



# Isotopic niche partitioning between two small cetacean species

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**ABSTRACT:** Commerson's dolphin *Cephalorhynchus commersonii* and Peale's dolphin *Lagenorhynchus australis* live in sympatry along the southwestern South Atlantic Ocean, suggesting the existence of some degree of habitat partitioning to reduce their competition for resources. Both species are usually associated with coastal environments, but information on their trophic ecology is scarce. Here we explored the existence of trophic resource partitioning between these 2 sympatric species using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . From 2007 to 2013, we analyzed a total of 14 Commerson's dolphin and 34 Peale's dolphin skin samples from a marine protected area in Argentina. Significant differences in  $\delta^{13}\text{C}$  values indicated intra- and interspecific spatial partitioning. Three different Peale's dolphin feeding groups (FGs) were identified: FG1 exclusively exploited the pelagic habitat, FG2 occupied more pelagic/inshore habitats (similar to Commerson's dolphins), and FG3 occupied more benthic/inshore habitats. Isotopic niche breadth varied between species and feeding groups, exhibiting less variation in prey selection among Commerson's dolphins. According to Bayesian standard ellipse area analysis, isotopic niche overlap was found between FG2 and FG3 from 2007 to 2012, and between FG2 and Commerson's dolphins. Mixing models suggest that FG3 has a diet mainly based in benthic fish, while FG2 and Commerson's dolphins feed predominantly on pelagic fish. Overall, this study indicates segregation in the use of trophic resources between 2 sympatric dolphin species, showing different foraging strategies that promote coexistence and reduce intra- and interspecific competition. Furthermore, the presence of 3 Peale's dolphin feeding groups segregated at a small geographic scale suggests a previously unknown ecological complexity.

**KEY WORDS:** Stable isotopes · Trophic niche segregation · Feeding strategies · Commerson's dolphin · *Cephalorhynchus commersonii* · Peale's dolphin · *Lagenorhynchus australis* · Marine protected area

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## 1. INTRODUCTION

The presence of sympatric species implies the existence of some degree of resource partitioning that has reduced competition through evolutionary processes (Roughgarden 1976). According to niche theory and as a consequence of competitive exclusion, niche divergence allows species with similar ecological requirements to coexist (Pianka 1974, 2011). Par-

ticularly in dolphins, this divergence usually occurs at the trophic niche level related to prey availability resulting in different habitat use or dietary divergence within the same habitat (Bearzi 2005). This occurs even in species that form mixed groups as a strategy to improve their foraging efficiency (Loizaga de Castro et al. 2017). Therefore, identifying the requirements of each species is the main objective of ecological studies as a strategy for understanding the

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mechanism of coexistence and is also key to biodiversity conservation under a climate change scenario (Gavrilchuk et al. 2014).

Dolphins have the potential for long-range dispersal in addition to occupying a wide environment without physical barriers, which hinder direct observations of their feeding habits. Using stomach content to study food habits of marine mammals has become common practice. Despite numerous advantages of this method, it presents some disadvantages related to biases in sampling (stranded animals) and the temporal nature of the information (data for only the most recent feeding events) (Pasquaud et al. 2007). In contrast, the analysis of stable isotopes is useful to understand the trophic ecology of dolphins through the trophic niche (Ambrose et al. 2013, Loizaga de Castro et al. 2016, 2017 Giménez et al. 2017). Diet studies based on stable isotope analysis of tissues provide integrated information of all assimilated prey, without the need for direct observations of marine taxa, over an extended period of time, depending on the turnover rate of the tissue used for the analysis (Koch 2007, Kiszka et al. 2014). In addition, this technique requires only a small piece of tissue (Michener & Kaufman 2007).

Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) are the main stable isotopes used in studies of marine mammal trophic ecology (Newsome et al. 2010). The  $^{13}\text{C}/^{12}\text{C}$  ratio allows separation between pelagic/offshore and benthic/inshore habitats, based on the source of organic carbon, which may come from phytoplankton or macroalgae (Rubenstein & Hobson 2004, Fry 2006). These differences are also related to other factors that can affect  $\delta^{13}\text{C}$  values in the marine environment, mainly dissolved  $\text{CO}_2$  concentration, temperature, algal growth rate, source and supply of inorganic carbon, and cell size and geometry (O'Leary 1988, Goericke & Fry 1994, Laws et al. 1995, Popp et al. 1998). The  $^{15}\text{N}/^{14}\text{N}$  ratio is an indicator of trophic level, with the relative abundance of heavy stable isotope increasing from prey to predator due to preferential excretion of the light stable isotope (Cabana & Rasmussen 1996). The combination of both of these stable isotopes allows the estimation of the isotopic niche occupied by a species, as well as an estimate of the overlap among intra- and interspecific isotopic niches (Newsome et al. 2007). The isotopic niche can be defined as an area (in  $\delta$ -space) with isotopic values ( $\delta$ -values) as coordinates where the  $\delta$ -space is comparable to the  $n$ -dimensional space that contains the ecological niche. This approximation is based on the assumption that the chemical composition of

a consumer is directly affected by what it consumes and its habitat, as long as they are different in their isotopic values (Newsome et al. 2007).

In the southwestern South Atlantic Ocean, 2 endemic species of small cetaceans occur in partial sympatry along the Patagonian marine coast. The distribution of Peale's dolphins *Lagenorhynchus australis* primarily spans  $38^\circ$ – $56^\circ\text{S}$  in the South Atlantic Ocean, including the Falkland (Malvinas) Islands (Heinrich & Dellabianca 2019). The species can measure up to 218 cm in total length, and it appears to be confined to shelf waters off southern South America, where it inhabits different nearshore habitats including open coast over shallow continental shelf, fiords, and deep bays (de Haro & Iñíguez 1997, Goodall et al. 1997, Lescrauwaet 1997, Brownell et al. 1999, Dellabianca et al. 2016); but it can also be found in the open sea up to ~300 km from the coast (Dellabianca et al. 2016). Peale's dolphin is associated with the kelp forest, where it can be seen swimming through it or along the edge (Heinrich & Dellabianca 2019).

