81	0.31	0.09–0.76	1.6	0.03–4.72	0.2	6	40	0.49	0.00–0.92	11.39	0.00–18.41	2.8	3
S. tenera	DB								40	0.32	0.00–0.97	0.04	0.00–0.14	0.08	2
Unknown ceph. sp. 1	NA	3.7	0.05	0.00–0.26				1							
Annelids															
Eunereis patagonica	P								40	1.94	0.00–4.40				12
								1,946							618

Stripped weakfish, *Cynoscion guatucupa*, occurred in more than 37% of the stomachs and determined the high frequency of occurrence of demersal-benthic group.

The overall estimated length of prey taken ranged from 4.5 to 37.0 cm and the estimated weight range was 0.7–416.1 g. Ninety-eight percent of the prey eaten by the common dolphins were concentrated in classes ranging between 10 and 25 cm, and modal individual mass was less than 50 g. These small prey were pelagic fish and cephalopods, and the tail of the length distribution was formed by Argentine hake, *M. hubbsi*, and conger, *Bassanago albescens*.

At the prey species level, the Argentine anchovy consumed by common dolphins had a mean length of 12.7 ± 3.5 cm. The length-frequency distribution (Fig. S1) was bimodal with modes at 9 and 17 cm. The minor mode, including juveniles, corresponded to anchovy consumed by coastal common dolphins. The anchovy eaten by offshore common dolphins were mostly mature (Hansen 1994), over 13–14 cm. SA long-fin squid showed a unimodal length-frequency distribution (Fig. S2) with a mean of 12.2 ± 2.6 cm and a mode at 13 cm of DML. These sizes corresponded to mature individuals (Barón and Ré 2002). Silver warehou ranged from 8.5 to 16.7 cm (Fig. S3), with a mean of 13.5 ± 1.8 cm and a peak at 14 cm, which comprised juvenile sizes (Perier and Di Giácomo 2002).

No relationship was found between length of prey and predator SL ($r_s = 0.09$, $n = 1,899$, $P > 0.05$). Average individual wet weight of anchovy, SA long-fin squid and silver warehou was 16.5 ± 13, 55.9 ± 29.6 and 32.5 ± 10.9 g, respectively.

Dusky dolphin body size ranged from 157 to 175 cm, and estimated age ranged from 3.5 to 11 yr. All stomachs analyzed contained food remains. The total number of prey found in northern dusky dolphins was 618 and the total estimated biomass was 16.5 kg. The mean number of prey items per stomach was 123.6 ± 52.3, and there was no difference in prey number per stomach between stranded and bycaught individuals.

The stomach contents were composed almost exclusively of fish, which made up 93.5% of the prey (5 species, 564 individuals), while the remainder was composed of squids (3 species, 42 individuals) and one species of annelid (12 individuals; Table 2). Argentine anchovy was the most frequent prey, occurring in all the stomachs and representing 59.5% of the estimated weight and 85.1% of the total number of prey. SA long-fin squid was the second most important prey, representing 5.9% of the total number and 4.1% of the total weight of prey ingested, with an overall occurrence of 60%. Silver warehou, hake and Argentine short-fin squid, *Illex argentinus*, also represented important items in dusky dolphin diet, with an *IRI%* greater than 2%. In terms of ecological groups, the pelagic species dominated the diet.

The anchovy length-frequency distribution was bimodal with modes at 10 and 16 cm (Fig. S4). SA long-fin squid consumed by dusky dolphin had a DML between 2.1 and 13.6 cm (Fig. S2) whereas the silver warehou were mostly between 21 and 39 cm (Fig. S3). A low positive relationship was found between length of prey and predator SL ($r_s = 0.63$, $n = 603$, $P < 0.05$). Average individual wet weight of anchovy, SA long-fin squid and silver warehou was 18.7 ± 9.67 g, 18.2 ± 15.6 g, and 230.4 ± 188.6 g, respectively.

