Journal of Mammalogy Advance Access published November 9, 2015

Journal of Mammalogy, xx(x):1–11, 2015
DOI:10.1093/jmammal/gyv180

Feeding ecology of dusky dolphins *Lagenorhynchus obscurus*: evidence from stable isotopes

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The dusky dolphin *Lagenorhynchus obscurus* occurs in the Southern Hemisphere, where it is restricted to coastal temperate areas. This study aimed to characterize the feeding ecology of dusky dolphins inhabiting northern and central Patagonia by using δ^{13}C and δ^{15}N stable isotope ratios in skin samples. We searched for evidence of geographical and seasonal variation in diet and we explored dietary differences between sexes. Significant differences in the stable isotope ratios of dusky dolphins were found among the 4 gulfs under study. Skin samples from Golfo San Matías and Golfo San Jorge were ^{13}C-enriched and ^{15}N-depleted compared to those from Golfo Nuevo and Golfo San José. There was no seasonality in the diet at Golfo Nuevo, and no differences in the diet between sexes in any gulf. Furthermore, Bayesian ellipses of males and females were similar in size and the overlap was mostly symmetrical in Golfo San José and Golfo San Jorge, while in the Golfo San Matías and Golfo Nuevo, females had wider ranges of δ^{15}N, suggesting the exploitation of a wider trophic niche. Finally, pelagic fishes and demersal pelagic squids were identified as the main prey for this species of dolphin, although the proportion of each prey varied regionally.

El delfín oscuro *Lagenorhynchus obscurus* se distribuye ampliamente en el Hemisferio Sur, donde prefiere áreas templadas costeras. Este estudio tuvo como objetivo caracterizar la ecología trófica de delfines oscuros que habitan en el norte y centro de la Patagonia mediante el uso de isótopos estables de δ^{13}C y δ^{15}N en muestras de piel. Específicamente, buscamos evidencia de variación geográfica y estacional en la dieta de los delfines y exploramos la diferencia de dieta entre sexos. Se encontraron diferencias significativas en los valores de isótopos estables de los delfines entre los cuatro golfos bajo estudio. Las muestras de piel de Golfo San Matías y Golfo San Jorge se encuentran enriquecidas en ^{13}C y deprimidas en ^{15}N en comparación con las muestras del Golfo Nuevo y Golfo San José. No hubo estacionalidad en la dieta en el Golfo Nuevo, y no hay diferencias en la dieta entre sexos en ningún golfo. Además, las elipses bayesianas de machos y hembras fueron similares en tamaño y la superposición fue mayormente simétrica en el Golfo San José y el Golfo San Jorge, mientras que en el Golfo San Matías y el Golfo Nuevo, las hembras tienen rangos más amplios de δ^{15}N, lo que sugiere la explotación de un nicho trófico más amplio. Por último, los peces pelágicos y los calamares demersales pelágicos fueron identificados como la presa principal de esta especie de delfín, aunque la contribución de cada presa varió regionalmente.

Key words: Argentina, Bayesian ellipses, δ^{13}C, δ^{15}N, dusky dolphins, feeding ecology

The dusky dolphin *Lagenorhynchus obscurus* occurs exclusively in the Southern Hemisphere where its distribution is restricted to coastal temperate zones in cool mesopelagic waters around 42°S latitude that are highly productive (Leatherwood and Reeves 1983). Studies from Argentina (Koen Alonso et al. 1998; Romero et al. 2012), Peru (McKinnon 1994; García-Godos et al. 2007), New Zealand (Cipriano 1992; Benoit-Bird et al. 2004; Vaughn et al. 2007), South Africa (Sekiguchi et al. 1992; Best and Meÿer 2010), and Antarctic and sub-Antarctic (Goodall and Galeazzi 1985) found that small schooling fishes (e.g., anchovies, pilchards, mackerels, sculpins, myctophids) were dominant in the diet of *L. obscurus*, but that a large number of squid and demersal fish (e.g., hake, hoki) also contributed to their diet. Over the wide extent of the Patagonian Shelf, dusky dolphins forage almost exclusively on neritic pelagic fish and squid, whereas on the narrower continental shelf off Peru, Chile, and New Zealand, they feed on neritic prey and oceanic species that become available to them at night (Benoit-Bird et al. 2004; Dans et al. 2010). Seasonal changes in the feeding behavior of dusky dolphins have been reported from northern Patagonia (Würsig and Würsig 1980; Degrati et al. 2008), New Zealand (Benoit-Bird et al. 2004; Vaughn et al. 2007), and South Africa (Best and Meÿer 2010), but there were no seasonal differences in prey use from Peru (McKinnon 1994). Finally, no differences in diet between males and females have been found (McKinnon 1994; Amir et al. 2005; Niño-Torres et al. 2006).

In northern and central Patagonia, Argentine anchovy (*Engraulis anchoita*), Argentine hake (*Merluccius hubbsi*), butterfish (*Stromateus brasiliensis*), and squids (*Illex argentinus*, *Loligo* spp.) are the main prey, whereas few benthic prey are taken (Koen Alonso et al. 1998; Romero et al. 2012). Habitat selection models indicate that the highest encounter rate of dusky dolphins occurs in areas with the highest densities of anchovy (Garaffo et al. 2011). Dusky dolphins at Golfo San José and Golfo Nuevo (northern Patagonia) usually feed in herds mainly on small pelagic schooling fish but can change their feeding strategy into single or small groups depending on prey availability (Würsig and Würsig 1980; Degrati et al. 2008, 2012).

Ecological complexity of marine ecosystems can lead to a dependence on local habitats and resulting a genetic differentiation of top predator populations (Valenzuela et al. 2009; Witteveen et al. 2009; Ohizumi and Miyazaki 2010; Fernández et al. 2011). Hence, specialization on local resources by a consolidation of different foraging strategies among groups could promote philopatry and progressively lead to genetic isolation (Baker et al. 1990, 1993; Hoelzel et al. 1998; Natoli et al. 2004, 2005). In this sense, it has been suggested that the strong matrilineal structure and female philopatry of dusky dolphins inhabiting the Patagonian gulfs (Golfo San Matías, Golfo San José, Golfo Nuevo and Golfo San Jorge) are influenced by specialization in the use of local resources (Loizaga de Castro 2013; Loizaga de Castro et al. 2015).

The combination of traditional methods to determine diets (i.e., stomach contents) with stable nitrogen and carbon isotope analysis (δ^{15}N, δ^{13}C) has improved the resolution of trophic interactions (Post 2002). While the former technique provides a precise taxonomic description of the prey consumed (Hobson and Wassenaar 1999), the latter technique offers a long-term integrated measure of all assimilated prey in the diet (Tieszen et al. 1983; Michener and Schell 1994). Stable nitrogen and carbon isotope ratios have proven to be particularly useful in determining the trophic ecology of dolphins (Barros et al. 2010; Kiszka et al. 2010, 2014; Riccialdelli et al. 2010, 2012, 2013; Botta et al. 2011; Fernández et al. 2011; Meissner et al. 2011; Bisi et al. 2013). In particular, δ^{15}N values can provide data on trophic level (Post 2002), while δ^{13}C values can reveal information on feeding habitat (i.e., inshore/benthic versus offshore/pelagic habitat—France 1995; Rubenstein and Hobson 2004; Cardona et al. 2007). Finally, stable isotope analysis contributes to ecological stock assessment and the identification of critical areas for management purposes (Barros et al. 2010; Fernández et al. 2011; Gómez-Campos et al. 2011; Aurioles-Gamboa et al. 2013; Bisi et al. 2013; Browning et al. 2014a).

This study uses stable isotope analysis of dusky dolphins from northern and central Patagonia to test the hypothesis that the specialization in trophic resources is an important factor in determining the genetic structure of this population. We expected to find evidence of geographical and seasonal variation in the diet, and also differences in diet between sexes that can promote philopatry, and progressively lead to population isolation. Consequently, results from this study would increase the knowledge on dusky dolphin's trophic ecology along the Argentine coast and could contribute to the design of conservation areas.

