Isotopic niche of two coastal dolphins in a tropical marine area: specific and age class comparisons

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Niche differentiation is the process by which species evolve different forms of resource use, and is used to explain the co-occurrence in a variety of habitats. The Bayesian framework of isotopic niche through quantitative niche metrics was applied to estimate and compare the niche breadth of two sympatric coastal dolphins Pontoporia blainvillei *and* Sotalia guianensis *in a tropical marine area. The standard ellipse areas (SEAs) based on species were quite similar, but the SEAs based on age class showed that the matures' niche space is larger than the immatures' for both dolphins. A probabilistic comparison of SEAs indicated that specific differences are negligible compared with age class differences. Trophic level measures ($\delta^{15}N$ range) indicated that the dolphins are comparable as top predators, and that immature specimens have a lower range of trophic levels than mature ones. In terms of variability of food sources ($\delta^{13}C$ range),* S. guianensis *showed a larger value than* P. blainvillei *and mature specimens had larger $\delta^{13}C$ range than immatures for both species. In general,* P. blainvillei *and* S. guianensis *were similar in the niche metrics, with SEAs overlap of 52.1 and 39.7%. The immature specimens showed reduced isotopic niche overlap between species (<3%). In conclusion,* Pontoporia blainvillei *and* S. guianensis *specimens have similar isotopic niches, but pronounced differences between immature and mature specimens, both intraspecific and interspecific. Isotopic niche and quantitative metrics along with previous data on stomach contents provide a strong representation of species niche and their relationships.*

INTRODUCTION

Species that co-occur and require similar feeding resources usually minimize the diet overlap by using different areas or capturing different prey, which is especially important when feeding resources are scarce (Pimm, 2002). In this sense, the niche differentiation among species is the process by which they evolve different forms of resource use, and has been used to explain their co-occurrence (Levins, 1968; MacArthur, 1972).

Considering the marine mammals, species using similar feeding resources may reduce niche overlap due to differences in their movement pattern and, consequently, their distributional range and feeding ground (Whitehead *et al.*, 2003). For species that share similar distribution, size and morphology, the niche differentiation can be explained by differences in preferred habitat (e.g. coastal *vs.* offshore; pelagic *vs.* benthic) and behavioural budgets (e.g. diurnal *vs.* nocturnal activities) (Kiszka *et al.*, 2011).

In the last two to three decades, stable isotope ratios have provided complementary data on animals' trophic ecology. This technique presents time-integrated information on food assimilation, and evaluates differences in trophic niche, trophic level and foraging sites (e.g. Hobson & Welch, 1992;

Cherel *et al.*, 2005; Di Beneditto *et al.*, 2011, 2013). Layman *et al.* (2007) introduced a number of metrics, borrowed from ecomorphological studies, to summarize quantitative information from stable isotope data sets, describing trophic structure at the species or community level. Additionally, Jackson *et al.* (2011) developed a Bayesian method for the comparison of these metrics among groups. This approach has recently been expanded, allowing a robust comparison of isotopic niches across species (e.g. Jackson & Britton, 2014; Knickle & Rose, 2014) and communities (e.g. Abrantes *et al.*, 2014; Zapata-Hernández *et al.*, 2014).

The target species of the present study are the coastal dolphins *Pontoporia blainvillei* (Gervais & D'Orbigny, 1844) and *Sotalia guianensis* (Van Bénedèn, 1864). These species are the most vulnerable dolphins along the South-western Atlantic Ocean due to interactions with fisheries (Secchi *et al.*, 2003; Barreto *et al.*, 2010; IUCN, 2015). The feeding habits of these dolphins were previously described and compared in a sympatric area by Di Beneditto & Ramos (2001) and (2004), and Di Beneditto *et al.* (2011). Twenty-five prey species were recorded in the stomach contents of *P. blainvillei*, among which five (three pelagic and two demersal) are preferentially ingested; whereas 36 prey species were recorded for *S. guianensis*, and two (one pelagic and one demersal) are most ingested.

In the present study, we analysed for the first time the isotopic niche breadth of *P. blainvillei* and *S. guianensis* through quantitative niche metrics using a Bayesian framework. The

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isotopic data were compared with previous data on feeding habits to assess the feeding overlap between species and age classes, and to evaluate specific and age class strategies related with their co-occurrence. We hypothesize that (i) the niche breadth of *P. blainvillei* and *S. guianensis* is similar, considering that these dolphins have coastal habits and both pelagic aand demersal prey are consumed by them; and (ii) the niche breadth of mature specimens is larger than immatures for both dolphins, because in cetacean species mature individuals have more experience in selectivity and prey capture (Perrin *et al.*, 2009) and have larger body size which allow the ingestion of more diverse range of prey (Segura *et al.*, 2015).

