Niche overlap and diet composition of three sympatric coastal dolphin species in the southwest Atlantic Ocean

Clarissa R. Teixeira1,3 | Silvina Botta2 | Fábio G. Daura-Jorge1 | Luiza B. Pereira1 | Seth D. Newsome3 | Paulo C. Simões-Lopes1

1Laboratório de Mamíferos Aquáticos (LAMAQ), Programa de Pós-Graduação em Ecologia, Universidade Federal de Santa Catarina; Florianópolis, Santa Catarina, Brazil
2Laboratório de Ecologia e Conservação da Megafauna Marinha (ECOMEGA), Universidade Federal do Rio Grande, Rio Grande, Brazil
3Department of Biology, University of New Mexico, Albuquerque, New, Mexico

Abstract
Sympatric species are expected to differ in ecological requirements to minimize niche overlap and avoid competition. Here we assess the trophic interactions among three coexisting dolphin species from southern Brazil: the franciscana dolphin (Pontoporia blainvillei), the Guiana dolphin (Sotalia guianensis), and the Lahille's bottlenose dolphin (Tursiops truncatus geyhreus). We evaluated temporal variation in carbon (δ13C) and nitrogen (δ15N) isotope values of bone collagen to examine potential dietary shifts resulting from increased fishing activity over the past three decades. We estimated the degree of niche overlap among these species and the contribution of potential prey sources to their diet. δ15N values were consistent among species and across years, while δ13C values increased for Guiana dolphins and decreased for bottlenose dolphins, suggesting changes in diet and/or foraging habitats through time. The similar δ13C and δ15N values and the high niche overlap between Guiana and bottlenose dolphins indicate that these species are primarily feeding on demersal prey. The franciscana diet is primarily composed of pelagic prey, resulting in a lower niche...
overlap in comparison with the other dolphin species. Our study provides further information about the foraging ecology of this unique dolphin community in southern Brazil with implications for its management and conservation.

KEYWORDS
isotopic niche, Pontoporia blainvillei, Sotalia guianensis, stable isotopes, trophic position, Tursiops truncatus gephreus

1 | INTRODUCTION

The concept of niche is essential for understanding how biotic and abiotic variables regulate resource use and competition among species. Niche theory predicts that sympatric species can partition resources through variation in foraging strategies or through variation in when and/or where resources are exploited (Plank, 1980; Schoener, 1974). Therefore, quantifying niche overlap of sympatric species can provide insights into the underlying mechanisms that enable coexistence, such as how species share or compete for resources. This information may eventually be used to predict community responses to natural or anthropogenic ecosystem change, especially those related to prey distribution and abundance (Chase & Leibold, 2003; Geange, Pledger, Burns, & Shima, 2011).

Resource partitioning through variation in foraging strategies can be attributed to morphological differences among coexisting species (Schoener, 1974). This is mainly due to the influence of an organism’s morphology on its foraging performance, which can limit the range of prey that can be efficiently captured (Taylor, 1987). On the coast of Santa Catarina, Brazil in the Southwest Atlantic Ocean (SWAO), a direct sympatry (sensu Bearzi, 2005) among three dolphin species with marked differences in morphological traits—the franciscana dolphin (Pontoporia blainvillei), the Guiana dolphin (Sotalia guianensis), and the coastal ecotype of the bottlenose dolphin (Tursiops truncatus gephreus)—provides an interesting opportunity to evaluate resource partitioning (Figure 1). The franciscana dolphin (Pontoporidae) is usually grouped within the so-called river dolphins, that consist of relict dolphin lineages (Cassens et al., 2000). These species have a unique combination of morphological features such as a flexible neck, elongated skull, narrow jaw, and rostrum (Cassens et al., 2000) with a relatively large number (up to 250) of small needle-like teeth (Werth, 2006). The Guiana and bottlenose dolphins are grouped within the more diverse delphinid family characterized by blunt heads, wider jaws, and a lower number of robust and conical teeth (up to 100) in comparison to river dolphins (Werth, 2006). These three species also have different body dimensions (Botta, Muelbert, & Secchi, 2012; Cremer et al., 2018; Rosas & Monteiro-Filho, 2002; Venuto, Botta, Barreto, Secchi, & Frue, 2020) and life history traits (i.e., growth rates and age at maturity; Barreto & Rosas, 2006; Botta et al., 2010; Frue, Daura-Jorge, Möller, Genoves, & Secchi, 2015; Rosas & Monteiro-Filho, 2002; Venuto et al., 2020) that likely result in contrasting energetic demands, which in turn can affect their behavior and ability to catch prey, and by extension their dietary preferences.

