Original Article

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Trophic ecology and foraging areas of cetaceans sampled in the coastal waters of south-eastern Brazil assessed through skin δ^{13}C and δ^{15}N‡

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Abstract

We investigated the habitat use and feeding ecology of 10 cetacean species encountered along the south-eastern coast of Brazil (24–26°S) using carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes. Hierarchical cluster analysis distinguished two main groups based on their isotopic patterns. One group included migratory baleen whales (*Megaptera novaeangliae* and *Eubalaena australis*) with the lowest δ^{13}C and δ^{15}N values, reflecting baseline isotopic values of their Subantarctic feeding grounds and consumption of lower trophic level prey. Resident species and those occasionally occurring in Brazilian coastal waters highly differed from the migratory whales in their isotopic values. In this group, *Tursiops truncatus* had the highest δ^{13}C and δ^{15}N values, indicating coastal habits and relatively higher trophic position. Similar δ^{13}C values were observed in *Sotalia guianensis*, *Pontoporia blainvillei*, *Orcinus orca* and *Steno bredanensis*. However, the former two species had lower δ^{15}N values than the latter two, indicating different trophic positions. The relatively lower δ^{13}C values observed in *Stenella frontalis* suggest greater influence of pelagic prey in their diet. Furthermore, the lower δ^{13}C values observed in *Delphinus delphis* and *Balaenoptera edeni* were associated with upwelling events that occur along the region, affecting the isotopic values of their main prey. Juvenile *M. novaeangliae* had higher δ^{13}C and δ^{15}N than the adults, which may indicate feeding in areas with different isoscapes and consumption of pelagic schooling fish with relatively higher trophic levels than krill. This study provides preliminary information that are useful to understand the habitat use and coexistence of cetacean species occurring in south-eastern Brazil.

Introduction

Cetaceans are known to play several ecological roles in the ecosystems they inhabit, including the control of prey populations, and vertical and horizontal transport of nutrients (Roman et al., 2014). To date, eight baleen whale and 27 odontocete species have been recorded in south-eastern Brazilian waters (Santos et al., 2010; Miranda et al., 2019; Figueiredo et al., 2020). Except for the Bryde's whale (*Balaenoptera edeni*), for which movement knowledge is limited in south-eastern Brazil (Siciliano et al., 2004; Santos et al., 2019), the other species of baleen whales are seasonal visitors during their migration to their reproductive areas in tropical regions (e.g. Lodi et al., 1996; Zerbini et al., 2006). Odontocete species include resident species such as franciscana (*Pontoporia blainvillei*) and Guiana dolphins (*Sotalia guianensis*), which occur in the inner part of the continental shelf and estuaries along the region (Figueiredo et al., 2020). Other species, such as the Atlantic spotted dolphin (*Stenella frontalis*) and bottlenose dolphin (*Tursiops truncatus*) occur in coastal waters mainly in the 20–50 m isobaths (Santos et al., 2017; Figueiredo et al., 2020; Paschoalini & Santos, 2020). Some other species such as the common dolphin (*Delphinus delphis*) and orcas (*Orcinus orca*) are assumed to be occasional visitors (Santos et al., 2010, 2019). Although their patterns of habitat use are poorly known in this region, these odontocetes seem to occur more frequently in shallow waters during the austral spring and summer (Tavares et al., 2010; Santos et al., 2019).

Sympatric species with similar ecological niches compete when resources are limiting (Roughgarden, 1976). For that reason, they may develop niche segregation mechanisms to facilitate their coexistence and, consequently, minimize competition (Pianka, 1974). Such mechanisms are extremely important for maintaining the diversity of an environment (Chesson, 2000), and include foraging at different depths, time of the day or the consumption of distinct prey species (e.g. Gross et al., 2009). Assessing the foraging areas and trophic ecology of co-occurring species may help in the understanding of the niche differentiation mechanisms developed among them (e.g. Browning et al., 2014a; Young et al., 2017). Additionally, information on species feeding behaviour and habitat use helps to define their

ecological roles in the ecosystems they inhabit, which can be used for conservation measures (Liu *et al.*, 2015). The coastal waters along south-eastern Brazil are strongly influenced by anthropogenic pressures, such as harbours, oil and fishing industries (Santos *et al.*, 2010; Figueiredo *et al.*, 2017), with several potential negative consequences for cetacean species. Therefore, investigating the ecological traits of local populations may help explain how these threats are affecting these species. Only a few studies have evaluated the feeding habits and trophic relationships of cetacean species in the region (e.g. Gross *et al.*, 2009; Bisi *et al.*, 2013; Liu *et al.*, 2015), and this information remains limited.

The analysis of carbon and nitrogen stable isotopes (expressed as $\delta^{13}C$ and $\delta^{15}N$, respectively) provides a good complementary method for a better understanding of the ecological traits among living organisms (e.g. Kelly, 2000; Newsome *et al.*, 2010). This is because the $\delta^{13}C$ and $\delta^{15}N$ of a consumer reflect those of its prey (Peterson & Fry, 1987), with a small increase at each trophic level due to metabolic processes that discriminate against the light isotopes. Consequently, there is a mean increase of $\sim+1$‰ and $+3$‰ in $\delta^{13}C$ and $\delta^{15}N$ values, respectively, for each trophic level increase (Minagawa & Wada, 1984; Peterson & Fry, 1987). Therefore, $\delta^{15}N$ values are applied to estimate the relative trophic position of individuals within food webs (e.g. Vander Zanden & Rasmussen, 2001), while $\delta^{13}C$ values are good indicators of the carbon source at the base of the food webs (Kelly, 2000). However, different studies have demonstrated that diet-to-tissue discriminations may vary largely, depending on the species and the tissue analysed (Borrell *et al.*, 2012; Browning *et al.*, 2014b; Giménez *et al.*, 2016), the quality of dietary protein (Robbins *et al.*, 2005) and consumers' trophic position (Hussey *et al.*, 2014).

Carbon stable isotope ratios vary considerably among primary producers (e.g. Michener & Kaufman, 2007), allowing differentiation between terrestrial and marine, coastal and oceanic, or benthic and pelagic ecosystems (Peterson & Fry, 1987; France, 1995). Moreover, there is a latitudinal gradient in $\delta^{13}C$ values, in which higher and lower $\delta^{13}C$ values are related with tropical and polar regions, respectively (Rau *et al.*, 1982). Similarly, $\delta^{15}N$ values of primary producers vary according to the nitrogen sources available (N_2, NH_4^+ and NO_3^-) and their concentration in the environment (Montoya, 2007), resulting in spatial and temporal gradients in $\delta^{15}N$ at the base of the food webs (Graham *et al.*, 2010). Therefore, $\delta^{13}C$ and $\delta^{15}N$ values provide useful information to investigate the feeding habits (e.g. relative trophic position) and foraging areas used by marine species (e.g. Gross *et al.*, 2009; Graham *et al.*, 2010; Chouvelon *et al.*, 2012).