Commerson's dolphins *Cephalorhynchus commersonii* are among the smallest dolphins (maximum 146 cm) and are found more frequently near shore (<60 km from the coast) (Dellabianca et al. 2016). However, this distribution may be skewed by sighting effort. Several individuals have been recorded beyond the limit of the continental shelf, about 370 km away (Pedraza 2007). The distribution of this species covers  $40^\circ$ – $56^\circ\text{S}$  in Argentina and at the Falkland (Malvinas) Islands (Crespo et al. 2017). Commerson's dolphins share the same coastal habitats with Peale's dolphins, although they usually prefer areas with a wide continental shelf, wide tidal cycles, and cool waters influenced by the Malvinas Current (Goodall et al. 1988, Goodall 1994, Coscarella 2005, Loizaga de Castro et al. 2013a, Dellabianca et al. 2016).

Traditional diet studies based on stomach content analyses along the coast of Argentina have suggested that Commerson's dolphins prefer pelagic-demersal fish in coastal habitats. Bastida et al. (1988) reported the presence of mysids, fish (mainly pelagic), squids, and crustaceans in the diet of this species in Tierra del Fuego. In addition, stable isotope analyses conducted in the same region are consistent with traditional diet studies and suggest that Commerson's dolphins primarily consume coastal and pelagic fish, followed by benthopelagic species, with a difference in the relative contribution according to age classes (Riccialdelli et al. 2013). Moreover, based on 9 stomach contents from central Patagonia, Koen

Alonso (1999) found that Commerson's dolphins feed on pelagic fish, squids, and crustaceans. Little information is available on the diet of Peale's dolphins along the coast of Argentina, as few studies have reported the dietary preferences of this species. Schiavini et al. (1997) found that dolphins in Tierra del Fuego appeared to be feeding on demersal and bottom prey associated with kelp forest. In Puerto Deseado, a diet study based on 3 stomach contents suggested that Peale's dolphins are coastal generalist predators, highlighting the presence of hagfish eggs (*Myxine* sp.) (Iñiguez & de Haro 1994), which is indicative of a benthic feeding strategy—as was reported by Schiavini et al. (1997). Finally, based on a single stomach from central Patagonia, 3 prey species were reported including a pelagic–demersal fish, a benthic–demersal fish, and a squid (Lichter 1992).

In order to better understand the trophic relationships between Commerson's and Peale's dolphins, the objective of this study was to assess the habitat use and explore the isotopic niche of these 2 endemic dolphins that live in sympatry in the Argentine Sea. We hypothesized that both species

use trophic resources differentially, thereby avoiding competition and promoting life in sympatry. Consequently, no significant overlap in isotopic niche was anticipated, given the expected existence of different feeding strategies between both species.

## 2. MATERIALS AND METHODS

### 2.1. Study area and sample collection

Fieldwork took place on the northern coast of Golfo San Jorge, Argentina ( $45^{\circ}04'34.5''$  S,  $65^{\circ}38'37.2''$  W), in a marine protected area (MPA), the Austral Patagonian Interjurisdictional Coastal Marine Park (Parque Interjurisdiccional Marino Costero Patagonia Austral, PIMCPA; Fig. 1). This area covers a total surface of 132 124 ha, including terrestrial and marine ecoregions. The national park protects around 180 km of marine coastline (1.8 nautical miles from the coast) and over 55 islands, all of which are characterized by the presence of numerous coves and small bays (APN 2018).