MATERIALS AND METHODS

The specimens of *P. blainvillei* and *S. guianensis* analysed in this study were incidentally captured from 2001 to 2005 through commercial gillnet fisheries practiced in south-eastern Brazil, from 21°35′S to 22°25′S, in waters from 0.4 to 47 km from the coastline, and in depths varying from 6 to 30 m. Each dolphin specimen was grouped into immature or mature according to age, calculated by the number of teeth growth layers (Ramos *et al.*, 2000). For *P. blainvillei* and *S. guianensis*, specimens ≤2 years old and ≤4 years old, respectively, were considered as immature. Specimens that were still suckling were excluded from this study due to the great influence of the mother's milk in their isotopic ratios. Thus, our sample was composed of 13 specimens of *P. blainvillei* (seven immatures and six matures), and 18 of *S. guianensis* (six immatures and 12 matures).

A sub-sample from the back dorso-lateral muscle was removed from the dolphins. The tissue samples were freeze-dried and homogenized with a mortar and pestle for stable isotope analyses (δ^{15}N and δ^{13}C). The isotopic analyses were performed with a ThermoQuest Finnigan Delta Plus (Finnigan MAT) mass spectrometer coupled to an elemental analyser. Pee Dee Belemnite carbonate and atmospheric nitrogen were standard values for carbon and nitrogen analyses, respectively:

$$\delta^{j/i}X = \left({}^{j}X/{}^{i}X\right)_{sample} - 1$$

$$\left({}^{j}X/{}^{i}X\right)_{standard}$$

where ${}^{j}X$ is the heavier isotope (^{15}N or ^{13}C), and ${}^{i}X$ is the lighter isotope (^{14}N or ^{12}C). The analytical precision was ±0.3‰ for δ^{15}N and ±0.2‰ for δ^{13}C, determined in triplicate at each of five samplings. Lipids were not extracted from the muscle samples prior to analysis; however, the C/N ratios were lower than 3.5, indicating low levels of lipids. Therefore, the interpretation of the results of δ^{13}C was not compromised (Post *et al.*, 2007).

Quantitative metrics based on the position of individuals in the niche space formed by δ^{13}C and δ^{15}N were applied to estimate isotopic niche breadth (Layman *et al.*, 2007; Jackson *et al.*, 2011). Metrics were calculated using the functions for Stable Isotope Bayesian Ellipses in R (SIBER – Jackson *et al.*, 2011), available within the package Stable Isotope Analysis in R (SIAR) (Parnell *et al.*, 2010; R Development Core Team, 2011). Six metrics were calculated as described below. The first four reflect trophic diversity in the

δ^{13}C-δ^{15}N scatterplot, and the other two represent trophic redundancy (how closely positioned individuals in species are to each other within their respective niches).

The metrics are described as: (1) δ^{15}N range (NR): distance between maximum and minimum δ^{15}N values for a given species (*P. blainvillei* and *S. guianensis*) or age class within species (immature and mature) which indicates the difference between trophic levels. A large NR implies higher trophic levels within species or age class; (2) δ^{13}C range (CR): distance between maximum and minimum δ^{13}C values which indicates the variability of food sources consumed. A large CR implies difference in basal resources within trophic levels (e.g. benthic *vs.* pelagic; coastal *vs.* oceanic); (3) Standard ellipse area (SEA): trophic niche breadth for a given species or age class. The standard ellipse is centred on the group centroid and scaled to encompass a 40% chance of including a subsequently sampled datum; (4) Mean distance to centroid (CD): average Euclidean distance of each individual to the group centroid (mean δ^{15}N and δ^{13}C value), which provides the average degree of trophic diversity within a species or age class; (5) Mean nearest neighbour distance (MNND): average Euclidean distances to the individual's nearest neighbour in scatterplot space which provides a measure of the overall species or age class packing. A set of many individuals with similar trophic ecologies would show a smaller MNND than a set in which individuals are more varied in terms of diet; and (6) Standard deviation of nearest neighbour distance (SDNND): a measure of evenness of species or age class packing in the scatterplot, in which low values indicate a more even distribution of individuals in the trophic niche space.