The diet of these three sympatric dolphin species was previously described via stomach content analysis (Basso, 2005; Daura-Jorge, Wedekin, & Simões-Lopes, 2011; Milmann, Danilewicz, Machado, Santos, & Ott, 2016), which revealed that the most important prey species for both Guiana and bottlenose dolphins is the pelagic Trichiurus lepturus, while the demersal Stellifer rastrifer is the preferred prey for the franciscana dolphin. Studies suggest that the franciscana dolphin feeds mainly on small size prey (Bittar & di Benedetto, 2009; Cremer, Pinheiro, & Simões-Lopes, 2012), which might be related to its rather unique skull morphology. In contrast, Guiana and bottlenose dolphins exhibit a high degree of dietary plasticity with respect to prey size (Daura-Jorge et al., 2011; Milmann et al., 2016).

Although T. lepturus is not considered an important resource for fisheries in southern Brazil, the high bycatch mortality of this pelagic species by the bottom trawling fleet (Haimovic & Mendonça, 1996; Haimovic &
Fischer, 2007) may negatively impact *T. lepturus* stocks and by extension influence the diet of Guiana and bottlenose dolphins. Other important prey consumed by these three sympatric dolphins are demersal species (e.g., *Mugil liza*, *Micropogonias furnieri*, *Macrodon atricuda*, *Umbrina canosa*, and *Cynocion guatucupa*), which have decreased in abundance over time, with stocks now considered fully exploited and/or at risk of collapse (Haimovici & Cardoso, 2017). Together, these demersal fish species represent more than half of local marine fish landings in southern Brazil. The ecological impact of overfishing has been monitored for decades along the southern Brazilian coast (Castello, Sunyé, Haimovici, & Hellebrandt, 2009; Haimovici & Cardoso, 2017; Vasconcellos & Gasalla, 2001) and has likely influenced the foraging behavior and diet composition of these dolphin species and possibly other coastal marine top consumers in this region. During the last decade, franciscana and bottlenose dolphins from Rio Grande in southern Brazil showed a temporal change in diet composition that likely corresponds to increased fishing pressure in this region, which impacted the availability of their primary prey sources (e.g., *M. furnieri* and *Menticirrhus* sp.; Secchi, Ott, & Danilewicz, 2003; Secchi et al., 2017). Thus, detailed information on feeding ecology can help elucidate how increasing fishing activities in this region can influence diet composition and trophic relationships among these top predators, supporting more effective management for the conservation of coastal marine mammal populations and the ecosystems that support them.

Stable isotope analysis has emerged as a useful tool to assess trophic interactions and resource partitioning among marine mammals and has been used extensively to study sympatric dolphin species (e.g., Kiszka et al., 2011; Loizaga de Castro, Saporiti, Vales, Cardona, & Crespo, 2017). As applied to marine top consumers, this approach
commonly utilizes carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analysis to characterize foraging habitats and trophic level (DeNiro & Epstein, 1978; Fry, 2006; Newsome, Clementz, & Koch, 2010). The ecological niche of a population or species can thus be depicted by its isotopic composition or isotopic niche (Bearhop, Adams, Waldron, Fuller, & MacLeod, 2004; Newsome, Martinez del Rio, Bearhop, & Phillips, 2007) in which $\delta^{13}C$ vs. $\delta^{15}N$ are the environmental axes that combine both habitat and resource related components. Isotopic niches can be quantified using metrics (Jackson, Inger, Parnell, & Bearhop, 2011; Layman, Arrington, Montanà, & Post, 2007) that allow for the assessment of trophic relationships and niche overlap within and among individuals (e.g., Zhao, Villéger, Lek, & Cucherousset, 2014), populations (e.g., Santos-Carvallo et al., 2015), and even species (e.g., Franco-Trecu, Drago, Costa, Dimitriadis, & Passadore, 2017).

