



Original investigation

What are you eating? A stable isotope insight into the trophic ecology of short-beaked common dolphins in the Southwestern Atlantic Ocean

Rocío Loizaga de Castro^{a,*}, Fabiana Saporiti^b, Damián G. Vales^a, Néstor A. García^a, Luis Cardona^b, Enrique A. Crespo^a

^a Marine Mammal Lab, Centre for the Study of Marine Systems (CESIMAR-CENPAT-CONICET, National Research Council), Bvd. Brown 2915, CP U9120ACV Puerto Madryn, Chubut, Argentina

^b Department of Animal Biology and IRBio, Faculty of Biology, University of Barcelona, Diagonal 643, 08071 Barcelona, Spain



ARTICLE INFO

Article history:

Received 26 June 2015

Accepted 11 July 2016

Handled by Jennifer Burns

Available online 18 July 2016

Keywords:

Short-beaked common dolphins

Delphinus delphis

Stable isotopes

Trophic ecology

Argentina

ABSTRACT

As the feeding habits of marine mammals are particularly difficult to observe, stable isotope analysis has become an essential tool to investigate several aspects of dolphin's trophic ecology. Short-beaked common dolphins (*Delphinus delphis*) occur off Argentina coastline from 36°S to 42°S, but nothing is known about latitudinal changes in diet. A stable isotope analysis has been performed on three short-beaked common dolphins groups: Buenos Aires group ($n=20$), Golfo San Matías inshore group ($n=24$), and Golfo San Matías offshore group ($n=16$). Highly significant differences in average $\delta^{15}\text{N}_{\text{skin}}$ values were found among the three groups of dolphins considered. Differences were also statistically significant for the average $\delta^{13}\text{C}_{\text{skin}}$ and Suess corrected $\delta^{13}\text{C}_{\text{skin}}$ values. Furthermore, no significant differences were found in the $\delta^{13}\text{C}_{\text{skin}}$ values of the dolphins from the inshore group sampled during summer and winter seasons at Golfo San Matías, although the $\delta^{15}\text{N}_{\text{skin}}$ values changes seasonally, suggesting that probably dolphins forage at a higher trophic level in summer. The SIAR model indicated that juvenile Argentine hake (*Merluccius hubbsi*) had the highest mean feasible contribution to the diet of short-beaked common dolphins inhabiting the continental shelf off Buenos Aires and northern Patagonia, whereas the Argentine anchovy (*Engraulis anchoita*) did it for short-beaked common dolphins inhabiting the Golfo San Matías. The results obtained in this study increase the knowledge of trophic ecology for high trophic level predators such as short-beaked common dolphins along the Argentina coast in support of effective conservation and management programs.

© 2016 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Introduction

The exploitation of marine ecosystems is causing a rapid decrease in the abundances of top predators around the world, and as a result food webs are suffering great changes in their structure and function (Pauly et al., 1998; Jackson and Sala, 2001; Myers and Worm, 2003). Cetaceans, as top predators, have an essential role in marine ecosystems (Bowen, 1997), and, as K strategists, they are likely to experience the most severe impact from anthropogenic stressors in the marine environment (Bowen, 1997; Bearzi et al., 2003; MacLeod et al., 2005).

Through diet, marine mammals are linked with other components of marine food webs and thus changes in diet are the first symptom of changes in the structure of food webs.

The feeding habits of marine mammals are particularly difficult to observe, and detailed data on long-term trends are rare in these animals (Walker and Macko, 1999; Drago et al., 2009a). A conventional tool to study the diet of marine mammals is the stomach content analysis, but this usually only provides a snapshot of the animals' diet (Sekiguchi et al., 1992; Kaschner et al., 2006). Alternatively, stable isotope analysis on different body tissues represents a new tool for studying changes in the diets of marine mammals, both short and long term, due to the fact that tissues with different turnover rates integrate dietary information over multiple temporal scales (Walker and Macko, 1999; Newsome et al., 2010). In particular nitrogen and carbon stable isotopes, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ respectively, have proven to be useful to explore several aspects of dolphin's trophic ecology (Kiszka et al., 2010, 2014; Ricciardelli et al., 2010, 2012, 2013; Botta et al., 2011; Meissner et al., 2011; Bisi et al., 2013). Finally, an isotopic approach may provide critical information to assess stocks and identify critical areas for management purposes

* Corresponding author.

E-mail address: rocio@cenpat-conicet.gob.ar (R. Loizaga de Castro).

(Barros et al., 2010; Fernández et al., 2011; Gómez-Campos et al., 2011; Auriolos-Gamboa et al., 2013; Browning et al., 2014a).

Common dolphins in genus *Delphinus* are distributed worldwide in temperate, subtropical, and tropical regions and show a high degree of morphological variation (Heyning and Perrin, 1994; Perrin, 2002; Jefferson et al., 2008, 2009). Common dolphins occur along the Argentine coastline from 36°S to 42°S and two morphotypes have been identified on the basis of the rostral index: short-beaked and long-beaked common dolphins (Tavares et al., 2010). Morphological variation in the rostrum of common dolphins may be related more to a local adaptation to prey capture and habitat use rather than the differentiation along phylogenetic lineages (Natoli et al., 2006; Pinela et al., 2011, 2015). Accordingly, only different morphotypes of *D. delphis* would occurred off Argentina (Natoli et al., 2006), a conclusion supported more recently by the genetic evidence gathered by Cunha et al. (2015).

The short-beaked common dolphin is listed by the IUCN as "Least Concern" (IUCN Red List Program, 2010) and is one of the most abundant small cetaceans in the Southwestern Atlantic Ocean (Crespo and Dans, 2008), also it is susceptible to incidental mortality in trawl and purse seine off Argentina (Corcueria et al., 1994; Crespo et al., 2000). Many aspects of its ecology are still unknown and there is a lack of biological information along its distribution off Argentina, recent research has focused on the incidental catch (Crespo et al., 2000), parasites (Berón-Vera et al., 2007) and just one in diet (Romero et al., 2012).

The bulk of the diet of short-beaked common dolphins consists of a combination of the locally most abundant species of small pelagic schooling fish or cephalopods inhabiting the continental shelves worldwide (e.g., Young and Cockcroft, 1994; Meynier, 2004; Pusineri et al., 2007). However, the foraging ecology of short-beaked common dolphins in the Southwestern Atlantic Ocean has remained unstudied, but with one exception (Romero et al., 2012). The authors showed that short-beaked common dolphins off northern Patagonia feed primarily on Argentine anchovy, *Engraulis anchoita*, and South American long-fin squid, *Doryteuthis (Loligo) sampaullensis* (Romero et al., 2012). Recently Saporiti et al. (in press), reported a poleward increase in trophic overlap among air-breathing marine predators along the Patagonian shelf, likely due to a decrease in the diversity of prey species. If this was also true for the short-beaked common dolphin, diet is expected to change

with latitude. Therefore, the main objective of this study is look for geographical and seasonal variation in diet. Consequently, the information provided here will contribute to design conservation areas and increase the knowledge on short-beaked common dolphins' ecology along the Argentine coast.

Material and methods

Study area

The study area includes the entire distribution of short-beaked common dolphins in Southwestern South Atlantic Ocean, from Buenos Aires coast (38° 40'S) to Golfo San Matías (40° 45'S). Based on the availability of different trophic resources throughout the whole region (e.g. prey species composition and relative abundance prey), three subareas were recognized: Buenos Aires group (BA), Golfo San Matías offshore group (SMo) and Golfo San Matías inshore group (SMi) (Fig. 1).

