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POPULATION ECOLOGY – ORIGINAL RESEARCH

Ecologically driven differences in individual diet specialization across three populations of Guiana dolphin

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Abstract

Populations usually considered foraging generalists may include specialized individuals that feed on a restricted subset of the prey spectrum consumed by the population. By analyzing the time series of δ^{13}C and δ^{15}N values in sequential growth layer groups within tooth dentin, we measured population- and individual-level variation in resource use of three populations of Guiana dolphins (*Sotalia guianensis*)—Caravelas River, Babitonga Bay, and Norte Bay—along a latitudinal gradient in the southwestern Atlantic Ocean. We show that the Guiana dolphin at Caravelas River is a generalist population consisting of individual dietary specialists, likely due to the absence of other resident dolphin populations thus allowing individuals to target prey across a wide range of habitats. The Babitonga Bay population is also composed of individual specialists potentially due to the selective foraging behavior of some individuals on high-quality prey sources within and near the bay. In contrast, the Norte Bay population comprises individual generalists, which likely reflects its distinctive cohesive social organization, coexistence with two other dolphin species, and an opportunistic foraging strategy in response to resource fluctuations inherent to the southern limit of the species distribution. Although the Guiana dolphin is generally considered to be a dietary generalist at the population level, our findings reveal that the total niche width of populations and the degree of individual diet specialization are highly context dependent, suggesting dietary plasticity that may be related to a latitudinal gradient in resource availability and environmental conditions.

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Fabio Daura Jorge and Paulo C Simoes Lopes both co-authors contributed equally to the paper.

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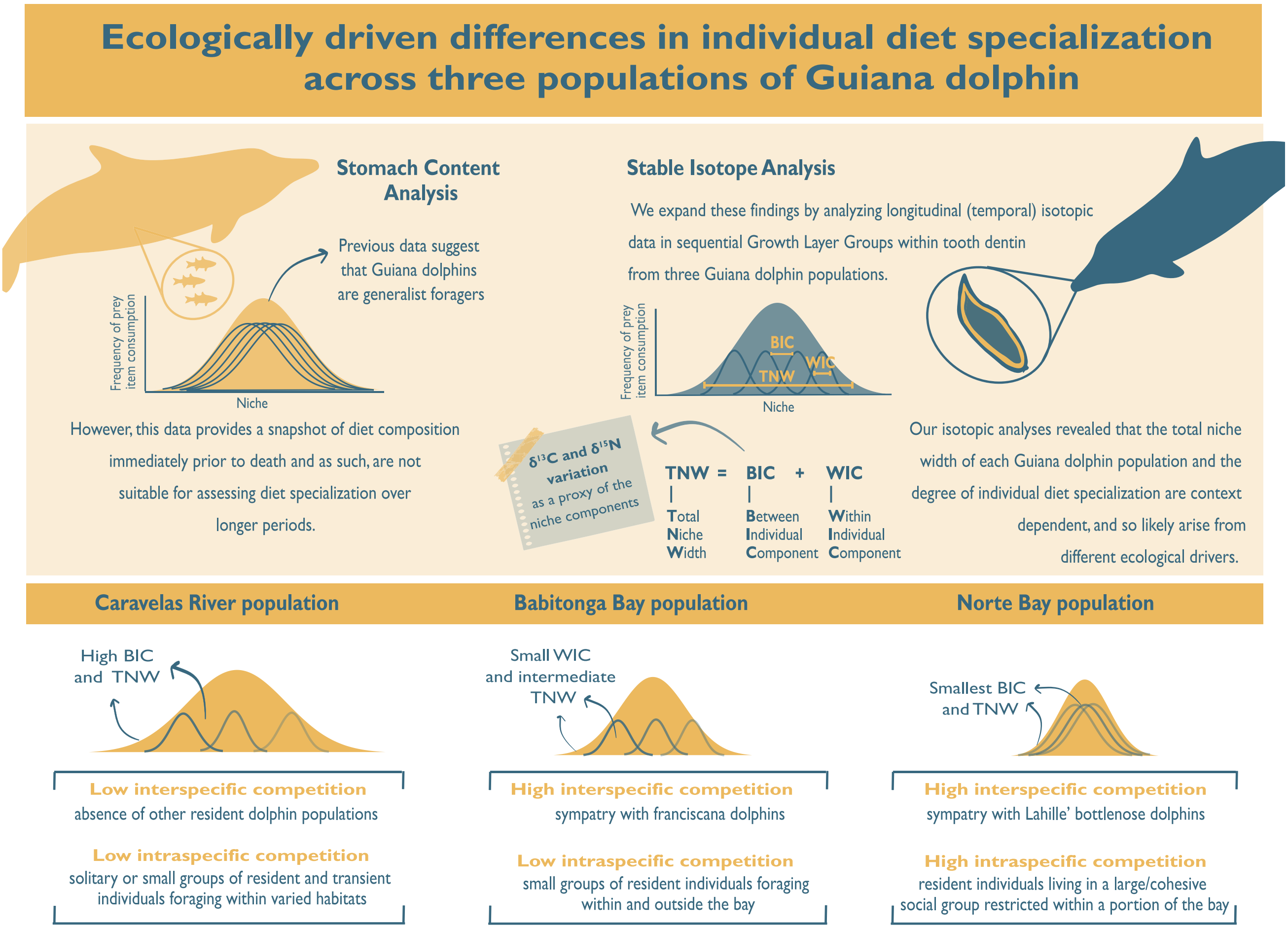
Graphical abstract



Ecologically driven differences in individual diet specialization across three populations of Guiana dolphin

Stomach Content Analysis

Previous data suggest that Guiana dolphins are generalist foragers

However, this data provides a snapshot of diet composition immediately prior to death and as such, are not suitable for assessing diet specialization over longer periods.

Stable Isotope Analysis

We expand these findings by analyzing longitudinal (temporal) isotopic data in sequential Growth Layer Groups within tooth dentin from three Guiana dolphin populations.

$\delta^{13}C$ and $\delta^{15}N$ variation as a proxy of the niche components

TNW = BIC + WIC

Total Niche Width

Between Individual Component

Within Individual Component

Our isotopic analyses revealed that the total niche width of each Guiana dolphin population and the degree of individual diet specialization are context dependent, and so likely arise from different ecological drivers.

Caravelas River population

High BIC and TNW

Low interspecific competition
absence of other resident dolphin populations

Low intraspecific competition
solitary or small groups of resident and transient individuals foraging within varied habitats

Babitonga Bay population

Small WIC and intermediate TNW

High interspecific competition
sympatry with franciscana dolphins

Low intraspecific competition
small groups of resident individuals foraging within and outside the bay

Norte Bay population

Smallest BIC and TNW

High interspecific competition
sympatry with Lahille' bottlenose dolphins

High intraspecific competition
resident individuals living in a large/cohesive social group restricted within a portion of the bay

Keywords Niche width · Intraspecific variation · Stable isotopes · Foraging ecology · Competition

Introduction

Natural populations can be composed of ecologically heterogeneous individuals that vary in their foraging strategies and feed on different prey types (Bolnick et al. 2002; Bearhop et al. 2004). Such variation in resource use among co-occurring individuals has long been recognized between sexes (Elorriaga-Verplancken et al. 2013), age or ontogenetic stage (Polis 1984), and discrete polymorphisms (Skúlason and Smith 1995). However, individual diet specialization is a widespread phenomenon in which organisms have narrower dietary niches than their population's irrespective of age, sex, or morphology (Bolnick et al. 2003) and instead results from predation, intra- versus inter-specific competition, and/or ecological opportunity (resource diversity and/or abundance). As these ecological drivers can vary along environmental gradients, the degree of individual diet specialization across populations of the same species likely reflects contrasting biotic interactions and abiotic conditions.