Materials and Methods

Study area.—The study area is located on the Atlantic coast of northern and central Patagonia including the following gulfs: Golfo San Matías (San Matías; 40°45′–42°14′S and 65°05′–63°48′W), Golfo San José (San José; 42°13′–42°25′S and 64°37′–64°02′W), Golfo Nuevo (Golfo Nuevo; 42°29′–42°56′S and 65°03′–64°0′W), and Golfo San Jorge (San Jorge; 44°–47°S and 65°31′–66°18′W; Fig. 1).

Sample collection.—Skin and blubber samples were collected with a biopsy pole (Loizaga de Castro et al. 2013a) from dusky dolphins in Golfo San Matías (n = 15), Golfo Nuevo (n = 15), and Golfo San José (n = 15) during the 2008–2009 field season. In addition, skin samples were obtained from 15 dusky dolphins incidentally caught in mid-water trawlers targeting Argentine red shrimp (*Pleoticus muelleri*) at Golfo San Jorge during 1993–1994. All samples were stored in 20% dimethylsulphoxide (DMSO) solution saturated with NaCl (Amos and Hoelzel 1991).

Sex determination.—Dolphins from fisheries bycatch were sexed through visual examination during necropsy, whereas those dolphins whose gender was unknown (biopsy samples) were sexed by amplifying portions of the genes ZFX and ZFY as described in Bérubé and Palsbøll (1996).

Stable isotope analyses.—Biopsy samples were dried at 60°C for 4 days and then ground with a mortar and pestle. Each sample was washed in successive rinses of deionized water to remove DMSO (Marcoux et al. 2007; Lesage et al. 2010; Foote et al. 2012). Lipid extraction was carried out with rinses of a 2:1 mixture of chloroform and methanol every 24 h over 5–9 days (Bligh and Dyer 1959). Samples were dried at 60°C for 48 h prior to stable isotope analysis. Stable isotope analysis was performed on the resultant skin samples with a continuous-flow isotope-ratio mass spectrometer at the Instituto de Geocronología y Geología Isotópica (INGEIS-CONICET/UBA). International isotope secondary standards provided by the International Atomic Energy Agency (IAEA) were used to

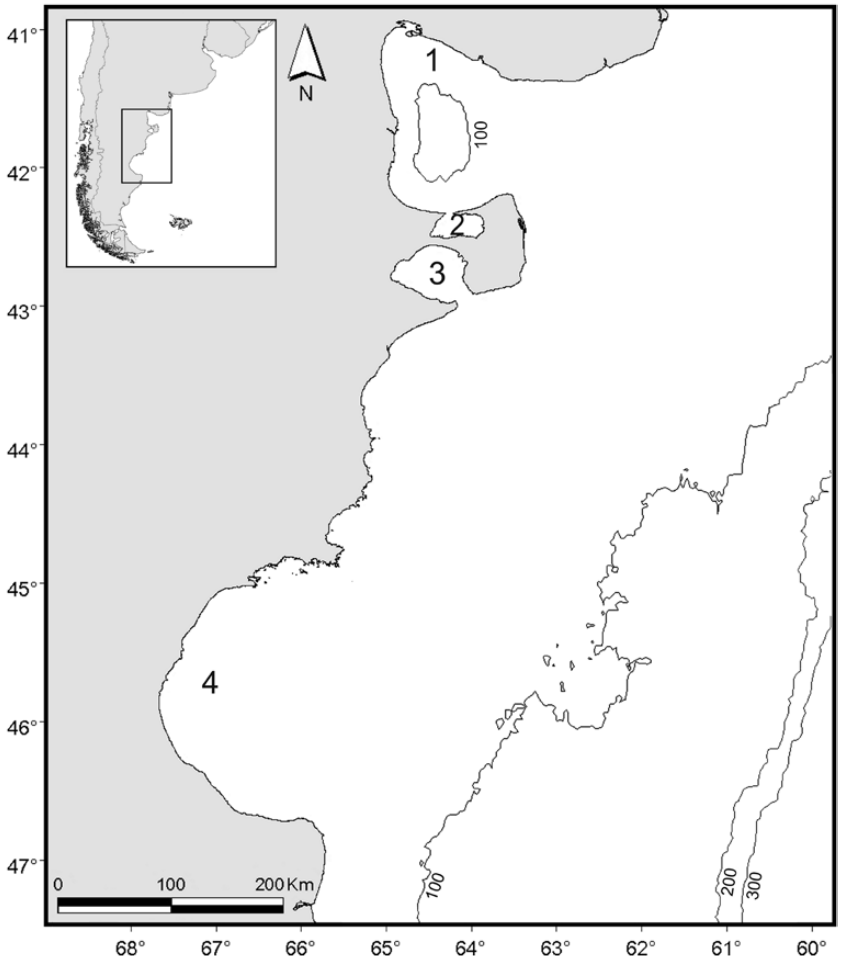

Fig. 1.—Map of northern and central Patagonia and its 4 gulfs: 1: Golfo San Matías; 2: Golfo San José; 3: Golfo Nuevo; and 4: Golfo San Jorge.

calibrate estimates of nitrogen and carbon to 0.2%. Results are expressed in δ notation relative to PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively, as:

$$\delta X = (R_{\text{sample}} / R_{\text{standard}} - 1),$$

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). The carbon to nitrogen ratio (C:N) also was calculated to indicate whether lipid had been removed effectively (Lesage et al. 2010).

Values for stable isotope ratios from the white dorsal muscle of pelagic fish and mantle of cephalopods were taken from the available literature (Drago et al. 2009a, 2009b; Silva et al. 2014); the prey species considered for this study were Argentine anchovy (*E. anchoita*), Argentine hake (*M. hubbsi*), butterfish (*S. brasiliensis*), South American long-fin squid (*Loligo sanpaulensis*), Patagonian squid (*Loligo gahi*), Argentine short-fin squid (*I. argentinus*; Table 1).

Data analysis.—Data were tested for normality and homoscedasticity with a Shapiro–Wilk test and Levene's test. Two-way analysis of variance (ANOVA) followed by a post hoc Tukey test was used to assess the effect of sex and locality (San Matías, San José, Golfo Nuevo, San Jorge) on stable isotope ratios of dusky dolphins ($\delta^{13}C$; Suess-corrected $\delta^{13}C$ and $\delta^{15}N$). Additionally, a 1-way ANOVA was performed to investigate whether diet changed between the warm ($n = 8$) and cold ($n = 6$) seasons for the Golfo Nuevo group because the biopsy samples were taken in both seasons only for this locality.

The stable carbon-13 isotope content in atmospheric CO_2 has decreased 0.022 per mil/year since 1960, largely attributed to use of fossil fuels (Francey et al. 1999; Indermühle et al. 1999; Zenteno et al. 2015). Accordingly, a correction for this Suess effect was applied to the stable isotope values to eliminate variation in $\delta^{13}C$ attributable to the change in atmospheric CO_2. The corrected $\delta^{13}C$ values were referenced to 2009.

SIBER (Stable Isotope Bayesian Ellipses in R—Jackson et al. 2011a) was used to calculate the standard ellipses corrected for small samples (SEA_c) and isotopic overlap between sexes. The standard ellipse measures the breadth of the isotopic niche at the population level. The corrected standard ellipse area (SEA_c) provides a suitable estimate for all sample sizes (e.g., Jackson et al. 2011a, 2011b; Syväranta et al. 2013 cited in Browning et al. 2014b) and should be used as a measure of the mean core population isotopic niche. SEA_c overlap between males and females was estimated in the 4 gulfs. For all data analyses, R-2.15.2 statistical software was used (Parnell et al. 2008, 2010; Parnell and Jackson 2013).

Table 1.—Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope ratios (mean ± *SD*), code of species, number of individuals analyzed (*n*), group considered (group) of dusky dolphin (*Lagenorhynchus obscurus*) from northern and central Patagonia and its potential prey species.

