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Using stable isotopes to assess whether two sympatric dolphin species share trophic resources

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According to niche theory, the coexistence of sympatric species requires some degree of resource partitioning, achieved through the differential use of microhabitats, temporal variations in habitat use, or different foraging tactics (Pianka 1974, 1981; Roughgarden 1976). Sympatric species of the family Delphinidae usually differ in diet and habitat use patterns as a strategy for coexistence (Bearzi 2005, Wang *et al.* 2012), but may also form mixed groups (Quérouil *et al.* 2008, Kiszka *et al.* 2011, Browning *et al.* 2014a) to avoid predators, improve foraging efficiency, or take certain social or reproductive advantages (Stensland *et al.* 2003).

In the southwestern South Atlantic Ocean, the dusky dolphin, *Lagenorhynchus obscurus*, and the short-beaked common dolphin, *Delphinus delphis*, overlap in their distribution along the Patagonian shelf and beyond the shelf-break from 38°S to 42°S (Leatherwood and Reeves 1983, Tavares *et al.* 2010) (Fig. 1). In coastal waters, these species can be found living in sympatry in the Golfo San Matías (40°45'S and 42°14'S), although they differ in their habitat use patterns. In this sense, short-

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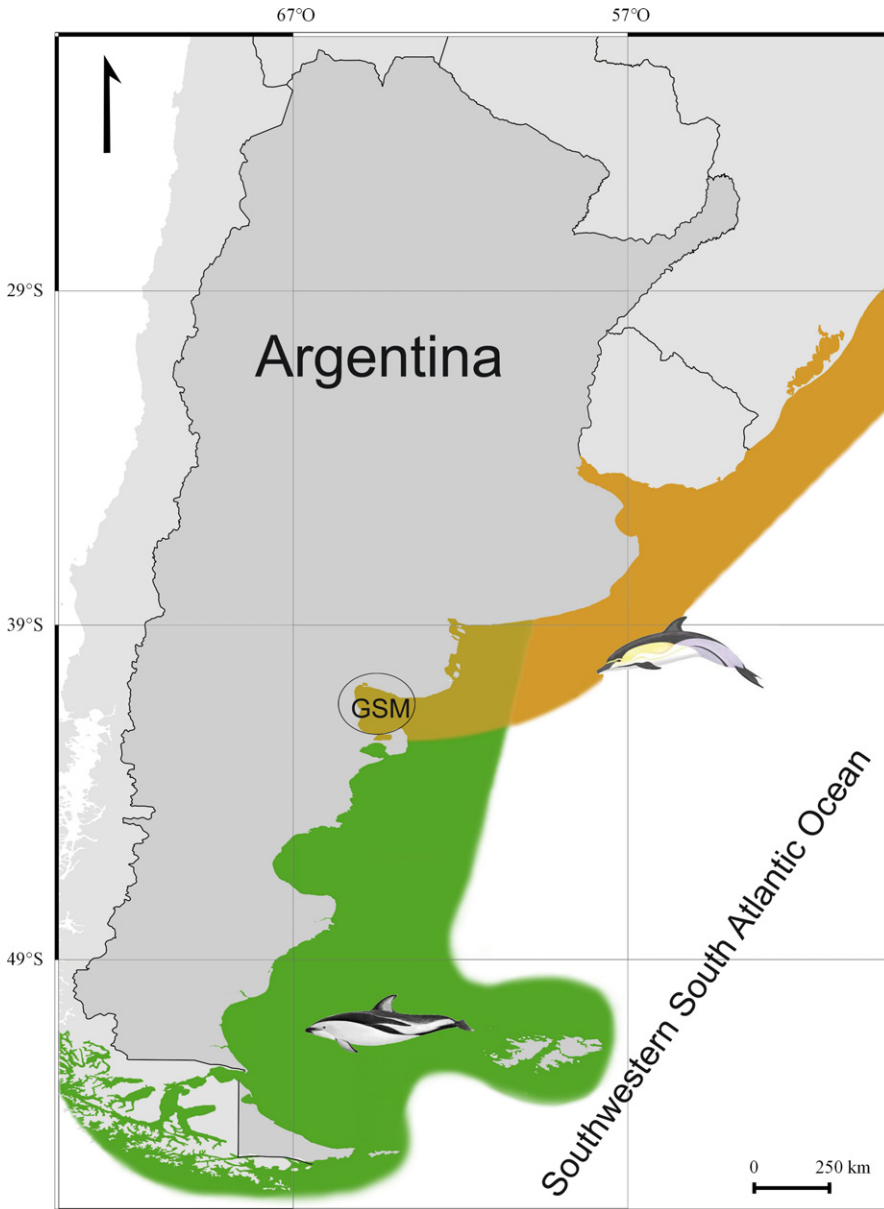


Figure 1. Distribution of the short-beaked common dolphin (orange) and the dusky dolphin (green) in the southwestern South Atlantic ocean. Overlap distribution for both species (brown). GSM: Golfo San Matías, study area (black ellipse).

beaked common dolphins prefer habitats located in the northwest section of the gulf far from the coast; whereas dusky dolphins prefer areas with steep slopes close to the coast in the southwestern sector of the gulf (Svendsen *et al.* 2015).