Here, we used $\delta^{13}C$ and $\delta^{15}N$ analysis to assess the foraging ecology and potential dietary overlap among sympatric franciscana, Guiana, and bottlenose dolphins along the southern Brazilian coast. Specifically, we compared the width and degree of overlap in the isotopic niche among these species and used a Bayesian mixing model to quantify the proportional contribution of primary prey sources to their diet. Based on differences in morphology, we hypothesized that we would observe significant differences in their isotopic niche, with larger niche overlap among the two most closely related species, Guiana and bottlenose dolphins. Second, we analyzed $\delta^{13}C$ and $\delta^{15}N$ values of individuals collected across the past three decades (1985–2017) to investigate historical dietary shifts that may be related to increased fishing pressure on some of their primary prey species during this period.

2 | MATERIAL AND METHODS

2.1 | Study area

The coast of Santa Catarina in southern Brazil is composed of a mosaic of bays, rocky coastal islands, sandy coastline, estuaries, lagoons, and mangrove forests. This region is influenced by Subantarctic Shelf Water transported northward by the Malvinas/Falkland Current and Tropical Water and South Atlantic Central Water carried southward by the Brazil Current, characterizing the Subtropical Convergence (Ciotti, Odebrecht, Fillmann, & Möller, 1995; Möller, Piola, Freitas, & Campos, 2008). This system generates high nutrient concentration and biological productivity (Muelbert et al., 2008). In addition to marine currents, discharge of freshwater from the La Plata River and, to a lesser extent, the Patos Lagoon Estuary also influences nutrient dynamics in the coastal zone (Muelbert et al., 2008).

2.2 | Sample collection

We subsampled vertebral epiphysis from 75 stranded carcasses ($n_{\text{franciscana dolphin}} = 34$; $n_{\text{Guiana dolphin}} = 23$; $n_{\text{bottlenose dolphin}} = 18$) found along the Santa Catarina coast from Itajaí (26°91’S, 48°67’W) to Laguna (28°30’S, 48°50’W) between 1985 and 2017 (see Supplementary Material Figure S1). The specimens are archived in the scientific collection of the Aquatic Mammals Laboratory (LAMAQ) at the Universidade Federal de Santa Catarina (UFSK).

We selected potential prey species based on the percent frequency of occurrence (%FO) from previous stomach content analyses for local and adjacent populations of franciscana (Bassoii, 2005), Guiana (Daura-Jorge et al., 2011) and bottlenose dolphins (Milmann et al., 2016). We focused on species with %FO > 10% based on stomach content analysis. Given that stable isotope values may vary geographically, we attempted to obtain prey with artisanal fishers of the southern Brazilian coast from the same regions where the stranded carcasses were found. We could not collect five fish species (M. atricauda, U. canosai, Engraulis anchoita and Urophycis brasiliensis), and hence, we relied on isotope values for these species collected in the southern Brazil and previously reported in the literature (Bugoni, McGill, & Furness, 2010; Zenteno et al., 2015). Due to the potential correlation between fish length/size and isotopic composition (Nagata, Moreira, Pimentel, & Morandini, 2015), we also considered the average size of prey consumed.
by each dolphin species when selecting samples for analysis. We analyzed stable isotope values of a total of 92 prey specimens from 17 fish and one cephalopod species (see Supplementary Material Table S2).

2.3 | Stable isotope analysis

We extracted bone collagen via demineralization in 0.2 N hydrochloric acid (HCl) for ~96 hr at room temperature with replacement of the acid solution every ~24 hr. Each sample was washed with successive rinses of deionized (DI) water and lipids were extracted by repeated soaks in a 2:1 chloroform:methanol solvent solution, rinsed with DI water, and dried for ~15 hr in a freeze-dryer. White dorsal muscle of fishes and the mantle of cephalopods were stored at −20°C until preparation for isotope analyses.

We then collected a section of muscle tissue from each fish from the region between the lateral line and the dorsal fin. We rinsed samples with deionized water to remove external contaminants and dried them at 60°C for 48 hr. We then ground the dried tissues to a fine powder using a mortar and pestle. No lipid corrections were applied to prey δ13C values because muscle samples had weight percent C:N ratios (<3.5), indicating negligible lipid contents (Post et al., 2007).