Analysis of the feeding strategy based on the Amundsen graphical method shows that common and dusky dolphins off North Patagonia exhibited a mixed feeding pattern with a dominance of Argentine anchovy (Fig. 2). SA long-fin squid occurred at high frequency (*%FO*) but only accounted for a small proportion of the food when present. These species in conjunction with silver warehou are categorized as common items. The prey species with a low frequency of occurrence and a low prey-specific
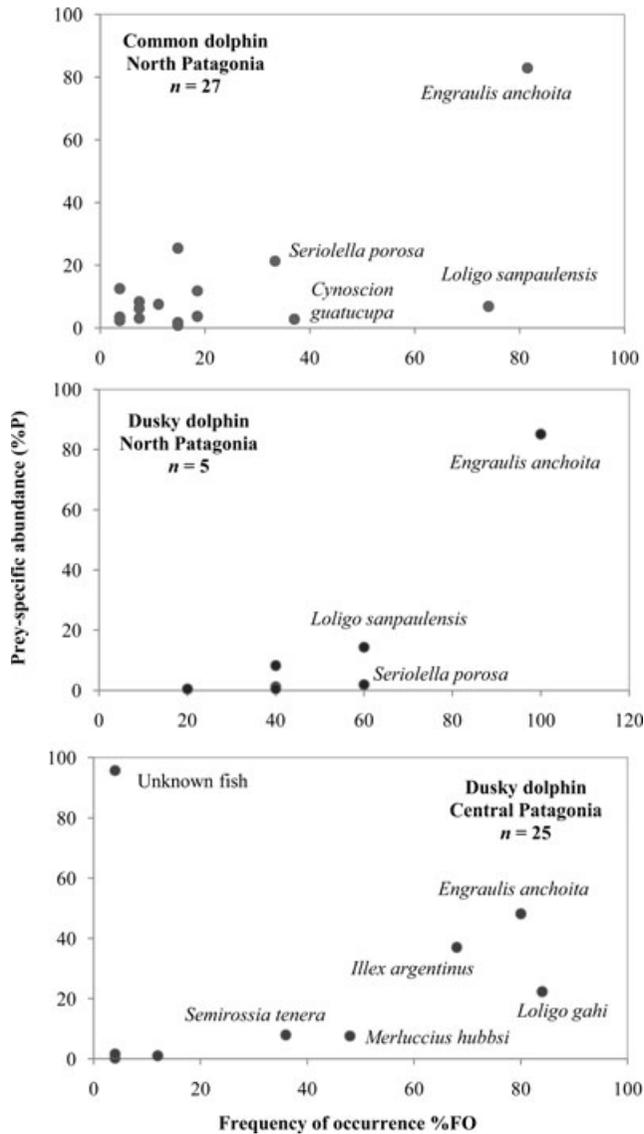
Figure 2. Amundsen diagrams, showing the feeding pattern of common dolphin, *D. delphis*, and dusky dolphin, *L. obscurus*. Prey-specific abundance (%P) in number plotted against frequency of occurrence (%FO) of prey items.

abundance (%P), located in the lower left corner, are considered complementary food items.

Comparing the information about dusky dolphins feeding in Central Patagonia (Koen Alonso *et al.* 1998) with northern samples, some differences in feeding strategy were found (Fig. 2). The southern dusky dolphins showed less preference for Argentine anchovy, with a more generalist feeding strategy. Opposite to that found

for common and dusky dolphins in North Patagonia, the diet of southern dusky dolphins was based on a mixture of fish and cephalopods in similar proportions (Koen Alonso *et al.* 1998).

The length-frequency distribution of prey consumed by each species according to its feeding area also exhibited some differences. The common and dusky dolphin samples collected in San Matías Gulf contained smaller anchovy (with a mode between 9 and 11 cm) than that found in stomachs from offshore areas (with a mode between 15 and 17 cm) (Fig. S1, S4). The silver warehou and SA long-fin squid were common items for dolphins feeding in North Patagonia. However, comparing the SA long-fin squid sizes consumed by the two dolphin species, the common dolphins fed on bigger sizes (4.5–19.0 cm) than the dusky dolphins (2.1–13.6 cm, Fig. S2). This relationship was reversed in the case of silver warehou (common dolphin: 8.5–16.7 cm; dusky dolphin: 19.7–37.5 cm) (Fig. S3).

This study represents the first attempt at quantifying the diet and feeding habits of short-beaked common dolphins, *D. delphis*, off North Patagonia, the austral limit of their distribution. It goes beyond the description of the diet of this species addressing the question of how it is sharing resources with a sympatric delphinid, the dusky dolphin, *L. obscurus*. In spite of the small sample size of this species, the description and brief quantification of the diet of dusky dolphin provides essential information for their conservation and management in an area where little is known about delphinid species.