Marine mammals have often been the focus of studies examining the ecological drivers of individual diet specialization. For example, the prevalence of individual diet specialization in sea otters (*Enhydra lutris*) varies in response to intraspecific competition (Estes et al. 2003; Tinker et al. 2008) and habitat type (Newsome et al. 2015). Population total niche width (TNW) and degree of individual diet specialization vary among ringed seal (*Pusa hispida*) and beluga (*Delphinapterus leucas*) populations across an Arctic latitudinal gradient likely in response to spatial variation in ecological opportunity (Yurkowski et al. 2016). Antarctic (*Arctocephalus gazella*) and sub-Antarctic fur seals (*Arctocephalus tropicalis*) have greater TNW when in allopatry than in sympatry (Kernaléguen et al. 2015). These patterns are potentially related to the niche variation hypothesis, which predicts that a release from or reduction in interspecific competition results in an expansion of population TNW that permit greater phenotypic variation in diet composition at the individual level (Van Valen 1965). Subsequent theoretical work suggests that population TNW can expand in two ways (Roughgarden 1972): *(i)* via minimization in resource use overlap among conspecifics that reduces the within-individual component (WIC) of the niche relative to TNW; or *(ii)* via an expansion of the WIC such that most individuals become more generalists and use the full spectrum of available resources. By constraining population TNW, interspecific competition forces conspecifics to forage on similar prey types, which dampens the degree of individual diet specialization (Bolnick et al. 2003).

Optimal foraging theory predicts that when resources are abundant, individuals will select prey based on their energetic benefits relative to handling time costs. As preferred prey become scarce, individuals may become more opportunistic and explore less profitable prey (MacArthur and Pianka 1966; Schoener 1971) or use specialized foraging tactics to outcompete conspecifics for a particular prey type. Foraging specialization is well-established for marine mammals, such as sea otters that learned to forage on a limited set of invertebrate species (Estes et al. 2003; Tinker et al. 2008) or killer whales (*Orcinus orca*) that specialize on salmonids or marine mammals (Ford and Ellis 2006). The learning process of specialized foraging tactics may require cognitive abilities and motor skills that can vary between conspecifics, widening the population TNW and increasing individual diet specialization (Stephens and Krebs 1986; Bolnick et al. 2010). Thus, ecological factors that regulate intra-and interspecific competition such as ecological opportunity, population density, social organization, and habitat use can lead to dietary variation between conspecifics that influences the total niche width of a population (Krause et al. 2002; Estes et al. 2003; Newsome et al. 2015; Sheppard et al. 2018).

The Guiana dolphin, *Sotalia guianensis*, provides a good model to evaluate the relationship between ecological factors (e.g., competition and resource availability) and individual diet specialization. This species is distributed along a latitudinal gradient in coastal waters of the southwestern Atlantic Ocean (Borobia et al. 1991) in populations of mostly resident individuals (e.g., Flores and Bazzalo 2004; Hardt et al. 2010; Cantor et al. 2012; Cremer et al. 2018). At tropical latitudes, the Guiana dolphin is the only cetacean that inhabits the coastal waters of the Caravelas River (Rossi-Santos et al. 2006). In contrast, Guiana dolphin populations that occur in subtropical latitudes are usually sympatric with other dolphin species. For example, Guiana dolphins coexist with the franciscana dolphin (*Pontoporia blainvillei*) in Babitonga Bay (Cremer et al. 2018), while they are sympatric with both franciscana and Lahille's bottlenose dolphins (*Tursiops truncatus gephyreus*) in Norte Bay (Flores and Bazzalo 2004). These differences in patterns of coexistence with other dolphin species change the potential for inter and intra-competition, which likely influences the TNW and the degree of individual diet specialization of Guiana dolphin populations across their range.

Data derived from stomach content analysis revealed that these three Guiana dolphin populations are opportunistic and generalist foragers at the population level, with a diet primarily consisting of demersal fish and cephalopods (Daura-Jorge et al. 2011; Cremer et al. 2012; Rodrigues et al. 2020). Some studies have also explored trophic interactions between Guiana dolphins and other sympatric dolphin populations in Norte Bay and Babitonga Bay using stable isotope analysis, showing some trophic overlap with the Lahille’s bottlenose (Teixeira et al. 2021) and franciscana dolphins (Hardt et al. 2013), respectively. However, no study to date has evaluated individual diet specialization within or across Guiana dolphin populations, likely because longitudinal foraging records required to quantify this information are particularly challenging to obtain for large mobile predators living in marine ecosystems.

Stable isotope analysis can reconstruct foraging and movement patterns at the individual level and has been especially useful for studying mobile and elusive animals like marine mammals (e.g. Rossman et al. 2015; Yurkowski et al. 2016). In general, variation in carbon isotope (δ^{13}C) values among marine consumers reflect the sources of primary production (e.g. phytoplankton vs macroalgae vs seagrass) that fuel the habitats where consumers forage (e.g. inshore versus offshore vs estuarine), whereas nitrogen isotope (δ^{15}N) values are commonly used as proxies for consumer trophic position (DeNiro and Epstein 1978, 1981; Newsome et al. 2010). Furthermore, the isotopic composition of metabolically inert but continuously growing tissues such as baleen plates, tooth dentin, or vibrissae provides a sequential archive of ecological information over different timescales (Walker and Macko 1999). Isotopic variation can be used as a proxy of TNW, which is the sum of the within- (WIC) and between-individual (BIC) components of the niche (e.g. Newsome et al. 2009; Yurkowski et al. 2016). When other confounding factors that influence consumer isotope values can be constrained, such as movement across baseline isotopic gradients (Graham et al. 2010; Troina et al. 2020), this approach can be used to evaluate the relative prevalence of specialist versus generalist foraging strategies at the individual level (Newsome et al. 2009, 2015; Vander Zanden et al. 2013).

Here we generated a δ^{13}C and δ^{15}N dataset from serially sampled teeth to quantify individual- and population-level niche components of three Guiana dolphin populations with different behavioral traits (i.e. social organization, home range, and spatial overlap) that live in contrasting ecological contexts (i.e. sympatry with other dolphin species, and habitat use). Based on well-established theory, we hypothesized that these ecological conditions will predictably influence the population TNW and degree of individual diet

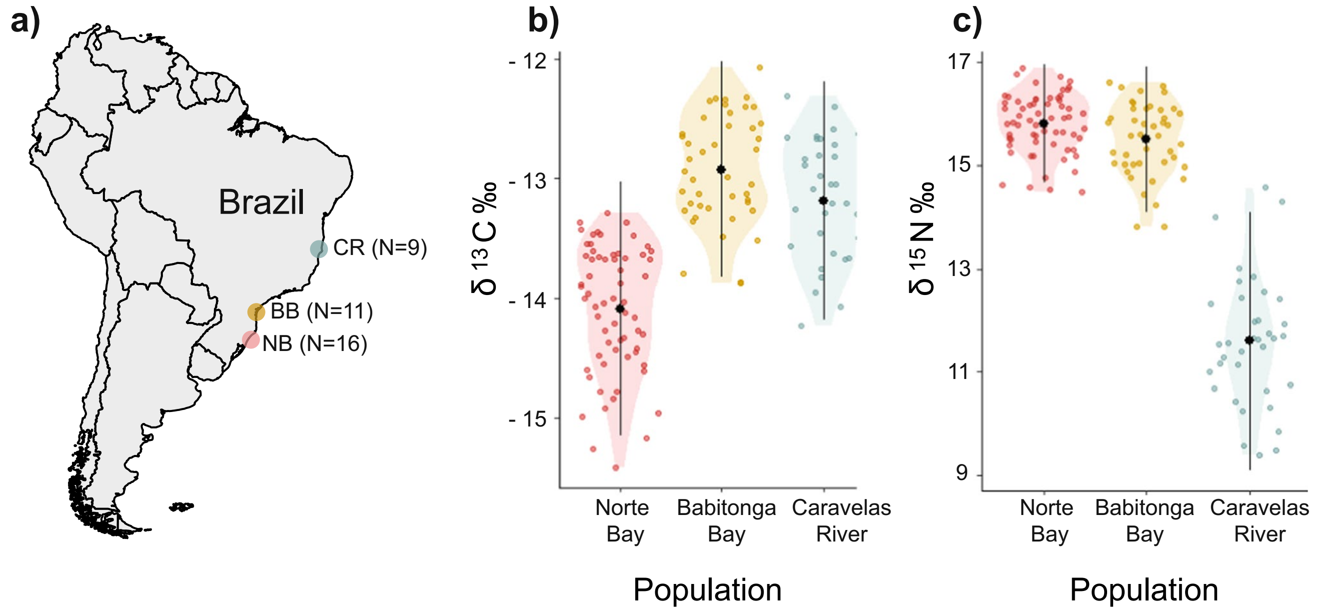


Fig. 1 **a** Location of the Guiana dolphin populations from Norte Bay (NB, 27°30′S, 48°32′W; red circles), Babitonga (BB, 26°28′S, 48°50′W; yellow circles) and Caravelas River (CR, 17°30′S, 39°30′W; green circles) along the Brazilian coast and the total of individuals sampled in each population; **b** Violin plots of tooth dentin Growth Layer Groups δ^{13}C and **c** δ^{15}N values for each population. Black circles are population mean δ^{13}C and δ^{15}N values and error bars indicate standard deviation

specialization among the three Guiana dolphin populations. Our predictions for each of the three populations are that: *(i)* In Caravelas River, the absence of interspecific competition with other dolphin species enables Guiana dolphins to maintain a large TNW, which increases the opportunity for individual diet specialization; *(ii)* In Babitonga Bay, the direct sympatry with franciscana dolphins and the high overlap of core areas and home range increases interspecific competition to produce a relatively narrow TNW with dietary generalists; and *(iii)* In Norte Bay, the sympatry of the Guiana dolphin population with two other dolphin species (franciscana and Lahille's bottlenose dolphin), combined with a distinctive aggregation in a large and stable social group within a small home range, results in a narrow TNW and a population of dietary generalists.