We weighed dried collagen or muscle/mantle tissue (~0.6 mg) into tin capsules and measured δ13C and δ15N values using a Costech 4010 Elemental Analyzer (Valencia, CA) coupled to a Thermo Scientific Delta V Plus (Bremen, Germany) isotope ratio mass spectrometer at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM). Results are expressed in parts per thousand (‰) and delta notation (δ) using the equation: δsample = [Rsample / Rstandard − 1] × 1,000, where Rsample and Rstandard are the 13C/12C or 15N/14N ratios of the sample and standard, respectively (Peterson & Fry, 1987). The standards are Vienna Pee Dee Belemnite limestone (V-PDB) for δ13C and atmospheric N2 for δ15N. The analytical precision based on the within-run standard deviation of protein reference materials (casein and acetonilide) was ≤0.2‰ for both δ13C and δ15N. To directly compare the carbon isotope composition of historical and modern specimens, we applied a correction factor of 0.022%/year to δ13C values of historical specimens to account for the Suess effect, or the anthropogenic decrease in the δ13C values of atmospheric CO2 caused by burning of fossil fuels (Francey et al., 1999; Indermühle et al., 1999). We also measured the C:N ratios of each sample, which were in the expected range (2.8–3.5) for pure protein (Ambrose, 1990; see Supplementary Material Table S1).

2.4 | Data analysis

2.4.1 | δ13C and δ15N variation among species and years

We fitted Gamma generalized linear models (GLM) with an inverse link function (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) to model δ13C and δ15N values (response variables) as a function of species and stranding year (explanatory variables). As δ13C values are negative and Gamma family requires positive data values, we used δ13C absolute values. We ran models separately for δ13C and δ15N considering additive, interactive, and isolated relations between response and explanatory variables. Model selection was performed through a stepwise backward procedure, and the best model was identified by adjusted Akaike's information criterion (AICc) and Akaike weights (Burnham & Anderson, 2002). Significant models with delta AICc ≤2 were considered suitable to explain the variation in δ13C and δ15N values and residuals were checked to ensure normality.

2.4.2 | Isotopic niche width and overlap

We compared the isotopic niche width of each species by generating bivariate ellipses in SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al., 2011), which employs Markov-Chain Monte Carlo (MCMC) simulations to
construct parameters of ellipses based on sampling points. We estimated the standard ellipse area corrected for small sample sizes (SEAC, expressed as %²), which represents the mean core area of each species’ isotopic niche (Jackson et al., 2011; Layman et al., 2007). We used the SEAC to estimate the proportional niche width overlap among species. Additionally, we calculated the Bayesian standard ellipse area (SEAB) to obtain unbiased estimates of the isotopic niche widths with credibility intervals (Jackson et al., 2011). To test for significant differences, we ran 20,000 MCMC iterations and constructed 95% credible intervals around the mean of each species.

2.4.3 Stable isotope mixing models

We estimated the relative contribution of prey species from different trophic levels to the diet of the three dolphin species using the Stable Isotope Mixing Models in R (simmr) package (Parnell, 2016). This Bayesian framework uses robust probability estimates to assess the distribution of sources contribution to the assimilated diet of consumers (Parnell et al., 2010) and incorporates δ¹³C and δ¹⁵N of consumers, δ¹³C and δ¹⁵N means and standard deviation of both the sources of prey (see Supplementary Material Table S2) and trophic discrimination factors (TDFs) defined as the difference in isotopic values between consumers and their diet. We ran mixing models separately for each dolphin species with prey sources identified from previous stomach content analysis of individuals stranded in our study area and adjacent areas (Bassoi, 2005; Daura-Jorge et al., 2011; Milmann et al., 2016); note that the suite of prey differed among models for each dolphin species (Table S2). This approach enabled us to compare the long-term contribution of prey from different trophic levels to the diet of each dolphin species.

As there are no estimates of δ¹³C and δ¹⁵N TDFs values for dolphin bone collagen, we used the published mean (± SD) value of diet-to-skin TDF estimates for the bottlenose dolphin of 1.0% ± 0.4% for δ¹³C and 1.6% ± 0.5% for δ¹⁵N (Gimenez, Ramirez, Almunia, Forero, & de Stephanis, 2016), and adjusted them using δ¹³C and δ¹⁵N values of paired skin and bone collagen of franciscana dolphin (n = 7) (S.B., unpublished data). The mean difference between paired skin and collagen δ¹³C values was +2.6% and +0.5% for δ¹³C and δ¹⁵N values, respectively. These mean values were added to the reported TDFs values for bottlenose dolphin (Gimenez et al., 2016) to yield final values of Δ¹³C = 3.6% ± 0.4% and Δ¹⁵N = 2.1% ± 0.5%.