Species	Common name	Tissue	Code	*n*	Group	δ^{13}C (‰)	Suess-corrected δ^{13}C (‰)	δ^{15}N (‰)
Prey								
Engraulis anchoita	Argentine anchovy	Muscle	Ea	5	Northern and central Patagonia	−17.9 ± 0.2		15.7 ± 0.8
Merluccius hubbsi (< 30 cm)	Argentine hake	Muscle	Mh	5	Northern and central Patagonia	−16.8 ± 0.2		16.6 ± 0.4
Stromateus brasiliensis	Butterfish	Muscle	Sb	5	Northern and central Patagonia	−18.1 ± 0.6		15.6 ± 0.4
Loligo sanpaulensis	South American long-fin squid	Muscle	Ls	5	Northern and central Patagonia	−16.7 ± 0.2		17.1 ± 0.3
Loligo gahi	Patagonian squid	Muscle	Lg	5	Northern and central Patagonia	−17.6 ± 0.4		15.7 ± 0.6
Illex argentinus	Argentine short-fin squid	Muscle	Ia	5	Northern and central Patagonia	−17.0 ± 0.6		13.7 ± 0.7
Predator								
Lagenorhynchus obscurus	Dusky dolphins	Skin		15	Golfo San Matías	−16.6 ± 0.29	−16.6 ± 0.29	18.3 ± 0.37
Lagenorhynchus obscurus	Dusky dolphins	Skin		15	Golfo San José	−16.2 ± 0.23	−16.2 ± 0.41	18.8 ± 0.30
Lagenorhynchus obscurus	Dusky dolphins	Skin		15	Golfo Nuevo	−15.7 ± 0.22	−15.8 ± 0.2	18.6 ± 0.32
Lagenorhynchus obscurus	Dusky dolphins	Skin		15	Golfo San Jorge	−16.4 ± 0.30	−16.8 ± 0.3	17.8 ± 0.44

Mixing models were applied with SIAR (Stable Isotope Analysis in R—Parnell et al. 2010) to estimate the proportional contribution of potential prey taxa to diets of dusky dolphin in each gulf. SIAR incorporates specific trophic enrichment factors (TEFs) and the *SD* for each prey source (Bond and Diamond 2011). TEFs and amount of change in isotope ratios between diet and consumer tissue (Phillips and Gregg 2003) were included in mixing models. Among marine mammal species, enrichment factors are considered to be relatively conservative for the same tissue (Lesage et al. 2001; Kiszka et al. 2014). Therefore, TEFs should be carefully selected to obtain robust results and make ecological inferences accurately. Given that the diet of the dusky dolphin is comprised mainly by fatty prey, such as anchovies, we used TEF from skin of bottlenose dolphins, *Tursiops truncatus*, which is based on a lipid-enriched diet. In this study, we used δ^{13}C 2.04‰ ± 0.14 and δ^{15}N 2.96‰ ± 0.12 (Browning et al. 2014b). Data are shown as mean ± *SD*, unless otherwise stated.

Results

Stable isotope ratios of potential prey species of dusky dolphins studied are shown in Table 1. Nitrogen and carbon isotope ratios were normally distributed for all geographic locations (δ^{15}N: $W = 0.9627$, $P = 0.0675$; δ^{13}C: $W = 0.9886$, $P = 0.8572$) and they also had similar variances (Levene's test δ^{13}C = 0.88, $P = 0.45$ and Levene's test δ^{15}N = 1.52, $P = 0.217$).

Isotopic data for females and males also were normally distributed for δ^{15}N ($W = 0.9886$, $P = 0.8572$) and for δ^{13}C ($W = 0.9886$, $P = 0.8572$) and also had similar variance (Levene's test δ^{15}N = 2.15, $P = 0.14$ and Levene's test δ^{13}C = 2.0628, $P = 0.15$).

No significant differences were found in the δ^{13}C and δ^{15}N values between warm and cold seasons at Golfo Nuevo (1-way ANOVA; δ^{13}C: $F_{1,57} = 0.472$, $P > 0.05$; δ^{15}N: $F_{1,51} = 1.823$, $P > 0.05$). High intraspecific variability was observed for both stable isotope ratios, indicating large individual variability in habitat use by dolphins (Fig. 2). This result is not attributable to differences in lipid content because the C:N ratio from skin samples of dusky dolphins was < 4, indicating good lipid removal efficiency (Kiszka et al. 2010). Significant differences in nitrogen isotope ratios were found among Patagonian gulfs ($F_{3,51} = 14.8$, $P < 0.001$; Table 1); all post hoc Tukey test were significant ($P < 0.001$), except for San José versus Golfo Nuevo ($P = 0.583$). The average δ^{13}C values also were significantly different among the gulfs ($F_{3,51} = 25.6$, $P < 0.001$); all post hoc Tukey test were significant ($P < 0.001$), except for San Matías versus San Jorge ($P = 0.463$; Fig. 3). Average Suess-corrected δ^{13}C values also were significantly different among the gulfs ($F_{3,51} = 37.9$, $P < 0.001$). Carbon-13 and Suess-corrected ^{13}C values showed that samples from Golfo San Matías and Golfo San Jorge were more depleted in ^{13}C and ^{15}N with respect to those from Golfo San José and Golfo Nuevo (Table 2).

No significant differences in the δ^{13}C and δ^{15}N values were found between males and females in any gulf (2-way ANOVA; δ^{13}C: $F_{1,51} = 0.2$, $P > 0.05$; Suess-corrected δ^{13}C: $F_{1,51} = 0.2$, $P > 0.05$; δ^{15}N: $F_{1,51} = 0.017$, $P > 0.05$); the sex × area interaction was not significant for any stable isotope ratio (δ^{13}C: $F_{3,51} = 1.3$, $P > 0.05$; Suess-corrected δ^{13}C: $F_{3,51} = 1.2$, $P > 0.05$; δ^{15}N: $F_{3,51} = 0.5$, $P > 0.05$). The ellipses of males were smaller than those of females in San Matías and Golfo Nuevo. The overlap between ellipses reflects niche overlap. This overlap was highly asymmetrical, higher for males than for females (Table 2). However, male and female ellipses were similar in size and overlap was mostly symmetrical in San José and San Jorge (Fig. 4; Table 2). In San Matías and Golfo Nuevo, females had wider ranges of δ^{15}N (Table 2), suggesting that they consumed prey at a higher trophic level than males. Conversely, females

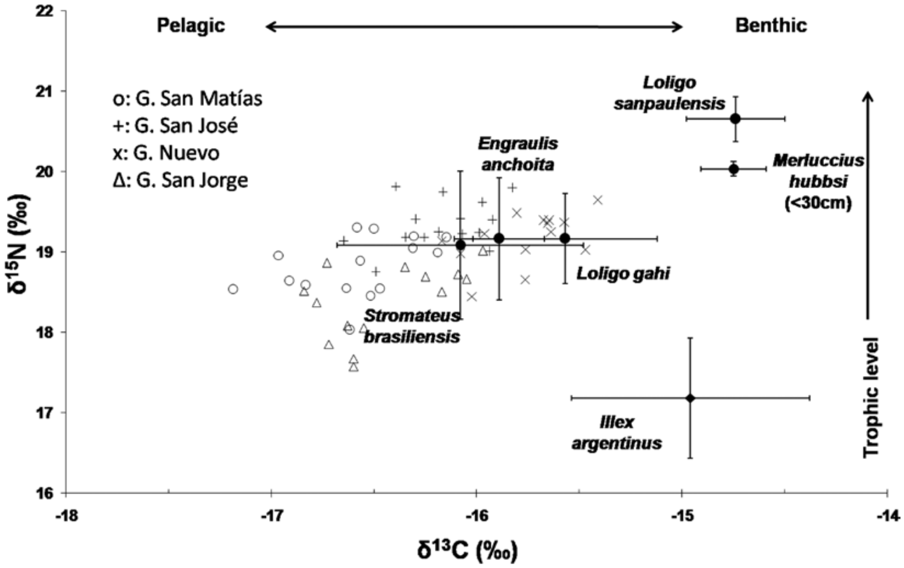

Fig. 2.—Nitrogen and carbon stable isotope values (δ^{15}N and δ^{13}C) of dusky dolphins and its potential prey species (mean ± *SD*) among 4 gulfs of Patagonia. Stable isotope ratios in dolphins have been corrected for diet-to-predator fractionation.

consumed mainly prey at lower trophic levels than males in Golfo Nuevo.