Material and methods

Sampling sites and collection

Teeth were collected from 36 carcasses of Guiana dolphin specimens stranded at three localities: Caravelas River estuary ($n = 9$ specimens) on the northeast coast of Brazil, as well as Babitonga ($n = 11$) and Norte Bay ($n = 16$) along the southern coast (Fig. 1a). The specimens are archived in the scientific collections of the Instituto Baleia Jubarte (IBJ), the Acervo Biológico Iperoba (ABI) at the Universidade da Região de Joinville (UNIVILLE), and the Aquatic Mammals Laboratory (LAMAQ) at the Universidade Federal de Santa Catarina (UFSC), Brazil.

The Caravelas River (17°30′S, 39°30′W) estuary is adjacent to the Abrolhos Bank, an extension of the continental shelf influenced by a large estuarine-mangrove complex (Herz 1991). The estuary system has the second largest mangrove forest along the northeast coast of Brazil with an area of ~ 66 km^2 (Herz 1991) and is characterized by a diverse suite of habitats including coral reefs and seagrass beds (Rossi-Santos et al. 2007). The Guiana dolphin population from this site is composed of ~ 57–124 resident and transient individuals (Rossi-Santos et al. 2007, Cantor et al. 2012) organized in solitary and small groups of ~ 6 individuals that are known to use all these habitats (Rossi-Santos et al. 2006). Babitonga Bay (26°28′S, 48°50′W) is one of the largest estuarine complexes in southern Brazil encompassing 160 km^2 (IBAMA 1998) and characterized by small islands, mangroves, rocky shores, and beaches. The local Guiana dolphin population is estimated at ~ 208 individuals (Cremer et al. 2011) organized in small groups of 5–6 individuals that primarily use the innermost area of the bay (Cremer et al. 2011, 2018) but also occur in adjacent waters. Norte Bay (27°30'S, 48°32'W) is located between Santa Catarina Island and the mainland and comprises a protected area of ~ 250 km^2 characterized by rocky shores, sandy beaches, and mangrove forests with oceanographic features influenced by the adjacent open ocean

(Cerutti 1996). The Guiana dolphin population in Norte Bay is estimated at ~ 130 individuals (L. Wedekin, unpublished data) characterized by a single large and cohesive group restricted to the western area of the bay (Flores and Bazzalo 2004).

Sample preparation and isotope analysis

For 29 out of the 36 specimens, more than one tooth was available, which were used to estimate age based on counting Growth Layer Groups (GLGs; Perrin and Myrick 1980) in dentine to guide the micromilling process for the collection of subsamples for stable isotope analysis. We cut each tooth into a 3 mm longitudinal mid-section using a Buehler IsoMet® saw with a diamond-embedded blade. We then fixed this thick section in 10% formalin for ~ 12 h, rinsed the section with deionized water and decalcified it in a rapid decalcifier solution (RDO®, Apex Engineering Products Corporation, Aurora, IL) for 7–17 h; hydrochloric acid is the active component of RDO®. The time interval required for decalcification varied with the age of the individuals, with shorter times for younger individuals. Once the teeth were flexible and transparent, they were washed with running water and then cut into 25 µm thin sections using a freezing microtome. We stained the sections in Mayer's hematoxylin, submerged them in an ammonia solution for a few seconds to intensify the coloration, and mounted on microscope slides with 100% glycerin (Hohn et al. 1989). Using a microscope, we took photomicrographs of each slide at 40–100 × magnification and GLGs were counted in the dentin by three observers without reference to biological data to avoid any possible bias in age estimates. To properly characterize within the individual component (WIC) of niche width, one must generate a longitudinal record of ecological (dietary) information. As older individuals have larger teeth containing more GLGs, we restrict our samples to adults males ≥ 6 years and/or with a body length greater than or equal to 170 cm, and females ≥ 5 years and/or with a body length greater than or equal to 164 cm (Ramos et al. 2000; Rosas et al. 2003). By focusing on older individuals, we also constrained possible ontogenetic effects including the ^{15}N-enrichment during the nursing period (Niño-Torres et al. 2006).

To prepare teeth for stable isotope analyses, we used a water-cooled diamond-blade saw to cut teeth in two mid-longitudinal sections. To accentuate the definition of GLGs, we polished the longitudinal sections with successive sheets of sandpaper with decreasing grit sizes (340, 500, 600, 1200 and 12,000). The inner surface of each tooth was immersed in 25% formic acid for 1.0–1.5 h, rinsed with deionized water and then air-dried for 24 h (Newsome et al. 2006). Such treatment does not influence the tooth's isotopic composition because the surface portion of the tooth represents only a small fraction of the total sample.

We mounted the polished tooth on a glass slide and subsampled ~ 1 mg of bulk dentin using a computer-guided micromill (Merchantek®) fitted with a 300 µm-diameter carbide drill bit at a depth of 250 µm. We milled five tracks from each tooth and due to the small size of Guiana dolphin teeth, sampling tracks reflecting older stages of an individual's life closer to the pulp cavity contained more GLGs (mean = 5 GLGs per track) than tracks near the neonatal line representing the youngest years (mean = 2 GLGs per track). Despite the high precision provided by the micromill system, some factors such as the tooth size, and the conical arrangement of the dentin layers in Guiana dolphins constrain the collection of enough powder from each GLG for isotope analysis. Several studies have shown that decalcification may not be necessary when measuring bulk dentin stable isotope values in teeth of modern odontocetes likely due to the low concentration of lipids and carbonates, and the similarity in δ^{13}C values of dentin collagen and carbonate (Brault et al. 2014; Matthew and Ferguson 2014; Groom 2018). Therefore, we chose to avoid sample loss associated with decalcification.

We collected a total of 180 powdered dentin subsamples (Caravelas River = 45; Babitonga Bay = 55; Norte Bay = 80), which were placed directly into tin capsules for carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope analysis. We measured δ^{13}C and δ^{15}N values of these subsamples using a Costech 4010 Elemental Analyzer (Valencia, CA, USA) 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] * 1000, where Rsample and Rstandard are the ^{13}C/^{12}C or ^{15}N/^{14}N ratios of the sample and standard, respectively (Peterson and Fry 1987). The standards are Vienna Pee Dee Belemnite limestone (VPDB) for δ^{13}C and atmospheric N_2 for δ^{15}N. The analytical precision based on the standard deviation of the standard laboratory replicas (Acetanilide) was ≤ 0.1‰ for both δ^{13}C and δ^{15}N. To ensure that our samples did not contain any ^{13}C-depleted lipids, we also measured the C:N ratio of each sub-sample. Values ranged from 2.8 to 3.6, well within the expected range that characterizes pure protein (Ambrose 1990).

Data analysis

As our samples were restricted to the last two decades, we did not apply a Suess correction. We also excluded the δ^{13}C and δ^{15}N values of the first GLG of each tooth from the analysis as they may reflect milk consumption during the nursing period (Niño-Torres et al. 2006; Rosas et al. 2010).