The Buenos Aires coast and waters off Golfo San Matías are characterized by an estuarine temperate zone where several marine fronts occur and promote high biological production (Acha et al., 2004). Typical small and medium pelagic fish species from this region are the Argentine anchovy, the Argentine hake *Merluccius hubbsi*, the rough scad *Trachurus lathami*, the silver warehou *Seriola porosa* and the silverside *Odontesthes smitti*; whereas the demersal fish community is dominated by sciaenids, like the white croaker *Micropogonias furnieri*, and the striped weakfish *Cynoscion guatucupa* among others species (Balech and Ehrlich 2008; Cousseau and Perrotta, 2013). The cephalopods assemblage is characterized by the South American long-fin squid and the Argentine short-fin squid *Illex argentinus* (Brunetti et al., 1999).

Golfo San Matías (GSM) is the most extensive of the northern Patagonian gulfs and belongs to the tidal Patagonian zone (Acha et al., 2004). The number of fish species and its relative abundance is lower than in the adjoining continental shelf (Cousseau and Perrotta, 2013). The pelagic community of Golfo San Matías is dominated by the Argentine hake, the Argentine anchovy, the butterfish *Stromateus brasiliensis*, the silver warehou, and the hoki *Macruronus magellanicus* (Brunetti et al., 1998). Among cephalopods the community is characterized by the South American long-fin squid, the Argentine short-fin squid, and the Patagonian squid *Doryteuthis*

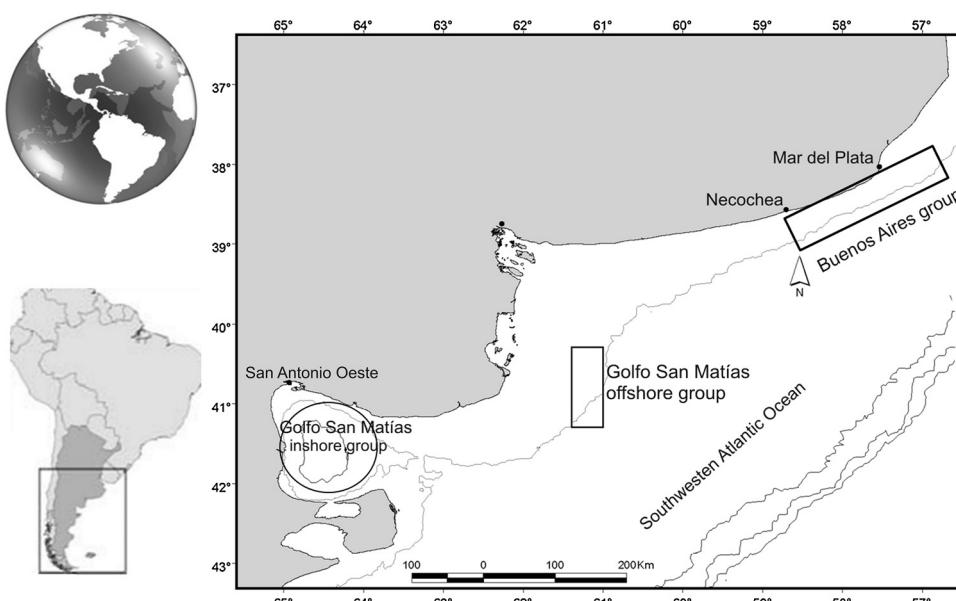


Fig. 1. Study area, three sampling sites for short-beaked common dolphins, *Delphinus delphis*.

(*Loligo*) *gahi*, although the abundance of the latter increases with latitude (Brunetti et al., 1998; Barón, 2001).

Sample collection

Short-beaked common dolphins' biopsy samples (skin and blubber) were collected during 2009–2010 field seasons in coastal waters off Necochea and Mar del Plata cities (off Buenos Aires coast, hereafter BA; n = 20) and in Golfo San Matías waters (hereafter SMi; n = 24). Biopsy sampling was performed with a biopsy pole system as described by Loizaga de Castro et al. (2013). On the other hand, short-beaked common dolphins' skin samples from waters off Golfo San Matías, between 40°30'–41°30'S and 61°00'–61°40'W, came from individuals accidentally caught by mid-water trawlers targeting Argentine anchovy in January 1999 (hereafter SMo; n = 16). All samples were stored in 20% dimethylsulphoxide (DMSO) solution saturated with NaCl (Amos and Hoelzel, 1991).

Prey of short-beaked common dolphins previously identified by stomach analysis (Romero et al., 2012) were collected to determine their isotopic ratios. Prey samples from the temperate estuarine zone (Buenos Aires and Golfo San Matías offshore) were obtained from fishermen at Mar del Plata (38°08'S, 57°32'W) and Puerto Quequén, Necochea (38°35'S, 58°42'W), and also taken from the literature (Drago et al., 2009a,b; Silva et al., 2014); whereas samples from Golfo San Matías inshore waters were obtained from fishermen at San Antonio Oeste City.

Stable isotope analyses

For each dolphin biopsy sample, blubber was removed with a scalpel blade and only skin was processed for isotopic analysis. Skin samples, white dorsal muscle of fish and mantle of cephalopod were dried at 60 °C for 5–9 days and then ground up with mortar and pestle. Each skin sample was washed in successive rinses of deionised water to remove DMSO effects as suggested in previous studies on marine mammals (e.g., Marcoux et al., 2007; Lesage et al., 2010; Foote et al., 2012). Lipid extraction was carried out to all the samples with several rinses of a 2:1 mixture of chloroform and methanol every 24 h during 4 days. Finally, samples were dried at 60 °C for 48 h and were ready for isotopic analysis. Skin samples, white dorsal muscle of fish and mantle of cephalopod were analysed at the Instituto de Geocronología y Geología Isotópica (INGEIS-CONICET/UBA), where international isotope secondary standards given by the International Atomic Energy Agency (IAEA) were used for calibration at a precision of 0.2‰ for both nitrogen and carbon. Results are expressed in δ notation relative to PeeDee Belemnite and atmospheric N₂ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, according to the equation: $\delta\text{X} = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$ where X is ^{13}C or ^{15}N and R is the isotope ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ (Bond and Hobson, 2012). Carbon to nitrogen percent ratio (C:N) was also calculated to indicate good lipid removal efficiency (Lesage et al., 2010).

^{13}C content in atmospheric CO₂ has decreased 0.022 per mil/year since 1960, due largely to fossil fuel burning (Francey et al., 1999; Indermühle et al., 1999), thus Suess effect correction was estimated in order to eliminate this factor as a possible cause of variation in $\delta^{13}\text{C}$ isotope values; all the corrected $\delta^{13}\text{C}$ values were referenced to 2010, last year of biopsy sampling (Loizaga de Castro et al., 2015; Zenteno et al., 2015).

Data analysis

Data were tested for normality and homoscedasticity with a Shapiro Wilks test and Levene test respectively. One-way ANOVA followed by a post hoc Tukey test was used to assess the effect of locality (BA, SMi, SMo) on short-beaked common dolphins' skin stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Additionally, one-way ANOVA