Furthermore, $\delta^{13}C$ and $\delta^{15}N$ values can be used to quantify a population's isotopic niche, which is considered an indicator of their ecological niche dimensions (Newsome *et al.*, 2007). Advanced statistical models, such as the *Stable Isotope Bayesian Ellipses in R* (SIBER, Jackson *et al.*, 2011), have been developed to estimate the isotopic niche width of populations. Such information can be applied to evaluate the level of trophic diversity (e.g. generalist *vs* specialist feeders) and overlap in isotopic niches among species or populations (e.g. Vighi *et al.*, 2014; Liu *et al.*, 2015; Kanaji *et al.*, 2017).

Studies of habitat use and trophic relationships among distinct cetacean species shed light to understand the ecological role of these mammals in aquatic food webs in the South-western Atlantic Ocean (e.g. Melo *et al.*, 2010; Bisi *et al.*, 2013; Di Beneditto & Monteiro, 2016). Therefore, the main objective of the present study is to investigate the habitat use and feeding ecology of 10 cetacean species encountered in south-eastern Brazil. Carbon and nitrogen stable isotope analyses were applied to evaluate their foraging areas, identify trophic relationships, and niche segregation mechanisms among different species.

Cetacean species investigated here include migratory baleen whales and resident toothed whales that occur in estuarine, coastal and oceanic environments along the study area.

Materials and methods

Study site

Cetacean samples were obtained along the coastal region of south-eastern Brazil, between Paraná state and the south of Rio de Janeiro state (24–26°S) (Figure 1). The region is influenced mainly by three water masses: the Coastal Water (CW), the Tropical Water (TW) and the South Atlantic Central Water (SACW) (Castro *et al.*, 2006). The CW is a low salinity water formed by the mixing between continental water and seawater and is encountered manly near the estuaries. The TW is a warm (>20°C), high salinity (>36 psu) water positioned between 0 and 200 m. The nutrient-rich SACW is positioned between depths of 200 and 500 m but surfaces along the coast of south-eastern Brazil mainly in summer months (Castro *et al.*, 2006), significantly influencing local productivity (Matsuura, 1996). The south-eastern Brazilian coast presents a great diversity of oceanographic features, such as estuaries, bays and coastal islands (Tessler *et al.*, 2006), which could influence the local biological productivity and prey abundance. The Cananéia–Iguape estuarine complex, for example, located in the southern portion of the study site, drains large amounts of organic matter to the coast and functions as a nursery area for several species of fish and invertebrates (Schaeffer-Novelli *et al.*, 1990). Similarly, the presence of islands along the coast may also contribute to increased primary productivity, by influencing physical processes that affect local nutrient concentrations (Gilmartin & Relevante, 1974).

Sampling

Skin samples of cetacean species were collected from biopsied, bycaught or stranded individuals along the south-eastern coast of Brazil between 2011 and 2016 (Table 1). Biopsies were collected during oceanographic cruises using a crossbow (125 lb) with floating darts adapted to extract small portions of epithelial tissue. The biopsies were collected from the dorsal region of the cetacean body and were no more than the size of a pencil eraser. Bycaught cetaceans were accidentally killed in gillnet fisheries and skin samples were collected with the individuals still fresh (condition score 2, freshly dead). Lastly, skin samples from stranded cetaceans were collected during beach surveys along the coast when carcass condition scores were either 2 or 3 (moderately decomposed) (Geraci & Lounsbury, 2005). All samples were stored at −20°C without the use of any preservative until analysis.

Stable isotope analyses and lipid correction

After drying at 60°C for 72 h, ∼0.3–0.7 mg of skin samples were weighed into tin capsules and sent to the Stable Isotope Core Laboratory (Washington State, USA) for analyses of carbon and nitrogen stable isotope ratios. Analyses were performed using an Isotope Ratio Mass Spectrometer (IRMS, Delta PlusXP, Thermofinnigan) connected to an Elemental Analyser (EA, ECS 4010, Costech Analytical, Valencia, CA). The analytical precision for both $\delta^{13}C$ and for $\delta^{15}N$ was < 0.1‰. Isotopic measurements are reported in the delta (δ) per mil (‰) notation, in relation to the international reference standards for $\delta^{13}C$ (Vienna Pee Dee Belemnite) and $\delta^{15}N$ (atmospheric nitrogen, N_2).