We first assessed variation in GLG $\delta^{13}C$ and $\delta^{15}N$ values among Guiana dolphin populations with a Gaussian generalized linear mixed model (GLMM) with a log link function that included sex as a covariate and individual as a random effect. Given that our data exploration suggested a lack of interaction between sex and population, we did not include interactive terms between these two factors to avoid overparameterization of the models. The model selection procedure was based on Akaike's information criterion (AIC) and Akaike weight (Burnham and Anderson 2002) using the R package 'MuMIn' (Bartoń 2019). We checked for scaled residuals using the DHARMa package (Hartig 2018). The threshold for significance in all statistical tests was 95% ($p < 0.05$).

We measured the degree of individual diet specialization within each population following Roughgarden`s (1979) framework adapted by Bolnick et al. (2003), which partitioned the total niche width of a population into two components: the within-individual component (WIC) that reflects the average of individual niche widths, and the between-individual component (BIC) that represents the variance among each individuals' niche. We estimated TNW as the variance of $\delta^{13}C$ and $\delta^{15}N$ values of all individuals that comprise the population, BIC as the total standard deviation in $\delta^{13}C$ and $\delta^{15}N$ values of sampled individuals (Bolnick et al. 2003), and WIC as the mean standard deviation in $\delta^{13}C$ and $\delta^{15}N$ values obtained along the longitudinal growth layers within individuals. Therefore, we used (1) the mean variability within individuals (WIC) as a measure of temporal consistency, which reflects how variable individuals are in their resource use through time, and (2) the degree of individual specialization (WIC/TNW) as the percent of within-individual component (WIC) of total niche width (TNW). Low WIC/TNW ratios (close to zero) indicate a higher degree of individual diet specialization (IS) and high values (close to 1) indicate a lower prevalence of individual specialization (Bolnick et al. 2003). We calculated TNW, WIC, BIC, and IS values using the R package 'RInSp' (Zaccarelli et al. 2013). We ran Monte Carlo permutations to test whether observed IS values differed significantly from a random distribution of values calculated for 10,000 replicate datasets. When the observed values were lower than the 95% confidence interval (CI) of the random distribution, they validated the null hypothesis that all individuals are generalists (Bolnick et al. 2002).

Results

We found no influence of sex on mean tooth GLG $\delta^{13}C$ (estimate = − 0.00463, se: 0.01065, z-value: − 0.43, $p < 0.664$; Model 1; Table 1) and $\delta^{15}N$ values (estimate = -− 0.02696, se: 0.01780, z-value: − 1.51, $p < 0.130$; Model 1; Table 1). The GLMMs showed significantly lower $\delta^{13}C$ values in Norte Bay compared to Caravelas River (estimate = 0.08628, se: 0.01194, z-value: 7.22, $p < 0.001$; Model 3; Table 1) and Babitonga Bay (estimate = 0.06643, se: 0.01269, z-value: 5.24, $p < 0.001$; Model 3; Table 1), whereas $\delta^{15}N$ values are

Table 1 Generalized linear mixed models (GLMMs) ranked by the lowest Akaike Information Criterion (AICc). Relative support for the models is assessed by the difference in delta AIC and AIC weights, while the model's goodness of fit is given by log-likelihood (logLink); df denotes degrees of freedom

GLMMs		*df*	logLink	AICc	delta AIC	AIC weight
$\delta^{13}C$						
Model 3	$\delta^{13}C \sim population + (1\|ID)$	5	− 71.09	152.6	0.00	0.73
Model 1	$\delta^{13}C \sim population + sex + (1\|ID)$	6	− 71.00	154.6	1.99	0.27
Model 2	$\delta^{13}C \sim sex + (1\|ID)$	4	− 87.45	183.2	30.58	0.00
$\delta^{15}N$						
Model 1	$\delta^{15}N \sim population + sex + (1\|ID)$	6	− 146.40	305.4	0.00	0.51
Model 3	$\delta^{15}N \sim population + (1\|ID)$	5	− 147.51	305.5	0.05	0.49
Model 2	$\delta^{15}N \sim sex + (1\|ID)$	4	− 182.34	373.0	67.56	0.00

Table 2 Within individual component (WIC), between individual component (BIC), total isotopic niche width (TNW) and individual specialization index (IS) for $\delta^{13}C$ and $\delta^{15}N$ values of Guiana dolphin populations from the Norte Bay, Babitonga Bay and Caravelas River. Estimated population size; number of individuals sampled in each population and the total number of sampling tracks (subsamples) obtained from each population are reported

Population	Population size	Individuals sampled	Total sampling tracks	WIC		BIC		TNW		IS	
				$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Norte Bay	~ 130	16	80	0.072	0.223	0.204	0.098	0.276	0.321	0.261	0.693
Babitonga Bay	~ 208	11	55	0.069	0.100	0.128	0.384	0.198	0.485	0.349	0.207
Caravelas River	~ 57–124	9	45	0.076	0.254	0.162	1.266	0.239	1.521	0.320	0.167

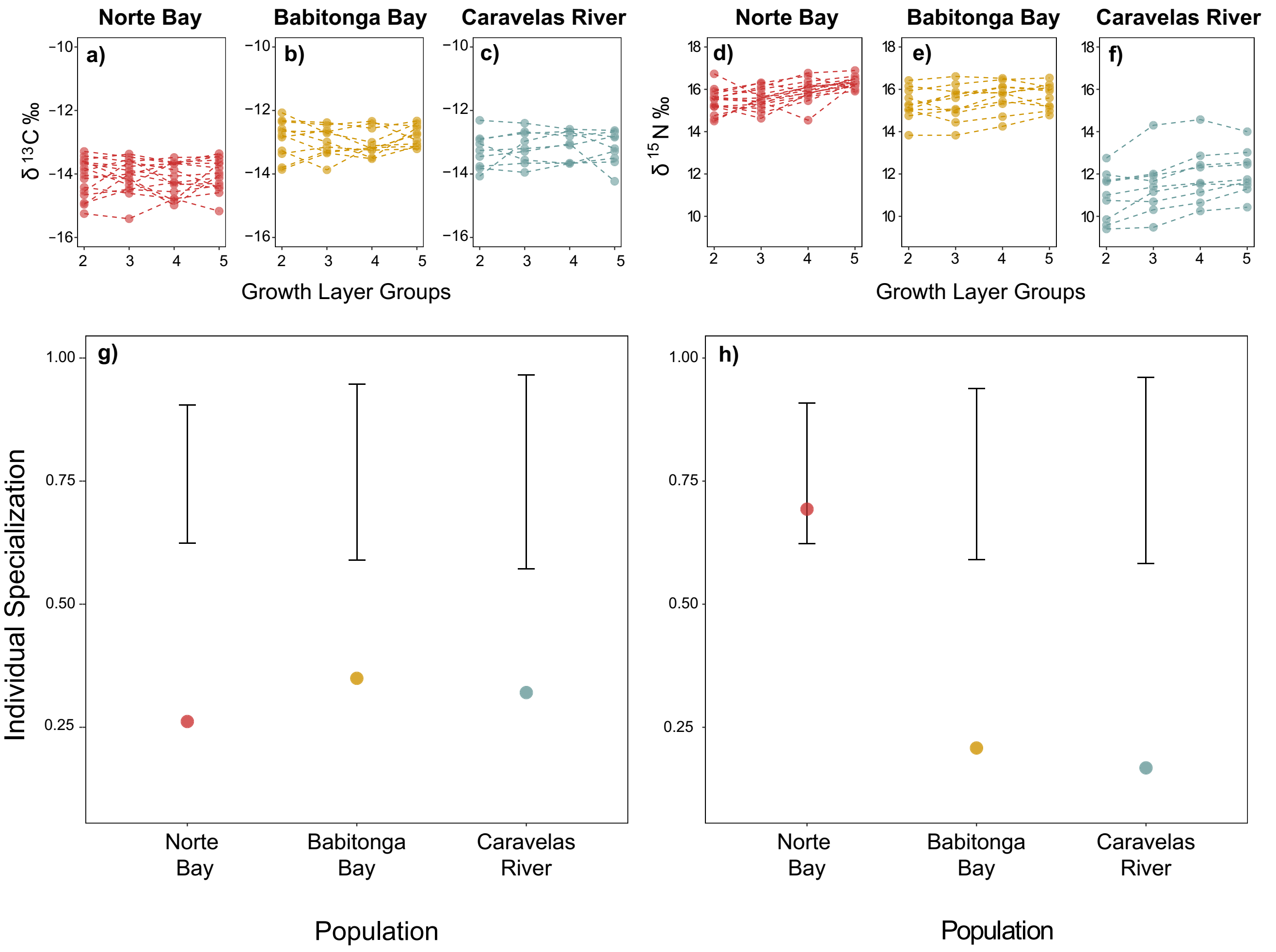


Fig. 2 δ^{13}C (**a–c**) and δ^{15}N (**d–f**) values in sequential growth layer groups within tooth dentin of Guiana dolphin individuals from Norte Bay (NB; $n = 16$), Babitonga Bay (BB; $n = 11$), and Caravelas River (CR; $n = 9$); each parallel line covers the lifetime of each sampled individual. Degree of individual diet specialization (IS) for **g** δ^{13}C and **h** δ^{15}N values of Guiana dolphin populations from NB, BB, and CR. IS values range from 0 (all individuals are specialists) to 1 (all individuals are generalists), and error bars indicate a null model depicted as the 95% confidence interval generated from a random distribution of IS values calculated for 10,000 replicate datasets