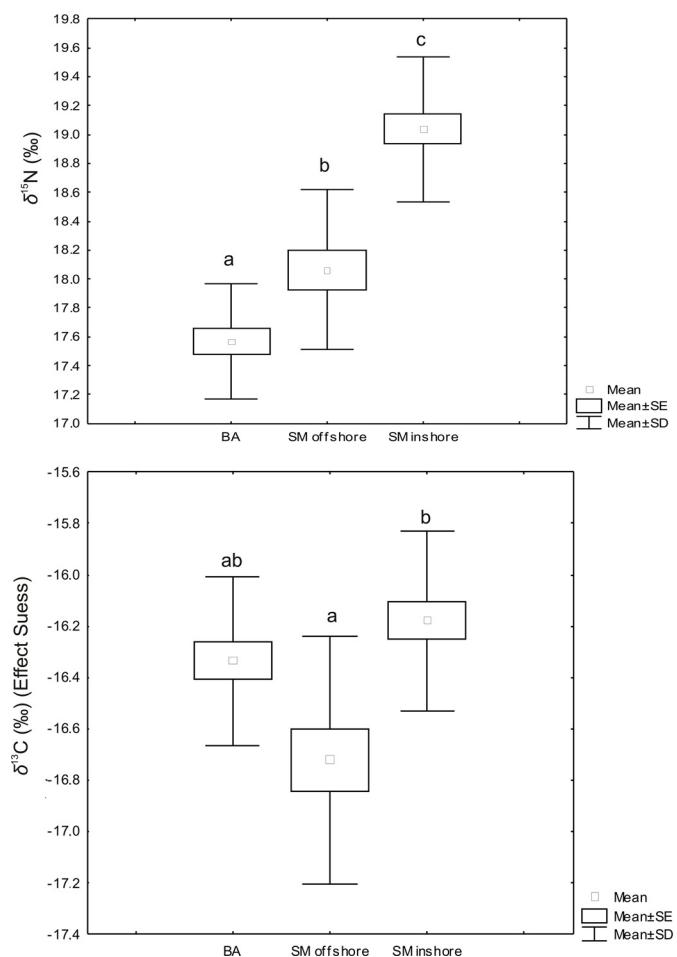


Fig. 2. Mean nitrogen and carbon stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of short-beaked common dolphins among the three groups considered. BA: Buenos Aires inshore; SMo: Golfo San Matías offshore, SMi: Golfo San Matías inshore. Letters indicate post hoc Tukey highly significance differences $p < 0.01$.

was performed to investigate potential seasonal changes in diet for Golfo San Matías inshore group, considering samples collected in summer (n = 14) and winter (n = 10).

Finally, mixing models were applied with the package SIAR (Stable Isotope Analysis in R; Parnell et al., 2010) to estimate the proportional contribution of potential prey taxa to the short-beaked common dolphin's diet in each locality. SIAR allows to incorporate specific trophic enrichment factors (TEFs), i.e. the difference in isotope ratios between diet and consumer tissue (Phillips and Gregg, 2003), and also the standard deviation for each prey source (Bond and Diamond, 2011). Among marine mammal species, enrichment factors are considered to be relatively conservative for the same tissue (Lesage et al., 2001; Kiszka et al., 2014). Trophic enrichment factor has to be carefully selected to obtain robust results and make ecological inferences accurately. Given that the short-beaked common dolphin's diet is expected to be composed mainly by fatty prey, such as anchovies; in this study, we used a TEF from skin of bottlenose dolphins based on a lipid enriched diet. In this study we used $\delta^{13}\text{C}$ 2.04‰ ± 0.14 and $\delta^{15}\text{N}$ 2.96‰ ± 0.12 (Browning et al., 2014b). Isotopic data are shown as mean ± sd, unless otherwise stated.

Results

Isotopic data for $\delta^{15}\text{N}$ were normally distributed for all geographic locations; ($W_{\text{BA}} = 0.9186, P = 0.09308$; $W_{\text{SMoffshore}} = 0.8869$,

Table 1

Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios (mean \pm SD), code of species, tissue, number of individuals analysed (n), group considered (group) of short-beaked common dolphins (*Delphinus delphis*) along its Argentine distribution and its potential prey species.

Species							
Prey	Common name	Tissue	n	Group	$\delta^{13}\text{C}(\text{‰})$	$\delta^{15}\text{N}(\text{‰})$	C/N
<i>Engraulis anchoita</i>	Argentine anchovy	Muscle	5	Buenos Aires/Golfo San Matías offshore	-18.2 \pm 0.3 ^a	15.5 \pm 0.5 ^a	
<i>Merluccius hubbsi</i> (<30 cm)	Argentine hake	Muscle	5	Buenos Aires/Golfo San Matías offshore	-18.4 \pm 0.08 ^a	17.3 \pm 0.5 ^a	
<i>Cynoscion guatucupa</i>	Stripped weakfish	Muscle	5	Buenos Aires/Golfo San Matías offshore	-17.2 \pm 0.2 ^a	17.6 \pm 0.2 ^a	
<i>Raneya brasiliensis</i>	Banded cuskeel	Muscle	5	Buenos Aires/Golfo San Matías offshore	-16.2 \pm 0.4 ^a	17.3 \pm 0.5 ^a	
<i>Stromateus brasiliensis</i>	Butterfish	Muscle	5	Buenos Aires/Golfo San Matías offshore	-16.9 \pm 0.6 ^a	17.3 \pm 0.4 ^a	
<i>Loligo sanpaulensis</i>	South American long-fin squid	Mantle	5	Buenos Aires/Golfo San Matías offshore	-16.7 \pm 0.2 ^a	18.6 \pm 0.2 ^a	
<i>Illex argentinus</i>	Argentine shortfin squid	Mantle	5	Buenos Aires/Golfo San Matías offshore	-17.5 \pm 0.4 ^a	14.7 \pm 0.5 ^a	
<i>Engraulis anchoita</i>	Argentine anchovy	Muscle	5	Golfo San Matías inshore	-17.9 \pm 0.2 ^a	15.7 \pm 0.7 ^a	
<i>Merluccius hubbsi</i> (<30 cm)	Argentine hake	Muscle	5	Golfo San Matías inshore	-17.7 \pm 0.5 ^a	17.6 \pm 0.2 ^a	
<i>Cynoscion guatucupa</i>	Stripped weakfish	Muscle	5	Golfo San Matías inshore	-17.2 \pm 0.2 ^a	17.6 \pm 0.2 ^a	
<i>Raneya brasiliensis</i>	Banded cuskeel	Muscle	5	Golfo San Matías inshore	-17.1 \pm 0.4 ^a	16 \pm 0.4 ^a	
<i>Stromateus brasiliensis</i>	Butterfish	Muscle	5	Golfo San Matías inshore	-16.9 \pm 0.6 ^a	16.0 \pm 0.4 ^a	
<i>Loligo sanpaulensis</i>	South American long-fin squid	Mantle	5	Golfo San Matías inshore	-16.7 \pm 0.2 ^a	18.6 \pm 0.2 ^a	
<i>Loligo gahi</i>	Patagonian squid	Mantle	5	Golfo San Matías inshore	-17.6 \pm 0.4 ^a	15.7 \pm 0.5 ^a	
<i>Illex argentinus</i>	Argentine shortfin squid	Mantle	5	Golfo San Matías inshore	-17 \pm 0.6 ^a	13.7 \pm 0.8 ^a	
<i>Seriorella porosa</i>	Silver warehou	Muscle	6	Golfo San Matías inshore	-17.4 \pm 0.5 ^b	19.31 \pm 0.5 ^b	
<i>Engraulis anchoita</i>	Argentine anchovy	Muscle	5	Golfo San Matías inshore	-17.5 \pm 0.4 ^b	17 \pm 0.3 ^b	
<i>Stromateus brasiliensis</i>	Butterfish	Muscle	5	Golfo San Matías inshore	-17.3 \pm 0.5 ^b	17.6 \pm 1.1 ^b	
<i>Merluccius hubbsi</i> (<30 cm)	Argentine hake	Muscle	5	Golfo San Matías inshore	-16.6 \pm 0.1 ^b	19.28 \pm 0.7 ^b	
<i>Loligo spp</i>		Mantle	5	Golfo San Matías inshore	-16 \pm 0.3 ^b	17.62 \pm 0.3 ^b	
<i>Illex argentinus</i>	Argentine shortfin squid	Mantle	5	Golfo San Matías inshore	-15.8 \pm 0.3 ^b	18.32 \pm 0.6 ^b	
Predator							
<i>Delphinus delphis</i>	Common dolphins	Skin	20	Buenos Aires	-16.3 \pm 0.3 ^b	17.6 \pm 0.4 ^b	3.64 \pm 0.07 ^b
<i>Delphinus delphis</i>	Common dolphins	Skin	18	Golfo San Matías offshore	-16.5 \pm 0.5 ^b	18.1 \pm 0.5 ^b	3.84 \pm 0.2 ^b
<i>Delphinus delphis</i>	Common dolphins	Skin	24	Golfo San Matías inshore	-16.2 \pm 0.3 ^b	19 \pm 0.5 ^b	3.6 \pm 0.1 ^b

^a Drago et al. (2009a,b); Silva et al. (2014).

