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Movements and habitat use of bottlenose dolphins, *Tursiops truncatus*, in south-eastern Brazil

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Abstract

Bottlenose dolphins (*Tursiops truncatus*) have been surveyed for at least two decades on the southern Brazilian coast. However, little is known about their distribution and habitat use in lower latitudes of the South-western Atlantic Ocean. Aiming to study the movements and distribution of the species along the south-eastern Brazilian coast, we made a comparison of photo-identified individuals of the species catalogued in 21 cruises conducted between 2012 and 2015. Additionally, we performed stable isotope analyses of carbon and nitrogen in skin samples (N = 35) to provide some insights of dolphin habitat use and trophic ecology through comparisons among individuals of distinct surveyed sectors (northern and southern) and sex. A total of 177 individuals were identified. Re-sightings (N = 24) occurred at intervals from 82 to 979 days at distances from 7 to 179 km. No individual was sighted in both sectors, suggesting spatial segregation. Isotopic comparisons showed no significant differences in carbon and nitrogen signatures between distinct sectors. However, ecological divergences were found when we divided the samples by gender. Wider isotopic niches were found for the northern bottlenose dolphins *vs* the southern ones, which could be related to temporal and spatial variation in the availability of resources, as well as possible differences in the home ranges of males and females in each region. This study represents a preliminary evaluation of ecological aspects of bottlenose dolphins along the Brazilian south-eastern coast, however, long-term studies on the feeding ecology and habitat use of this species are important to further improve our knowledge.

Introduction

The bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), is a cosmopolitan species distributed in tropical and temperate waters around the world, including coastal and offshore open waters, bays, estuaries, lakes and lagoons (Wells & Scott, 1999). Two ecotypes have been described showing regional differences in ecology, physiology, genetics and morphology: a coastal and an offshore form (Wells & Scott, 2017), which have already been described in Brazilian waters (see Moreno *et al*., 2009). In recent years, morphological and genetic evidence has indicated that two distinct forms inhabit the South-western Atlantic Ocean (SAO): one in the south and the other in the north of 28°S. According to the authors, these forms appear to show differences in cranial morphology and a variation in their distribution (see Ott *et al*., 2016; Fruet *et al*., 2017; Costa *et al*., 2019). The southern form is usually sighted in salt lagoons and estuaries of the southern coast of Brazil, Uruguay and Argentina (see Simões-Lopes & Fabian, 1999; Fruet *et al*., 2011; Giacomo & Ott, 2016; Wickert *et al*., 2016; Genoves *et al*., 2018), and has been proposed as a new species for the genus, *T. gephyreus* (see Wickert *et al*., 2016; Genoves *et al*., 2018). In contrast, the distribution of the northern form varies greatly, being commonly found from shallower to deeper waters (see Zerbini *et al*., 2004; Lodi & Monteiro-Neto, 2012; Milmann *et al*., 2017).

Several movement patterns have been described in the species since the 1970s, such as seasonal migration, stable residence, temporary residence, and residence with seasonal loyalty (Shane *et al*., 1986). These patterns may be influenced by seasonal variation in oceanographic and physical conditions such as water temperature, salinity and depth, directly affecting productivity, thus the availability of prey (Jaquet & Whitehead, 1996; Bearzi, 2005). Bottlenose dolphins are opportunistic and generalist feeders, with a diet based on a large variety of pelagic and demersal fish, cephalopods and crustaceans (Shane *et al*., 1986; Barros & Clarke, 2009). Furthermore, bottlenose dolphins seem to exhibit variations in feeding habits that may vary according to habitat characteristics, prey availability and life stage (see Fernández *et al*., 2011; Rossman *et al*., 2015; Giménez *et al*., 2018; Louis *et al*., 2018).

Combination of multiple methodologies has the potential to explain plasticity in the distribution of bottlenose dolphins in ocean basins and better understand habitat use. Traditionally, photo-identification has been used as a basic technique to follow naturally marked individuals in surveyed areas (see Würsig & Jefferson, 1990). This technique has several limitations, such as the non-detection of usage in non-surveyed areas and substantial time and energy demands in conjunction with the high costs of boat-based surveys in longer-term studies. Carbon and nitrogen stable isotope analyses (SIA) provide a complementary alternative tool to better understand cetacean movements and feeding ecology (Kelly, 2000; Newsome *et al.*, 2010).

The basic principle of SIA is that the stable isotope ratios of a consumer ($^{13}C/^{12}C$, $\delta^{13}C$ and $^{15}N/^{14}N$, $\delta^{15}N$) are related to those of its prey (Peterson & Fry, 1987; Newsome *et al.*, 2010). Consumers that use similar environments and occupy the same trophic position have similar isotopic profiles (Renaud *et al.*, 2011). The utility of this technique resides on the isotopic fractionation (i.e. reaction difference between the heavy and light isotope) (Peterson & Fry, 1987), which results in an isotopic enrichment of the consumer relative to its prey (Sulzman, 2007). $\delta^{15}N$ generally increases by 3 to 4‰ with each step in the food web, offering a good indicator of the trophic level (Peterson & Fry, 1987). However, recent studies have shown that this rate could be lower for high trophic level organisms (Vanderklift & Ponsard, 2003; Hussey *et al.*, 2014). $\delta^{13}C$ values are indicators of primary production at the base of the food web and have a smaller increase that usually varies from 0.5–1‰ between trophic levels (Peterson and Fry, 1987). In marine environments, several studies have shown that there are significant differences between the carbon isotopic composition of animals living in pelagic and benthic systems and among those that live in coastal and oceanic environments (e.g. France, 1995; Newsome *et al.*, 2007, 2010). Therefore, carbon isotope values can be used as an indicator of the foraging habitat of a species and its habitat use (DeNiro & Epstein, 1978; Peterson & Fry, 1987; Fry, 2008). Some studies have shown that $\delta^{15}N$ can also inform aspects regarding the habitat use of a species. This isotopic ratio may also indicate differences when considering distinct habitats (e.g. inshore and offshore systems, latitudes and among oceanic basins) (see Chouvelon *et al.*, 2012; Ruiz-Cooley *et al.*, 2012). Additionally, carbon and nitrogen stable isotopes have also been used to quantify niche dimensions using the concept of 'isotopic niche' (Newsome *et al.*, 2007), which is comparable to the ecological niche because an animal's isotopic composition is directly influenced by its prey and the habitat in which it lives (Newsome *et al.*, 2007).