Butterfish were identified as the main prey item in the diet of dusky dolphins along the Patagonian coast (Fig. 5), although their relative contribution to the diet varied among gulfs. In Golfo San Matías, butterfish, Argentine anchovy, and Argentine short-fin squid were the main prey items in the diet with means of 29%, 23%, and 19%, respectively. In Golfo San José, butterfish were the main prey item comprising a mean of 35% of the diet; Argentine anchovy and Patagonian squid also were included in the diet comprising 18% and 28% of the diet, respectively. In Golfo Nuevo, the Argentine anchovy and the butterfish contributed equally to the diet, 29% and 28%, respectively. The Patagonian squid represented a smaller portion of the diet (23%). In Golfo San Jorge, the diet included Argentine short-fin squid (32%), butterfish (29%), and Argentine anchovy (19%; Fig. 5).

DISCUSSION

Earlier studies on the diet of dusky dolphins in the Southwestern Atlantic Ocean and waters off of Patagonia were based on analyses of stomach contents (Koen Alonso et al. 1998; Romero et al. 2012). Ours is unique in analyzing the foraging ecology of dusky dolphins using stable isotopes and covering a large geographic area. The present study and stomach content analysis (Koen Alonso et al. 1998; Romero et al. 2012) agree that the diet of dusky dolphins in the Southwestern Atlantic is primarily comprised of pelagic items. In northern Patagonia, the Argentine anchovy, the Argentine short-fin squid, and the South American long-fin squid are the most abundant pelagic resources (Brunetti et al. 1998; Barón and Ré 2002; Hansen et al. 2009). Hence, it seems that dusky dolphins forage opportunistically on available prey species, preferring pelagic fish with schooling behavior, perhaps because they are the most energetically profitable prey for a cooperative predator (Meynier et al. 2008). According to analyses of stomach contents, Argentine anchovies prevail in the dusky dolphin's diet (Koen Alonso et al. 1998; Romero et al. 2012), whereas butterfish dominate their diet according to stable isotope analyses. However, both species of pelagic fishes (e.g., anchovies, butterfish) have similar δ^{13}C and δ^{15}N values, which hinder the capacity of SIAR to discriminate between them. Nevertheless, the model clearly demonstrates that other pelagic species such as the South American long-fin squid and the Argentine hake are not important items in the diet of dusky dolphins.

SIAR revealed similar diets for dusky dolphins from Golfo San Matías and Golfo San Jorge, but the relative importance of the Argentine short-fin squid differed. In the other hand, Patagonian squid had a main role in the diet of dusky dolphins from the smallest gulfs (Golfo San José and Golfo Nuevo). Information on abundance of cephalopods is available from Golfo San Matías and Golfo San Jorge because of the fishery industry in these gulfs, but information on abundance of cephalopods from Golfo Nuevo and Golfo San José is lacking because fishing in these gulfs is forbidden. Argentine short-fin squid is quite similar in abundance and availability from 43°S to 51°S, corresponding to the "summer spawning stock" (SDV, for its acronym in Spanish) and the "south-Patagonian stock" (SSP, for its acronym in Spanish—Brunetti et al. 1998). The size of squids consumed by dusky dolphins corresponds to the size of pelagic juveniles which can be found at 50–100 m depths year-round because of continuous spawning (Brunetti and Ivanovic 1992; Ivanovic and Brunetti 1994; Crespi-Abril and Barón 2012). At Golfo San José and Golfo Nuevo, butterfish and Argentine anchovy contribute almost in equal proportion to the diet of dusky dolphin. In the other hand, the Patagonian squid increased its contribution in Golfo Nuevo than Golfo San Matías and San José.

The use of different foraging tactics, pointed out by the consumption of both pelagic schooling fish and squids, has

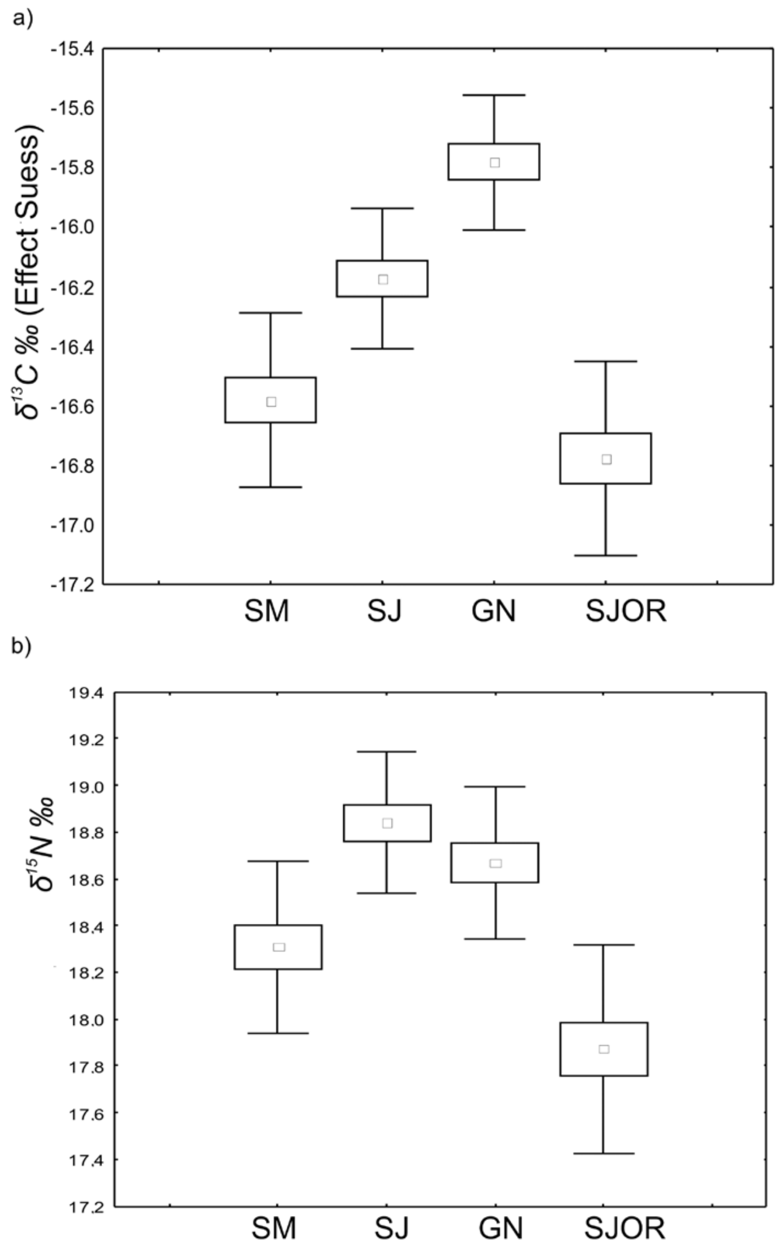

Fig. 3.—a) Suess-corrected carbon ($\delta^{13}C$ ‰) and b) mean nitrogen ($\delta^{15}N$ ‰) stable isotope ratios of dusky dolphins among 4 gulfs of Patagonia. SM: Golfo San Matías; SJ: Golfo San José; GN: Golfo Nuevo; SJOR: Golfo San Jorge.

Table 2.—Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios (mean ± *SD*) of dusky dolphins (*Lagenorhynchus obscurus*) in 4 gulfs from northern and central Patagonia. Overlap as a percentage of standard ellipses corrected for small samples (SEA_c) for dusky dolphins, females and males, in northern and central Patagonia, Argentina.