Our results indicate that common dolphins in the southwestern South Atlantic feed primarily on Argentine anchovy, *E. anchoita*, which accounted for over 80% in number and 62% in weight of all prey taken. SA long-fin squid, *L. sanpaulensis*, also constituted an important component of common dolphin diet in this region. Although generally more than three prey species were found per stomach, anchovy and SA long-fin squid made up most of the diet representing 85 and 12%, respectively (*IRI%*). The Argentine anchovy was also the main food item in the diet of northern dusky dolphins, representing 85% (*IRI%*) of prey. This preliminary value was higher than recorded by Koen Alonso *et al.* (1998) for Central Patagonia where anchovy accounted for only 48% (*IRI%*) of diet.

Inferences on foraging habits by interpreting dietary results are often limited by the inherent biases in any methods of diet analyses (*e.g.*, da Silva and Neilson 1985, Jobling and Breiby 1986, Meynier *et al.* 2008). Dead individuals found onshore are likely to misrepresent the diet of healthy individuals because sickness and poor body condition may influence the type of prey that can be consumed (De Pierrepont *et al.* 2005). However in our sample, there were many more stomachs recovered from common dolphins caught incidentally than from stranded individuals, and in the case of northern dusky dolphins, the stranded individuals were in good condition and contained a high number of prey items.

On the other hand, the diet information could be biased depending on the degree of stomach content digestion. The use of several (and complementary) hard remains and the fact that only undamaged otoliths were measured, allowed us to reduce the bias due to the degree of stomach content digestion. Thus, estimating prey size by regressions avoided underestimating the importance of small or highly digested prey. Nevertheless, the importance of squid in the diet might be slightly overestimated due to the low digestibility rate of beaks compared with fish bones and otoliths.

In Patagonia, both dolphin species feed mainly on prey exhibiting pelagic and schooling behavior. This finding is broadly in agreement with other studies on dolphin diet. Peruvian long-beak common and dusky dolphins seem to depend

on pelagic and mesopelagic prey, mainly large schooling fish species, such as anchovy, *Engraulis ringens*, mycthophids, mote sculpin, *Normanictys crockery*, mackerel, *Trachurus picturatus*, and hake, *Merluccius gayi* (García-Godos *et al.* 2007). In the eastern North Atlantic, common dolphins forage both in oceanic and neritic habitats, preying on small schooling species available in the epipelagic layer (Pusineri *et al.* 2007). In New Zealand waters, myctophid fish and arrow squid are important food resources for New Zealand dusky dolphins (Cipriano 1992).

Another feature of the feeding behavior of the two dolphin species is that they feed mainly on the locally most abundant species. In the offshore North Pacific, the prey composition of common dolphins which consists mainly of highly abundant myctophids, may reflect the features of the subarctic front (Ohizumi *et al.* 1998). On the Portuguese coast, the sardine, *Sardina pilchardus*, was the dominant prey in the diet of common dolphins and is one of the most abundant pelagic fish off the Iberian coast (Silva 1999). In the Bay of Biscay, common dolphins feed primarily on anchovy, *Engraulis encrasicolus*, sardine, horse mackerel, *Trachurus* spp. and *Trisopterus* spp., which are abundant fish in this region and temporal variability in diet composition was associated with changes in prey availability (Meynier *et al.* 2008). The myctophid fish and arrow squid consumed by New Zealand dusky dolphins were described as very abundant and widely distributed (Robertson *et al.* 1978).

In the North Patagonia ecosystem, the Argentine anchovy, the Argentine short-fin squid, *Illex argentinus*, and the SA long-fin squid are the most important pelagic resources (Brunetti *et al.* 1998, Barón and Ré 2002, Hansen *et al.* 2009). Hence, it seems that common and dusky dolphins forage opportunistically on available prey species, but selectively based on their social behavior, prefer small schooling species. This is in broad agreement with Koen Alonso *et al.* (1998) who documented dusky dolphin feeding habits in Central Patagonia. Preying on schooling species is probably the most energetically profitable foraging tactic for a cooperative predator (Meynier *et al.* 2008).