Lipids are known to be depleted in ^{13}C (DeNiro & Epstein, 1977), which can lead to an underestimation of $\delta^{13}C$ values in the tissues of an organism (Tieszen *et al.*, 1983). The lipid content
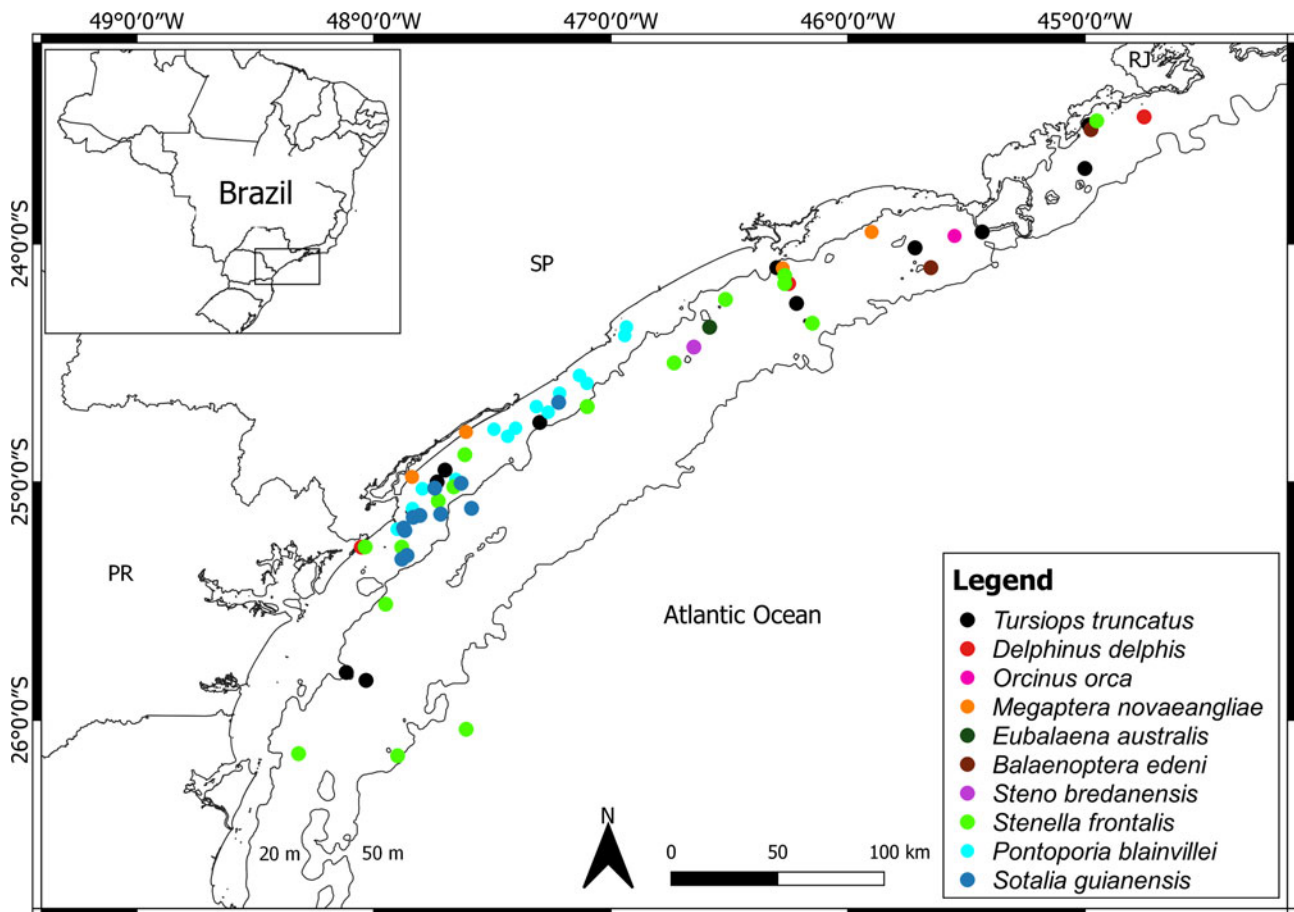
Fig. 1. Study area in south-eastern Brazil. The dots indicate the locations where cetacean skin samples were collected between 2011 and 2016. The different states along the coast are indicated as SP (São Paulo), PR (Paraná) and RJ (Rio de Janeiro).

of a sample is correlated to its C/N ratio, and high values correspond to high quantities of lipids (McConnaughey & McRoy, 1979). In this study, we corrected δ^{13}C values of all samples with C/N ratios higher than 3.0, as recommended for cetacean skin (Lesage *et al.*, 2010). To promote the lipid correction, we used the equations proposed by McConnaughey & McRoy (1979) with adjustments of the constants suggested by Lesage *et al.* (2010):

$$L = 93 / \left[1 + \left(0.246 \times \frac{C}{N} - 0.775 \right)^{-1} \right]$$

$$\delta^{13}\text{Ccor} = \delta^{13}\text{C} + 6.386 \times \left[0.004 + 3.90 / \left(1 + \frac{287}{L} \right) \right]$$

where *L* is the quantity of lipids in the sample, *C/N* is the ratio of carbon to nitrogen, δ^{13}C and δ^{13}Ccor are sample measured and mathematically corrected δ^{13}C, respectively.

Data analyses

As data did not meet the assumptions of normality and homoscedasticity (tested using the Shapiro–Wilk and Bartlett test, respectively), δ^{13}C and δ^{15}N values were compared using Welch's Analyses of variance (Welch's ANOVA), followed by the Games–Howell *post-hoc* test for pair-wise comparisons between species. Only species with four or more samples were included in the statistical analyses to ensure the reliability of the results.

A *P* value < 0.05 was used to indicate statistical significance. Additionally, hierarchical cluster analysis using the complete linkage method and Euclidean distances was carried out to detect isotopic similarities among the cetacean species. Due to the influence of milk on the isotopic ratios of nursing calves (Fogel *et al.*, 1989), the calf of southern right whale (*Eubalaena australis*) was not included in this analysis. All statistical analyses were performed using R version 3.6.1 (R Core Team, 2020).

To better understand the trophic relationships among species, their isotopic niches were estimated using the Stable Isotope Bayesian Ellipses package in R (SIBER) (Jackson *et al.*, 2011). Only species with five or more samples were considered for these analyses as SIBER requires at least five samples for reliable isotopic niche determination. Each species' isotopic niche width was estimated by calculating the standard ellipse area (SEA) corrected for small sample sizes (SEA_C) and the Bayesian SEA based on the posterior distribution (SEA_B). Isotopic niche widths were compared using the SEA_B, for which we calculated the probabilities of real differences among niche widths based on 100,000 posterior draws. The overlap among the isotopic niches was computed from SEA_C. All these estimations considered a prediction interval (p-interval) of 40% (Jackson *et al.*, 2011).

Results

Skin samples were obtained from 10 different cetacean species (seven toothed whales and three baleen whales) between 2011 and 2016 (Table 1). The mean δ^{13}C and δ^{15}N values for each species are displayed in Table 1 and Figure 2. The humpback whales (*Megaptera novaeangliae*) included one adult and three juveniles,