	Females			Males			% Overlap	
	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Males	Females
Golfo San Matías	8	−16.6 ± 0.307	18.3 ± 0.391	7	−16.6 ± 0.303	18.4 ± 0.309	59.89	29.86
Golfo San José	7	−16.1 ± 0.199	18.9 ± 0.306	8	−16.2 ± 0.243	18.8 ± 0.323	56.91	63.17
Golfo Nuevo	6	−15.9 ± 0.291	18.6 ± 0.403	8	−15.8 ± 0.227	18.7 ± 0.324	90.78	40.11
Golfo San Jorge	12	−16.5 ± 0.303	17.9 ± 0.471	3	−16.5 ± 0.313	17.9 ± 0.201	67.78	74.45

been reported for other delphinids (Ballance et al. 2006; Loizaga de Castro et al. 2013b) and seasonal changes in feeding behavior and prey availability were described for dusky dolphins at Golfo San José and Golfo Nuevo (Würsig and Würsig 1980; Degrati et al. 2008, 2012). On the other hand, we did not find any differences in $\delta^{15}N$ and $\delta^{13}C$ values for dusky dolphins in Golfo Nuevo between warm and cold seasons. However, because this analysis was based on only 1

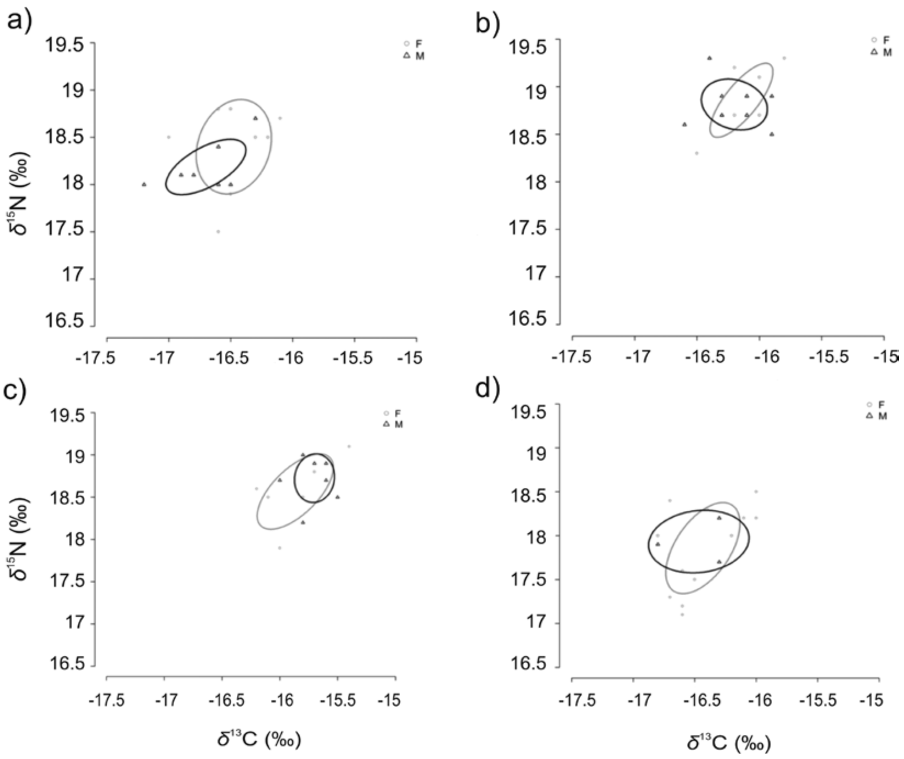

Fig. 4.—Bayesian ellipses of dusky dolphins according to stable isotope ratios in skin; a) Golfo San Matías; b) Golfo San José; c) Golfo Nuevo; d) Golfo San Jorge; F: female, gray ellipses and M: male, black ellipses.

gulf, a seasonal sample from all 4 gulfs should be undertaken by future studies.

An important feature of stable isotope analysis is the use of proper, species- and diet-specific TEFs for $\delta^{15}N$ and $\delta^{13}C$; as they are of great significance for using stable isotope mixing models to predict the dietary sources of a consumer (Newsome et al. 2010; Caut et al. 2011; Borrell et al. 2012; Kiszka et al. 2014). However, currently there are no TEFs for dusky dolphins; therefore, a literature search was conducted to find the most appropriate TEF for this species. We used TEF for $\delta^{15}N$ and $\delta^{13}C$ from the skin of bottlenose dolphins based on a lipid-enriched diet that consisted of 80% (by mass) Pacific saury and 20% Atlantic mackerel (Browning et al. 2014b). Because the diet of dusky dolphin is composed mainly of prey of high nutritional value, such as anchovy, these correction factors were chosen as the most ones appropriate for this study.

The dusky dolphins included in the present study were sampled in coastal areas, but this species occurs beyond the 200-mile limit of the continental slope (Crespo et al. 1997). Myctophids are the dominant schooling pelagic fish over the continental slope (Sánchez and de Ciechomsky 1995), have a very high energy density (Ichii et al. 2007), and have been reported in the diet of the dusky dolphins in New Zealand and South Africa (Cipriano 1992; Sekiguchi et al. 1992; Benoit-Bird et al. 2004; Vaughn et al. 2007; Würsig et al. 2007; Best and Meÿer 2010). In the Southwestern Atlantic, myctophids are highly depleted in ^{13}C and ^{15}N ($\delta^{13}C = -21.9 \pm 0.7$; $\delta^{15}N = 11.7 \pm 0.9$—Ciancio et al. 2008), so any contribution to the diet of the individuals included in the present study is extremely unlikely. However, 1 dusky dolphin stranded in Playa Bonita (Chubut), and not included here, had a totally different stable isotope ratio ($\delta^{13}C = -17.6‰$; $\delta^{15}N = 12.1‰$), indicative of off-shore foraging on myctophids. Furthermore, for this particular individual was reported the presence of cysts of *Phyllobothrium delphini*, a typical helminth recorded in several off-shore pelagic and deep feeder cetaceans (Loizaga de Castro et al. 2014), thus suggesting the exploitation of more oceanic foraging grounds.

The main advantage of stable isotope analysis lies in the long-period integration of the diet data (Tieszen et al. 1983; Michener and Schell 1994). The skin tissue we used integrates dietary inputs over 2–3 months (Tieszen et al. 1983; Hobson et al. 1996; Kiszka et al. 2014), hence it can overcome any biases from time to digestion (Hobson et al. 1996). As expected in a dolphin species with no sexual dimorphism in body size (Cipriano 1992; Van Waerebeek 1993; Best and Meÿer 2010) and that forages in mixed groups (Würsig and Würsig 1980), no differences were found in the average stable isotope ratios of males and females in any of the 4 gulfs. However, the Bayesian ellipses of females were larger and encompassed those of males in Golfo San Matías and Golfo Nuevo, which may reflect a broader trophic diversity for females than for males. This is not a consistent difference along the Southwestern Atlantic as males and females of dusky dolphins at Golfo San José and Golfo San Jorge have similar SEA_c values and symmetric overlap. Consequently, the hypothesis that the genetic structure proposed by Loizaga de Castro (2013) was mainly determined by differences in feeding ecology should be rejected. It should also be noted that the use of a tissue such as skin with a short time integrating the diet may not detect such differences between ecotypes. Further analysis combining stable isotopes with

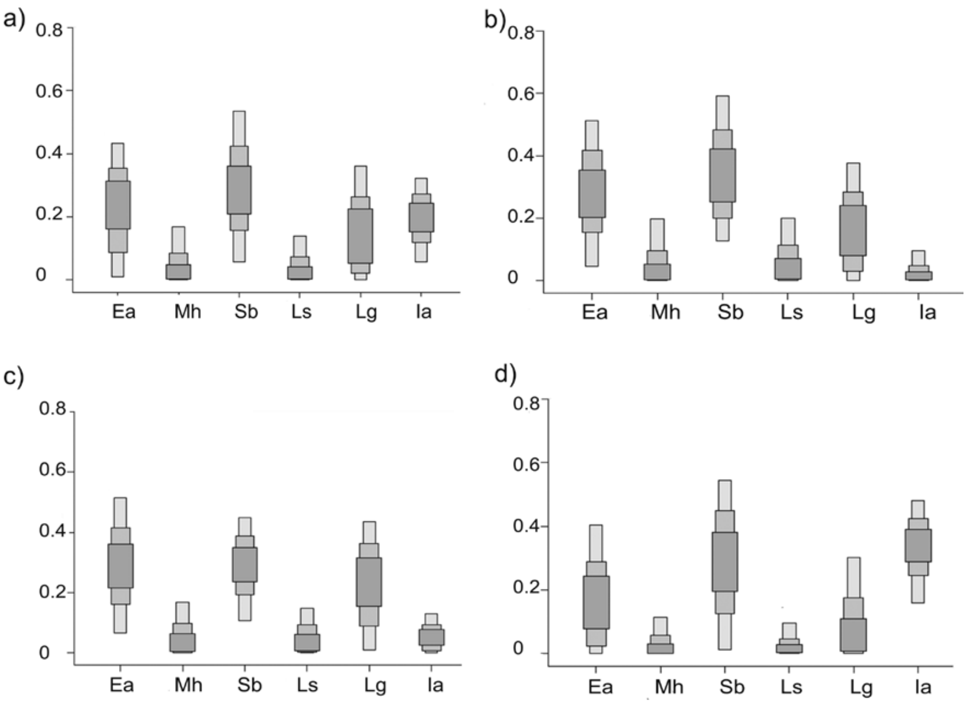

Fig. 5.—Feasible composition of the diet of dusky dolphins in 4 gulfs from northern and central Patagonia; a) Golfo San Matías; b) Golfo San José; c) Golfo Nuevo; d) Golfo San Jorge. Median 50%, 75%, and 95% *CI*s (Argentine anchovy Ea: *Engraulis anchoita*; Argentine hake Mh: *Merluccius hubbsi*; butterfish Sb: *Stromateus brasiliensis*; South American long-fin squid Ls: *Loligo sanpaulensis*; Patagonian squid Lg: *Loligo gahi*; Argentine short-fin squid Ia: *Illex argentinus*).

matrilineally inherited mtDNA will provide a mean to compare simultaneously both the matrilineal relatedness and foraging ecotype of large numbers of individuals. Potentially, if the offspring remain faithful to maternally introduced regions of fine-scale foraging habitat, this behavior might reinforce selection for natal site philopatry by adult females as reported for southern right whales (*Eubalaena australis*—Valenzuela et al. 2009) and killer whales (*Orcinus orca*—Hoelzel et al. 2007).