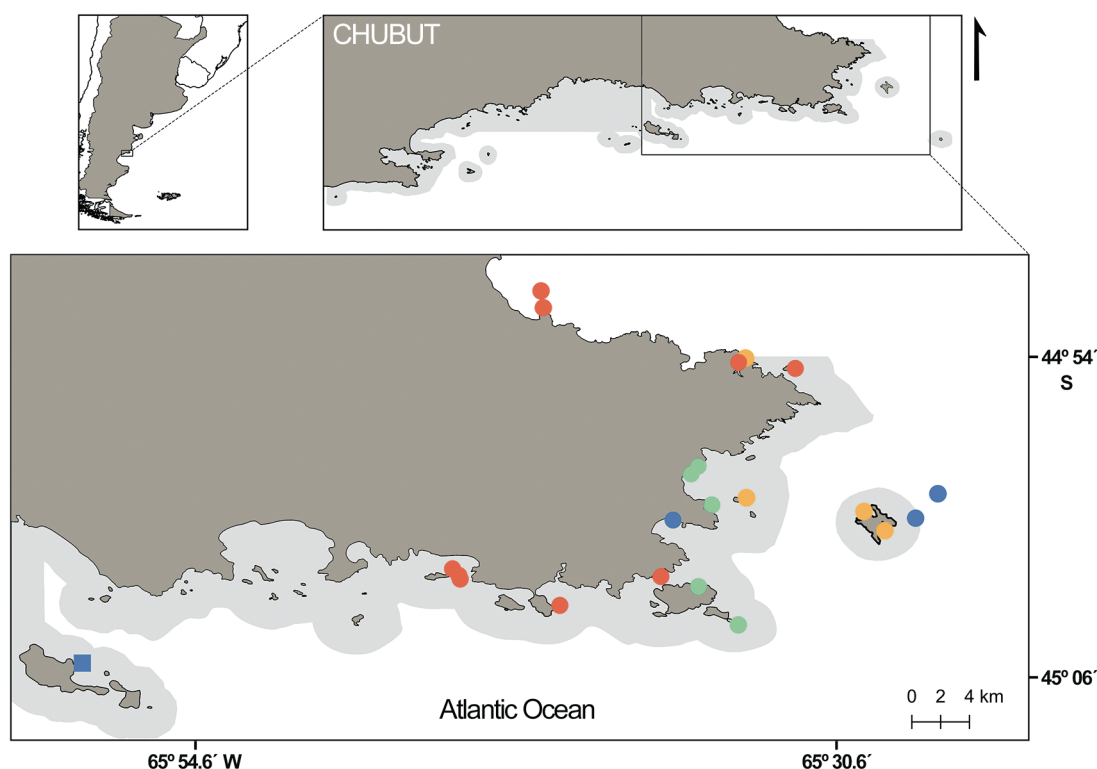


Fig. 1. Study area detailing the marine protected area in light gray. Circles show biopsy sampling sites; the square marks the location of a dead stranded individual. Colors represent species and feeding groups (FGs): *Cephalorhynchus commersonii* (red), and *Lagenorhynchus australis* FG1 (yellow), FG2 (green), and FG3 (blue)

We collected 14 and 34 biopsy skin samples of Commerson's and Peale's dolphins, respectively, in December of 3 consecutive years (2007–2009) and 2013 in the MPA (Fig. 1). Samples were taken from adult individuals using a pole system (Loizaga de Castro et al. 2013b). Additionally, a single Peale's dolphin skin sample was obtained from an individual found stranded dead on the coast in 2012. All samples were preserved in 20% dimethyl sulfoxide (DMSO) solution saturated with sodium chloride (NaCl) and stored at  $-20^{\circ}\text{C}$  until analysis (Amos & Hoelzel 1991). For the biopsy skin samples, molecular sexing was performed by amplifying the ZFX and ZFY regions following Bérubé & Palsbøll (1996). Potential prey species were selected according to the stomach contents and information about the dolphins' ecology. Stable isotope values from white dorsal muscle of pelagic fish and mantles of cephalopods were taken from the available literature, considering the same oceanographic region (Forero et al. 2004, Drago et al. 2009a,b, Vales et al. 2015). For those prey without previous information, samples were obtained from fisheries ( $n = 12$ ) and the corresponding isotopic analysis were performed (see Section 2.2).

## 2.2. Stable isotope analysis

All samples (dolphin skin and prey samples) were lipid-extracted with 2:1 chloroform:methanol solution in successive 24 h washes (3–5 times). Skin samples were then rinsed 5 consecutive times with deionized water to remove the solvent (to avoid the potential influence of DMSO on the isotopic composition of samples) and lyophilized at  $-80^{\circ}\text{C}$  (Newsome et al. 2018). Nitrogen and carbon ratios were measured with approximately 0.5–0.6 mg of dried sample using a continuous-flow isotope ratio mass spectrometer connected to an elemental analyzer (EA-IRMS) at the University of New Mexico Center for Stable Isotopes. Results are reported in  $\delta$  notation in per mil units (‰) based on PeeDee Belemnite and atmospheric  $\text{N}_2$  as internationally accepted standards for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively:

$$\delta X = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000 \quad (1)$$

where  $R$  represents the relationship between heavy and light isotope ( $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ) for samples and standards, and  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$  (Peterson & Fry 1987). International isotope secondary standards given by the International Atomic Energy Agency were used to calibrate estimates of nitrogen and carbon at a

precision of 0.30 and 0.20‰, respectively. The carbon:nitrogen ratio (C:N) from all samples was  $<4$ , indicating effective lipid extraction (Kiszka et al. 2010).

## 2.3. Data analysis

To eliminate atmospheric changes, a correction for the Suess effect ( $0.022\text{‰ yr}^{-1}$ ) was applied to the stable isotope values (Loizaga de Castro et al. 2016) using as a reference the average year between the years of sampling of potential prey (2005) following Vales et al. (2020). Using IBM SPSS Statistics (IBM SPSS 2017), generalized linear models (GLMs) were performed to understand the isotopic variation ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) for Peale's dolphin samples from 2007 to 2012, taking into consideration sampling year, sex (1:1 sex ratio, Durante et al. 2020), and distance to coast as variables. For the last variable, we defined 2 different habitats according to the site where dolphins were sampled, dividing those samples that were taken close to the coast (Habitat A =  $<200$  m), even into the small bays or coves, and those samples obtained away from the coast (Habitat B =  $>200$  m). All possible models were compared to the base model (without factors) using an omnibus test. Models were selected using the lowest value for Akaike's information criterion corrected for small sample sizes ( $\text{AIC}_c$ ) and with significance values from the omnibus test. Also, 1-way ANOVAs followed by a post hoc Tukey test were used to compare the differences in stable isotope ratios of feeding groups (FGs) and species. Prior to ANOVA, data were tested for normality (Shapiro-Wilk) and homoscedasticity (Levene's test).

To estimate the isotopic niche width for each species and the isotopic overlap between species and feeding groups, Bayesian standard ellipse areas ( $\text{SEA}_B$ ), expressed in  $\text{‰}^2$ , were calculated using the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al. 2011).  $\text{SEA}_B$  contains 95% of the data regardless of sample size and it allows for the estimation of a range of probable values for the calculated standard ellipse (Jackson et al. 2011). Overlap in  $\text{SEA}_B$  between species/feeding groups was estimated by using SEA code and was used as a measure of isotopic niche partitioning, where the proportion of overlap between 2 SEAs is expressed as a percentage (%) (Garcia et al. 2018).