Table 1. Cetacean species analysed in the present study

Species	STR	IC	BP	N	C/N Mean + SD	δ^{13}C Mean + SD	δ^{13}C$_{cor}$ Mean + SD	δ^{15}N Mean + SD
Toothed whales								
Tursiops truncatus	–	–	35	35	3.5 ± 0.6	−16.2 ± 1.0	−15.6 ± 0.8	+17.3 ± 0.8
Stenella frontalis	–	–	30	30	3.1 ± 0.3	−16.6 ± 0,8	−16.3 ± 0.5	+14.8 ± 0.9
Sotalia guianensis	–	12	–	12	4.6 ± 0.6	−17.8 ± 0.7	−15.9 ± 0.2	+13.9 ± 0.4
Pontoporia blainvillei	–	11	–	11	4.9 ± 0.6	−18.0 ± 0.5	−15.6 ± 0.2	+14.0 ± 0.7
Delphinus delphis	–	1	4	5	4.7 ± 0.2	−19.3 ± 0.5	−17.3 ± 0.3	+14.6 ± 0.4
Steno bredanensis	–	–	3	3	3.4 ± 0.5	−16.3 ± 0.6	−15.8 ± 0.4	+14.5 ± 0.1
Orcinus orca	–	–	2	2	3.7 ± 0.2	−16.5 ± 0.9	−15.6 ± 0.5	+14.6 ± 1.0
Baleen whales								
Balaenoptera edeni	–	–	3	3	3.7 ± 0.3	−17.6 ± 0.8	−16.6 ± 0.5	+13.4 ± 1.1
Eubalaena australis	–	–	2	2	3.8 ± 0.1	−22.5 ± 1.0	−21.4 ± 0.8	+7.8 ± 0.5
Adults	–	–	1	1	3.7	−21.7	−20.8	+7.2
Calves	–	–	1	1	3.9	−23.2	−22.0	+8.3
Megaptera novaeangliae	2	–	2	4	4.1 ± 0.6	−20.4 ± 3.2	−19.0 ± 2.7	+11.4 ± 1.6
Adults	–	–	1	1	4.7	−25.0	−23.0	+9.1
Juveniles	2	–	1	3	3.9 ± 0.3	−18.8 ± 0.8	−17.7 ± 0.7	+12.1 ± 0.5

The number of skin samples obtained from stranded (STR), incidentally caught (IC) or biopsied (BP) individuals and the total number of samples (N) for each species; Mean (± SD) of C/N ratios, measured and mathematically corrected carbon (δ^{13}C and δ^{13}C$_{cor}$, respectively), and nitrogen stable isotopes (δ^{15}N).

while the *E. australis* included a mother and her calf. Juveniles *M. novaeangliae* had considerably higher δ^{13}C and δ^{15}N values in comparison to the adult. The calf *E. australis* had higher δ^{15}N and lower δ^{13}C values than the adult female. δ^{13}C and δ^{15}N varied significantly among the six species from which we had enough data to allow for statistical comparisons (Welch's ANOVA, $P < 0.05$, Table 2). The pair-wise comparisons were significant for all species regarding the δ^{13}C values, except between *T. truncatus* and both *S. guianensis* and *P. blainvillei* (Table 2). Nitrogen stable isotopes were significantly higher in *T. truncatus* than in the remaining species (Figure 2). In contrast, *M. novaeangliae* had significantly lower δ^{15}N than the other cetacean species. Lastly, δ^{15}N were significantly higher in *D. delphis* and *S. frontalis* than in *S. guianensis* but did not show significant differences between any of these species and *P. blainvillei* (Table 2).

Our hierarchical cluster analysis identified two main groups based on mean δ^{13}C and δ^{15}N values (node 1, Figure 3). One group included only baleen whales (*M. novaeangliae* and *E. australis*), with the lowest δ^{13}C and δ^{15}N values. Yet, these two species showed considerable dissimilarity in their isotopic values, as evidenced by the large Euclidean distance between them (node 4, Figure 3). The second main group included those species with higher δ^{13}C and δ^{15}N and was comprised mostly by toothed whales (aside from *B. edeni* and the juveniles *M. novaeangliae*). Within this group, *T. truncatus* (node 2) and the juveniles *M. novaeangliae* (node 3) were split from the other species, evidencing their large isotopic differences pertaining to their higher and lower δ^{15}N values, respectively. Further, our cluster analysis identified large isotopic dissimilarity between *D. delphis* and *B. edeni* (node 6, Figure 3), and between these species and the remaining toothed whales (node 5). The highest isotopic similarities were found between *O. orca* and *S. bredanensis*, and between *P. blainvillei* and *S. guianensis* (node 8).

Tursiops truncatus, followed by *S. frontalis*, had the largest isotopic niche areas estimated by the SIBER model, while the smallest niche width was observed in *S. guianensis* (Table 3, Figure 4). Intermediate niche widths were observed in *D. delphis* and in

P. blainvillei. Furthermore, our analyses showed small isotopic niche overlap only between *P. blainvillei* and *S. guianensis* (Figure 4).

Discussion

In the present study we analysed carbon and nitrogen stable isotopes in 10 cetacean species sampled along the coastal waters of south-eastern Brazil. We discuss our results from isotopic data in relation to the patterns of habitat use and feeding habits, as well as the level of overlap in the use of resources among the co-occurring species.