The Patagonian Shelf is extensively used as foraging area for several top predators like penguins, sea lions, dolphins, whales, and elephant seals, which play key roles in the marine ecosystem (Falabella et al. 2009) and are indicators of important coastal and pelagic marine areas. Dusky dolphins seems to forage on small pelagic prey, similar to South American fur seals (*Arctocephalus australis*—Vales et al. 2015) and Magellanic penguin (*Spheniscus magellanicus*—Forero et al. 2002, 2004; Silva et al. 2014). Therefore, the knowledge of trophic ecology for high trophic level predators along the Argentine coast is an important component of a broader study supporting effective conservation and management programs.

Acknowledgments

The authors are indebted to many people and institutions who collaborated in this research. Centro Nacional Patagónico (National Research Council of Argentina), Instituto de Biología Marina y Pesquera Almirante Storni, and Universidad Nacional de la Patagonia San Juan Bosco provided logistic and institutional support. Collection of samples was approved by Secretaría de Turismo and Dirección de Fauna y Flora Silvestre de la Provincia del Chubut (Research permit N° 23/07) and Government Agency Provincia de Rio Negro. Skin samples were exported under CITES permit N° 032423, 31374/75/76, from the Ministerio de Salud y Ambiente, Secretaria de Ambiente y Desarrollo Sustentable, Buenos Aires, Argentina. Funds were received from Agencia Nacional de Promoción Científica y Tecnológica (PICT N° 11679 and 33934), Project PNUD ARG-02/018 (B-B27), and the Mohamed bin Zayed Species Conservation Fund Project N°0925516. We also thank G. Cameron (University of Cincinnati, Ohio) who helped us to improve the English grammar. At the time this manuscript was written, RLC was supported by a Postdoctoral Fellowship and DGV by a Ph.D. Fellowship from the National Research Council of Argentina (CONICET).

Literature Cited

Amir, O. A., P. Berggren, S. G. M. Ndaro, and N. S. Jiddawi. 2005. Feeding ecology of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) incidentally caught in the gillnet fisheries off Zanzibar, Tanzania. Estuarine, Coastal and Shelf Science 63:429–437.

Amos, W., and A. R. Hoelzel. 1991. Long-term preservation of whale skin for DNA analysis. Report of International Whaling Commission, Special Issue 13:99–103.

Aurioles-Gamboa, D., M. Rodríguez-Pérez, L. Sánchez-Velasco, and M. F. Lavín. 2013. Habitat, trophic level, and residence of marine mammals in the Gulf of California assessed by stable isotope analysis. Marine Ecology Progress Series 488:275–290.

Baker, C. S., S. R. Palumbi, R. H. Lambertsen, M. T. Weinrich, and J. Calambokidis. 1990. Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. Nature 344:238–240.

Baker, C. S., Perry A., J. L. Bannister, M. T. Weinrich, and R. B. Abernethy. 1993. Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. Proceedings of the National Academy of Sciences 90:8239–8243.

Ballance, L. T., R. L. Pitman, and P. C. Fiedler. 2006. Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. Progress in Oceanography 69:360–390.

Benoit-Bird, K. J., B. Würsig, and C. J. McFadden. 2004. Dusky dolphin (*Lagenorhynchus obscurus*) foraging in two different habitats: active acoustic detection of dolphins and their prey. Marine Mammal Science 20:215–231.

Barón, P. J., and M. E. Ré. 2002. Reproductive cycle and population structure of *Loligo sanpaulensis* in the northeastern coast of Patagonia. Bulletin of Marine Science 71:175–186.

Barros, N. B., P. H. Ostrom, C. A. Stricker, and R. S. Wells. 2010. Stable isotopes differentiate bottlenose dolphins off west-central Florida. Marine Mammal Science 26:324–336.

Bérubé, M., and P. J. Palsbøll. 1996. Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. Molecular Ecology 5:283–287.

Best, P. B., and M. A. Meÿer. 2010. Neglected but not forgotten—Southern Africa's dusky dolphins. Pp. 291–311 in The dusky dolphin: master acrobat off different shores (B. Würsig and M. Würsig, eds.). Academic Press, San Diego, California.

Bisi, T. L., et al. 2013. Trophic relationships and habitat preferences of delphinids from the Southeastern Brazilian Coast determined by carbon and nitrogen stable isotope composition. PLoS One 8:e82205.

Bligh, E., and W. Dyer. 1959. A rapid method of total lipid extraction and purification. Journal of Cellular Biochemistry B 37:911–917.

Bond, A. L., and A. W. Diamond. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecological Applications 21:1017–1023.

Borrell, A., N. Abad-Oliva, E. Gómez-Campos, J. Giménez, and A. Aguilar. 2012. Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. Rapid Communications in Mass Spectrometry 26:1596–1602.

Botta, S., A. A. Hohn, S. A. Macko, and E. R. Secchi. 2011. Isotopic variation in delphinids from the subtropical western South Atlantic. Journal of the Marine Biological Association of the United Kingdom 92:1689–1698.

Browning, N. E., C. Dold, J. I-Fan, and G. A. J. Worthy. 2014b. Isotope turnover rates and diet-tissue discrimination in skin of ex situ bottlenose dolphins (*Tursiops truncatus*). Journal of Experimental Biology 217:214–221.

Browning, N. E., S. D. McCulloch, G. D. Bossart, and G. A. J. Worthy. 2014a. Fine-scale population structure of estuarine bottlenose dolphins (*Tursiops truncatus*) assessed using stable isotope ratios and fatty acid signature analyses. Marine Biology 161:1307–1317.

Brunetti, N. E., and M. L. Ivanovic. 1992. Distribution and abundance of early stages of squids (*Illex argentinus*) in the south-west Atlantic. ICES Journal of Marine Science 49:175–183.

Brunetti, N. E., M. Ivanovic, G. Rossi, B. Elena, and S. Pineda. 1998. Fishery biology and life history of *Illex argentinus*. Pp. 217–232 in Contributed paper to international symposium on large pelagic squid (T. Okutani, ed.). Japan Marine Fishery Resources Research Center, Tokyo, Japan.

Cardona, L., M. Revelles, M. Sales, A. Aguilar, and A. Borrell. 2007. Meadows of the seagrass, *Posidoniaoceanica*, are a relevant source of organic matter for adjoining ecosystems. Marine Ecology Progress Series 335:123–131.

Caut, S., S. Laran, E. Garcia-Hartmann, and K. Das. 2011. Stable isotopes of captive cetaceans (killer whales and bottlenose dolphins). Journal of Experimental Biology 214:538–545.

Ciancio, J. E., M. Pascual, F. Botto, E. Frere, and O. Iribarne. 2008. Trophic relationships of exotic anadromous salmonids in the Southern Patagonian Shelf as inferred from stable isotopes. Limnology and Oceanography 53:788–798.

Cipriano, F. W. 1992. Behavior and occurrence patterns, feeding ecology, and life history of dusky dolphins (*Lagenorhynchus obscurus*) off Kaikoura, New Zealand. Ph.D. dissertation, University of Arizona, Tucson.