To estimate the proportional contribution of potential prey (sources) to diets of dolphins (consumers),

the 'MixSIAR' package was used (Bayesian Mixing Models in R: Stock & Semmens 2016). MixSIAR uses isotopic values and a trophic discrimination factor (TDF), which is defined as the difference between the isotope values of consumer bulk tissue (e.g. skin, bone, muscle) and the isotope value of the average prey consumed. The MixSIAR model allows estimating the assimilated diet of the consumer considering uncertainty in isotopic variability (consumers and sources), TDF, and multiple sources (Moore & Semmens 2008). Particularly for the last point, when considering 2 variables ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ), it is recommended to use a maximum of 7 sources (Phillips et al. 2014). For this reason, and due to the lack of information about trophic ecology in Peale's dolphins at the study site, their potential prey was grouped according to ecological groups in order to define 5 sources: decapod crustaceans, benthic fish, demersal-benthic fish, pelagic fish, and squids. Each model was run with 3 Markov chain Monte Carlo (MCMC) simulations using 1 000 000 iterations, removing 500 000 iterations as burn-in and thinning by 500. TDF values (mean  $\pm$  SE) of  $\delta^{13}\text{C} = 2.04 \pm 0.14\text{‰}$  and  $\delta^{15}\text{N} = 2.96 \pm 0.12\text{‰}$  were used, according to reported data for skin samples of *Tursiops truncatus* in controlled experiments with a lipid-enriched diet (Browning et al. 2014), similar to that expected for the species under study. Gelman-Rubin and Geweke diagnostic tests were used to assess if each MCMC chain had converged on the true posterior distribution for each variable in the model (Stock & Semmens 2016). A mixing polygon simulation was therefore constructed to determine if the mixing model design and TDF used were appropriate, i.e. using a Monte Carlo simulation of mixing polygons to apply the point-in-polygon assumption to mixing models. This test provides a quantitative basis for model acceptance or rejection based on a frequentist probability that the mixing model proposed can correctly calculate source contributions to explain a consumer's isotopic value (Smith et al. 2013).

### 3. RESULTS

#### 3.1. Feeding groups

Three feeding groups (FGs) of Peale's dolphins and 1 FG of Commerson's dolphins were identified in

the central Patagonian MPA based on the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (Fig. 2). Stable isotope ratios of Commerson's dolphins, Peale's dolphins, and their potential prey species are shown in Table 1 and illustrated in Fig. 3. For Peale's dolphins, all samples from 2013 were grouped in a single FG (FG1) showing an extreme position. Alternatively, samples taken between 2007 and 2009 in addition to the only sample of 2012 showed 2 FGs: FG2 was more pelagic/inshore and FG3 occupied benthic/inshore habitat. Both species were segregated by both stable isotopes (ANOVA,  $\delta^{13}\text{C}$ :  $F_{3,47} = 153.8$ ,  $p < 0.05$ ;  $\delta^{15}\text{N}$ :  $F_{3,47} = 15.9$ ,  $p < 0.05$ ), except for FG1 versus Commerson's dolphin in  $\delta^{15}\text{N}$  values (Tukey post hoc,  $p = 0.74$ ). For FG2 and FG3, the GLMs with 'distance to coast' as the only factor were the best fitting models according to  $\text{AIC}_c$  (Table 2), and we found significant differences in both stable isotopes between Habitats A and B (Wald  $\chi^2 = 61.37$ ,  $\text{df} = 1$ ,  $p < 0.01$ ).

With regard to isotopic niche, Commerson's dolphins showed the smallest isotopic  $\text{SEA}_B$ , with an estimated isotopic niche area of  $1.61\text{‰}^2$ , followed by Peale's dolphin FGs:  $\text{SEA}_B = 2.01\text{‰}^2$  for FG1,  $2.06\text{‰}^2$  for FG2, and  $9.37\text{‰}^2$  for FG3 (Table S1 in the Supplement at: [www.int-res.com/articles/suppl/m659p247\\_supp.pdf](http://www.int-res.com/articles/suppl/m659p247_supp.pdf)). We performed a sensibility test (Smith et al. 2013) using the TDF reported by Giménez et al. (2016), Caut et al. (2011), and Browning et al. (2014) to choose the most appropriate to run the models. The TDF reported by Browning was chosen to run mixing models. Overlap was only observed between Peale's dolphin FG2 and FG3, and between FG2 and Commerson's dolphin (Fig. 2). The propor-

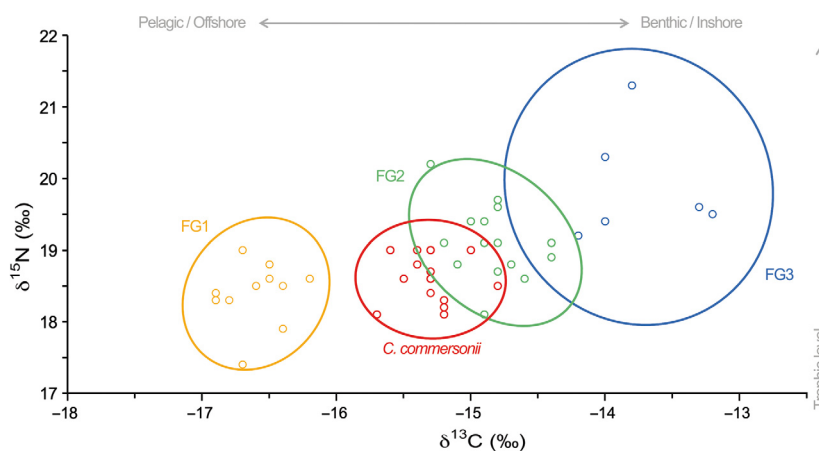


Fig. 2.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  biplot illustrating the isotopic niche for *Cephalorhynchus commersonii* and *Lagenorhynchus australis* feeding groups (FGs). Each point represents an individual, and solid ellipses represent area at 95% (standard ellipse area)



Table 1.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios, sample size (n), C:N ratio, and sampling date (year) of consumers (*Lagenorhynchus australis* feeding groups, FGs; and *Cephalorhynchus commersonii*) in the PIMCPA marine protected area and their potential sources (prey species or group of prey species)