The differences between species and age classes regarding δ^{15}N and δ^{13}C values were assessed via two-way ANOVA. The SEAs of species (*P. blainvillei* and *S. guianensis*) and age classes (immature and mature) were compared probabilistically with the posterior Bayesian distributions, calculating the proportion of ellipses for group 1 that was larger than ellipses for group 2 in the simulated draws (Jackson *et al.*, 2011). The per cent of overlapping SEA between species and age classes was the measure of isotopic niche overlap. Two-way ANOVAs were also used to assess differences and interactions between species and age classes considering CD and MNND. The statistic SDNND, being a standard deviation, was compared between groups by an F-ratio test. The *P* values were interpreted as strengths of evidence toward null hypotheses, rather than on the dichotomic scale of significance testing (Hurlbert & Lombardi, 2009).

RESULTS

The isotopic values for *P. blainvillei* and *S. guianensis* are presented in Figure 1. For *P. blainvillei*, the mean values for δ^{15}N and δ^{13}C were +13.8 ± 0.3‰ and −16.0 ± 0.3‰ (immature specimens) and +13.2 ± 1.1‰ and −15.7 ± 0.6‰ (mature specimens), respectively. Considering *S. guianensis*, the mean values for δ^{15}N and δ^{13}C were +14.0 ± 0.5‰ and −15.4 ± 0.3‰ (immature specimens) and +14.1 ± 1.1‰ and −15.8 ± 0.8‰ (mature specimens), respectively. The two-way ANOVAs were unable to detect differences in the means of the isotopic values between species ($F = 2.6$, df = 1, 27, $P = 0.12$ for δ^{15}N, $F = 1.14$, df = 1, 27, $P = 0.29$ for δ^{13}C,) and maturity ($F = 0.6$, df = 1, 27, $P = 0.44$ for

δ^{15}N, $F = 0.05$, df $= 1$, 27, $P = 0.82$ for δ^{13}C). No interactions were detected between species and age class factors ($F = 1.2$, df $= 1$, 27, $P = 0.28$ for δ^{15}N, $F = 1.9$, df $= 1$, 27, $P = 0.18$ for δ^{13}C). This result was expected given that within-group variation is considerably large compared with the differences among groups (see Figure 1 for details). The diagnostic plots of residuals and fitted values (not shown) did not indicate noticeable departures from assumptions of normality and homoscedasticity.

The SEAs based on species were similar in size and position in the δ^{13}C – δ^{15}N scatterplot. However, the SEAs based on age class showed that the mature ellipses are larger than the immatures' for both dolphins (Figure 1 and Table 1). A probabilistic comparison between the ellipses areas based on the posterior distribution of simulated ellipses indicated that specific differences ($P = 0.32$) are negligible compared with age class differences ($P = 0.04$ for *P. blainvillei*, $P = 0.13$ for *S. guianensis*).

The quantitative metrics to estimate the isotopic niche breadth are in Table 1. Trophic level measures (δ^{15}N range) indicate that the dolphin species are comparable as predators, and that immature specimens have a lower range of trophic levels than mature ones. In terms of variability of food sources (δ^{13}C range), *S. guianensis* showed a larger value than *P. blainvillei*. For both species, mature specimens have larger δ^{13}C range than immatures.

Neither CD, MNND or SDNND presented a clear difference between species (CD $P = 0.39$, MNND $P = 0.84$, SDNND $P = 0.31$), indicating similarities in the average degree of trophic diversity, redundancy and evenness. Both CD and MNND differed between age classes regardless of species (CD $P = 0.01$, MNND $P = 0.01$) as no interaction of factors was detected (CD $P = 0.72$, MNND $P = 0.23$). The average degree of trophic diversity (CD) in mature specimens is two times larger than that of the immatures. Comparing SDNND between age classes within species, we observed that immatures presented smaller values than matures in both species (*P. blainvillei* $P < 0.01$; *S guianensis* $P = 0.01$). The distribution of immatures in trophic space is tighter and more even (based on MNND and SDNND) than the distribution of mature specimens (Table 1). The diagnostic plots of residuals and fitted values for the two-way ANOVAs, as well as the SDNND comparison, indicated normal but heteroscedastic residuals for both metrics (CD and MNND). Logarithmic transformations corrected the deviation from model assumptions but maintained the conclusions unchanged.