^b Present study.

$P=0.0510$; $W_{\text{SMinshore}}=0.9641$, $P=0.5265$). Also Suess corrected $\delta^{13}\text{C}$ was normally distributed for SM offshore and inshore ($W_{\text{SMoffshore}}=0.9275$, $P=0.2226$; $W_{\text{SMinshore}}=0.939$, $P=0.1551$), however data were not normally distributed for Buenos Aires ($W_{\text{BA}}=0.8592$, $P=0.007$) nonetheless ANOVA is robust to non-normality. Also isotopic data had similar variance (Levene-test; $F_{\delta^{15}\text{N}}=0.7476$, $P=0.4781$, $F_{\delta^{13}\text{C}\text{Suesscorrected}}=2.2501$, $P=0.1147$).

Highly significant differences in short-beaked common dolphins average $\delta^{15}\text{N}$ values were found among the three groups considered ($F_{2,57}=52.18$, $P<0.001$) and all the post hoc Tukey test were highly significant ($P<0.001$). The average Suess corrected $\delta^{13}\text{C}$ values were also significantly different among the regions ($F_{2,57}=3.227$, $P<0.05$), but the post hoc Tukey test was significant only between the inshore and off shore groups from Golfo San Matías ($P<0.05$) (Fig. 2 and Table 1).

Stable isotope ratios of potential prey species of short-beaked common dolphins studied are shown in Table 1. The distribution of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for common dolphins along the Argentine coast is given in Fig. 3. High intraspecific variability was observed for both stable isotope ratios, indicating large individual variation in dolphins' habitat use patterns and clearly showed differences among dolphins feeding along the continental shelf and inside the gulf (Fig. 3a and b). This is not because differences in lipid contents, as the carbon to nitrogen ratio (C:N) from short-beaked common dolphins skin samples were lower than 4, indicating good lipid removal efficiency (Table 1, Kiszka et al., 2010). Short-beaked common dolphins from Golfo San Matías inshore group seems to prefer more prey from continental shelf rather than prey from inside the gulf (Fig. 3a and b). No significant differences were found in $\delta^{13}\text{C}$ values between summer and winter seasons at Golfo San Matías inshore group (One-way ANOVA; $\delta^{13}\text{C}$: $F_{1,22}=0.152$, $P>0.05$); however significant differences were found in $\delta^{15}\text{N}$ ($F_{1,22}=7.188$, $P<0.05$), indicating that in summer short-beaked common dolphins seems to forage at a higher trophic level than in winter (Fig. 4).

Finally, estimates of potential dietary contributions identified Argentine hake (<30 cm) and Argentine anchovy as the main prey for short-beaked common dolphins along its distribution off Argentina, although their feasible relative contribution varied regionally. In Buenos Aires, the Argentine hake represented the bulk of the diet, and contributed with 79% and a very minor contribution of the Argentine anchovy 7.2% and the Argentine short-fin squid 8.9%. In Golfo San Matías offshore, Argentine hake also seems to dominate the diet 56%, but the contribution of the Argentine anchovy 22% and the Argentine shortfin squid 11% increased. In Golfo San Matías inshore group, the Argentine anchovy and the Argentine hake contributed to common dolphins' diet with 38% and 19% respectively and the Patagonian squid was also an important prey contributing 15.0% to diet (Fig. 5).

Discussion

In the present study, we reported stable isotope data from short-beaked common dolphin skin samples, describing the habitat use and trophic ecology along the Argentine continental shelf. Variation on stable isotopes of carbon and nitrogen reflect variation associated with habitat use, suggesting considerable differences between individuals and among groups along the coast in the exploitation of food resources and, most likely, their habitat. Stable isotopes showed a more complex diet for short-beaked common dolphins than diet reflected by the stomachs content studies.

In marine mammals, the use of naturally occurring stable isotopes of carbon and nitrogen has provided complementary data to their feeding ecology and habitat use (Hobson and Wassenaar, 1999). There exist two methods for analyzing prey to gain insight into predator trophic ecology: analyzing stable isotopes of the entire fish, or only analyzing muscle tissue from the fish. Dolphins swallow they whole prey, so analyzing the entire potential prey may seem the best approach at a first glance. On the other hand, processing small samples of muscle is more practical, particularly when dealing with bulky prey. Experimental evidence