Mean δ¹³C and δ¹⁵N values of prey for each dolphin species were analyzed with a cluster analysis (Ward’s minimum variance method) to group them for running the mixing models. Ecological groups were defined considering the clusters, the prey habitat type (pelagic vs. demersal) and trophic levels, including high and low trophic level pelagic fish, high and low trophic level demersal fish, and cephalopods (see Supplementary Material Figures S2, S3, and S4, Table S2). Results are reported as mean ± standard deviation (SD) unless otherwise stated.

3 RESULTS

3.1 δ¹³C and δ¹⁵N variation among species

δ¹³C values were similar among the three dolphin species varying from −13.4‰ ± 0.4‰ for franciscana, −12.9‰ ± 0.4‰ for Guiana, and −12.7‰ ± 0.7‰ for the bottlenose dolphin. In contrast, franciscana dolphin had the highest mean δ¹⁵N values (16.9‰ ± 0.8‰), followed by Guiana (16.1‰ ± 0.6‰) and the bottlenose dolphin (15.5‰ ± 1.6‰) (Figure 2a).

The most parsimonious models in our two candidate set had contrasting δ¹³C and δ¹⁵N values for species (Table 1), with δ¹³C values significantly lower (t = −5.170, p < .001) and δ¹⁵N values significantly higher (t = −4.734, p < .001) for franciscana in relation to Guiana and the bottlenose dolphin. No residual patterns were evident in the validation of these models. The model that included the dolphin species and year of collection was also one of the best candidate models, suggesting a temporal effect in δ¹³C values dependent of species; the AIC value of this model
was 1.2 units higher than the model that only included species as an explanatory variable. $\delta^{13}C$ decreased for the bottlenose dolphin but increased for Guiana across years; there was no significant temporal trend in franciscana (Figure 2b). The fitted model for $\delta^{15}N$ values suggests variation among species with no temporal effect within each dolphin species (Figure 2c).

### 3.2 | Isotopic niche width and overlap

![FIGURE 2](image-url) (a) Bone collagen $\delta^{13}C$ and $\delta^{15}N$ mean values for the franciscana (Pontoporia blainvillei), Guiana (Sotalia guianensis), and Lahille’s bottlenose (Tursiops truncatus gephyreus) dolphin. (b) Temporal trends in bone collagen $\delta^{13}C$ and (c) $\delta^{15}N$ values of franciscana (red triangles), Guiana (gray triangles), and Lahille’s bottlenose (blue triangles) dolphins collected from 1985 to 2017.

The Bottlenose dolphin had the largest standard ellipse area (SEAC; $3.5\%o^2$ and SEAB: $3.2\%o^2$; CI: $1.9\%o^2$–$5.1\%o^2$) while Guiana (SEAc: $0.8\%o^2$ and SEAB: $0.8\%o^2$; 95% CI: $0.5\%o^2$–$1.2\%o^2$) and franciscana (SEAc: $0.9\%o^2$ and SEAB: $0.9\%o^2$; 95% CI: $0.6\%o^2$–$1.2\%o^2$) had much smaller areas. Based on SEAC estimates, Guiana (0.1%o²) and the bottlenose dolphin (0.2%o²) had minimal overlap with franciscana (Figure 3). In contrast, the SEAc ellipses of Guiana and the bottlenose dolphin overlapped by 0.9%o², which represent 100% of the former and 24.4% of the latter species isotopic niche width.
### 3.3 Stable isotope mixing models

Stable isotope composition of potential prey items varied from $-18.1\, \text{‰} \pm 0.4\, \text{‰}$ to $-14.2\, \text{‰} \pm 0.5\, \text{‰}$ for $\delta^{13}\text{C}$ and from $13.3\, \text{‰} \pm 0.5\, \text{‰}$ to $17.0\, \text{‰} \pm 0.3\, \text{‰}$ for $\delta^{15}\text{N}$. Bayesian mixing model-based estimates of trophic levels revealed interspecific differences among the three species (Table 2). Low trophic level pelagic fish contributed a median of 51% (CI: 0.14% – 0.80%) to the diet of franciscana, while low trophic level demersal fish contributed a median of 46% (CI: 0.25% – 0.58%) to the diet of Guiana. Low trophic level demersal fish were also important for the bottlenose dolphin and contributed a mean of 72% (CI: 0.45% – 0.94%) to this species diet (Figure 4, Table 2).
**TABLE 2**  Stable isotope mixing model results with predicted diet proportions (2.5% and 97.5% quantiles) of each prey group to the diet of the franciscana (*Pontoporia blainvillei*), Guiana (*Sotalia guianensis*) and Lahille’s bottlenose (*Tursiops truncatus gephyreus*) dolphin off the coast of Santa Catarina, southern Brazil. Mean values are in parentheses and bold values represent the highest prey item contribution.