The percentages of SEA overlap between *P. blainvillei* and *S. guianensis*, and *S. guianensis* and *P. blainvillei* were 52.1 and 39.7%, respectively. For both dolphins, there is a high isotopic niche overlap between immature and mature specimens (Table 2), because the immature ellipses are almost completely contained by the mature ellipses. Comparing age classes between species, it was noted that immatures of *P. blainvillei* and *S. guianensis* have a minimal niche overlap (<3%), whereas the percentage for mature specimens was greater ($\sim45 – 55$%) (Table 2).

DISCUSSION

This study compared the isotopic niche breadth of the coastal dolphins *P. blainvillei* and *S. guianensis*, showing to what extent they are sharing or segregating feeding resources in a sympatric area. The comparison of quantitative niche metrics indicated that specific differences (*P. blainvillei vs. S. guianensis*) are negligible compared with age class differences (immature *vs.* mature specimens). For both species, the niche breadth of immature specimens is smaller than mature ones.

The δ^{15}N values are generally applied as measures of trophic level (predators have higher values than their prey), and δ^{13}C values may indicate the origin of feeding resources (e.g. coastal *vs.* oceanic sources; pelagic *vs.* benthic sources) (Hobson & Welch, 1992; Cherel *et al.*, 2005). In the study area ($\sim21 – 22°$S), previous studies using stable isotopes (δ^{15}N and δ^{13}C) as diet proxies showed that *P. blainvillei* and *S. guianensis* are top predators whose main feeding resources are associated with coastal waters (Di Beneditto *et al.*, 2011, 2013; Kehrig *et al.*, 2013). The isotopic values of the present study corroborate these findings, but the large δ^{13}C range in *S. guianensis* might indicate a wider movement along the continental shelf and, consequently, a mixture of coastal and oceanic influences in the set of prey. This is corroborated by the record of *Ariosoma opistophthalmum* in its stomach contents, which is a fish species typically found more distant from the coastline (Di Beneditto & Ramos, 2004; Froese & Pauly, 2015).

In general, *P. blainvillei* and *S. guianensis* were similar in the niche metrics, with SEA overlap, which confirms the first hypothesis of this study. Similarities in niche metrics
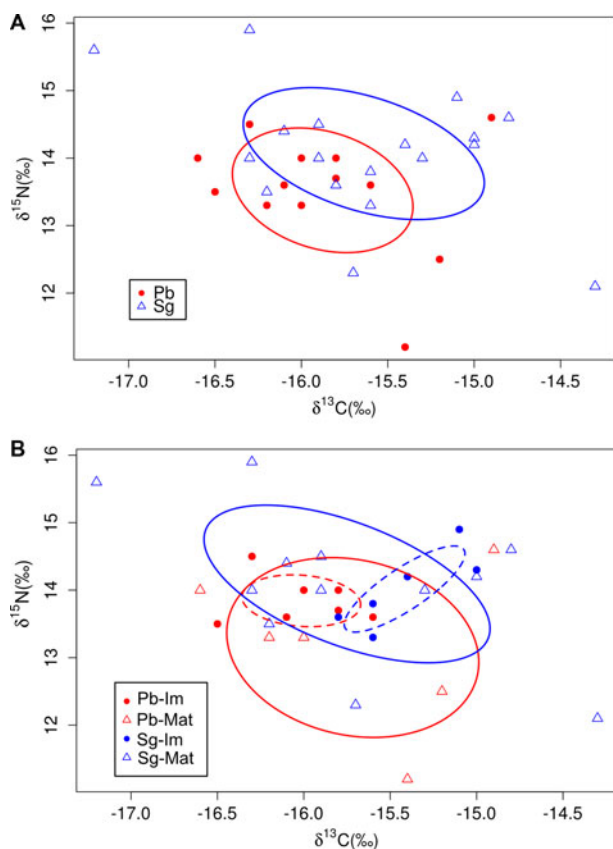

Fig. 1. Stable isotopes values of the dolphin species *Pontoporia blainvillei* and *Sotalia guianensis* for (A) the entire sample, and (B) separating age classes. Lines depict the standard ellipse (the 40% confidence interval) for the isotopic niches with solid lines for *P. blainvillei* and dashed lines for *S. guianensis*. Pb, *Pontoporia blainvillei*; Sg, *Sotalia guianensis*; Im, immatures; Mat, matures.

Table 1. Quantitative niche metrics by species and age classes.