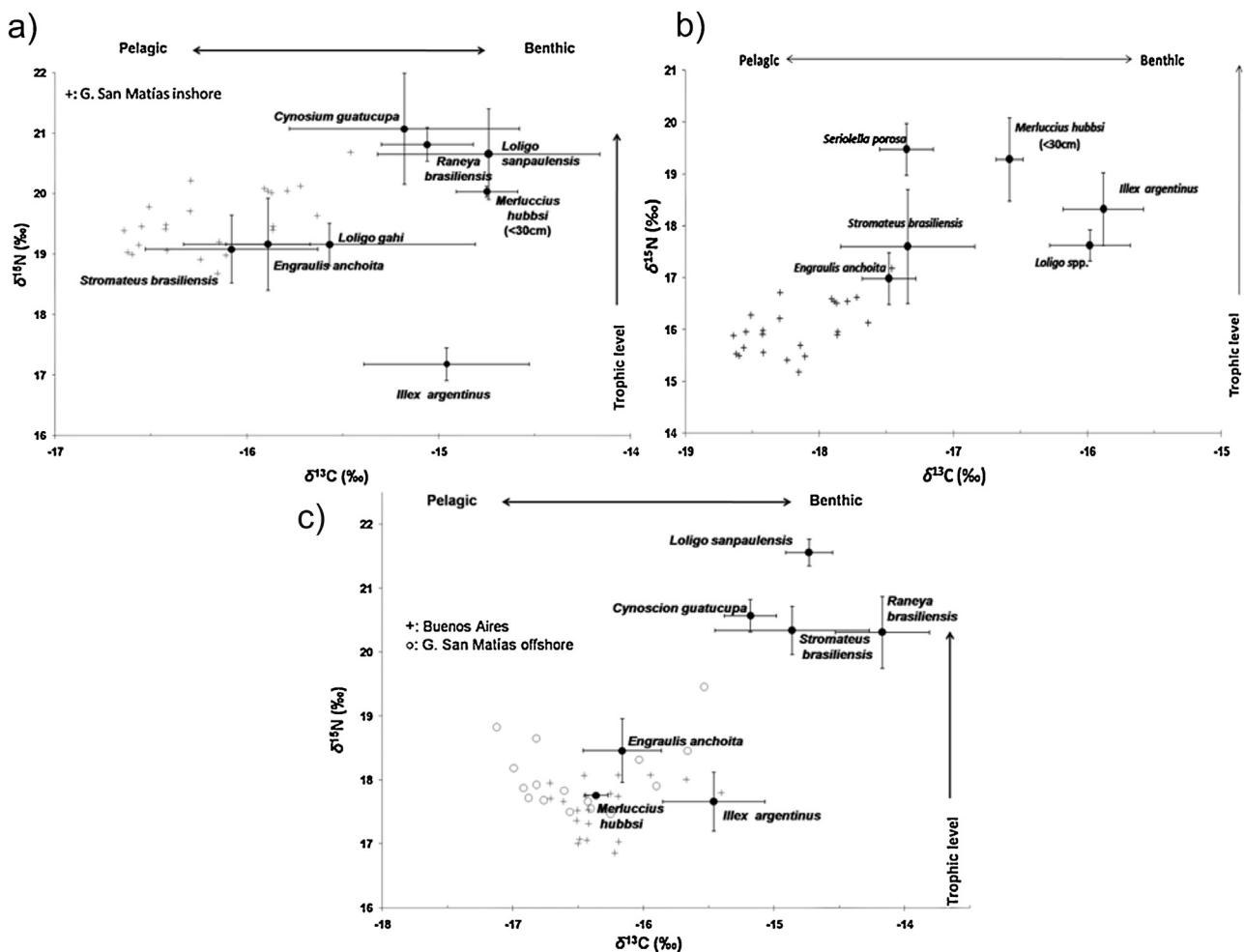


Fig. 3. Nitrogen and carbon stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of short-beaked common dolphins (individual values) and their potential prey after correcting for the trophic discrimination factor (mean \pm SD for each species); a) Golfo San Matías inshore group, b) Golfo San Matías offshore group and potential prey species sampled in Golfo San Matías c) cross: Buenos Aires group; circles: Golfo San Matías offshore group.

demonstrates that diet-to-tissue discrimination values did not differ for fish muscle and the whole fish, as far as lipids had been previously removed (Giménez et al., 2016), and hence analyzing muscle is not introducing any relevant bias. An important feature of stable isotope analysis is the use of appropriate, species- and diet-specific TEFs for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$; as they are key to predict the dietary sources of a consumer using the mixing models (Newsome et al., 2010; Kiszka et al., 2014). Nevertheless, currently there are no TEFs for short-beaked common dolphins; therefore, a literature search was conducted to find the most proper TEF. We used TEF for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from the skin of bottlenose dolphins based on a lipid enriched diet (Browning et al., 2014b). Because the diet of short-beaked common dolphins is composed mainly of prey of high nutritional value, these correction factors were chosen as the most accurate for this study.

Differences were found in $\delta^{15}\text{N}$ among short-beaked common dolphins groups considered, nonetheless the Buenos Aires group and Golfo San Matías offshore group showed similar values indicating a similar trophic level in contrast to the Golfo San Matías inshore group, that showed higher values of nitrogen isotopes ratios indicating that dolphins inside the gulf are probably feeding at higher trophic level in the trophic network. Also differences in $\delta^{13}\text{C}$ among short-beaked common dolphins groups considered in this study could indicate the presence of offshore and inshore ecotypes along the Argentine Sea. Beak morphology has been related to dietary differences along an offshore-inshore gradient in other populations of

common dolphins (Pinela et al., 2011), but only short-beaked common dolphins exist in Argentina (Cunha et al., 2015) so other factors need to be considered.

In any case, stable isotope analysis of skin samples (this study) and stomach contents analysis (Romero et al., 2012) agree in that *Delphinus delphis* off the Argentine coast rely primarily on pelagic schooling fish and squids, but species composition vary locally. According to stomach contents analysis, the diet of short-beaked common dolphins inhabiting Golfo San Matías was dominated by one prey species, the Argentine anchovy, which made up over 80% of their prey intake by number (Romero et al., 2012). SIAR also agreed in identifying the Argentine anchovy as the main prey of short-beaked common dolphins from inshore areas of Golfo San Matías, but revealed that juvenile Argentine hakes dominated diet in off-shore locations. This pattern is consistent with previous reports indicating that the Argentine hake represents the bulk of diet of most air-breathing predators in northern Patagonia, but not off Buenos Aires, where a higher diversity of small pelagic fishes and squids exist (Saporiti et al., in press).

The Argentine anchovy, the Argentine hake, the Argentine short-fin squid, and the 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). Hence, it seems that short-beaked common dolphins forage opportunistically on available prey species, but selectively prey on small schooling species. Feeding on schooling species is probably the most energetically

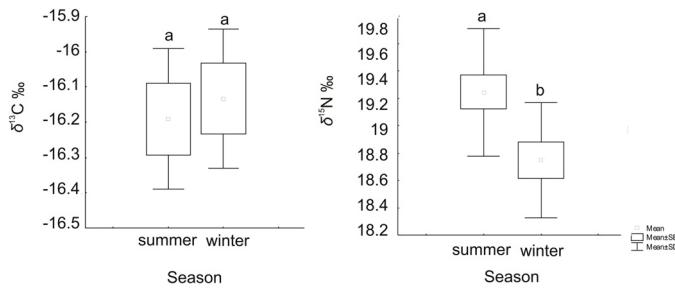


Fig. 4. Mean nitrogen and carbon stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of short-beaked common dolphins at Golfo San Matías inshore group during summer and winter seasons. Letters indicate post hoc Tukey highly significant differences $p < 0.01$.

profitable foraging tactic for a cooperative predator (Meynier et al., 2008a). It is important to highlight that at every single locality, the diet of short-beaked common dolphins is dominated by only one or two pelagic species, although species richness in the environment may be higher; this adaptation to feeding on the locally most abundant prey is a common feature of the feeding strategy of common dolphins worldwide (Pusineri et al., 2007). Young and Cockcroft (1994) proposed that common dolphins off South Africa consume the most abundant, easily catchable prey, and that their diet may be a reliable and accurate proxy of the abundance and distribution of local, neritic resources. In the offshore North Pacific, the prey composition of common dolphins consisting mainly of highly abundant myctophids, may reflect the features of the subarctic front (Ohizumi et al., 1998). Meynier et al. (2008a) identified only three dominant species in the diet of the common dolphins off New Zealand, despite the overall diet appearing quite diverse. Peruvian long-beaked common dolphins seem to depend on pelagic and mesopelagic prey, mainly large schooling fish species (García-Godó 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). Long-term comparisons between fluctuations in local fish stocks and the prey consumed by dolphins helps to determine how the diet of the common dolphins reflects prey species abundance (Meynier et al., 2008b).

Dependence on juvenile hake of short-beaked common dolphins inhabiting the continental shelf is a matter of concern, particularly off Buenos Aires. The Argentine hake is the main fishery resource in the region (Aubone et al., 2000) and inhabits the waters of the Southwestern Atlantic Ocean between 22° and 55°S, at depths ranging from 50 to 500 m (Cousseau and Perrota, 2013). Two fishing stocks exist, north and south to 41°S parallel. During the late 1990s, the spawning biomass and the recruitment indices of both stocks declined drastically because of increased exploitation (Aubone et al., 2000; Renzi and Irusta, 2006). Decline was particularly serious for the northern stock, inhabiting waters of the Argentine-Uruguayan Common Fishing Zone (Aubone et al., 2000; Renzi and Irusta, 2006). Currently, this stock is supported by just a few age classes and the 2-year age class represented the bulk of the commercial landings during the period 1986–2005 (Renzi and Irusta, 2006; Rodriguez and Macchi, 2010). This scenario clearly indicates a negative population trend, which could lead to the disappearance of larger groups and in fact may have consequences on the reproductive potential of the northern hake stock (Aubone et al., 2000). Bearzi et al. (2003) reported similar changes in the abundance and distribution of the prey species of the short-beaked common dolphin in the western Mediterranean Sea as the most likely cause of the decline in the abundance of this species in that region. In view of the resulting possible indirect and/or direct com-