<table>
<thead>
<tr>
<th>Species</th>
<th>Pel HL</th>
<th>Pel LL</th>
<th>Dem HL</th>
<th>Dem LL</th>
<th>Dem</th>
<th>Ceph</th>
</tr>
</thead>
<tbody>
<tr>
<td>Franciscana dolphin</td>
<td>0.02–0.39  (0.16)</td>
<td>0.14–0.80  (0.51)</td>
<td>—</td>
<td>—</td>
<td>0.02–0.47 (0.18)</td>
<td>0.03–0.30 (0.15)</td>
</tr>
<tr>
<td>Guiana dolphin</td>
<td>0.01–0.20  (0.06)</td>
<td>0.01–0.57  (0.15)</td>
<td>0.05–0.42 (0.27)</td>
<td>0.25–0.58 (0.46)</td>
<td>—</td>
<td>0.01–0.12 (0.04)</td>
</tr>
<tr>
<td>Bottlenose dolphin</td>
<td>0.01–0.23  (0.07)</td>
<td>—</td>
<td>0.01–0.41 (0.14)</td>
<td>0.45–0.94 (0.72)</td>
<td>—</td>
<td>0.01–0.06 (0.07)</td>
</tr>
</tbody>
</table>

Note. Pel HL = pelagic fish from high trophic levels, Pel LL = pelagic fish from low trophic levels, Dem = demersal fish, Dem HL = demersal fish from high trophic levels, Dem LL = demersal fish from low trophic levels, Ceph = cephalopods. See Supplementary Material Table S2 for prey species included in each ecological group as they may not include the same items for each dolphin species.
DISCUSSION

Our study is the first to assess resource partitioning among franciscana, Guiana, and Lahille's bottlenose dolphins within the unique area where these three species coexist. Our main findings suggest some degree of spatial segregation in foraging behavior and prey preferences for these species along the southern Brazilian coast. Stable isotope
analysis showed that franciscana primarily consumes low trophic level pelagic prey like *E. anchoita*, while Guiana and the bottlenose dolphin tend to consume demersal fish species such as *Mugil curema* and *M. liza*, respectively. Relative to the size of the distribution of each species, their sympatry along the southern Brazilian coast seems to be restricted to a rather small latitudinal band (Figure 1). Locally, franciscana uses open waters with mean depth of 30 m (Danilewicz et al., 2009), which may favor selection of pelagic prey in the water column or near the surface. In contrast, the Guiana and the coastal ecotype of the bottlenose dolphin along the southern Brazilian coast use shallower waters with a mean depth of 3 m (Di Tullio, Fruet, & Secchi, 2015; Simões-Lopes et al., 2019; Wedekin, Daura-Jorge, & Simões-Lopes 2010), which favors selection of demersal prey captured on or near the bottom. Indeed, the minimal isotopic overlap observed between franciscana and the delphinid species can be associated with this broader distribution of franciscana in open waters that likely results in low $\delta^{13}C$ values.

The different trophic position occupied by the two delphinid species was a result of low $\delta^{15}N$ values of Guiana and the bottlenose dolphin compared to franciscana, which likely reflect consumption of prey sources from different habitat types (pelagic vs. demersal). The $\delta^{13}C$ and $\delta^{15}N$ mean values and the high degree of isotopic niche overlap between Guiana and the bottlenose dolphin suggest similar foraging areas and/or prey preferences with both species occupying equivalent trophic positions. This high degree of overlap can be related to the important contribution of demersal fish species to both Guiana and the bottlenose dolphin's diet. Although prey sources used for mixing models differ among delphinid species, it is important to note that both Guiana and the bottlenose dolphin are primarily consuming mullet species along the southern Brazilian coast (Daura-Jorge et al., 2011; Milmann et al., 2016). *Mugil curema* and *M. liza* are common dolphin prey that consume a mixed diet of macroalgae, microphytobenthos, and small benthic invertebrates and thus likely occupy a lower trophic level than more pelagic prey (Cardona, 2001; García et al., 2018; Drake, Arias, & Gállego, 1984). Consumption of these omnivorous prey could contribute to the similar and lower $\delta^{15}N$ values of Guiana and the bottlenose dolphin relative to franciscana. In contrast, pelagic fish assemblages are usually planktrophic or piscivorous, which may explain the relatively high $\delta^{15}N$ values and by extension higher trophic level of franciscana dolphin compared to the other species.