Resident species

We considered *T. truncatus*, *S. frontalis*, *S. guianensis* and *P. blainvillei* as resident species, based on available information resulting from sightings, strandings and accidental catches along the south-eastern coast of Brazil (Santos *et al.*, 2010, 2017, 2019), as well as recent results on local cetacean niche modelling (Figueiredo *et al.*, 2020). The large Euclidean distance between *T. truncatus* and the remaining odontocetes is related to its significantly higher δ^{15}N values in comparison to the remaining cetacean species. This was evident in the isotopic niche space, which showed niche segregation between *T. truncatus* and the other odontocete species, with complete lack of overlap in δ^{15}N values (Figure 4). The isotopic values estimated for *T. truncatus* indicate the consumption of coastal/benthic prey and relatively higher trophic position than the other species analysed. This is in agreement with previous studies on the same species in south-eastern Brazil, that also suggested the use of inshore areas along the 16 and 45 m isobaths (Figueiredo *et al.*, 2020; Paschoalini & Santos, 2020) and high trophic level (Bisi *et al.*, 2013). Additionally, stomach content analyses of *T. truncatus* from south-eastern Brazil showed a great importance of demersal piscivorous fish, such as cutlass fish (*Trichiurus lepturus*), banned grunt (*Conodon nobilis*) and Atlantic midshipman (*Porichthys*
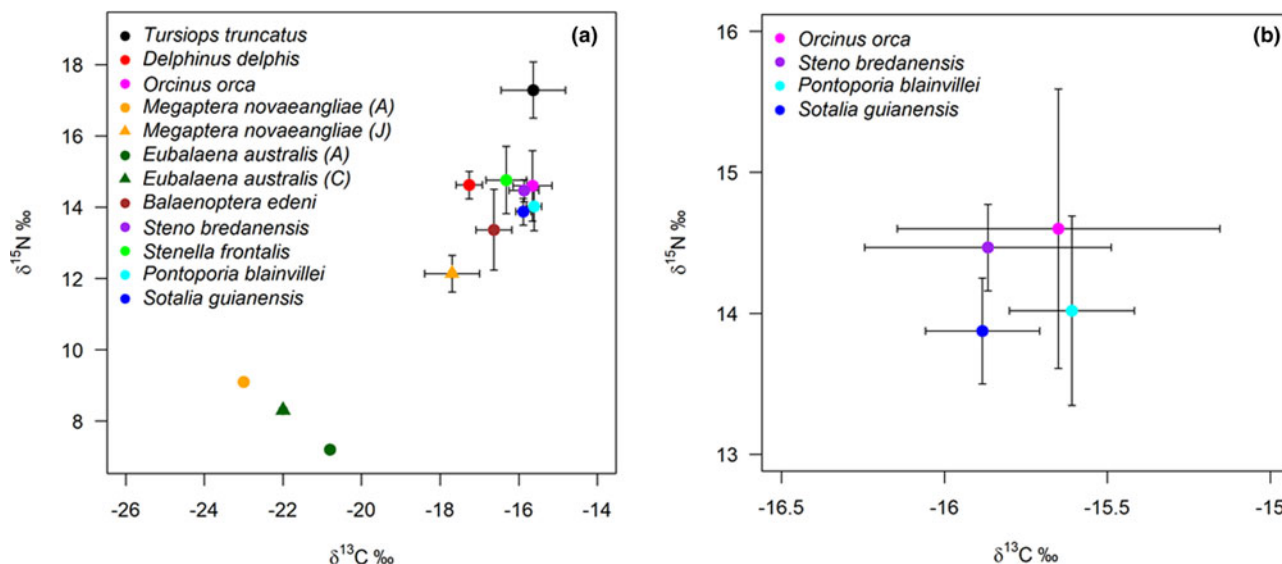
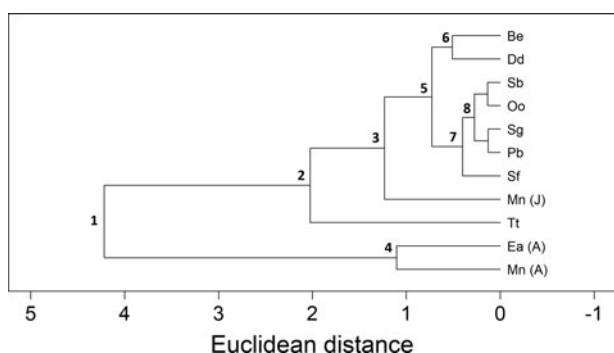**Fig. 2.** Mean (±SD) stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes measured in (A) all cetacean species sampled in south-eastern Brazil between 2011 and 2016; and (B) focusing on *Orcinus orca*, *Steno bredanensis*, *Sotalia guianensis* and *Pontoporia blainvillei*. A – adult; C – calf; J – juvenile.

Table 2. Results of the Games–Howell *post hoc* test for the pair-wise comparisons of mean carbon ($\delta^{13}C$; lower-left) and nitrogen ($\delta^{15}N$; upper-right) stable isotopes measured in skin samples of cetacean species from south-eastern Brazil, between 2011 and 2016

	Tt	Dd	Sf	Pb	Sg	Mn
Tt		**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Dd	**0.00**		0.98	0.19	**0.04**	**0.00**
Sf	**0.02**	0.07		0.06	**0.00**	**0.00**
Pb	1.00	**0.01**	**0.01**		0.97	**0.00**
Sg	0.50	**0.02**	**0.02**	**0.02**		**0.00**
Mn	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	

Significant differences ($P < 0.05$) are highlighted in bold. Only species with four or more samples available were considered: *Tursiops truncatus* (Tt); *Delphinus delphis* (Dd); *Stenella frontalis* (Sf); *Pontoporia blainvillei* (Pb); *Sotalia guianensis* (Sg); *Megaptera novaeangliae* (Mn).

Table 3. Standard ellipse area corrected for small sample sizes (SEA$_C$; ‰^{2}) and Bayesian standard ellipse area (SEA$_B$, ‰^{2}) with the 95% confidence interval (CI) calculated for the cetacean species sampled in south-eastern Brazil between 2011 and 2016

Species	N	SEA$_C$	SEA$_B$ (95% CI)
Tursiops truncatus	35	2.10	2.00 (1.43–2.80)
Stenella frontalis	30	0.90	0.90 (0.80–1.00)
Sotalia guianensis	12	0.20	0.17 (0.10–0.32)
Pontoporia blainvillei	11	0.34	0.33 (0.18–0.63)
Delphinus delphis	5	0.50	0.30 (0.22–0.43)

Only species with five samples or more were considered.

Fig. 3. Hierarchical cluster analysis based on mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes of the cetacean species sampled on the south-eastern coast of Brazil between 2011 and 2016. *Tursiops truncatus* (Tt); *Pontoporia blainvillei* (Pb); *Sotalia guianensis* (Sg); *Stenella frontalis* (Sf); *Orcinus orca* (Oo); *Steno bredanensis* (Sb); *Delphinus delphis* (Dd); *Balaenoptera edeni* (Be); *Megaptera novaengliae* (Mn); *Eubalaena australis* (Ea). A – adult; J – juvenile. The numbers indicate where the branches are separated based on their isotopic values.

porossimus) (Di Beneditto *et al.*, 2001; Melo *et al.*, 2010; Moura *et al.*, 2016), which could justify the high values estimated for both stable isotopes. Demersal prey have relatively higher $\delta^{13}C$

values than pelagic prey (e.g. Corbisier *et al.*, 2006), which are related to the greater ^{13}C-enrichment that usually occurs in the coastal/benthic isotopic baselines (France, 1995). In addition, feeding upon mesopredators (i.e. piscivorous fish) (Figueiredo *et al.*, 2002) would result in higher trophic positions, hence higher $\delta^{15}N$ values.