significantly higher in Babitonga (estimate = 0.29420, se: 0.02320, z-value: 12.68, $p < 0.001$; Model 1; Table 1) and Norte Bay (estimate = 0.30631, se: 0.02190, z-value: 13.99, $p < 0.001$; Model 1; Table 1) compared to Caravelas River population. δ^{13}C values ranged from − 15.4 to − 13.3‰ (mean ± *SD*: − 14.0 ± 0.5‰) for the Norte Bay population; from − 14.2 to − 12.3‰ (mean ± *SD*: − 13.1 ± 0.4‰) for the Caravelas River population, and from − 13.8 to − 12.0‰ (mean ± *SD*: − 12.9 ± 0.4‰) for the Babitonga Bay population (Fig. 1b). δ^{15}N values ranged from 9.4 to 14.5‰ (mean ± *SD*: 11.6 ± 1.2‰) for the Caravelas River population, from 13.8 to 16.6‰ (mean ± *SD*: 15.5 ± 0.7‰) for the Babitonga Bay population, and from 14.5 to 16.9‰ for the Norte Bay population (mean ± *SD*: 15.8 ± 0.5‰) (Fig. 1c).

The WIC, BIC, TNW, and individual diet specialization index for δ^{13}C values were similar among all Guiana dolphin populations. For δ^{15}N, WIC was higher for the Caravelas River and Norte Bay populations, while BIC and TNW were higher for the Caravelas River population (Table 2, Fig. 2). The Monte Carlo resampling procedure we used to evaluate the individual diet specialization relative to a null model (population of generalist individuals) revealed a lower prevalence of individual specialization than expected by chance for δ^{13}C values from all populations (Fig. 2a–c, g) and for δ^{15}N values for the Caravelas River and Babitonga Bay ($p < 0.01$) (Fig. 2d–f, h). The lack of significance ($p = 0.18$) for individual specialization at Norte Bay relative to the null model suggests that this population is comprised of more generalist individuals whereas the Caravelas River and Babitonga Bay populations are comprised of more individual dietary specialists.

Discussion

There is a longitudinal trend in marine environments where benthic nearshore habitats are more ^{13}C enriched in comparison to pelagic and offshore habitats (Clementz and Koch 2001; Lesage et al. 2001; Rossman et al. 2016). The overlap in δ^{13}C values among the three Guiana dolphin populations suggests they use habitats fueled by similar source(s) of primary production. Thus, our discussion is focused on patterns in δ^{15}N niche metrics that differed among populations indicating individual-level variability in prey consumption and varying degrees of individual dietary specialization. These results indicate that although the Guiana dolphin is typically considered to be an opportunistic dietary generalist (Daura-Jorge et al. 2011; Cremer et al. 2012; Rodrigues et al. 2020), variation in the diet at the individual level may arise from distinct ecological contexts.

A diverse set of oceanographic and ecological factors that vary along a tropical to subtropical gradient likely influences the observed variation in δ^{15}N niche metrics among the three populations. For example, Babitonga Bay and Norte Bay are highly productive areas due to the confluence of the northward flow of cold nutrient-rich waters of the Malvinas Current and the southward flow of oligotrophic tropical waters of the Brazil Current (Ciotti et al. 1995), with additional nutrient inputs from the La Plata River and Patos Lagoon estuaries (Carreto et al. 1986; Muelbert et al. 2008). The freshwater discharged by the La Plata River induces a large-scale buoyant plume (i.e. the Plata Plume Waters; Piola et al. 2008) that fertilizes the southern Brazilian shelf area and fuels one of the most productive fisheries in Brazil (Moreira da Silva 1971; Castello et al. 1990). Although the Caravelas River is surrounded by productive ecosystems (i.e. coral reefs and mangrove forests) and its physiography provides an area for phytoplankton production (Travassos et al. 2006), it is also primarily influenced by warm nutrient-poor waters of tropical Brazil Current that limit biological productivity (Ekau 1999) when compared to Norte Bay and Babitonga Bay. The Caravelas River Guiana dolphin population has the broadest TNW for δ^{15}N, largest between-individual component of a diet, and the highest degree of individual diet specialization (lowest WIC/TNW) compared to the other populations. These niche metrics suggest a generalist population comprised of individual dietary specialists and support the niche variation hypothesis (Van Valen 1965), in which the release from interspecific competition with other dolphin species promotes niche expansion via greater inter-individual variation. Another factor that likely contributed to this relatively large TNW is that even though individuals use a smaller area (~66 km^2; Herz 1991) in comparison to Babitonga Bay (~160 km^2; IBAMA 1998) and Norte Bay (~250 km^2; Cerutti 1996), this small population (~57–124 individuals) is composed of a mixture of resident and transient individuals (Rossi-Santos et al. 2007; Cantor et al. 2012) that forage in solitude or in small groups (Rossi-Santos et al. 2010) in a diverse set of habitats in the river and adjacent coastal waters (Rossi-Santos et al. 2007).

Previous studies based on stomach content analysis and stable isotope analysis showed some degree of overlap in the diet of the two dolphin species that occupy Babitonga Bay, with 13 shared prey species that represents 62% and 46% of the total prey spectrum consumed by franciscanas and Guiana dolphins, respectively (Cremer et al. 2011; Paitach 2015). Babitonga Bay is an estuary with high productivity (IBAMA 1998; Schettini et al. 2002; Brandini et al. 2006; Costa and Souza-Conceição, 2009; Gerhardinger et al. 2020), and the adjacent coastal area is situated in productive subtropical waters (Cioti et al. 1995; Muelbert et al. 2008). However, some areas of its surroundings are densely populated and have great industrial activity, resulting in water pollution, intense boat traffic, and illegal modification of mangrove habitats. Along with this, the bay has two large port areas, both close to the access channel. These factors influence the distribution of prey and the distribution of franciscana and Guiana dolphins' populations, causing both to have their main concentration area in the central portion of the bay (Cremer and Simões-Lopes 2005; Cremer et al. 2011; Cremer et al. 2018). The strong interspecific competition with the franciscanas may be the reason why the Babitonga Bay Guiana dolphin population has a much lower TNW (0.485) in comparison to Caravelas River (1.521) where Guiana dolphins occur in allopatry. Despite the relatively low TNW, the Guiana dolphin population at Babitonga Bay has a similar degree of individual diet specialization (Table 2) compared to the Caravelas River, because the former population has the lowest estimate of WIC of all the populations examined. A possible explanation for this pattern is that some individuals of the Babitonga Bay Guiana dolphin population selectively forage on the prey of high nutritional quality (*Mugil curema* and *Micropogonias furnieri*) that occur in low abundance within and near the bay (Cremer 2012). In the Cananeia Estuary, for example, females accompanied by calves specialize in a hunting technique to capture mullet species on sloping beaches. Using specialized skills to hunt in littoral habitats likely decreases the amount of energy required to capture prey while enabling them to closely monitor their young in shallow areas (Santos 2010).