Stomach content analysis suggests that dusky and short-beaked common dolphins have overlapping diets, feeding primarily on small pelagic schooling fishes and squids of the same size, specifically the Argentine anchovy (*Engraulis anchoita*) and the South American long-fin squid (*Doryteuthis (Loligo) sanpaulensis*) (Koen Alonso *et al.* 1998, Romero *et al.* 2012). On the other hand, studies based on stable nitrogen and carbon isotope analysis ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) in skin suggest that both species feed on Argentine anchovy in Golfo San Matías, but dusky dolphins also feed on butterfish (*Stromateus brasiliensis*) and Argentine shortfin squid (*Illex argentinus*), whereas short-beaked common dolphins feed on Argentine hake (*Merluccius hubbsi*) and Patagonian squid (*Doryteuthis [Loligo] gahi*) (Loizaga de Castro *et al.* 2016a, b).

Despite these differences, the two species of dolphins occasionally engage in apparent cooperative fish herding (Dans *et al.* 2010). In order to better understand the trophic relationships between these two sympatric species, we have analyzed the stable nitrogen and carbon isotope ratios of individuals from a mixed group. Therefore, the goal of this study was to investigate dietary differences in two sympatric dolphin species that appear to exploit the same resource.

Stable isotope ratios are useful to reconstruct the diet of predators, but also to assess the overlap in their isotopic niches (Bearhop *et al.* 2004, Newsome *et al.* 2007). The isotopic niche can be defined as an area (in δ -space) with isotopic values (δ -values) as coordinates; the δ -space is comparable to the n -dimensional space that contains what ecologists refer to as the ecological niche (Hutchinson 1978), because an animal's chemical composition is directly influenced by what it consumes (bionomic) as well as the habitat in which it lives (scenopoetic) (Newsome *et al.* 2007). Stable isotopes of nitrogen and carbon have proven extremely useful when studying marine mammal ecology (Newsome *et al.* 2010). $\delta^{15}\text{N}$ values can provide data on trophic level (Post 2002), and also be used to indicate feeding habitats, since strong variation in $\delta^{15}\text{N}$ values has been registered between inshore and offshore systems, due to biochemical properties of the habitat (Chouvelon *et al.* 2012, Ruiz-Cooley and Gerrodette 2012). Similarly, $\delta^{13}\text{C}$ values provide information on feeding habitat (*i.e.*, inshore/benthic *vs.* offshore/pelagic habitat) but also on trophic level due to a slight prey to predator fractionation (France 1995, Rubenstein and Hobson 2004). Additionally, stable isotope ratios integrate the diet data over a range of time scales, depending on the tissue (Tieszen *et al.* 1983, Michener and Schell 1994), whereas traditional diet studies provide a snapshot of the diet (Browning *et al.* 2014b). Stable isotope ratios in the skin of cetaceans integrate dietary information over 1–3 mo (Hicks *et al.* 1985, Browning *et al.* 2014b, Giménez *et al.* 2016).

On 25 March 2009, a mixed group of dusky and short-beaked common dolphins was sighted in the Golfo San Matías (GSM; $40^{\circ}45' - 42^{\circ}14'S$, $65^{\circ}05' - 63^{\circ}48'W$) and biopsy samples (skin and blubber) were collected. The group consisted of more than 100 short-beaked common and dusky dolphins, mainly adults and juveniles engaged in slow travel during the entire survey. Biopsy samples were taken only from adult dolphins, using a biopsy pole as described by Loizaga de Castro *et al.* (2013). For each dolphin biopsy sample, blubber was removed with a scalpel blade and only skin was processed for isotopic analysis. A total of 27 skin samples; 14 from short-beaked common dolphins and 13 from dusky dolphins were analyzed.