The isotopic niche area estimated for *T. truncatus* was considerably larger than those of the other cetacean species (Figure 4 and Table 3). Large niche area may indicate the use of a wide diversity of prey items, foraging on isotopically distinct prey and/or habitats (e.g. benthic *vs* pelagic), and feeding at different trophic positions. The large isotopic niche area observed in the present study is in agreement with the large spatial niche estimated for *T. truncatus* in a recent study using distributional data coupled with environmental variables in south-east Brazil (Figueiredo *et al.*, 2020). Additionally, *T. truncatus* have been described as generalist feeders (e.g. Leatherwood, 1975; Shane *et al.*, 1986) showing large variation in the isotopic values of populations in other regions (e.g. Borrell *et al.*, 2006, 2021; Browning *et al.*, 2014*b*). The ability to consume a large diversity of prey is especially beneficial for populations occurring in areas highly impacted by anthropogenic activities that may affect the availability of resources. For example, temporal changes in the most important prey species have been reported for a coastal population of *T. truncatus* from southern Brazil based on data from stomach contents coupled with stable isotope analyses (Secchi *et al.*, 2016). This temporal change in their feeding habits
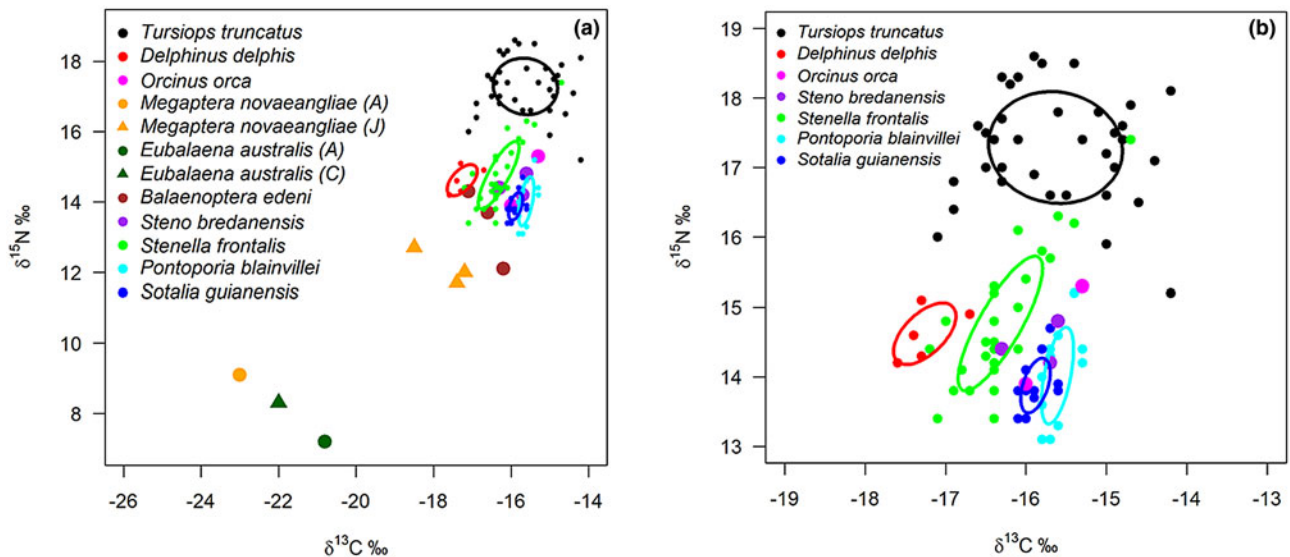
Fig. 4. Standard ellipse area corrected for sample size (SEA$_C$) estimated for species with total number of samples (N) > 5, and $\delta^{13}C$ – $\delta^{15}N$ biplots of individual cetaceans from which N < 5 in (A) all cetacean species sampled in south-eastern Brazil between 2011 and 2016; and (B) zoomed ellipses to show increased detail of (A). A – adult; C – calf; J – juvenile.

was attributed to the overfishing of their main prey species in the 1970s (whitemouth croaker *Micropogonias furnieri*), resulting in increased consumption of other prey species in recent years. This was also observed for *T. truncatus* populations in other regions, where the great proportion of pelagic in comparison to demersal prey in their diet may be related to human-related eutrophication that is affecting the local populations of demersal species (Borrell *et al.*, 2021). This illustrates the importance of long-term studies assessing cetacean feeding habits to better understand the effects of anthropogenic actions on cetacean populations.

The second largest isotopic niche area was estimated for *S. frontalis* (Figure 4), which suggests foraging on isotopically variable prey and areas. This is in line with the large geographic niche observed for the species in the same region (Figueiredo *et al.*, 2020). Additionally, *S. frontalis* had relatively lower $\delta^{13}C$ values (Figure 2) in comparison to the other isotopically similar species identified by our cluster analysis (Figure 3), but its mean $\delta^{15}N$ was similar to those of *S. bredanensis* and *O. orca* (Table 2). The species has been recorded throughout the year in the shallow coastal waters (20–43 m) of south-eastern Brazil (Santos *et al.*, 2017; Figueiredo *et al.*, 2020) and dietary studies analysing stomach contents have identified great importance of pelagic prey, such as the tropical arrow squid (*Dorytheuthis plei*), the knobby (*Argonauta nodosa*) and the rough-scad (*Trachurus lathami*) (Melo *et al.*, 2010; Lopes *et al.*, 2012*a*). The dominance of pelagic prey could explain their $\delta^{13}C$ values, since organisms occurring in the pelagic environments usually present lower $\delta^{13}C$ values than demersal/benthic organisms (France, 1995).

Despite the statistical differences in $\delta^{13}C$ values, *S. guianensis* and *P. blainvillei* were placed together in our cluster analysis (Figure 3) and slightly overlapped in their isotopic niche areas (Figure 4). Similar $\delta^{13}C$ and $\delta^{15}N$ values have also been observed based on muscle tissues of these species in the central coast of Rio de Janeiro in south-eastern Brazil (Baptista *et al.*, 2016). This similarity in the isotopic ratios agrees with their local distribution, as both species are strongly associated with shallow waters and estuarine regions, where they feed mainly on small pelagic and demersal neritic prey (Di Beneditto *et al.*, 2009; Campos *et al.*, 2020). However, *S. guianensis* and *P. blainvillei* from south-eastern Brazil differ in terms of prey preferences, as demonstrated

in studies based on stomach contents. While the main prey of *S. guianensis* include the banded croaker (*Paralonchurus brasiliensis*) and the cutlass fish (Lopes *et al.*, 2012*b*), the diet of *P. blainvillei* is dominated by the American coastal pellona (*Pellona harroweri*) and the bigtooth corvina (*Isopisthus parvipinnis*) (Campos *et al.*, 2020). Furthermore, the observed gradient in $\delta^{13}C$ values may be explained by small-scale differences in areas used (Figueiredo *et al.*, 2020), as *S. guianensis* were mainly sampled near the Cananéia estuary, while *P. blainvillei* samples were more uniformly distributed along the coast. Thus, the relatively small overlap in isotopic niche areas and the differences in $\delta^{13}C$, even though both species are associated with coastal/estuarine waters, may suggest ecological and spatial segregation between these species. Nevertheless, our study counted only a small sample size for both species, thus our results should be interpreted with caution. Therefore, continued research is recommended for better understanding of the ecology and habitat use by these co-occurring odontocetes.