Crespi-Abril, A. C., and P. J. Barón. 2012. Revision of the population structuring of *Illex argentinus* (Castellanos, 1960), and a new interpretation based on modelling the spatio-temporal environmental suitability for spawning and nursery. Fisheries Oceanography 21:199–214.

Crespo, E. A., et al. 1997. Distribution of dusky dolphins, *Lagenorhynchus obscurus* (Gray, 1828), in the Southwestern South Atlantic Ocean with notes on herd size. Report of the International Whaling Commission 47:693–697.

Dans, S. L., E. A. Crespo, M. Koen-Alonso, T. Markowitz, B. BeronVera, and A. Dahood. 2010. Dusky dolphin trophic ecology: their role in the food web. Pp. 49–74 in The dusky dolphin: master acrobat off different shores (B. Würsig and M. Würsig, eds.). Academic Press, San Diego, California.

Degrati, M., S. L. Dans, G. V. Garaffo, and E. A. Crespo. 2012. Diving for food: a switch of foraging strategy of dusky dolphins in Argentina. Journal of Ethology 30:361–367.

Degrati, M., S. L. Dans, S. N. Pedraza, E. A. Crespo, and G. V. Garaffo. 2008. Diurnal behaviour of dusky dolphins, *Lagenorhynchus obscurus*, in Golfo Nuevo. Journal of Mammalogy 89:1241–1247.

Drago, M., et al. 2009a. Historic diet change of the South American sea lion in Patagonia as revealed by isotopic analysis. Marine Ecology Progress Series 384:273–286.

Drago, M., L. Cardona, E. A. Crespo, and A. Aguilar. 2009b. Ontogenic dietary changes in South American sea lions. Journal of Zoology (London) 279:251–261.

Falabella, V., C. Campagna, and J. Croxall. 2009. Atlas del Mar Patagónico. Especies y espacios. Wildlife Conservation Society y Bird Life International, Buenos Aires, Argentina.

Fernández, R. S., et al. 2011. Stable isotope analysis in two sympatric populations of bottlenose dolphins *Tursiops truncatus*: evidence of resource partitioning? Marine Biology 158:1043–1055.

Foote, A. D., H. Vester, G. A. Víkingsson, and J. Newton. 2012. Dietary variation within and between populations of northeast Atlantic killer whales, *Orcinus orca*, inferred from $\delta^{13}C$ and $\delta^{15}N$ analyses. Marine Mammal Science 28:E472–E485.

Forero, M. G., G. R. Bortolotti, K. A. Hobson, J. A. Donazar, M. Bertelotti, and G. Blanco. 2004. High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. Journal of Animal Ecology 73:789–801.

Forero, M. G., K. A. Hobson, G. R. Bortolotti, J. A. Donázar, M. Bertelloti, and G. Blanco. 2002. Food resource utilisation by the Magellanic penguin evaluated through stable isotope analysis: segregation by sex and age and influence on offspring quality. Marine Ecology Progress Series 234:289–299.

France, R. L. 1995. Differentiation between littoral and pelagic foodwebs in lakes using stable carbon isotopes. Limnology and Oceanography 40:1310–1313.

Francey, R. J., et al. 1999. A 1000-year high precision record of δ^{13}C in atmospheric CO_2. Tellus B 51:170–193.

García-Godos, I., K. Van Waerebeek, J. C. Reyes, J. Alfaro, and M. Arias-Schreiber, 2007. Prey occurrence in the stomach contents of four small cetacean species in Peru. Latin American Journal of Aquatic Mammals 6:171–183.

Garaffo, G. V., et al. 2011. Modeling habitat use for dusky dolphin and Commerson's dolphin in Patagonia. Marine Ecology Progress Series 421:217–227.

Goodall, R. N. P., and A. R. Galeazzi. 1985. A review of the food habits of the small cetaceans of the Antarctic and Sub-Antarctic. Pp. 566–572 in Antarctic nutrient cycles and food webs (W. Siegfried, R. M. Laws, and P. Condy, eds.). Springer-Verlag Press, Berlin, Germany.

Gómez-Campos, E., A. Borrell, L. Cardona, J. Forcada, and A. Aguilar. 2011. Overfishing of small pelagic fishes increases trophic overlap between immature and mature striped dolphins in the Mediterranean Sea. PLoS One 6:e24554.

Hansen, J. E., C. C. Buratti, and A. D. Garciarena. 2009. Estado de la población de anchoita (Engraulis anchoita) al sur de 41ºS y estimación de capturas biológicamente aceptables en el año 2009. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), INIDEP Technical report 11/09:1–16.

Hobson, K. A., D. M. Schell, D. Renouf, and E. Noseworthy. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Canadian Journal of Fisheries and Aquatic Sciences 53:528–533.

Hobson, K. A., and L. I. Wassenaar. 1999. Stable isotope ecology: an introduction. Oecology 120:312–313.

Hoelzel, A. R., M. Dalheim, and S. J. Stern. 1998. Low genetic variation among killer whales (*Orcinus orca*) in the eastern North Pacific and genetic differentiation between foraging specialists. Journal of Heredity 89:121–128.

Hoelzel, A. R., J. Hey, M. E. Dahlheim, C. Nicholson, V. Burkanov, and N. Black. 2007. Evolution of population structure in a highly social top predator, the killer whale. Molecular Biology and Evolution 24:1407–1415.

Ichii, T., et al. 2007. Provisioning strategies of Antarctic fur seals and chinstrap penguins produce different responses to distribution of common prey and habitat. Marine Ecology Progress Series 344:277–297.

Indermühle, A., et al. 1999. Holocene carbon-cycle dynamics based on CO_2 trapped in ice at Taylor Dome, Antarctica. Nature 398:121–126.

Ivanovic, M., and N. E. Brunetti. 1994. Size, maturity, growth and food of squid *Illex argentinus* (Castellanos, 1960). ICES Journal of Marine Science C.M. 18, 18p (Doc mimeog).

Jackson, M. C., I. Donohue, A. L. Jackson, J. R. Britton, D. M. Harper, and J. Grey. 2011b. Population level metrics of trophic structure based on stable isotopes and their application to invasion ecology. PLoS One 7:e31757.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011a. Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80:595–602.

Kiszka, J., P. Méndez-Fernandez, M. R. Heithaus, and V. Ridoux. 2014. The foraging ecology of coastal bottlenose dolphins based on stable isotope mixing models and behavioural sampling. Marine Biology 16:953–996.

Kiszka, J., M. Oremus, P. Richard, M. Poole, and V. Ridoux. 2010. The use of stable isotope analyses from skin biopsy sampled to assess trophic relationships of sympatric delphinids off Moorea (French Polynesia). Journal of Experimental Marine Biology and Ecology 395:48–54.

Koen Alonso, M., E. A. Crespo, N. A. García, S. N. Pedraza, and M. Coscarella. 1998. Diet of dusky dolphins, *Lagenorhynchus obscurus*, in waters off Patagonia, Argentina. Fishery Bulletin US 96:366–374.

Leatherwood, S., and R. R. Reeves. 1983. The Sierra Club Handbook of whales and dolphins. Sierra Club Books, San Francisco, California.

Lesage, V., M. O. Hammill, and K. M. Kovacs. 2001. Marine mammals and the community structure of the Estuary and Gulf of St Lawrence, Canada: evidence from stable isotope analysis. Marine Ecology Progress Series 210:203–221.

Lesage, V., Y. Morin, E. Rioux, C. Pomerleau, S. H. Fergusson, and E. Pelletier. 2010. Stable isotopes and trace elements as indicators of diet and habitat use in cetaceans: predicting errors related to preservation, lipid extraction and lipid normalization. Marine Ecology Progress Series 419:249–265.

Loizaga de Castro, R. 2013. Genética de Poblaciones del delfín oscuro, *Lagenorhynchus obscurus*, en la costa de Argentina. Ph.D. dissertation, Universidad Nacional del Comahue, Bariloche, Argentina.

Loizaga de Castro, R., S. L. Dans, M. A. Coscarella, and E. A. Crespo. 2013b. Living in an estuary: Commerson's dolphin (*Cephalorhynchuscommersonii* (Lacépède, 1804)), habitat use and behavioural pattern at the Santa Cruz River, Patagonia, Argentina. Latin American Journal of Aquatic Research 41:985–991.