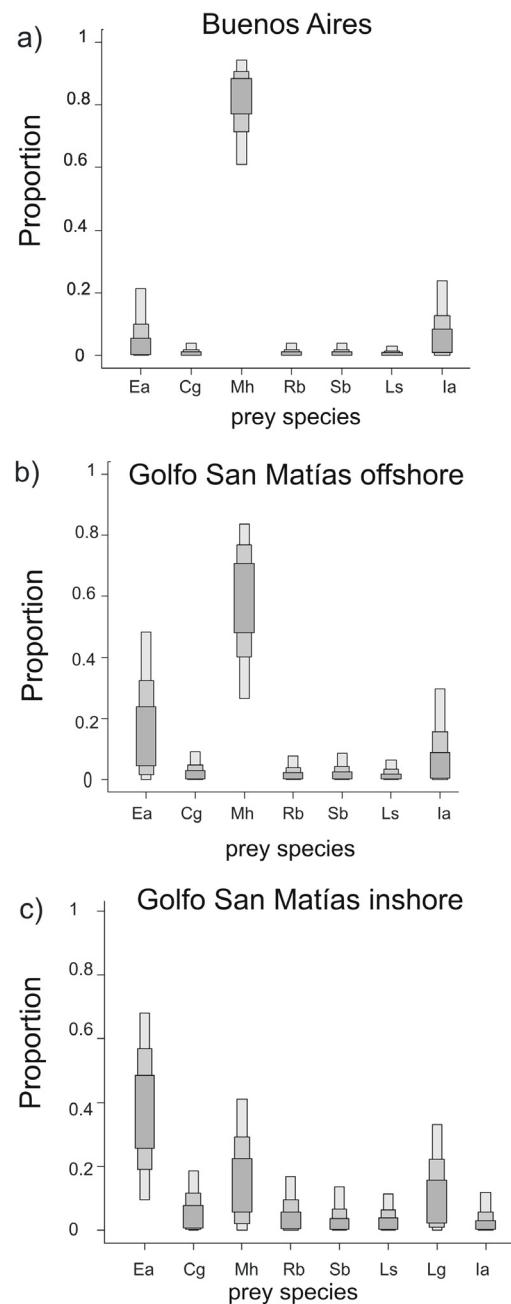


Fig. 5. Feasible composition of the diet of short-beaked common dolphins in three groups under study according to SIAR; a) Buenos Aires; b) Golfo San Matías offshore; c) Golfo San Matías inshore. Median 50%, 75% and 95% credibility intervals (respectively dark grey, light grey and white boxes) (Ea: *Engraulis anchoita*; Cg: *Cynoscion guatupupa*; Mh: *Merluccius hubbsi*; Rb: *Raneya brasiliensis*; Sb: *Stromateus brasiliensis*; Ls: *Loligo sanpaulensis*; Lg: *Loligo gahi*; Ia: *Illex argentinus*).

petition between dolphins and fisheries in northern Argentina, the biology of both predator and prey, need to be carefully studied.

Therefore the knowledge of feeding ecology for high trophic level predators such as short-beaked common dolphins along the Argentine coast is an important component of a broader study in support of effective conservation and management programs.

Acknowledgements

The authors are indebted to many people and institutions that collaborated in this research, Centro Nacional Patagónico (National Research Council of Argentina) and Universidad Nacional de la

Patagonia San Juan Bosco for logistic and institutional support. Also we thanks to Dr. Matías R. Ocampo for collecting the samples in San Antonio Oeste, Rio Negro. 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 Río Negro and Provincia de Buenos Aires. 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. Also RLC was supported by Grant-in-Aid from the Society of Marine Mammalogy. At the time this manuscript was written, DGV and RLC were supported by a Posdoc Fellowship from National Research Council of Argentina (CONICET).