Occasional species

We considered occasional species those for which data are limited in the region, although they seem to occur more frequently and more abundantly at certain seasons of the year. This includes the *O. orca*, *S. bredanensis*, *D. delphis* and *B. edeni* (Tavares *et al.*, 2010; Santos *et al.*, 2019). *Orcinus orca* and *S. bredanensis* were clustered together and had high isotopic similarity with *S. guianensis* and *P. blainvillei* (Figure 3). Their $\delta^{15}N$ values were higher than those of *S. guianensis* and *P. blainvillei* (Figure 2B), indicating relatively higher trophic levels. In south-eastern Brazil, *S. bredanensis* are mainly sighted in shallow coastal waters (Santos *et al.*, 2019; Figueiredo *et al.*, 2020) where cephalopods are the dominant prey item (Melo *et al.*, 2010). The high $\delta^{15}N$ values observed here for *S. bredanensis* are similar to those observed for this species in other regions of south-eastern Brazil (Baptista *et al.*, 2016). The authors attributed *S. bredanensis*' relatively higher $\delta^{15}N$ to the use of larger prey due to their higher energy requirements in comparison to the smaller odontocetes. The high $\delta^{15}N$ observed in individuals of *O. orca* are in agreement with the species' high trophic position. In the South-western Atlantic Ocean, they have been reported feeding on swordfish *Xiphias gladius*, tunas *Thunnus* spp. (Dalla Rosa & Secchi,

2007; Passadore *et al.*, 2015), blue shark *Prionace glauca* (Passadore *et al.*, 2015) and on small odontocetes, including *P. blainvillei* (Ott & Danilewicz, 1998; Santos & Netto, 2005). Thus, our isotopic data suggested that *S. bredanensis* and *O. orca* occupy relatively higher trophic positions than *P. blainvillei* and *S. guianensis*, although the former two species most likely differ considerably in terms of the main prey consumed.

The lower δ^{15}N values observed in *O. orca* in comparison to other cetacean species (e.g. *T. truncatus*, *S. frontalis* and *D. delphis*, Table 1) were unexpected, considering the prey types that could comprise their diet in the South-western Atlantic Ocean. Sightings of *O. orca* in the south-eastern Brazilian coast are more common between November and February (Siciliano *et al.*, 1999; Santos *et al.*, 2019), the same period the samples in our study were obtained (December). As there is a seasonality of occurrence along the region, the stable isotopes measured in *O. orca* skin may be representing the isotopic values of prey consumed in different feeding areas. The time it takes for the isotopic values of prey to be reflected on toothed whales' skin tissue has an average half-life of ~24 and 47 days for δ^{13}C and δ^{15}N, respectively (Giménez *et al.*, 2016). Accordingly, the nitrogen isotopic ratio observed in *O. orca* may be reflecting the isoscapes of other regions where they had been foraging during the previous months. If they had been foraging in offshore waters before approaching coastal regions, the lower δ^{15}N values from oceanic waters (Troina *et al.*, 2020a) could still be reflected in their skin isotopic values. Additionally, the diet-to-consumer discrimination could differ among these toothed whales, as diet-to-tissue (TDF) can be affected by consumers trophic level, the quality of dietary protein and prey isotopic values (Adams & Sterner, 2000; Robbins *et al.*, 2005; Hussey *et al.*, 2014). Accordingly, if *O. orca* has lower TDF than the remaining toothed whales, the resulting δ^{15}N values observed in their skin could be relatively lower, even if they feed on higher trophic level prey. Further studies using complementary tools such as the analysis of δ^{15}N in individual compounds could help resolve their trophic position.

Our cluster analysis also identified a subgroup formed by *D. delphis* and *B. edeni*. It is important to note that, although they were grouped together, the isotopic differences between these two species were considerably large (node 6, Figure 3). This is most likely due to the large difference in δ^{15}N (~1.2‰, Table 1) between these two species, indicating relatively higher trophic position for *D. delphis* than for *B. edeni*. Individuals of both species seem to occur seasonally in the coastal waters of south-eastern Brazil. Although sightings of these species happen throughout the year in the shallow waters of the study area, frequency is higher during late spring, summer and early autumn (Siciliano *et al.*, 2004; Tavares *et al.*, 2010; Santos *et al.*, 2019). Such seasonality has been linked to the influence of the SACW during these months (Castro *et al.*, 2006), which results in increased productivity in coastal waters off south-eastern Brazil and, consequently, increased prey availability (Brandini *et al.*, 2018). These physical events significantly affect baseline carbon isotopes, decreasing the δ^{13}C values in the organisms comprising the base of this food web (Troina *et al.*, 2020a). Among the organisms whose abundances are favoured by upwelling conditions of the SACW are small pelagic fishes and squids, such as the Brazilian sardine (*Sardinella brasiliensis*), the Argentine anchovy (*Engraulis anchoita*) (Bakun & Parrish, 1991; Matsuura, 1996) and the arrow squid (*Doryteuthis sanpaulensis*) (Haimovici & Perez, 1991). *Balaenoptera edeni* uses the south-eastern Brazilian coast mainly during warm months, apparently to forage upon large schools of Brazilian sardines (Siciliano *et al.*, 2004). Similarly, a diet rich on pelagic organisms has been suggested for *D. delphis* along its distribution in the Brazilian coast (Tavares *et al.*, 2010), although their diet may include relatively

higher trophic level prey such as the longfine inshore squid (Melo *et al.*, 2010). Thus, the lower δ^{13}C of *D. delphis* and *B. edeni* in comparison with the remaining species (Figure 2) could be reflecting foraging along the shelf breakwaters, where increased productivity due to upwelling events may provide important food sources for these species.

Despite the geographic overlap in occurrence between *S. frontalis* and *D. delphis* (Moreno *et al.*, 2005; Tavares *et al.*, 2010), we found no evidence for overlap in the use of resources, as indicated by the lack of isotopic similarity between these two species. Similar isotopic values have been observed in *S. frontalis* and *D. delphis* from southern Brazil (31–34°S) nearshore (Botta *et al.*, 2012) and oceanic populations (Troina *et al.*, 2020b). Nevertheless, the authors have concluded that despite the relatively high isotopic niche overlap between the oceanic populations of *D. delphis* and *S. frontalis*, the fact that they avoid one another (Di Tullio *et al.*, 2016) is a strategy to minimize competition (Troina *et al.*, 2020b). In south-eastern Brazil, data from stomach contents showed overlap in some prey species taken by these toothed whales, although they differed in terms of size-classes and the dominance of species (Melo *et al.*, 2010). Therefore, segregation in the use of resources seems to be plausible, although further studies with larger sample sizes are recommended, as they would help improve our understanding about the trophic ecology and overlap between these enigmatic species.