Loizaga de Castro, R., S. L. Dans, and E. A. Crespo. 2015. Spatial genetic structure of dusky dolphin, *Lagenorhynchus obscurus*, along the argentine coast: preserve what scale? Aquatic Conservation: Marine and Freshwater Ecosystems, DOI: 10.1002/aqc.2552.

Loizaga de Castro, R., A. R. Hoelzel, and E. A. Crespo. 2013a. Behavioural responses of Argentine coastal dusky dolphins (*Lagenorhynchus obscurus*) to a biopsy pole system. Animal Welfare 22:13–23.

Loizaga de Castro, R., D. G. Vales, M. Degrati, N. A. García, M. Fernández, and E. A. Crespo. 2014. First record of cestode cysts of *Phyllobothrium delphini* (Phyllobothriidae) from the dusky dolphins (*Lagenorhynchus obscurus*) off Argentine coast. Hidrobiológica 24:307–310.

Marcoux, M., H. Whitehead, and L. Rendell. 2007. Sperm whale feeding variation by location, year, social group and clan: evidence from stable isotopes. Marine Ecology Progress Series 333:309–314.

McKinnon, J. 1994. Feeding habits of the dusky dolphin, *Lagenorhynchus obscurus*, in the coastal waters of central Peru. Fishery Bulletin US 92:569–578.

Meissner, A., C. D. MacLeod, P. Richard, V. Ridoux, and G. Pierce. 2011. Feeding ecology of striped dolphins, *Stenella coeruleoalba*, in the north-western Mediterranean Sea based on stable isotopes. Journal of the Marine Biological Association of the UK 96:1677–1687.

Meynier, L., C. Pusineri, J. Spitz, M. B. Santos, G. J. Pierce, and V. Ridoux. 2008. Intraspecific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: importance of fat fish. Marine Ecology Progress Series 354:277–287.

Michener, R. H., and D. M. Schell. 1994. Stable isotope ratios as tracers in marine aquatic food webs. Pp. 138–157 in Stable isotopes in ecology and environmental science (K. Lajtha and R. H. Michener, eds.). Blackwell, Oxford, United Kingdom.

Natoli, A., V. M. Peddemors, and A. R. Hoelzel. 2004. Population structure and speciation in the genus *Tursiops* based on microsatellite and mitochondrial DNA analyses. Journal of Evolutionary Biology 17:363–375.

Natoli, A., A. Birkun, A. Aguilar, A. Lopez, and Hoelzel A. R. 2005. Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). Proceedings of the Royal Society of London, B. Biological Sciences 272:1217–1226.

Newsome, S. D., M. A. Clementz, and P. L. Koch. 2010. Using stable isotopes biogeochemistry to study marine mammal ecology. Marine Mammal Science 26:509–572.

Niño-Torres, C. A., J. P. Gallo-Reynoso, F. Galván-Magaña, E. Escobar-Briones, and S. A. Macko. 2006. Isotopic analysis of δ13C, δ15N and δ34S "a feeding tale" in teeth of the long beaked common dolphin, *Delphinus capensis*. Marine Mammal Science 22:831–846.

Ohizumi, H., and N. Miyazaki. 2010. Differences in stable isotope ratios of Dall's porpoises (*Phocoenoidesdalli*) between coastal and oceanic areas of the North Pacific. Fisheries Oceanography 19:257–261.

Parnell, A., R. Inger, S. Bearhop, and A. L. Jackson. 2008. SIAR: Stable Isotope Analysis in R. http://cran.r-project.org/web/packages/siar/ index.html. Accessed 10 December 2014.

Parnell, A. C., R. Inger, S. Bearhop, and A. L. Jackson. 2010. Source partitioning using stable isotopes: coping with too much variation. PLoS One 5:e9672.

Parnell, A., and A. Jackson. 2013. SIAR: Stable Isotope Analysis in R. http://cran.r-project. org/web/packages/siar/index.html. Accessed 10 December 2014.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293–320.

Phillips, D. L., and J. W. Gregg, 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136:261–269.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703–720.

Riccialdelli, L., S. D. Newsome, N. A. Dellabianca, R. Bastida, M. L. Fogel, and R. N. P. Goodall. 2013. Ontogenetic diet shift in Commerson's dolphin (*Cephalorhynchuscommersonii commersonii*) off Tierra del Fuego. Polar Biology 36:617–627.

Riccialdelli, L., S. D. Newsome, M. L. Fogel, and R. N. P. Goodall. 2010. Isotopic assessment of prey and habitat preferences of a cetacean community in the southwestern South Atlantic Ocean. Marine Ecology Progress Series 418:235–248.

Riccialdelli, L., S. D. Newsome, R. N. P. Goodall, M. L. Fogel, and R. Bastida. 2012. Insight into niche separation of Risso's dolphin (*Grampus griseus*) in the southwestern South Atlantic via δ^{13}C and δ^{15}N values. Marine Mammal Science 28:503–515.

Romero, M. A., S. L. Dans, N. A. García, G. M. Svendsen, R. González, and E. A. Crespo. 2012. Feeding habits of two sympatric dolphin species off North Patagonia, Argentina. Marine Mammal Science 22:364–377.

Rubenstein, D. R., and K. A. Hobson. 2004. From birds to butterflies: animal movements patterns and stable isotopes. Trends in Ecology & Evolution 19:256–263.

Sánchez, R. P., and J. D. de Ciechomsky. 1995. Spawning and nursery grounds of pelagic fish species in the sea-shelf off Argentina and adjacent areas. Scientia Marina 59:455–478.

Sekiguchi, K., N. T. W. Klages, and P. Best. 1992. Comparative analysis of the diets of smaller odontocete cetaceans along the coast of Southern Africa. African Journal of Marine Science 12:843–861.

Silva, L., et al. 2014. Differences in diet composition and foraging patterns between sexes of the Magellanic penguin (*Spheniscusmagellanicus*) during the non-breeding period as revealed by δ^{13}C and δ^{15}N values in feathers and bone. Marine Biology 161:1195–1206.

Syväranta, J., A. Lensu, T. J. Marjomäki, S. Oksanen, and R. I. Jones. 2013. An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data. PLoS One 8:e56094.

Tieszen, L. L., T. W. Boutton, K. G. Tesdahl, and N. A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for δ13 C analyses of diet. Oecologia 57:32–37.

Valenzuela, L. O., M. Sironi, V. J. Rowntree, and J. Seger. 2009. Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). Molecular Ecology 18:782–791.

Vales D. G., L. Cardona, N. A. García, L. Zenteno, and E. A. Crespo. 2015. Ontogenetic dietary changes in male South American fur seals *Arctocephalus australis* in Patagonia. Marine Ecology Progress Series 525:245–260.

Van Waerebeek, K. 1993. Geographic variation and sexual dimorphism in the skull of the dusky dolphin, *Lagenorhynchus obscurus* (Gray, 1828). Fishery Bulletin US 91:754–774.

Vaughn, R. L., D. S. Shelton, L. L. Timm, L. A. Watson, and B. Würsig. 2007. Dusky dolphin (*Lagenorhynchus obscurus*) feeding tactics and multi-species associations. New Zealand Journal of Marine and Freshwater Research 41:391–400.

Witteveen, B. H., G. A. J. Worthy, K. Wynne, and J. D. Roth. 2009. Population structure of North Pacific humpback whales on feeding grounds as shown by stable carbon and nitrogen isotope ratios. Marine Ecology Progress Series 379:299–310.

Würsig, B., N. Duprey, and J. Weir. 2007. Dusky dolphins (*Lagenorhynchus obscurus*) off Kaikoura New Zealand: present knowledge and goals for the future. DOC Science and Technical Publications, Research and Development Series 270, Department of Conservation, Wellington, New Zealand.

Würsig, B., and M. Würsig. 1980. Behaviour and ecology of dusky dolphins, *Lagenorhynchus obscurus*, in the South Atlantic. Fishery Bulletin 77:871–890.

Zenteno, L., et al. 2015. Dietary consistency of male South American sea lions (*Otaria flavescens*) in southern Brazil during three decades inferred from stable isotope analysis. Marine Biology 162:275–289.

Submitted 29 June 2015. Accepted 20 October 2015.

Associate Editor was Jeanette A. Thomas.