References

- Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M., Bava, J., 2004. Marine fronts at the continental shelves of austral South America, physical and ecological processes. *J. Mar. Syst.* 44, 83–105.
- Amos, W., Hoelzel A.R., 1991. Long-term preservation of whale skin for DNA analysis. Report of IWC, Special Issue 13, 99–103.
- Aubone, A., Bezzi, S., Castrucci, R., Dato, C., Ibañez, P., Irusta, G., Pérez, M., Renzi, M., Santos, B., Scarlato, N., Simonazzi, M., Tringali, L., Villarino, M.F., 2000. Los recursos pesqueros del Mar Argentino y su relación con las pesquerías. II. Recursos a recuperar: Merluza (*Merluccius hubbsi*). In: Bezzi, S., Akselman, R., Boschi, E. (Eds.), Síntesis del estado de las pesquerías marítimas argentinas y de la Cuenca del Plata. Años 1997–1998, con una actualización de 1999. Publicaciones Especiales. INIDEP, Mar del Plata, pp. 29–39.
- Auriolles-Gamboa, D., Rodríguez-Pérez, M., Sánchez-Velasco, L., Lavín, M., 2013. Habitat, trophic level, and residence of marine mammals in the Gulf of California assessed by stable isotope analysis. *Mar. Ecol. Prog. Ser.* 488, 275–290.
- Balech, E., Ehrlich, M.D., 2008. Esquema Biogeográfico del Mar Argentino. *Rev. Invest. Des. Pesq.* 19, 45–75.
- Barón, P.J., 2001. First description and survey of the egg masses of *Loligo gahi* D'Orbigny, 1835, and *Loligo sanpaulensis* Brakoniecki, 1984, from coastal waters of Patagonia. *J. Shellfish Res.* 20, 289–295.
- Barón, P.J., Ré, M.E., 2002. Reproductive cycle and population structure of *Loligo sanpaulensis* in the northeastern coast of Patagonia. *Bull. Mar. Sci.* 71, 175–186.
- Barros, N.B., Ostrom, P.H., Stricker, C.A., Wells, R.S., 2010. Stable isotopes differentiate bottlenose dolphins off west-central Florida. *Mar. Mamm. Sci.* 26, 324–336.
- Bearzi, G., Reeves, R.R., Notarbartolo di Sciara, G., Politi, E., Cañadas, A., Frantzis, A., Mussi, B., 2003. Ecology, status and conservation of short-beaked common dolphins *Delphinus delphis* in the Mediterranean Sea. *Mamm. Rev.* 33, 224–252.
- Berón-Vera, B., Crespo, E.A., Raga, J.A., Fernández, M., 2007. Parasite communities of common dolphins *Delphinus delphis* from Patagonia: the relation with host distribution and diet and comparison with sympatric hosts. *J. Parasitol.* 93, 1056–1060.
- Bisi, T.L., Dorneles, P.R., Lailson-Brito, J., Lepoint, G., Azevedo, A.d.F., Flach, L., Malm, O., Das, K., 2013. Trophic relationships and habitat preferences of delphinids from the southeastern Brazilian coast determined by carbon and nitrogen stable isotope composition. *PLoS One* 8(12), e82205, <http://dx.doi.org/10.1371/journal.pone.0082205>.
- Bond, A.L., Diamond, A.W., 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. *Ecol. Appl.* 21, 1017–1023.
- Bond, A.L., Hobson, K.A., 2012. Reporting stable-isotope ratios in ecology: recommended terminology, guidelines, and best practices. *Waterbirds* 35, 324–331.
- Botta, S., Hohn, A.A., Macko, S.A., Secchi, E.R., 2011. Isotopic variation in delphinids from the subtropical western South Atlantic. *J. Mar. Biol. Assoc. U. K.* 92, 1689–1698.
- Bowen, W.D., 1997. Role of marine mammals in aquatic ecosystems. *Mar. Ecol. Prog. Ser.* 158, 267–274.
- Browning, N.E., McCulloch, S.D., Bossart, G.D., Worthy, G.A.J., 2014a. Fine-scale population structure of estuarine bottlenose dolphins *Tursiops truncatus* assessed using stable isotope ratios and fatty acid signature analyses. *Mar. Biol.*, <http://dx.doi.org/10.1007/s00227-014-2420-z>.
- Browning, N.E., Dold, C., I-Fan, J., Worthy, G.A.J., 2014b. Isotope turnover rates and diet-tissue discrimination in skin of ex situ bottlenose dolphins *Tursiops truncatus*. *J. Exp. Biol.* 217, 214–221.
- Brunetti, N.E., Ivanovic, M., Rossi, G., Elena, B., Pineda, S., 1998. Fishery biology and life history of *Illex argentinus*. In: Okutani, T. (Ed.), Contributed paper to International Symposium on Large Pelagic Squid. Japan Marine Fishery Resources Research Center, Tokyo, Japan, pp. 217–232.
- Brunetti, N.E., Ivanovic, M.I., Sakai, M., 1999. Calamares de importancia comercial en la Argentina. In: Biología, distribución, muestreo biológico. INIDEP, Mar del Plata, Argentina, 45p.
- Corcuera, J., Monzón, F., Crespo, E.A., Aguilar, A., Raga, J.A., 1994. Interactions between marine mammals and coastal fisheries of Necochea and Claromecó Buenos Aires Province, Argentina. 1994 Gillnets and Cetaceans. In: Perrin, W. F., Donovan G. P., Barlow J. (Eds.) Rep. Int. Whal. Comm., Special Issue 15, 283–290.
- Cousseau, M., Perrotta, R.G., 2013. Peces marinos de Argentina. In: Biología, distribución, pesca, 4th ed. Publ. Esp. INIDEP, Mar del Plata, Argentina, 193pp.
- Crespo, E.A., Dans, S.L., 2008. Bases para el monitoreo y herramientas de gestión para el manejo de las poblaciones de mamíferos marinos afectadas por las actividades turísticas y recreativas en el litoral Patagónico. Tech. Report FMM/BIRF 28385-AR. Proyecto PNUD ARG 02/018. 16 pp.
- Crespo, E.A., Koen Alonso, M., Dans, S.L., García, N.A., Pedraza, S.N., Coscarella, M.A., González, R., 2000. Incidental catch of dolphins in mid-water trawls for southern anchovy off Patagonia. *J. Cetacean Res. Manag.* 2, 11–16.
- Cunha, H.A., Loizaga de Castro, R., Secchi, E.R., Crespo, E.A., Lailson-Brito, J., Azevedo, A.F., Lazoski, F., Solé-Cava, A.M., 2015. Molecular and morphological differentiation of common dolphins (*Delphinus sp.*) in the Southwestern Atlantic: testing the two species hypothesis in sympathy. *PLoS One* 10, e0140251, <http://dx.doi.org/10.1371/journal.pone.0140251>.
- Drago, M., Crespo, E.A., Aguilar, A., Cardona, L., García, N., Dans, S.L., Goodall, N., 2009a. Historic diet change of the South American sea lion in Patagonia as revealed by isotopic analysis. *Mar. Ecol. Prog. Ser.* 384, 273–286.
- Drago, M., Cardona, L., Crespo, E.A., Aguilar, A., 2009b. Ontogenetic dietary changes in South American sea lions. *J. Zool.* 279, 251–261.
- Fernández, R., García-Tiscar, S., Begoña Santos, M., López, A., Martínez-Cedeira, J.A., Newton, J., Pierce, G.J., 2011. Stable isotope analysis in two sympatric populations of bottlenose dolphins *Tursiops truncatus*: evidence of resource partitioning? *Mar. Biol.* 158, 1043–1055.
- Foote, A.D., Vester, H., Vikingsson, G.A., Newton, J., 2012. Dietary variation within and between populations of northeast Atlantic killer whales, *Orcinus orca*, inferred from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses. *Mar. Mamm. Sci.* 284, E472–E485.
- Francey, R.J., Allison, C.E., Etheridge, D.M., Trudinger, C.M., Enting, I.G., Leuenberger, M., Langenfelds, R.L., Michel, E., Steele, L.P., 1999. A 1000-year high precision record of $\delta^{13}\text{C}$ in atmospheric CO_2 . *Tellus B* 51, 170–193.
- Gómez-Campos, E., Borrell, A., Cardona, L., Forcada, J., Aguilar, A., 2011. Overfishing of small pelagic fishes increases trophic overlap between immature and mature striped dolphins in the Mediterranean Sea. *PLoS One* 6, e24554.
- García-Godoy, I., Van Waerebeek, K., Reyes, J.C., Alfaro, J., Arias-Schreiber, M., 2007. Prey occurrence in the stomach contents of four small cetacean species in Peru. *LAJAM* 6, 171–183.
- Giménez, J., Ramírez, F., Almunia, J., Forero, M.G., de Stephanis, R., 2016. From the pool to the sea: applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (*Tursiops truncatus*). *J. Exp. Mar. Biol. Ecol.* 475, 54–61.
- Hansen, J.E., Buratti, C.C., Garcíarena, A.D., 2009. Estado de la población de anchoita (*Engraulis anchoita*) al sur de 41°S y estimación de capturas biológicamente aceptables en el año 2009. INIDEP Technical report 11/09, pp. 1–16.
- Heyning, J.E., Perrin, W.F., 1994. Evidence for two species of common dolphins genus *Delphinus* from the eastern North Pacific. *Nat. Hist. Mus. Los Angel. Cty. Contrib. Sci.* 442, 1–35.
- Hobson, K.A., Wassenaar, I.I., 1999. Stable isotope ecology: an introduction. *Oecology* 120, 312–313.
- Indermühle, A., Stocker, T.F., Joos, F., Fischer, H., Smith, H.J., Wahlen, M., Deck, B., Mastrianni, D., Tschumi, J., Blunier, T., Meyer, R., Stauffer, B., 1999. Holocene carbon-cycle dynamics based on CO_2 trapped in ice at Taylor Dome, Antarctica. *Nature* 398, 121–126.
- Jackson, J., Sala, E., 2001. Unnatural oceans. *Sci. Mar.* 65, 273–281.
- Jefferson, T.A., Webber, M.A., Pitman, R.L., 2008. *Marine Mammals of the World: A Comprehensive Guide to Their Identification*. Academic Press, Elsevier, San Diego.
- Jefferson, T.A., Fertl, D., Bolaños-Jiménez, J., Zerbini, A.N., 2009. Distribution of common dolphins *Delphinus spp.* in the western Atlantic Ocean: a critical re-examination. *Mar. Biol.* 156, 1109–1124.
- Kaschner, K., Karpouzi, V., Watson, R., Pauly, D., 2006. Forage fish consumption by marine mammals and seabirds. In: Alder, J., Pauly, D. (Eds.), On the Multiple Uses of Forage Fish: From Ecosystem to Markets, vol. 143. FCR, 33–46.
- Kiszka, J., Oremus, M., Richard, P., Poole, M., Ridoux, V., 2010. The use of stable isotope analyses from skin biopsy sampled to assess trophic relationships of sympatric delphinids off Moorea French Polynesia. *J. Exp. Mar. Biol. Ecol.* 395, 48–54.
- Kiszka, J.J., Méndez-Fernandez, P., Heithaus, M.R., Ridoux, V., 2014. The foraging ecology of coastal bottlenose dolphins based on stable isotope mixing models and behavioural sampling. *Mar. Biol.* 16, 953–996.
- Lesage, V., Hammill, M.O., Kovacs, K.M., 2001. Marine mammals and the community structure of the Estuary and Gulf of St Lawrence, Canada: evidence from stable isotope analysis. *Mar. Ecol. Prog. Ser.* 210, 203–221.
- Lesage, V., Morin, Y., Rioux, E., Pomerleau, C., Ferguson, S.H., Pelletier, E., 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. *Mar. Ecol. Prog. Ser.* 419, 249–265.
- Loizaga de Castro, R., Hoelzel, A.R., Crespo, E.A., 2013. Behavioural responses of Argentine coastal dusky dolphins *Lagenorhynchus obscurus* to a biopsy pole system. *Anim. Welf.* 22, 13–23.
- Loizaga de Castro, R., Saporti, F., Vales, D.V., García, N.A., Cardona, L., Crespo, E.A., 2015. Feeding ecology of dusky dolphins *Lagenorhynchus obscurus*: evidence from stable isotopes. *J. Mamm.*, <http://dx.doi.org/10.1093/jmammal/gv180>.