The lowest levels of TNW, BIC, and degree of individual diet specialization were observed in the Norte Bay Guiana dolphin population, which can be explained by a series of fine-scale ecological factors. While this population inhabits productive subtropical waters, it is also restricted to the western margin of the bay (Flores and Fontoura 2006; Wedekin et al. 2007) and does not use the most productive eastern areas adjacent to mangrove and estuarine habitats (Wedekin et al. 2007). According to the optimal foraging theory (MacArthur and Pianka 1966), this limited home range may impose limits on their foraging strategies, forcing individuals to behave more opportunistically in response to seasonal fluctuations in resource availability. One likely explanation for the limited home range of Guiana dolphins in Norte Bay is the presence of Lahille`s bottlenose dolphins, which is believed to contribute to the distinctive social organization of the former species characterized by a single large, stable, and cohesive social group (Flores and Bazzalo 2004). Aggressive behaviors of this larger species (lengths of 316.5 cm for females and 351.6 cm for male bottlenose dolphins compared to 164 cm for females and 170 cm for male Guiana dolphins; Ramos et al. 2000, Rosas et al. 2003, Venuto et al. 2020) towards Guiana dolphins were previously reported in Norte Bay (Wedekin et al. 2007), and recent isotope-based evidence suggests that these delphinids compete for resources in this area, specifically demersal mullet species (*Mugil* spp.) (Teixeira et al. 2021). Thus, this unique social pattern relative to other Guiana dolphin populations could be a defensive behavior and/or a solution to reduce competition with bottlenose dolphins. Alternatively, it could result from adverse environmental conditions inherent to the southern limit of the species distribution (Lesica and Allendorf 1995).

Previous studies based on stomach content analysis showed that Guiana dolphin populations consume a diverse diet, concluding that Guiana dolphins are generalists and opportunistic foragers (Daura-Jorge et al. 2011; Cremer et al. 2012; Rodrigues et al. 2020). However, stomach content data provides a snapshot of diet composition immediately prior to death and as such are not suitable for assessing individual diet specialization over longer time periods. Our isotopic analyses expand these previous findings by revealing that the total niche width of each Guiana dolphin population and the degree of individual diet specialization are context-dependent, and so likely arise from ecological drivers including latitudinal variation in productivity, inter- and intraspecific competition, and the home range of each population. However, our approach also has two key limitations. First, we restricted our samples to mature individuals to obtain more subsamples, which resulted in a small sample size within populations as well as an uneven sample size among populations, as fewer mature individuals were available in some areas, which may limit direct comparisons. Second, since it was not possible to directly evaluate the diversity and abundance of prey sources in each area, we relied on the literature to assess variation in ecological opportunity available to each population. Yet, our results show how ecological features can influence niche metrics and encourage researchers to explore a wide range of potential drivers of varied foraging strategies within and among populations other than those studied. Given that ecological opportunity is a key driver of individual diet specialization (Araújo et al. 2011), and our data suggest it is an important factor for explaining niche variation among Guiana dolphin populations, future studies should further explore latitudinal gradients in resource availability to refine our understanding of the foraging tactics used by these cryptic predators. This will cast more light on how resource abundance and richness may promote and maintain individual diet specialization in cetacean species that are restricted to coastal areas in which resource availability is increasingly altered by human activities.

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Availability of data and materials The R code to reproduce the analyses is available in the supplementary material, and the dataset can be made available upon request.

Declarations

Conflict of interests The authors declare that they have no conflict of interests.

References

Ambrose SH (1990) Preparation and characterization of bone and tooth collagen for isotopic analysis. J Archaeol Sci 17:431–451. https://doi.org/10.1016/0305-4403(90)90007-R

Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. Ecol Lett 14:948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Bartoń K (2019) MuMIn: Multi-modal inference. Model selection and model averaging based on information criteria (AICc and alike). cran. r-project. org/web/packages/MuMIn/index. Html.

Bearhop S, Adams CE, Waldron S, Fuller RA, MacLeod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007–1012. https://doi.org/10.1111/j.0021-8790.2004.00861.x

Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanbäck R (2002) Measuring individual-level resource specialization. Ecology 83:2936–2941. https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2

Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:1–28. https://doi.org/10.1086/343878

Bolnick DI, Ingram T, Stutz WE, Snowberg LK, Lau OL, Paull JS (2010) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. Proc R Soc Biol Sci 277:1789–1797. https://doi.org/10.1098/rspb.2010.0018

Borobia M, Siciliano S, Lodi L, Hoek W (1991) Distribution of the South American dolphin sotalia fluviatilis. Can J Zool 69:1025–1039. https://doi.org/10.1139/z91-148

Brandini FP, Alquini F, Pereira RB, Leite RL (2006) Abundância e estrutura populacional da comunidade planctônica na baía da babitonga: subsídios para a avaliação de impactos ambientais. In: Cremer MJ, Morales PRD, Oliveira TMN (eds) Diagnóstico ambiental da baía da babitonga. Editora da Univille, Joinville

Brault EK, Koch PL, Gier E, Ruiz-Cooley RI, Zupcic J, Gilbert KN, McCarthy MD (2014) Effects of decalcification on bulk and compound-specific nitrogen and carbon isotope analyses of dentin. Rapid Commun Mass Spectrom 28:2744–2752. https://doi.org/10.1002/rcm.7073

Burnham KP, Anderson DR (2002) A practical information-theoretic approach model selection and multimodel inference, 2nd edn. Springer, New York

Cantor M, Wedekin LL, Daura-Jorge FG, Rossi-Santos MR, Simões-Lopes PC (2012) Assessing population parameters and trends of guiana dolphins (sotalia guianensis): an eight-year mark-recapture study. Mar Mamm Sci 28:63–83. https://doi.org/10.1111/j.1748-7692.2010.00456.x

Carreto JI, Negri RM, Benavides HR (1986) Algunas características del florecimiento del fitoplancton en el frente del río de la plata. I. los sistemas nutritivos. Revista De Investigación y Desarrollo Pesquero 5:7–29

Castello J, Duarte A, Moller OO, Niencheski F, Odebredcht C, Weiss G, Habiaga R, Bellotto V, Kitzmann D, Souto C, Souza R, Ciotti A; Fillmann G, Schwingell P, Bersano J, Cirano M, Freire K, Lima I, Mello R, Monteiro A, Resgalla C, Soares I, Suzuki M (1990) On the importance of coastal and subantartic waters for the shelf ecosystem off Rio Grande do Sul. Anais do II Simpósio de Estrutura, Função e Manejo de Ecossistemas da Costa Sul e Sudeste, São Paulo – Brazil 1:112–129

Cerutti RL (1996) Contribuição ao conhecimento da poluição doméstica na Baía Norte área da Grande Florianópolis, Universidade Federal de Santa Catarina, Brazil

Chase JM, Leibold MA (2003) Ecological niches: linking classical and contemporary approaches. University of Chicago Press

Ciotti ÁM, Odebrecht C, Fillmann G, JrOO M (1995) Freshwater outflow and subtropical convergence influence on phytoplankton biomass on the southern Brazilian continental shelf. Cont Shelf Res 15:1737–1756. https://doi.org/10.1016/0278-4343(94)00091-Z

Clementz MT, Koch PL (2001) Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. Oecologia 129:461–472. https://doi.org/10.1007/s004420100745

Costa MDP, Souza-Conceição JM (2009) Composição e abundância de ovos e larvas de peixes na baía da babitonga, Santa Catarina, Brasil. Pan-Am J Aquat Sci 4:371–382

Cremer MJ (2007) Ecologia e conservação de populações simpátricas de pequenos cetáceos em ambiente estuarino no sul do Brasil. Federal University of Paraná, Brazil

Cremer MJ, Simões-Lopes PC (2005) The occurrence of pontoporia blainvillei (gervais & d'orbigny) (cetacea, pontoporiidae) in an estuarine area in southern Brazil. Revista Brasileira De Zoologia 22:717–723. https://doi.org/10.1590/s0101-81752005000300032

Cremer MJ, Simões-Lopes PC (2008) Distribution, abundance, and density estimates of franciscanas, pontoporia blainvillei (cetacea: pontoporiidae), in babitonga bay, southern Brazil. Revista Brasileira De Zoologia 25:397–402. https://doi.org/10.1590/S0101-81752008000300003

Cremer MJ, Hardt FA, Tonello-Júnior AJ, Simões-Lopes PC (2011) Distribution and status of the guiana dolphin sotalia guianensis (cetacea, delphinidae) population in babitonga bay, Southern Brazil. Zool Stud 50:327–337