Migratory species

The cluster analyses identified the largest isotopic differences between the adults *M. novaeangliae* and *E. australis* and the remaining cetaceans (node 1, Figure 3), with both baleen whale species having the lowest δ^{13}C and δ^{15}N values (Figure 2). These species occur along the Brazilian coastal waters during the austral winter and early spring, when they use the region for mating and parental care (Lodi *et al.*, 1996; Zerbini *et al.*, 2006). Their low δ^{15}N values were expected as these two species occupy relatively lower trophic positions: their main food item is krill, but copepods and small schooling fish are also important for *E. australis* (e.g. Hoffmeyer *et al.*, 2010) and *M. novaeangliae* (Clapham, 2018), respectively. The low δ^{13}C most likely represents the isotopic baseline of Subantarctic and Antarctic waters (Brault *et al.*, 2018), their summer feeding grounds (Zerbini *et al.*, 2006). Considering estimated isotopic turnover of ~6 months in baleen whale skin (Busquets-Vass *et al.*, 2017), this would coincide with the period these whales were feeding in polar waters prior to sampling off south-eastern Brazil. The large isotopic dissimilarity between these baleen whales (node 4, Figure 3) could be attributed to feeding in different areas in Subantarctic and Antarctic waters and the gradient in these regions' isoscapes (McMahon *et al.*, 2013). While the population of *M. novaeangliae* that breed off Brazil feed in South Georgia and Sandwich Islands (Zerbini *et al.*, 2006), a variety of feeding grounds in the South Atlantic Ocean have been suggested for *E. australis*, including the Georgia and Sandwich Islands, the Antarctic Peninsula and areas close to the Antarctic Convergence (IWC, 2001; Valenzuela *et al.*, 2018).

The two *E. australis* sampled included an adult female and her calf. The calf's δ^{13}C and δ^{15}N values were, respectively, lower and higher than those of the mother (Table 1, Figure 2). This is probably due to the influence of the mother's milk on the isotopic values of the calf. As females produce milk by metabolizing their own tissues, the δ^{15}N in their nursing calves are relatively higher than in the mother (Fogel *et al.*, 1989). On the other hand, the high fat content in aquatic mammals' milk (Costa, 2002) result in lower δ^{13}C values in calves, due to the low ^{13}C/^{12}C in lipids (DeNiro & Epstein, 1977). Furthermore,

lactation can also influence $\delta^{13}C$ and $\delta^{15}N$ in the mothers' tissues. An increase in $\delta^{13}C$ may be observed in the tissues of lactating females due to the production of lipid-rich ^{13}C-depleted maternal milk (e.g. Borrell et al., 2016; Gellippi et al., 2020). Additionally, the protein synthesis during lactation reduces the $\delta^{15}N$ values in the maternal body protein (Kurle, 2002). Such patterns have been observed in northern elephant seals Mirounga angustirostris (Habran et al., 2010) and in polar bears Ursus maritimus (Polischuck et al., 2001). Bearing this in mind, we could not discard the possibility that both $\delta^{13}C$ and $\delta^{15}N$ values in the adult female E. australis were influenced by metabolism during lactation, as we assume this female was breastfeeding due to the presence of a calf.

In the present study we analysed one adult and three juveniles M. novaeangliae. The adult was a biopsied female that had the lowest $\delta^{13}C$ and $\delta^{15}N$ values (Table 1), while the juveniles' isotopic values were notably higher, resulting in their clustering closer to the other toothed whales and B. edeni (Figure 3). The high $\delta^{13}C$ and $\delta^{15}N$ values observed in these juveniles may be indicative of foraging in an area with a different isotopic baseline. Juveniles of M. novaeangliae have already been reported opportunistically feeding during their migration to temperate and tropical zones (Danilewicz et al., 2009; Sá Alves et al., 2009; Bortolotto et al., 2016). Baseline isoscapes are ^{13}C-enriched in temperate and tropical zones in comparison with Subantarctic and Antarctic regions (McMahon et al., 2013; Magozzi et al., 2017; Troina et al., 2020a). Additionally, the $\delta^{13}C$ and $\delta^{15}N$ values observed in juvenile M. novaeangliae were comparable to those of baseline organisms from the South-western Atlantic Ocean (McMahon et al., 2013; Troina et al., 2020a). Accordingly, our isotopic data suggest that the juveniles may be feeding during their displacement along the waters of the South-western Atlantic Ocean, which would consequently be influencing their skin isotopic values, averaging out the isotopic values from polar baselines. Such a pattern was also observed for M. novaeangliae specimens opportunistically feeding along the Australian coast, which had $\delta^{13}C$ and $\delta^{15}N$ values significantly higher than those of the same population that feed in Antarctica waters (Eisenmann et al., 2016). Additionally, higher $\delta^{15}N$ could indicate the consumption of other prey types such as small schooling fish that occupy a relatively higher trophic position than krill, which has been reported for the species in Brazilian waters (Sá Alves et al., 2009). Alternatively, nutritional stress could also have influenced the $\delta^{15}N$ values of these juveniles, as such conditions have been shown to increase $\delta^{15}N$ values due to the catabolism of tissues to balance energetic requirements (Hobson et al., 1993; Doi et al., 2017).

Conclusion

In the present study we used $\delta^{13}C$ and $\delta^{15}N$ values in skin samples to assess the feeding ecology and habitat use by distinct cetacean species occurring along the south-eastern coast of Brazil. It is important to note that our ecological inferences were limited given our small sample size, especially for the baleen whales, and for O. orca and S. bredanensis. Nevertheless, stable isotopes allowed us to identify patterns of habitat use, feeding habits and trophic interactions that are useful to understand how these cetacean species explore and coexist in this area. Although information on the forage areas and feeding strategies of cetaceans is extremely important for management purposes, little is known about this subject for populations occurring in the South-west Atlantic Ocean. Therefore, continued investigation with increased sample size is recommended, perhaps coupled with other methodologies such as stomach content analysis or telemetry. Additionally, future studies in south-eastern Brazil should focus

on sampling potential prey for isotopic measurements, as they would be extremely helpful to assess cetacean–prey relationships throughout the region.

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