The Argentine anchovy is distributed in waters of the Argentine continental shelf from southern Brazil (24°S) to Patagonia (48°S). This species is present in high biomass over the entire area (Angelescu 1982). Within their latitudinal range two main stocks have been reported: the Bonaerenses (northern) and Patagonian (southern) stocks (Brandhorst *et al.* 1974, Hansen *et al.* 1984). The maximum overlap between the stocks occurs during late spring and early summer, at around 41°S. It is possible that common and dusky dolphins in the sympatric zone are foraging alternatively on the Bonaerense and Patagonian anchovy stocks, depending on the migration of the anchovy stocks along the Argentine continental shelf.

The difference found in anchovy size range consumed according sample origin is concordant with results obtained from scientific surveys. Hansen (2007) studied the population size and structure of the Argentine anchovy in Patagonia and found that juveniles and small-sized adults of anchovy were prevalent in San Matías Gulf. The concordance between the size range consumed by dolphins and the availability in the environment also may support the hypothesis that dolphins feed mainly on the most abundant local resources.

The SA long-fin squid is a neritic-oceanic species, distributed from 20°S to 46°S. Its spawning grounds are in shallow and coastal waters, and it migrates to deeper waters to feed and grow (Barón and Ré 2002). In North Patagonian waters, the spawning season for this species is restricted to austral summer and early autumn. Based on the date of death of dolphins with SA long-fin squid remains in their

stomachs and the size range of squid eaten, feeding on this species may occur when spawning aggregations are formed.

In addition to both species having similar feeding habits and living in the same area, foraging interactions between common and dusky dolphins have been noted in North Patagonia. Common dolphins occasionally engage in apparent cooperative fish herding with dusky dolphins, together with sea lions and several species of seabirds (Crespo and Dans 2008, Dans *et al.* 2010). Interspecific associations between dolphins may be beneficial for at least one species (*e.g.*, increased feeding, decreased predation rates; Bearzi 2005). Field studies on dolphin sympatric associations have been mentioned in the literature, although not many of them cite mixed-species foraging aggregations (Perrin 2002, Bearzi 2005).

The high general similarity in diet composition, prey profiles and spatial distribution between common and dusky dolphins off North Patagonia could be interpreted in two ways. The similarity in the diet could cause a high degree of competition for food. However, if food availability is high enough, the two species may occur in trophic coexistence (Cowell and Futuyma 1971, Pianka 1974) as seems to apply in the North Patagonian ecosystem due to the high biomass of anchovy (Hansen *et al.* 2009). Furthermore, this high abundance of anchovy could support the mixed-species aggregations observed in the sympatric area, at least at certain times of the year.

Another possible source of competition is linked with fishery activity in the area. The Argentine anchovy represents an important economic resource, supporting a directed fishery on the Argentine continental shelf. Annual landings of southern anchovy in the last ten years have fluctuated between 2,400 and 3,300 t (Hansen *et al.* 2009). Comparing the anchovy size range consumed by dolphins and targeted by the fishery, an overlap was detected (7–20 cm in this study *vs.* 14–19 cm for anchovy caught in Patagonian waters) (Garciarena *et al.* 2002). Although the historical exploitation level of the anchovy fishery has been significantly below the biological potential for the southern stock (Hansen *et al.* 2009), if the fishery expands, there could be a potentially direct competition with the dolphins. The identification of potential hotspots of trophic overlap in North Patagonia is essential for marine mammal conservation in an ecosystem where fishery activity is growing steadily and where pelagic resources support a wide variety of predators.

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SUPPORTING INFORMATION

The following supporting information is available for this article online:

Figure S1. Length-frequency distribution of Argentine anchovy, *E. anchoita*, consumed by common dolphins, *D. delphis*, off North Patagonia. The sample set was split in two subsets: samples from San Matías Gulf and samples from offshore areas.

Figure S2. Length-frequency distribution of South American long-fin squid, *L. sanpaulensis*, eaten by common dolphins, *D. delphis*, and dusky dolphins, *L. obscurus*, off North Patagonia.

Figure S3. Length-frequency distribution of silver warehou, *S. porosa*, eaten by common dolphins, *D. delphis*, and dusky dolphins, *L. obscurus*, off North Patagonia.

Figure S4. Length-frequency distribution of Argentine anchovy, *E. anchoita*, eaten by dusky dolphins, *L. obscurus*. The sample off North Patagonia was split in two subsets: samples from San Matías Gulf and samples collected in Nuevo Gulf and offshore areas.