Cremer MJ, Pinheiro PC, Simões-Lopes PC (2012) Prey consumed by guiana dolphin sotalia guianensis (cetacea, delphinidae) and franciscana dolphin pontoporia blainvillei (cetacea, pontoporiidae) in an estuarine environment in southern Brazil. Iheringia Série Zoologia 102:131–137. https://doi.org/10.1590/S0073-47212012000200003

Cremer MJ, Holz AC, Sartori CM, Schulze B, Paitach RL, Simões-Lopes PC (2018) Behavior and ecology of endangered species living together: long-term monitoring of resident sympatric dolphin populations. In: Rossi-Santos MR, Finkl CW (eds) Advances in marine vertebrate research in Latin America. Springer, Cham, pp 477–508

Daura-Jorge FG, Wedekin LL, Simões-Lopes PC (2011) Feeding habits of the guiana dolphin, sotalia guianensis (cetacea: delphinidae), in norte bay, southern Brazil. Sci Mar 75:163–169. https://doi.org/10.3989/scimar.2011.75n1163

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506. https://doi.org/10.1016/0016-7037(78)90199-0

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:341–351. https://doi.org/10.1016/0016-7037(81)90244-1

Ekau W (1999) Topographical and hydrographical impacts on zooplankton community structure in the abrolhos bank region, East Brazil. Arch Fish Marine Res 47:307–320

Elorriaga-Verplancken F, Aurioles-Gamboa D, Newsome SD, Martinez-Diaz SF (2013) d^{15}N and d^{13}C values in dental collagen as a proxy for age and sex related variation in foraging strategies of California sea lions. Mar Biol 160:641–652. https://doi.org/10.1007/s00227-012-2119-y

Estes JA, Riedman ML, Staedler MM, Tinker MT, Lyon BE (2003) Individual variation in prey selection by sea otters: patterns, causes and implications. J Animal Ecol. https://doi.org/10.1046/j.1365-2656.2003.00690.x

Flores PAC, Bazzalo M (2004) Home ranges and movements patterns of the marine tucuxi Sotalia fluviatilis in baía norte, southern Brazil. Lat Am J Aquat Mamm 3:37–52. https://doi.org/10.5597/lajam00047

Flores PAC, Fontoura NF (2006) Ecology of marine tucuxi and bottlenose dolphins in baía norte, Santa Catarina state, southern Brazil. Lat Am J Aquat Mamm 5:105–115. https://doi.org/10.5597/lajam00101

Ford JK, Ellis GM (2006) Selective foraging by fish-eating killer whales orcinus orca in British columbia. Mar Ecol Prog Ser 316:185–199. https://doi.org/10.3354/meps316185

Gerhardinger LC, Herbst DF, Cunha SMB, Costa MDP (2020) Diagnóstico da ictiofauna do ecossistema babitonga. Revista CEPSUL. https://doi.org/10.3700/revistacepsul.vol9.693eb2020001

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behaviour of top predators in oceanic ecosystems. Isoscapes. Springer, Dordrecht, pp 299–318

Groom B (2018) Effects of decalcification, species, and mammalian order on bulk stable isotope values from marine mammal teeth unpublished master's thesis. University of California, San Diego

Hardt FAS, Cremer MJ, JrAJ T, Simões-Lopes PCA (2010) Residence patterns of the guiana dolphin sotalia guianensis in babitonga bay, south coast of Brazil. Lat Am J Aquat Mamm 8:117–121. https://doi.org/10.5597/lajam00160

Hardt FAS, Cremer MJ, Tonello Junior AJ, Bellante A, Buffa G, Buscaino G, Mazzola S, Barreto AS, Martinelli LA, Zuppi GM (2013) Use of carbon and nitrogen stable isotopes to study the feeding ecology of small coastal cetacean populations in southern Brazil. Biota Neotrop 13:90–98. https://doi.org/10.1590/S1676-06032013000400009

Hartig F (2018) DHARMa residual diagnostics for hierarchical multi-level mixed regression models R package v. 0.2.0. University of Regensburg, Regensburg

Herz R (1991) Manguezais do Brasil, USP

Hohn AA, Scott MD, Wells RS, Sweeney JC, Irvine AB (1989) Growth layers in teeth from known-age, free-ranging bottlenose dolphins. Mar Mamm Sci 5:315–342. https://doi.org/10.1111/j.1748-7692.1989.tb00346.x

Hutchinson GE (1957) The multivariate niche. Cold Spring Harb Symp Quant Biol 22:415–421

IBAMA (1998) Proteção e controle de ecossistemas costeiros: manguezal da Baía de Babitonga

Kernaléguen L, Arnould JP, Guinet C, Cherel Y (2015) Determinants of individual foraging specialization in large marine vertebrates, the Antarctic and subantarctic fur seals. J Anim Ecol 84:1081–1091. https://doi.org/10.1111/1365-2656.12347

Krause J, Ruxton GD, Ruxton G, Ruxton IG (2002) Living in groups. Oxford University Press, Oxford

Lesage V, Hammill MO, Kovacs KM (2001) Marine mammals and the community structure of the estuary and gulf of st lawrence, Canada: evidence from stable isotope analysis. Mar Ecol Prog Ser 210:203–221. https://doi.org/10.3354/meps210203

Lesica P, Allendorf FW (1995) When are peripheral populations valuable for conservation? Conserv Biol 9:753–760. https://doi.org/10.1046/j.1523-1739.1995.09040753.x

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100:603–609. https://doi.org/10.1086/282454

Matthews CJD, Ferguson SH (2014) Validation of dentine deposition rates in beluga whales by interspecies cross dating of temporal δ^{13}C trends in teeth. North Atl Marine Mamm Comm Sci Publ 10(7557/3):3196

Moreira da Silva PC (1971) Upwelling and its biological effects in southern Brazil. In: Costlow JD (ed) Fertility of the sea Gordon and Breach Science Publishers Inc. New York

Muelbert JH, Acha M, Mianzan H, Guerrero R, Reta R, Braga ES, Garcia VMT, Berasetegui A, Gomez-Erache M, Ramírez F (2008) Biological, physical and chemical properties at the subtropical shelf front zone in the SW Atlantic Continental Shelf. Cont Shelf Res 28:1662–1673. https://doi.org/10.1016/j.csr.2007.08.011

Newsome SD, Koch PL, Etnier MA, Aurioles-Gamboa D (2006) Using carbon and nitrogen isotope values to investigate maternal strategies in northeast Pacific otariids. Mar Mamm Sci 22:556–572. https://doi.org/10.1111/j.1748-7692.2006.00043.x

Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA (2009) Using stable isotopes to investigate individual diet specialization in California sea otters (enhydra lutris nereis). Ecology 90:961–974. https://doi.org/10.1890/07-1812.1

Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mamm Sci 26:509–572. https://doi.org/10.1111/j.1748-7692.2009.00354.x

Newsome SD, Tinker MT, Gill VA, Hoyt ZN, Doroff A, Nichol L, Bodkin JL (2015) The interaction of intraspecific competition and habitat on individual diet specialization: a near range-wide examination of sea otters. Oecologia 178:45–59. https://doi.org/10.1007/s00442-015-3223-8

Niño-Torres CA, Gallo-Reynoso JP, Galván-Magaña F, Escobar-Briones E, Macko SA (2006) Isotopic analysis of δ^{13}C, δ^{15}N, and δ^{34}S "a feeding tale" in teeth of the longbeaked common dolphin, delphinus capensis. Mar Mamm Sci 22:831–846. https://doi.org/10.1111/j.1748-7692.2006.00065.x

Paitach RL (2015) Ecologia alimentar e espacial da toninha (pontoporia blainvillei) e do boto-cinza (sotalia guianensis) na baía da babitonga. Federal University of Santa Catarina, Brazil

Perrin WF, Myrick CA (1980) Report of the workshop on growth of odontocetes and sirenians Age determination of toothed whales and sirenians. International Whaling Commission, Cambridge

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293–320

Piola AR, Romero SI, Zajaczkovski U (2008) Space–time variability of the plata plume inferred from ocean color. Cont Shelf Res 28:1556–1567. https://doi.org/10.1016/j.csr.2007.02.013

Polis GA (1984) Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? Am Nat 123:541–564. https://doi.org/10.1086/284221