All samples were stored in 20% dimethylsulphoxide (DMSO) solution saturated with NaCl (Amos and Hoelzel 1991). Each sample was washed in three successive rinses of deionized water to remove DMSO effects, as suggested in previous studies on marine mammals (*e.g.*, Lesage *et al.* 2010, Foote *et al.* 2012). Skin samples were dried at 60°C for 4 d and then ground up with mortar and pestle. Lipid extraction

was carried out with several rinses of a 2:1 mixture of chloroform and methanol every 24 h during 5–9 d (Bligh and Dyer 1959). Finally, samples were dried at 60°C for 48 h. Stable isotope analysis was performed with a continuous-flow isotope-ratio mass spectrometer at the Instituto de Geocronología y Geología Isotópica (INGEIS-CONICET/UBA). Results are expressed in δ notation relative to PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively, according to the equation: $\delta X = R_{\text{sample}}/R_{\text{standard}} - 1$, where X is ^{13}C or ^{15}N and R is the isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Peterson and Fry 1987). L-SVEC lithium carbonate and NBS 19 calcium carbonate (Coplen *et al.* 2006) were used for calibration at a precision of 0.2‰ for carbon. For nitrogen, international isotope secondary standards IAEA N1 and IAEN N2 were used for calibration at a precision of 0.3‰. Carbon:Nitrogen (C:N) ratios were calculated to assess lipid removal efficiency (Lesage *et al.* 2010, Newsome *et al.* 2010).

Data were tested for normality using Shapiro–Wilks tests (sample size <50) and for homogeneity of variance using Levene tests. Differences between species were explored separately for $\delta^{15}N$ and $\delta^{13}C$ using t -tests. SIBER (stable isotope Bayesian ellipses in R; Jackson *et al.* 2011) was used to calculate the standard ellipses corrected for small samples (SEAc) and the overlap of the isotopic niches of the two species. The Layman metric of convex hull area (Layman *et al.* 2007) can be converted directly to a measure of population niche area, but it is highly sensitive to sample size and as a result its value increases with increasing sample sizes (Jackson *et al.* 2011). The corrected standard ellipse area (SEAc) measures the breadth of the isotopic niche at the population level and provides an appropriate estimate for small sample sizes (Jackson *et al.* 2011), thus SEAc was used as a measure of the mean core population isotopic niche. For all data analyses, R-2.15.2 statistical software was used (Parnell *et al.* 2008, 2010; Parnell and Jackson 2013).

Nitrogen and carbon isotope ratios were normally distributed for short-beaked common dolphins (Dd after *Delphinus delphis*) and dusky dolphins (Lo after *Lagenorhynchus obscurus*) ($\delta^{15}N_{Dd}: W = 0.96, P = 0.79$; $\delta^{13}C_{Dd}: W = 0.89, P = 0.08$; $\delta^{15}N_{Lo}: W = 0.96, P = 0.82$; $\delta^{13}C_{Lo}: W = 0.89, P = 0.11$) and they also had homogeneous variances (Levene test $\delta^{13}C = 2.48, P = 0.12$ and Levene test $\delta^{15}N = 2.05, P = 0.16$). Dusky dolphins and short-beaked common dolphins differed significantly in both $\delta^{15}N$ and $\delta^{13}C$ (t -test; $\delta^{13}C: t = 3.1018, P < 0.001$; $\delta^{15}N: t = 6.0193, P < 0.001$), indicating that these species had distinct isotopic niches. This result is not attributable to differences in the lipid content of the samples, because the C:N ratio of the skin samples was always <4, indicating good lipid removal efficiency (Kiszka *et al.* 2010). Mean $\delta^{13}C$ values were $-16.6 \pm 0.3\text{‰}$ for dusky dolphins and $-16.2 \pm 0.4\text{‰}$ for short-beaked common dolphins (Fig. 2a) and mean values for $\delta^{15}N$ were $18.3\text{‰} \pm 0.3\text{‰}$ for dusky dolphins and $19.2\text{‰} \pm 0.5\text{‰}$ for short-beaked common dolphins (Fig. 2b). In addition, there was no overlap between the isotopic niche (SEAc) of short-beaked common dolphins and dusky dolphins. The corrected standard ellipse area of short-beaked common dolphins was larger (SEAc = 0.35‰^2) than that of dusky dolphins (SEAc = 0.32‰^2) (Fig. 3).