Lahille’s Bottlenose dolphin is known to exhibit behavioral flexibility with a wide variety of foraging strategies and prey selection via adaptation to local ecological conditions (Sargeant, Wirsing, Heithaus, & Mann, 2007). Patterns in SEA_C and SEA_B estimates among species show that bottlenose dolphins consume a more diverse set of prey than franciscana and Guiana dolphins. This pattern may be driven in part by the possibility that our sample of bottlenose dolphin represent a mixture of resident and transient individuals that use different foraging strategies (Fruet et al., 2014). A subset of the small and highly resident bottlenose dolphin population of Laguna in southern Brazil seasonally consumes a high proportion of *M. liza* in cooperation with artisanal fishermen, which is a unique and specialized foraging tactic (Daura-Jorge, Cantor, Ingram, Lusseau, & Simões-Lopes, 2012; Simões-Lopes, Fabian, & Menegheti, 1998). In contrast, coastal transient individuals forage over a broader geographical area in a variety of habitats and, by extension, likely have more diverse diets. The broader geographic range and the wide variety of foraging tactics showed by the bottlenose dolphin may explain why some individuals plot outside of the mixing polygon produced from analysis of the limited prey types analyzed here (see Supplementary Material Figure S5). The similarity between SEA_C and SEA_B observed for franciscana and Guiana has been previously observed for populations off the southeastern Brazilian coast (Di Beneditto & Monteiro, 2016). The narrowness of SEA_C and SEA_B of Guiana is consistent with the restricted home range and site fidelity of the resident population that inhabits the northern bay of Santa Catarina (Flores, 1999; Wedekin, Daura-Jorge, Placentini, & Simões-Lopes, 2007). In addition, this resident population seems to avoid productive areas near mangroves or the mouths of estuaries that are close to urban areas, thereby reducing their access to a more diverse array of prey types (Wedekin et al., 2007).

Guiana and the bottlenose dolphin had similar $\delta^{13}C$ values, suggesting that they tend to forage in similar habitats. Observational data, however, suggest a fine-scale segregation in habitat use between these two species, where the resident Guiana population is restricted to the western section of the northern bay of Santa Catarina and bottlenose dolphin occurs mostly in the eastern section of the bay (Flores & Fontoura, 2006; Wedekin et al., 2007). These habitat preferences likely reduce either interference or exploitative competition (Wedekin, Daura-Jorge,
Simões-Lopes, 2004). Interestingly, these two species showed opposite patterns in $\delta^{13}C$ values over time, and we hypothesize that the observed temporal shifts in $\delta^{13}C$ values through time may reflect changes in resource availability. Specifically, the increases in $\delta^{13}C$ values observed in Guiana through time is consistent with a recent shift in habitat use of this resident population, which moved from a small and open inlet to a wider and more protected inlet likely due to changes in prey abundance (Wedekin et al., 2007). It is important to note that we cannot rule out the possibility that the $\delta^{13}C$ values of potential prey has changed over time, which may contribute to the observed temporal variation in dolphin carbon isotope composition.

As mentioned above, the apparent interaction between foraging ecology and commercial fishing activities has been previously noted for franciscana and the bottlenose dolphin (Secchi et al., 2003, 2016) from adjacent waters in southern Brazil. Additionally, the mullet species (M. liza) consumed by bottlenose dolphins are increasingly over-exploited in southern Brazil (Chao et al., 2015; de Abreu-Mota et al., 2018; Haimovici, 1998; Haimovici & Cardoso, 2017). Not only are current landings of M. liza unsustainable (Sant’Ana & Kinas, 2018), Santa Catarina also has produced the largest proportion (45%) of total mullet (Mugil) landings for any region in southern Brazil over the past 30 years (de Abreu-Mota et al., 2018). The increased local fishing pressure on mullet and its high contribution to bottlenose dolphin diet raise concerns about resource competition with fisheries, which could lead to changes in diet composition, and by extension, influence how it coexists with the two other dolphin species in this region.