Ramos RMA (1997) Determinação de idade e biologia reprodutiva de Pontoporia blainvillei e da forma marinha de sotalia fluviatilis (cetacea, pontoporiidae e delphinidae) no norte do RIO DE JANEIRO. Universidade estadual do norte fluminense campos dos goytacazes, RJ, Brazil

Ramos RMA, Di Beneditto AP, Lima NRW (2000) Growth parameters of pontoporia blainvillei and sotalia fluviatilis (cetacea) in northern rio de janeiro, Brazil. Aquat Mamm 26:65–75

Resgalla C Jr (2011) The holoplankton of the Santa Catarina coast, southern Brazil. An Acad Bras Ciênc 83:575–588. https://doi.org/10.1590/s0001-37652011000200017

Rodrigues VLA, Wedekin LL, Marcondes MCC, Barbosa L, Farro APC (2020) Diet and foraging opportunism of the guiana dolphin (sotalia guianensis) in the abrolhos bank, Brazil. Mar Mamm Sci 36:436–450. https://doi.org/10.1111/mms.12656

Rosas FCW, Monteiro-Filho ELA (2002) Reproduction of sotalia guianensis on the coast of paraná, southern Brazil. J Mammal 83:507–515. https://doi.org/10.1644/1545-1542%282002%29083%3C0507:ROTEDS%3E2.0.CO;2

Rosas FCW, Barreto AS, Monteiro-Filho ELA (2003) Age and growth of the estuarine dolphin (sotalia guianensis) (cetacea, delphinidae) on the paraná coast, southern Brazil. Fish Bull 101:377–383

Rosas FCW, Marigo J, Laeta M, Rossi-Santos MR (2010) Natural history of dolphins of the genus sotalia. Lat Am J Aquat Mamm. https://doi.org/10.5597/lajam00154

Rossi-Santos MR, Wedekin LL, Sousa-Lima RS (2006) Distribution and habitat use of small cetaceans in the coast of the Abrolhos bank, eastern Brazil. Lat Am J Aquat Mamm 5:23–28. https://doi.org/10.5597/lajam00088

Rossi-Santos MR, Wedekin LL, Monteiro-Filho ELA (2007) Residence and site fidelity of sotalia guianensis in the caravelas river estuary, eastern Brazil. J Marine Biol Assoc UK 87:207–212. https://doi.org/10.1017/S0025315407055683

Rossi-Santos MR, Wedekin L, Monteiro-Filho ELA (2010) Habitat use of the guiana dolphin, sotalia guianensis (cetacea, delphinidae), in the caravelas river estuary, eastern Brazil. Lat Am J Aquat Mamm 8:111–116. https://doi.org/10.5597/lajam00159

Rossman S, Ostrom PH, Stolen M, Barros NB, Gandhi H, Stricker CA, Wells RS (2015) Individual specialization in the foraging habits of female bottlenose dolphins living in a trophically diverse and habitat rich estuary. Oecologia 178:415–425. https://doi.org/10.1007/s00442-015-3241-6

Rossman S, Ostrom PH, Gordon F, Zipkin EF (2016) Beyond carbon and nitrogen: guidelines for estimating three-dimensional isotopic niche space. Ecol Evol 6:2405–2413. https://doi.org/10.1002/ece3.2013

Roughgarden J (1972) Evolution of niche width. Am Nat 106:683–718. https://doi.org/10.1086/282807

Roughgarden J (1979) Theory of population genetics and evolutionary ecology: an introduction. Macmillan, New York

Santos MCDO (2010) Guiana dolphins (sotalia guianensis) displaying beach hunting behavior in the cananéia estuary, Brazil: social context and conservation issues. Braz J Oceanogr 58:143–152. https://doi.org/10.1590/s1679-87592010000200005

Schaeffer-Novelli Y, Cintrón-Molero G, Adaime RR, de Camargo TM (1990) Variability of mangrove ecosystems along the Brazilian coast. Estuaries 13:204–218. https://doi.org/10.2307/1351590

Schettini CAF, Truccolo EC, Resgalla Jr C, Rörig LR, Kuroshima KN (2002) O sistema estuarino da baía da Babitonga. In: Knie JLW (ed) Atlas ambiental da região de Joinville – Complexo hídrico da baía da Babitonga, FATMA/GTZ

Schoener TW (1971) Theory of feeding strategies. Annu Rev Ecol Syst 2:369–404. https://doi.org/10.1146/annurev.es.02.110171.002101

Sheppard CE, Inger R, McDonald RA, Barker S, Jackson AL, Thompson FJ, Vitikainen EIK, Cant MA, Marshall HH (2018) Intragroup competition predicts individual foraging specialisation in a group-living mammal. Ecol Lett 21:665–673. https://doi.org/10.1111/ele.12933

Simões-Lopes PC (1988) Ocorrência de uma população de sotalia fluviatilis (gervais, 1853) (cetacea, delphinidae) no limite sul de sua distribuição, santa catarina, Brasil. Biotemas 1:57–62. https://doi.org/10.5007/%25x

Skúlason S, Smith TB (1995) Resource polymorphism in vertebrates. Trends Ecol Evol 11:25–25. https://doi.org/10.1016/S0169-5347(00)89135-1

Stephens DW, Krebs JR (1986) Foraging theory. Princeton university press, Princeton

Svanbäck R, Bolnick DI (2005) Intraspecific competition affects the strength of individual specialization: an optimal diet theory method. Evol Ecol Res 7:993–1012

Teixeira CR, Botta S, Daura-Jorge FG, Pereira LB, Newsome SD, Simões-Lopes PC (2021) Niche overlap and diet composition of three sympatric coastal dolphin species in the southwest Atlantic ocean. Mar Mamm Sci 37:111–126. https://doi.org/10.1111/mms.12726

Tinker MT, Bentall G, Estes JA (2008) Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proc Natl Acad Sci 105:560–565. https://doi.org/10.1073/pnas.0709263105

Travassos MP, Krüger GT, Lopes EBP, Pinto JA (2006) Hydrochemical characteristics of the caravelas river estuary and surrounding seazone Brazil. J Coast Res 736:740

Troina GC, Botta S, Dehairs F, Di Tullio JC, Elskens M, Secchi ER (2020) Skin $\delta^{13}C$ and $\delta^{15}N$ reveal spatial and temporal patterns of habitat and resource use by free-ranging odontocetes from the southwestern Atlantic Ocean. Mar Biol 167:186. https://doi.org/10.1007/s00227-020-03805-8

Van Valen L (1965) Morphological variation and width of ecological niche. Am Nat 99:377–390. https://doi.org/10.1086/282379

Vander Zanden HB, Bjorndal KA, Bolten AB (2013) Temporal consistency and individual specialization in resource use by green turtles in successive life stages. Oecologia 173:767–777. https://doi.org/10.1007/s00442-013-2655-2

Venuto R, Botta S, Barreto AS, Secchi ER, Fruet PF (2020) Age structure of strandings and growth of lahille's bottlenose dolphin (tursiops truncatus gephyreus). Mar Mamm Sci 36:813–827. https://doi.org/10.1111/mms.12683

Walker JL, Potter CW, Macko SA (1999) The diets of modern and historic bottlenose dolphin populations reflected through stable isotopes. Mar Mamm Sci 15:335–350. https://doi.org/10.1111/j.1748-7692.1999.tb00805.x

Wedekin LL, Daura-Jorge FG, Piacentini VQ, Simões-Lopes PC (2007) Seasonal variations in spatial usage by the estuarine dolphin, sotalia guianensis (van bénéden, 1864) (cetacea; delphinidae) at its southern limit of distribution. Braz J Biol 67:1–8. https://doi.org/10.1590/s1519-69842007000100002

Yurkowski DJ, Ferguson S, Choy ES, Loseto LL, Brown TM, Muir DC, Semeniuk CAD, Fisk AT (2016) Latitudinal variation in ecological opportunity and intraspecific competition indicates differences in niche variability and diet specialization of Arctic marine predators. Ecol Evol 6:1666–1678. https://doi.org/10.1002/ece3.1980

Zaccarelli N, Bolnick DI, Mancinelli G (2013) RInSp: an R package for the analysis of individual specialization in resource use. Methods Ecol Evol 4:1018–1023. https://doi.org/10.1111/2041-210X.12079