The pelagic community of Golfo San Matías is dominated by the Argentine hake, Argentine anchovy, butterfish, silver warehou (*Seriotelella porosa*), and hoki (*Macruronus magellanicus*) (Brunetti *et al.* 1998). On the other hand, the demersal community is dominated by striped weakfish (*Cynoscion guatucupa*), banded cusk-eel (*Raneya brasiliensis*), and Brazilian flathead (*Percophis brasiliensis*) (Romero *et al.* 2012). The small pelagic fish consumed by dolphins are depleted in ^{15}N and ^{13}C relative to the demersal and benthic prey. Among cephalopods the community is characterized by

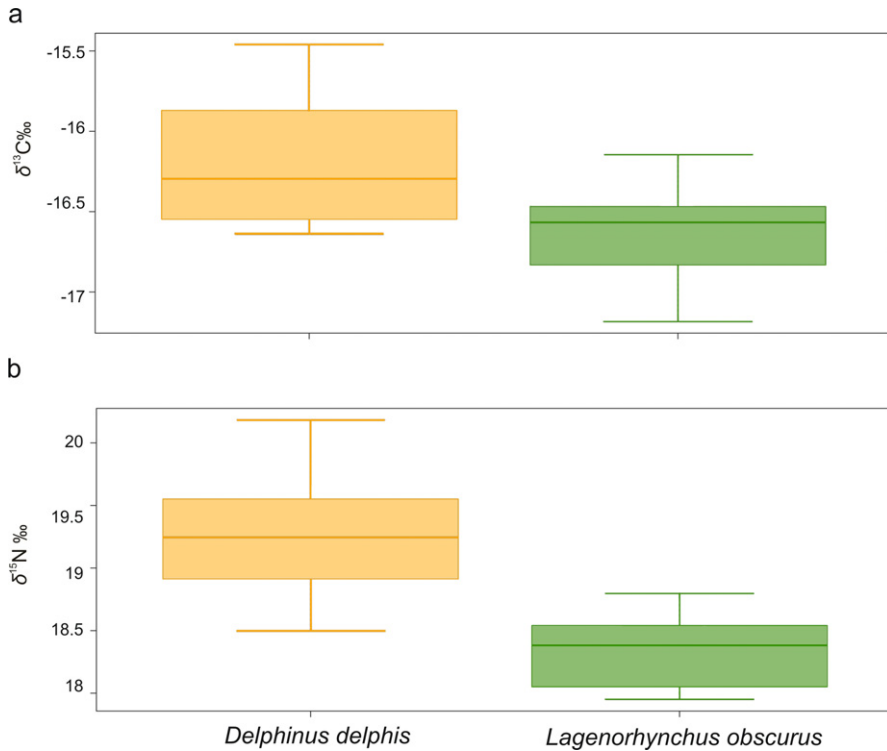


Figure 2. Mean stable nitrogen and carbon isotope ratios (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ of short-beaked common dolphins (*Delphinus delphis*) and dusky dolphins (*Lagenorhynchus obscurus*) from Golfo San Matías.

South American long-fin squid, Argentine short-fin squid, and Patagonian squid, although the abundance of the latter increases with latitude (Brunetti *et al.* 1998, Barón 2001).

The present study confirms that dusky and short-beaked common dolphins exploit different isotopic niches and hence that occurrence in mixed groups is temporary. According to stable isotope ratios, short-beaked common dolphins use more demersal and benthic resources than dusky dolphins, which prefer more pelagic resources. These results are consistent with previous studies based on stomach content analysis, revealing a larger consumption of demersal prey by the short-beaked common dolphin such as striped weakfish and banded cusk-eel compared to dusky dolphins. However, short-beaked common dolphins occasionally engage in apparent cooperative fish herding with dusky dolphins (Dans *et al.* 2010). Therefore, evidence suggests that short-beaked common dolphins may have a more diverse diet than dusky dolphins, and incorporate more prey species, being a more generalist predator. Large niche width indicates greater trophic diversity (generalist consumer) and a small niche width indicates a lower trophic diversity (specialist consumer) (Jackson *et al.* 2011, 2012). However, many generalist populations may be an assemblage of specialized individuals that segregate in the niche space (Bolnick *et al.* 2003, 2007).