	$\delta^{13}\text{C}$ ‰ mean $\pm$ SD	Suess-corrected $\delta^{13}\text{C}$ (‰) mean $\pm$ SD	$\delta^{15}\text{N}$ ‰ mean $\pm$ SD	n	C:N ratio	Year	Reference
<b>Consumers</b>							
<i>L. australis</i>							
FG1	$-16.8 \pm 0.2$	$-16.6 \pm 0.2$	$18.4 \pm 0.4$	11	3.2	2013	Present study
FG2	$-14.9 \pm 0.3$	$-14.8 \pm 0.3$	$19.1 \pm 0.5$	17	3.2	2007–2009	Present study
FG3	$-13.8 \pm 0.4$	$-13.7 \pm 0.4$	$19.9 \pm 0.8$	6	3.2	2007–2012	Present study
<i>C. commersonii</i>	$-15.4 \pm 0.2$	$-15.3 \pm 0.2$	$18.6 \pm 0.3$	14	3.2	2007–2009	Present study
<b>Sources</b>							
Decapod crustaceans							
<i>Pleoticus muelleri</i> <sup>a</sup>	$-15.9 \pm 0.4$	$-15.9 \pm 0.4$	$16.7 \pm 0.3$	5	2.9	2010	Vales et al. (2015)
Benthic fish							
<i>Genypterus blacodes</i>	$-14.7 \pm 0.4$	$-14.7 \pm 0.4$	$18.0 \pm 0.3$	5	3.1	2007	Present study
Demersal–benthic fish							
<i>Patagonotothen ramsayi</i> <sup>a</sup>	$-16.1 \pm 0.2$	$-16.1 \pm 0.2$	$18.6 \pm 0.2$	2	3.2	2010	Present study
<i>Riveiroclinus eigenmani</i>	$-16.7 \pm 0.2$	$-16.7 \pm 0.2$	$17.9 \pm 0.2$	8		2004	Forero et al. (2004)
Squids							
<i>Illex argentinus</i> <sup>a</sup>	$-17.0 \pm 0.6$	$-17.0 \pm 0.6$	$13.7 \pm 0.8$	5	3.0	2006	Drago et al. (2009a)
<i>Doryteuthis gahi</i>	$-17.6 \pm 0.4$	$-17.6 \pm 0.4$	$15.7 \pm 0.6$	4	3.0	2007	Drago et al. (2009a)
Pelagic fish							
<i>Sprattus fueguensis</i>	$-17.8 \pm 0.3$	$-17.8 \pm 0.3$	$17.2 \pm 0.2$	5	3.5	2000	Present study
<i>Engraulis anchoita</i>	$-17.7 \pm 0.1$	$-17.7 \pm 0.1$	$16.4 \pm 0.1$	18		2004	Forero et al. (2004)
<i>Merluccius hubbsi</i> (<30 cm) <sup>a</sup>	$-17.7 \pm 0.6$	$-17.7 \pm 0.6$	$15.9 \pm 0.5$	5	3.1	2006	Drago et al. (2009b)

<sup>a</sup>Prey selected for *C. commersonii* mixing model

tional overlap between them was asymmetric and varied from 8 to 40 % (Table S2).

### 3.2. Stable isotope mixing models

All data sets fit the mixing model assumptions according to Smith et al. (2013), except for Peale's dolphin FG1. Gelman-Rubin and Geweke diagnostic tests showed a convergence of each MCMC chain on the true posterior distribution for each variable in the model (Table S3). The isotopic mixing models indicated that continental shelf prey species contributed the most (80.8 %) to the diet of Commerson's dolphins, including Argentine hake <30 cm and Argentine shortfin squid, whereas the notothenid *Patagonotothen ramsayi* and Argentine red shrimp *Pleoticus muelleri* represented less than 10 % in the dolphins' diet (Fig. 4A; Table S4). For Peale's dolphins, the relative contribution of each potential prey species to diet varied according to feeding groups (Fig. 4B,C; Table S5). Pelagic resources were the most important prey according to the model for FG2, with a relative contribution of 41 and 28 % for 'pelagic fish' and 'squids,' respectively. In contrast,

'benthic fish' was the potential prey with the largest contribution (37 %) for FG3, followed by 'decapod crustaceans' (25 %), 'squids' (17 %), 'pelagic fish' (14 %), and 'demersal–benthic fish' (7 %).

## 4. DISCUSSION

Many different strategies are adopted by sympatric species to coexist in the same habitat depending on the availability of resources as well as the plasticity that each animal group possesses (Ruadreo et al. 2019). Trophic niche partitioning is one of the most frequent mechanisms employed by several taxa to minimize competition, including marine mammals (Pinela et al. 2010, Gibbs et al. 2011, Méndez-Fernandez et al. 2013, Wilson et al. 2017, Giménez et al. 2018). Through carbon and nitrogen stable isotope analysis, we studied the habitat use of sympatric dolphins to understand the trophic relationship between them. Based on the turnover rate of dolphin skin, which is estimated between 2 and 6 mo (Caut et al. 2011, Browning et al. 2014, Giménez et al. 2016), we report the segregation of 2 coastal small cetacean species during the warm season in the Southern