These dolphin species are all considered to be threatened to various degrees primarily by high bycatch-related mortality (Fruet et al., 2012; Secchi, 2010). Our isotope-based approach suggests that franciscana, Guiana, and the bottlenose dolphin may be threatened by resource competition with fisheries, which impacts how they partition prey sources and foraging habitats along the southern Brazilian coast. Some of the prey species shown by mixing models and previous stomach content analysis (Basso, 2005; Daura-Jorge et al., 2011; Milmann et al., 2016) to contribute significantly to dolphin diets are considered threatened by overexploitation. For example, M. atricauda has suffered a marked decrease in biomass in recent decades, indicating a decline of at least 50% in commercial stocks of this species (Carvalho-Filho, Santos, & Sampaio, 2010). Similarly, local artisanal fishers have reported a severe decline in catches of M. fumieri and M. liza (Martins, Medeiros, Di Domenico, & Hanazaki, 2018). Thus, changes in abundance of these prey sources—whether due to environmental effects or unsustainable fishing pressure—has the potential to impact resource and habitat use among these sympatric dolphin species and should be closely monitored. If food resources become limited, interspecific competition among these three sympatric species will increase, which may have a variety of ecological implications. For example, both inter- and intraspecific competition influence both the total niche width and prevalence of individual specialization (Araújo et al., 2010). Therefore, future studies on within and between individual diet variation could strengthen our understanding of how these three species coexist and are impacts by future changes in resource availability. By providing both population- and individual-level estimates of dietary niche, isotope analysis could be an effective tool to better understand franciscana, Guiana, and Lahille’s bottlenose dolphin population dynamics and contribute with species management and conservation plans.

ACKNOWLEDGMENTS
We sincerely thank Dr. Jorge Luiz Rodrigues Filho (Universidade Estadual de Santa Catarina - UDESC), the fisherman Elias and his wife Susy Andrade for providing samples of potential prey. We would also like to thank M.Sc. Gisela Costa Ribeiro (Núcleo de Estudos do Mar – Universidade Federal de Santa Catarina) for identifying the fish species. This research was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Cetacean Society International (CSI).

AUTHOR CONTRIBUTIONS
Clarissa Teixeira: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; software; supervision; validation; visualization; writing-original draft; writing-review and editing. Silvina Botta: Data curation; formal analysis; funding acquisition; methodology; resources; software; supervision; validation; visualization; writing-original draft; writing-review and editing. Fabio Daura-Jorge:
Conceptualization; data curation; formal analysis; funding acquisition; investigation; project administration; resources; software; supervision; validation; visualization; writing-original draft; writing-review and editing. **Luiza Pereira**: Conceptualization; formal analysis; investigation; visualization; writing-original draft; writing-review and editing. **Seth Newsome**: Data curation; formal analysis; funding acquisition; investigation; methodology; validation; visualization; writing-original draft; writing-review and editing. **P. C. Simoes Lopes**: Conceptualization; funding acquisition; investigation; project administration; resources; supervision; validation; visualization; writing-original draft; writing-review and editing.

**DATA AVAILABILITY STATEMENT**

The data that support the findings of this study are available from the corresponding author upon request.

**ORCID**

Clarissa R. Teixeira 🐦 https://orcid.org/0000-0002-6922-8877
Silvina Botta 🐦 https://orcid.org/0000-0001-6219-6932
Fábio G. Daura-Jorge 🐦 https://orcid.org/0000-0003-2923-1446
Paulo C. Simões-Lopes 🐦 https://orcid.org/0000-0002-7338-3669

**REFERENCES**


Cremer, M. J., Pinheiro, P. C., & Simões-Lopes, P. C. (2012). Presas consumidas pelo boto-cinza *Sotalia guianensis* (Cetacea, Delphinidae) e pela toninha *Pontoporia blainvillii* (Cetacea, Pontoporiidae) em ambiente estuarino no sul do Brasil [Prey consumed by the gray dolphin *Sotalia guianensis* (Cetacea, Delphinidae) and the porpoise *Pontoporia blainvillii* (Cetacea, Pontoporiidae) in an estuarine environment in southern Brazil]. *Iheringia Série Zoologia*, 102, 131–137.


SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.