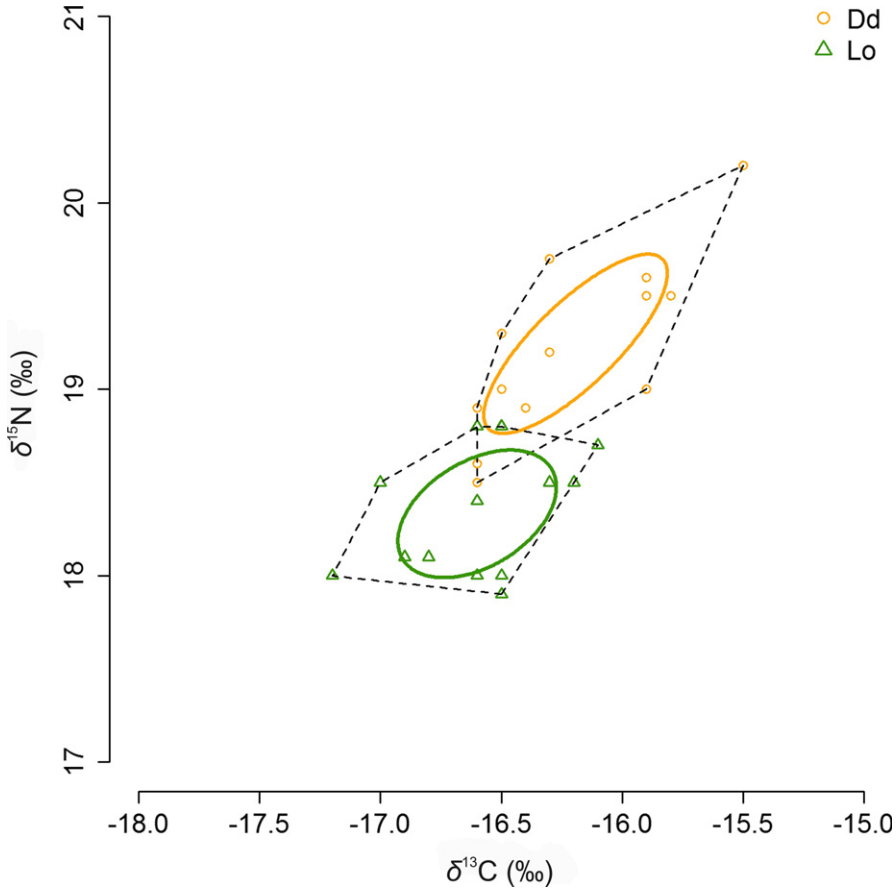


Figure 3. Stable isotope bi-plot illustrating isotopic niche space of two sympatric species, short-beaked common dolphins (*D. delphis*; orange) and dusky dolphins (*L. obscurus*; green). Standard ellipse area (SEAc, solid lines) and convex hull (TA, dashed lines) for each species.

The main prey species of these dolphin species (Argentine anchovy, Argentine hake, Argentine short-fin squid, and South American long-fin squid) are the most abundant small pelagic species of the Argentine Sea (Brunetti *et al.* 1998, Barón and Ré, 2002, Hansen *et al.* 2009), and the differences in the use of trophic resources by dolphins species reflect the plasticity and adaptation to feeding on the locally most abundant prey. The high levels of intraspecific variability in the stable isotope ratios of both dolphins species previously reported along the coast of Argentina revealed large individual variability in diet and habitat use (Loizaga de Castro *et al.* 2016a, b). Therefore, the formation of mixed groups of short-beaked and dusky dolphins should be temporary and opportunistic, and are likely taking advantage of a particularly abundant pelagic resources (Dans *et al.* 2010). Although, stable isotope results indicate that dusky and short-beaked common dolphins living in sympatry are feeding differently most of the time, the results do not preclude the possibility that when the species are together they are eating the same prey, such as Argentine anchovies, which

are recorded in the stomach contents of both dolphin species (Koen Alonso *et al.* 1998, Romero *et al.* 2012). Additionally, Coscarella *et al.* (2015) reported killer whales (*Orcinus orca*) preying on dusky dolphins at Golfo Nuevo, Península Valdes, 300 km away from the study area, so the predator avoidance hypothesis may also play some role in the formation of dolphin mixed-species groups. Nevertheless, the coexistence of these two species within the same community is probably favored by segregation in both the habitat dimension (Svendsen *et al.* 2015) and in the trophic resources (present study).

Although the results of the present study are based on only one mixed group and much remains to be learned, this study represents the beginning of new research based on a wider vision, looking at an ecosystem level and the interaction of sympatric species on the community. Systematic sampling throughout the year is needed, considering the 1–3 mo skin integration time, in order to extend the ecological inferences year round. Also, a tissue with low turnover rate and long integration time, such as bone (Tieszen *et al.* 1983), would allow comparison over longer time periods and help to understand the complexity of interaction among sympatric dolphin species over long timescales. This is a necessary step to determine species-specific requirements, and thus provide valuable information on how to manage areas effectively for the conservation of different species (Parra 2006). Specifically a greater understanding of the trophic relationships between sympatric species along the Argentine coast is essential for small cetacean conservation in an ecosystem where fishing, oil transportation, and tourism based on cetaceans is growing steadily.

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