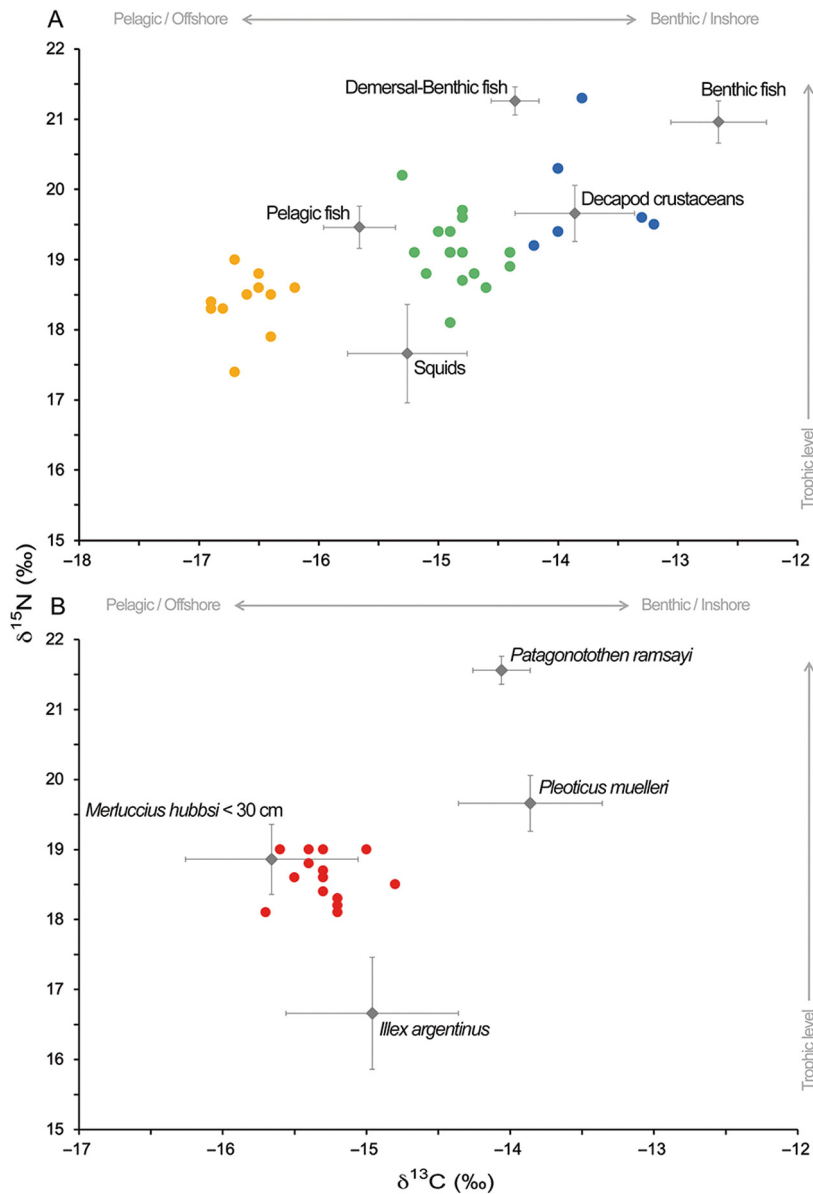


Fig. 3. (A) Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios in skin samples of *Lagenorhynchus australis* feeding groups (FGs) (individual values) (yellow = FG1, green = FG2, blue = FG3), and their potential prey after correcting for the trophic discrimination factor (mean  $\pm$  SD) grouped by ecological group. (B) Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios in skin samples of *Cephalorhynchus commersonii* (individual values in red) and their potential prey after correcting for the trophic discrimination factor (mean  $\pm$  SD)

Hemisphere, both in the spatial and the trophic niche dimensions, allowing their coexistence.

For Commerson's dolphins, our results are consistent with studies of stomach contents throughout their distribution in Argentina, where their diet comprises mainly pelagic fish and squids. Particularly, the results of our mixing models are in accordance with the diet identified in the region by Koen Alonso (1999); specifically, juveniles of Argentine hake *Merluccius hubbsi* (<30 cm) and Argentine shortfin squid *Illex argentinus* as main prey. Given that both techniques offer different diet information over different temporal scales, with a longer integration time for stable isotopes, the similarity across both techniques indicates a clear feeding preference for these prey species. Moreover, the smaller  $\text{SEA}_B$  observed in this study indicates less variability in prey selection among individuals, which sug-

Table 2. Results from generalized linear models, with Akaike's information criterion corrected for small sample size (AICc) and omnibus test p-values ( $\alpha = 0.05$ ). Best fitting models are highlighted in **bold**

Dependent variable	Model	AICc	Omnibus p
$\delta^{13}\text{C}$ ‰	<b>Distance to coast</b>	<b>20.02</b>	<b>&lt;0.001</b>
	Year	25.17	<0.001
	Sex	48.91	0.532
	Distance to coast + Year + Sex	32.93	<0.001
	<b>Distance to coast</b>	<b>37.35</b>	<b>&lt;0.001</b>
$\delta^{15}\text{N}$ ‰	Year	42.32	<0.001
	Sex	54.07	0.467
	Distance to coast + Year + Sex	48.74	<0.001

gests that this species has a specific use of pelagic habitats, feeding on small numbers of prey. Overall, Commerson's dolphins seem to occur close to the coast (Dellabianca et al. 2016) but exploit pelagic resources, in particular Argentine hake and Argentine shortfin squid in the north of the Golfo San Jorge.

For Peale's dolphins, our results revealed 3 different FGs, showing intraspecific isotopic niche partitioning within a small geographic area. All FGs showed significant differences among their mean  $\delta^{13}\text{C}$  values. FG1 exhibited lower  $\delta^{13}\text{C}$  values, suggesting an exclusively pelagic/offshore foraging habitat. In contrast, FG3 presented higher  $\delta^{13}\text{C}$  values as evidence of more benthic/inshore foraging