- MacLeod, C.D., Bannon, S.M., Pierce, G.J., Schweder, C., Learmonth, J.A., Reid, R.J., Herman, J.S., 2005. Climate change and the cetacean community of northwest Scotland. *Biol. Conserv.* 124, 477–483.
- Marcoux, M., Whitehead, H., Rendell, L., 2007. Sperm whale feeding variation by location, year, social group and clan: evidence from stable isotopes. *Mar. Ecol. Prog. Ser.* 333, 309–314.
- Meissner, A., MacLeod, C.D., Richard, P., Ridoux, V., Pierce, G., 2011. Feeding ecology of striped dolphins, *Stenella coeruleoalba*, in the north-western Mediterranean Sea based on stable isotopes. *J. Mar. Biol. Assoc. U.K.* 96, 1677–1687.
- Meynier, L., 63 pp. 2004. Food and feeding ecology of the common dolphin, *Delphinus delphis*, in the Bay of Biscay: intraspecific dietary variation and food transfer modelling. In: Master Thesis. University of Aberdeen, Aberdeen, United Kingdom.
- Meynier, L., Stockin, K.A., Bando, M.K.H., Duignan, P.J., 2008a. Stomach contents of common dolphin *Delphinus sp.* from New Zealand waters. *N. Z. J. Mar. Freshw. Res.* 42, 257–268.
- Meynier, L., Pusineri, C., Spitz, J., Begoña Santos, M., Piercemb, G.J., Ridoux, V., 2008b. Intraspecific dietary variation in the short-beaked common dolphin *Delphinus delphis* in the Bay of Biscay: importance of fat fish. *Mar. Ecol. Prog. Ser.* 354, 277–287.
- Myers, R., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Natoli, A., Cañadas, A., Peddemors, V.M., Aguilar, A., Vaquero, C., Fernández-Piqueras, P., Hoelzel, A.R., 2006. Phylogeography and alpha taxonomy of the common dolphin *Delphinus sp.* *J. Evol. Biol.* 19, 943–954.
- Newsome, S.D., Clementz, M.A., Koch, P.L., 2010. Using stable isotopes biogeochemistry to study marine mammal ecology. *Mar. Mamm. Sci.* 26, 509–572.
- Ohizumi, H., Yoshioka, M., Mori, K., Miyazaki, N., 1998. Stomach contents of common dolphins (*Delphinus delphis*) in the pelagic western North Pacific. *Mar. Mamm. Sci.* 14, 835–844.
- Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS One*, e9672.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F., 1998. Fishing down marine food webs. *Science* 279, 860–863.
- Perrin, W.F., 2002. Common dolphins *Delphinus delphis*, *D. capensis*, and *D. tropicalis*. In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (Eds.), Encyclopedia of Marine Mammals. Academic Press, San Diego, pp. 245–248.
- Phillips, D.L., Gregg, J.W., 2003. Source partitioning using stable isotopes: coping with too many sources. *Oecologia* 136, 261–269.
- Pinela, A.M., Borrell, A., Aguilar, A., 2011. Common dolphin morphotypes: niche segregation or taxonomy. *J. Zool.* 284, 239–247.
- Pinela, A.M., Borrell, A., Aguilar, A., 2015. Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope values in common dolphins (*Delphinus spp.*) worldwide, with particular emphasis on the eastern North Atlantic populations. *Rapid Commun. Mass Spectrom.* 29, 855–863.
- Pusineri, C., Magnin, V., Meynier, L., Spitz, J., Hassani, S., Ridoux, V., 2007. Food and feeding ecology of the common dolphin *Delphinus delphis* in the oceanic Northeast Atlantic and comparison with its diet in neritic areas. *Mar. Mamm. Sci.* 23, 30–47.
- Renzi, M., Irusta, G., 2006. Evaluación del estado del efectivo norte de 41ES de la merluza *Merluccius hubbsi* y estimación de la captura biológicamente aceptable correspondiente al año 2006. Tech. Report INIDEP NE39/06, 33 pp.
- Ricciardelli, L., Newsome, S.D., Fogel, M.L., Goodall, R.N.P., 2010. Isotopic assessment of prey and habitat preferences of a cetacean community in the southwestern South Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 418, 235–248.
- Ricciardelli, L., Newsome, S.D., Goodall, R.N.P., Fogel, M.L., Bastida, R., 2012. Insight into niche separation of Risso's dolphin *Grampus griseus* in the southwestern South Atlantic via d13C and d15N values. *Mar. Mamm. Sci.* 28, 503–515.
- Ricciardelli, L., Newsome, S.D., Dellabianca, N.A., Bastida, R., Fogel, M.L., Goodall, R.N.P., 2013. Ontogenetic diet shift in Commerson's dolphin *Cephalorhynchus commersonii* off Tierra del Fuego. *Polar Biol.* 36, 617–627.
- Rodríguez, K.A., Macchi, G.G., 2010. Spawning and reproductive potential of the Northern stock of Argentine hake (*Merluccius hubbsi*). *Fish. Res.* 106, 560–566.
- Romero, M.A., Dans, S.L., García, N.A., Svendsen, G.M., González, R., Crespo, E.A., 2012. Feeding habits of two sympatric dolphin species off North Patagonia, Argentina. *Mar. Mamm. Sci.* 22, 364–377.
- Saporiti, F., Bearhop, S., Vales, D.G., Silva, L., Zenteno, L., Tavares, M., Crespo, E.A., Cardona, L., 2016. Resource partitioning between marine air-breathing predators: are body size and mouth diameter the major determinants? *Mar. Ecol. (in press)*.
- Sekiguchi, K., Klages, N.T.W., Best, P.B., 1992. Comparative analysis of the diets of smaller odontocete cetaceans along the coast of Southern Africa. In: Payne, A.I.H., Brink, K.H., Mann, K.H., Hilborn, R. (Eds.), Benguela Trophic Functioning. S. Afr. J. Mar. Sci. 12, 843–861.
- Silva, L., Saporiti, F., Vales, D., Tavares, M., Gandini, P., Crespo, E.A., Cardona, L., 2014. Differences in diet composition and foraging patterns between sexes of the Magellanic penguin *Spheniscus magellanicus* during the non-breeding period as revealed by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in feathers and bone. *Mar. Biol.* 161, 1195–1206.
- Tavares, M., Moreno, I.B., Siciliano, S., Rodriguez, D., Santos, M.C.D., Lailson-Brito, J., Fabian, M.E., 2010. Biogeography of common dolphins genus *Delphinus* in the Southwestern Atlantic Ocean. *Mamm. Rev.* 40, 40–64.
- Walker, J.L., Macko, S.A., 1999. Dietary studies of marine mammals using stable carbon and nitrogen isotopic ratios of teeth. *Mar. Mamm. Sci.* 15, 314–334.
- Young, D.D., Cockcroft, V.G., 1994. Diet of common dolphins *Delphinus delphis* off the south-east coast of southern Africa: opportunism or specialization. *J. Zool.* 234, 41–53.
- Zenteno, L., Crespo, E.A., Vales, D.G., Silva, L., Saporiti, L., Oliveira, L.R., Secchi, E.R., Drago, M., Aguilar, A., Cardona, L., 2015. Dietary consistency of male South American sea lions (*Otaria flavescens*) in southern Brazil during three decades inferred from stable isotope analysis. *Mar. Biol.*, <http://dx.doi.org/10.1007/s00227-014-2597-1>.