	NR	CR	CD	MNND	SDNND	SEA (‰²)		
						LQ	Median	UQ
P. blainvillei	3.4	1.7	0.76	0.50	0.41	1.47	1.74	2.09
S. guianensis	3.8	2.9	0.92	0.46	0.36	1.76	2.05	2.41
P. blainvillei								
Immature	1.0	0.9	0.39	0.31	0.14	0.93	1.17	1.51
Mature	3.4	1.7	1.09	0.89	0.61	2.33	2.99	3.88
S. guianensis								
Immature	1.6	0.8	0.54	0.39	0.12	1.17	1.50	1.98
Mature	3.8	2.9	1.08	0.63	0.41	2.18	2.64	3.21

NR, δ^{15}N range; CR, δ^{13}C; SEA, standard ellipse area; CD, distance to centroid; MNND, mean nearest neighbour distance; SDNND, standard deviation of nearest neighbour distances; LQ, lower quartile; and UQ, upper quartile.

Table 2. Overlapping SEA (%) between age classes for *Pontoporia blainvillei* and *Sotalia guianensis* (isotopic niche overlap).

	P. blainvillei immature	*P. blainvillei* mature	*S. guianensis* immature	*S. guianensis* mature
	–	100.0	2.7	–
P. blainvillei – mature	13.6	–	–	45.8
S. guianensis – immature	2.8	–	–	86.3
S. guianensis – mature	–	55.1	13.8	–

can reflect prey's isotopic values, as previous recorded in Di Beneditto *et al.* (2011), and variations in food intake. *Pontoporia blainvillei* ingests prey with minor body size, but in greater amounts than *S. guianensis*. The first species feed mainly on juveniles or small-sized fish and cephalopod species, up to 15.0 cm length (Di Beneditto & Ramos, 2001; Danilewicz *et al.*, 2002), while the second species is a primarily piscivorous predator that has plasticity in relation to its prey size, varying from <10.0 to 100.0 cm length (Di Beneditto & Ramos, 2004; Di Beneditto & Siciliano, 2007). At least for some prey species the total amount (biomass) ingested in each meal is equivalent between the dolphins (Di Beneditto *et al.*, 2001). Variations in prey size and quantity of each prey ingested can lead to similar isotopic values in consumers (Lassalle *et al.*, 2014).

For both dolphins, mature specimens have greater trophic diversity (CD) and minor trophic redundancy (MNND) than immatures. Different age classes can differ in many ecological ways, including resources use (Bolnick *et al.*, 2003). In a population, groups with more generalized diet (as the mature specimens of both dolphins) tend to be more ecologically heterogeneous, exhibiting greater niche breadth (Bolnick *et al.*, 2007). The niche breadth of mature specimens enlarges the niche breadth of these dolphins' population as a whole, reducing the intraspecific competition (Bolnick *et al.*, 2011).

Differences between age classes regarding the niche breadth support our second hypothesis. This reveals the greater experience of matures in utilization of available feeding resources and capturing prey, expanding their niche breadth. It is expected in cetaceans due to their social behaviour, which includes long-term parental care and developed feeding strategies (e.g. Rendell & Whitehead, 2001; Perrin *et al.*, 2009; Tardin *et al.*, 2011; Oliveira *et al.*, 2013). In addition, animals with larger body size are able to ingest larger prey than smaller ones (Segura *et al.*, 2015). This condition may also explain the differences between the mature and immature dolphins, since small prey of a given species are in general less δ^{15}N enriched than large ones (Jennings *et al.*, 2002), which influences the isotopic value of predator.

The immatures' isotopic niche has high overlap with mature ones. This indicates an intraspecific sharing of food resources and feeding grounds, typical in cetacean species that live in groups (Tardin *et al.*, 2011). The immature specimens in turn, show reduced isotopic niche overlap between species. This niche divergence might facilitate the species' co-existence during the beginning of solid food ingestion.

In conclusion, *P. blainvillei* and *S. guianensis* specimens have similar isotopic niches, but pronounced differences between immature and mature specimens. Isotopic niche and quantitative metrics associated together with previous data on stomach contents provide a strong representation of species niche and their relationships, both intraspecific and interspecific. Moreover, the utilization of multiple methods to analyse feeding preferences reduces bias in data interpretation and may elucidate much more about species' behaviour and movement pattern (Di Beneditto *et al.*, 2011, 2015; Kehrig *et al.*, 2013).

ACKNOWLEDGEMENTS

FINANCIAL SUPPORT

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