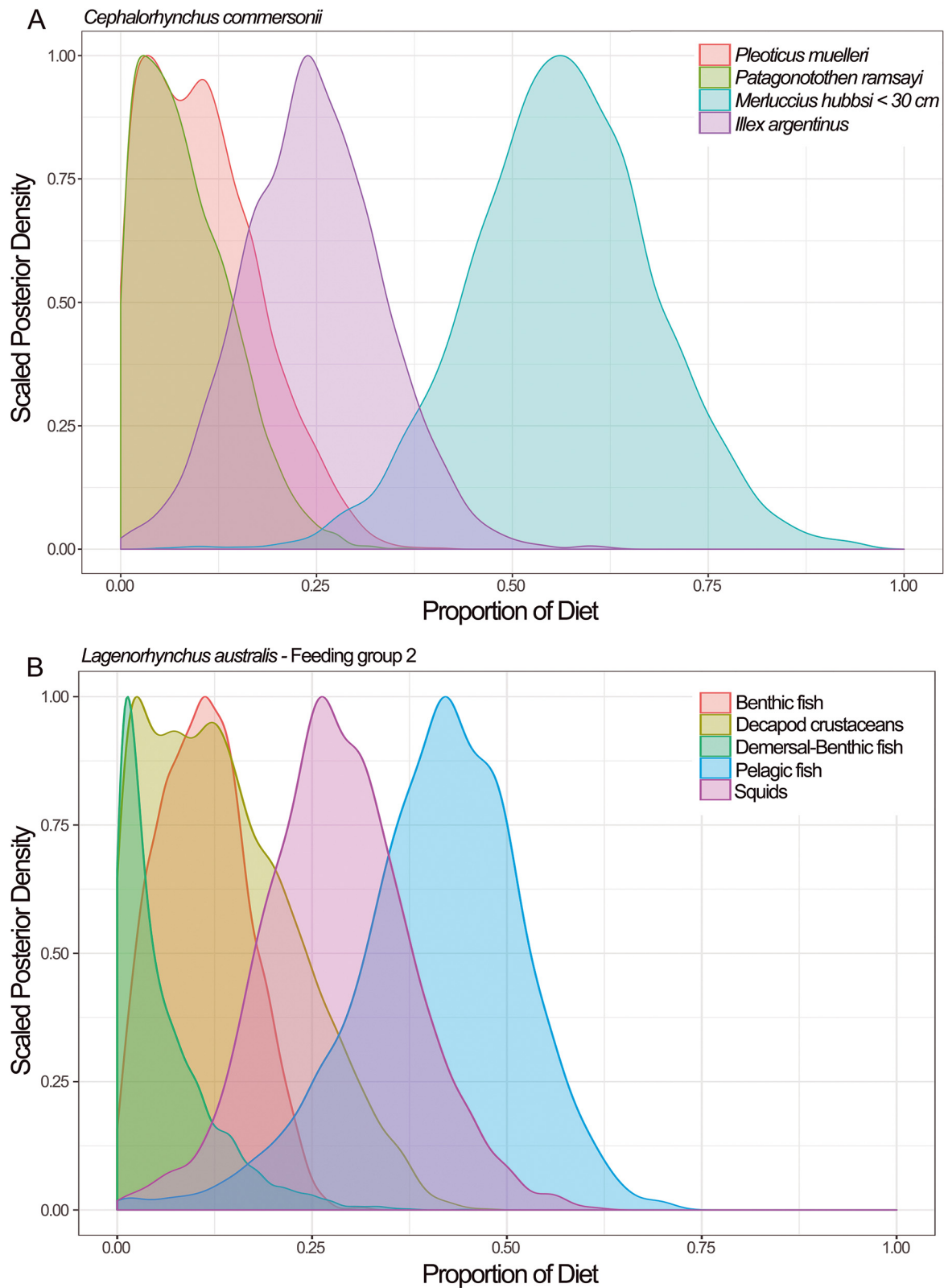


Fig. 4. Mixing models results (MixSIAR) as proportion of (A) potential prey of Commerson's dolphin or (B,C) potential prey group of Peale's dolphin feeding groups 2 and 3

Fig. 4. continued on next page



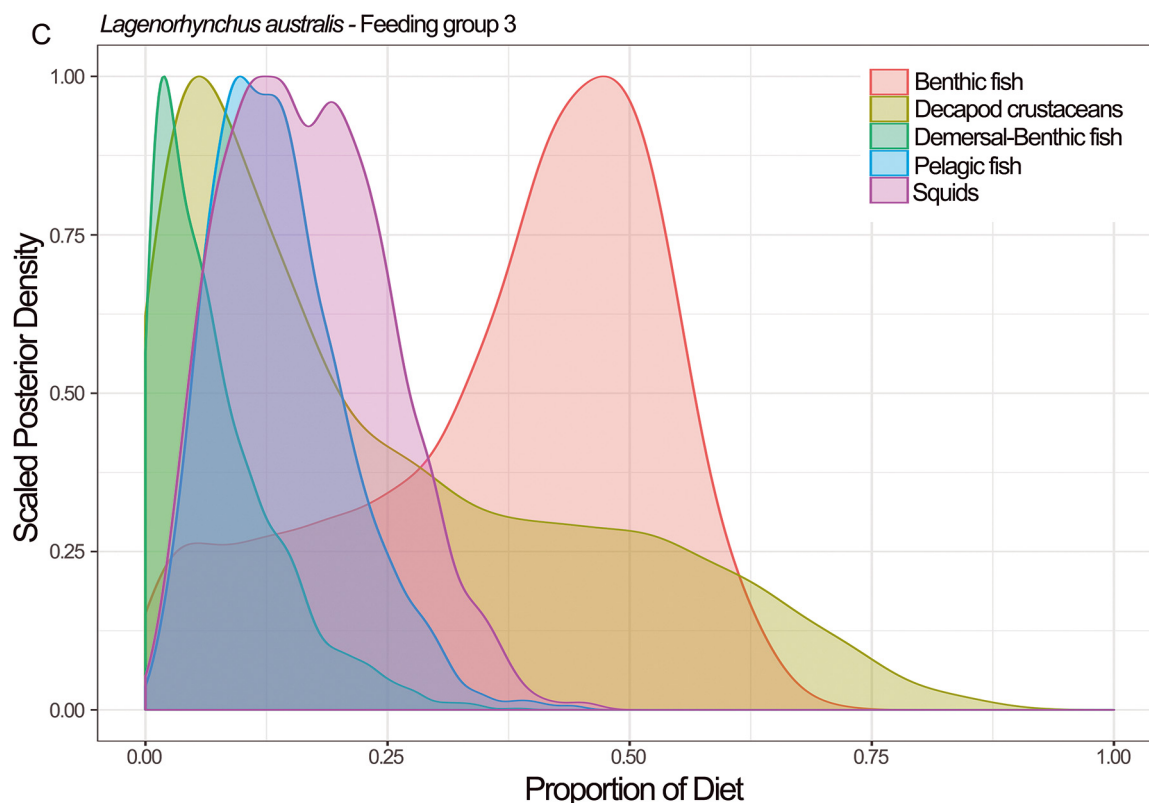


Fig. 4. (continued)

habitats, while FG2 showed intermediate values of  $\delta^{13}\text{C}$ . The isotopic niche widths of all 3 FGs were small, with some degree of overlap between FG2 and FG3. These results suggest that Peale's dolphins are capable of displaying different foraging strategies that are segregated in space. The wide isotopic niche of FG3, in terms of  $\text{SEA}_\text{B}$ , can be a consequence of the low sample size and the spatial geometry of the data, which in some cases, could be biasing the model (Jackson et al. 2011). According to this, the spatial overlap of  $\text{SEA}_\text{B}$  with FG2 is not necessarily indicative of trophic competition and can instead be explained by overestimation of the isotopic niche. The isotopic data indicate that there are dolphins from FG3 that exhibit 2‰ differences between the nitrogen isotope values; therefore, the variability in FG3 is greater compared to the other groups, independent of the sampling effort.

One result to be highlighted is the absence of correspondence between the stable isotope signals and the habitat where some Peale's dolphins were sampled. Unexpectedly, FG2 (more pelagic) was sampled closer to the coast (<200 m), inside of coves, whereas FG3 (benthic extreme) was sampled far from the coast (>200 m). Considering that the

cetacean skin incorporation rate is approximately 2 to 6 mo and that they usually have a high dispersal range, it is very unlikely that sampling of Peale's dolphin skin in a specific area reflects feeding occurring in that habitat. Therefore, the results suggest that in spite of Peale's dolphins frequently occurring in coastal environments, dominated by macroalgal forests and small bays, foraging strategies are not the only explanation for their occurrence in these habitats and other behaviors could be involved, such as nursing (Hartman et al. 2008).

Our mixing model results represent a first approximation of the diet preference of Peale's dolphins, and they showed different ecological/taxonomical clusters as the main prey items for FG2 and FG3. However, the dolphins could potentially be feeding on the same prey due to partial overlap. The remaining feeding group (FG1) could not be directly compared with potential prey resources, due to missing potential prey species that were not included in the models. Unfortunately, information on stomach contents for the species that provides the finest-scale resolution of prey taxa is lacking (Di Benedetto et al. 2011). Thus, more studies based on this technique are needed in order to obtain a more complete under-

standing of their feeding preferences (Giménez et al. 2017). Also, it is worth taking into consideration that all FG1 samples were collected in the same year, and changes in the ecosystem baseline may influence the isotopic values of predators.

Interspecific spatial overlap seems to occur in pelagic/offshore habitats between Commerson's and Peale's dolphins (FG2). However, it is not necessarily related to ecological or dietary overlap, since different prey species can exhibit similar isotopic signatures (Ramírez et al. 2011, Giménez et al. 2018). The most important resources in the Argentine Sea are Argentine hake, Argentine anchovy *Engraulis anchoita*, Patagonian sprat *Sprattus fuegensis*, Argentine shortfin squid, Patagonian squid *Doryteuthis gahi*, and Argentine red shrimp (Barón & Ré 2002, Hansen et al. 2009, Salas et al. 2011, Romero et al. 2012, Loizaga de Castro et al. 2016, 2017). All of these taxa have characteristics in common that make them preferred prey of marine mammals, including their wide distribution and availability, relatively small size, tendency to form large groups of individuals, and high nutritional value (Cousseau & Perrota 1998, Ciancio et al. 2007). In addition, within each ecological group, they have similar isotopic composition (Table 1), making it impossible to discriminate at the taxonomic level using stable isotope analysis.

The present study revealed that both dolphin species occur in the same habitat, but are segregated in terms of trophic resources. In the region, Commerson's dolphin is a specialist predator that has a small trophic niche width, whereas Peale's dolphin is a clear example of a species that can be considered a generalist that occupies a wide trophic niche (Bolinick et al. 2007). This conclusion is supported by the high plasticity reflected in different feeding groups within a small geographic area as was shown here, and represents an ecological complexity not yet described for Peale's dolphins along the southwestern Atlantic Ocean. An endemic species with hints of high philopatry in a small geographic area (Durante et al. 2020), that develops different strategies to reduce intra- and interspecific competition, suggests high adaptability of the species in response to prey availability and local habitat conditions. Therefore, future studies on the trophic ecology of both dolphin species throughout their distribution are recommended, where different habitats, variation in the isotopic composition of prey, and new stomach content analysis should be considered. Furthermore, it is possible that competition is not the only selective force structuring the biological com-

munity, and predation could be also playing a role. If this is the case, these species could be below their population carrying capacity, with abundant feeding resources in the Argentine Sea, and with ecological niches allowing some degree of overlap without competition as a primary driving force. Thus, studies on predation in small cetacean species should be conducted to understand its role within the marine community structure. This information will allow a better understanding of the ecological role in coastal habitats and the dynamics of intra- and interspecific trophic interactions of these species. Moreover, in a scenario of global warming and continuous development of commercial and local fisheries, it will also help to determine the impact of potential threats to top predators and implement conservation policies that preserve them and their habitat.

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