Isotopic fractionation may vary extensively among tissues (Newsome *et al.*, 2010), body sizes (Caut *et al.*, 2011) and diet (Vander Zanden & Rasmussen, 2001). Similarly, turnover rates also vary among tissues, depending on their metabolic activity in relation to protein content (Martínez del Rio *et al.*, 2009). For bottlenose dolphins, isotopic fractionation and turnover rates have been evaluated for skin (Giménez *et al.*, 2016) and blood (Caut *et al.*, 2011). For skin, Giménez *et al.* (2016) calculated an isotopic fractionation of 1.01‰ for $\delta^{13}C$ and 1.57‰ for $\delta^{15}N$, while 'half-life' turnover rates were 24 and 47 days, respectively. Therefore, the skin isotopic ratio reflects the integrated diet over the last one or two months.

The presence of *Tursiops truncatus* in inshore environments of the southern Brazilian coast allowed the development of more studies on the species, which has been surveyed for at least two decades (see Simões-Lopes & Fabian, 1999; Fruet *et al.*, 2011; Daura-Jorge & Simões-Lopes, 2016; Fruet *et al.*, 2017). Available data on *T. truncatus* from lower latitudes of the SAO (≤28°S) comes mainly from scattered stranding records (see Santos *et al.*, 2010; Meireles *et al.*, 2016; Moura *et al.*, 2016), and a few survey efforts devoted to assessing live individuals near shore (e.g. Lodi *et al.*, 2008; Lodi & Monteiro-Neto, 2012). As a consequence, there are still no available data regarding their distribution and habitat use within coastal and offshore waters for lower latitudes of the SAO.

The movements and habitat use patterns of a species could affect the population distribution and abundance, habitat selection, species interactions and the population structure (Nathan *et al.*, 2008; Börger, 2016). Furthermore, the investigation of habitat preferences and trophic ecology of an individual is very important for understanding the roles and niches occupied by it (e.g. Das *et al.*, 2000; Gross *et al.*, 2009; Bisi *et al.*, 2013; Santos-Carvalho, 2015), which may in turn help with conservation strategies for populations (Owen *et al.*, 2011). In this sense, a coupled approach using photo-identification and SIA was applied to: (1) investigate the occurrence and movements of bottlenose dolphins along the south-eastern Brazilian coast; (2) evaluate their habitat use and the trophic ecology of the species in the region; (3) compare movements and isotopic signatures calculated here with previous studies.

Materials and methods

Data collection and sampling

We used samples collected on oceanographic cruises conducted between 2012 and 2015 to investigate the occurrence and distribution of cetaceans in coastal waters with bottom depths ranging from 15–50 m along 600 km of shoreline in south-eastern Brazil (24–26°S). Surveys were conducted using 15 m high-speed boats travelling at 10 knots following pre-established transects (Figure 1). Due to the dimensions of the surveyed area, transects were divided in two sectors: a northern (Transect 1) and southern (Transect 2) sector. Each transect was covered on three different days. This division was logistical and did not take into account environmental or biological characteristics.

When a group of cetaceans was sighted, the geographic position (latitude and longitude), surface temperature and salinity, bottom depth and group size were estimated (Figure 1 and Table 1). We defined a group as an aggregation of two or more dolphins distributed in a cohesive manner and observed within an area with ~100 m radius (see Wells *et al.*, 1999a). Group size was estimated visually considering the probable best, high and low group size, as given by Connor *et al.* (2000). Photographs of the dorsal fin were taken for individual identification using a digital SLR camera with a 70–400 mm lense, as proposed by Würsig & Jefferson (1990) for small cetaceans. Furthermore, skin samples were collected for genetic and isotopic analyses in the majority of the sightings (Table 1) using a 150 lb crossbow (permit SISBIO 37.206) and frozen in liquid nitrogen onboard.

Photo-identification analyses

Individuals were identified using the photo-ID technique of Würsig & Würsig (1977) and following the recommendations of Würsig & Jefferson (1990). Photographs of dorsal fins were analysed based on photograph quality and distinctiveness of natural marks. Regarding the quality, photos were classified into four categories: 0 – photographs that were taken just after a dolphin's dive and contained no image of the individual; 1 – photographs without adequate quality to identify individuals in the frame (e.g. blurred, without focus, sharpness); 2 – photographs with sufficient quality to identify individuals taken at distances ranging from 5 to 10 m; and 3 – photographs with sufficient quality to identify individuals taken at distances of up to 4 m. Photos in categories 2 and 3 were useful for identification purposes. Considering distinctiveness, when natural marks were present, the letter 'c' was attached to quality categories 2 and 3, representing the marked individuals. When no distinctive marks were shown along the dorsal fin border, the letter 's' would follow categories 2 and 3, representing the unmarked dolphins. Additionally, the proportion of the dorsal fin out of the water and the amount of water splash were also considered in the appropriate choice of photos (for more details, see Santos &

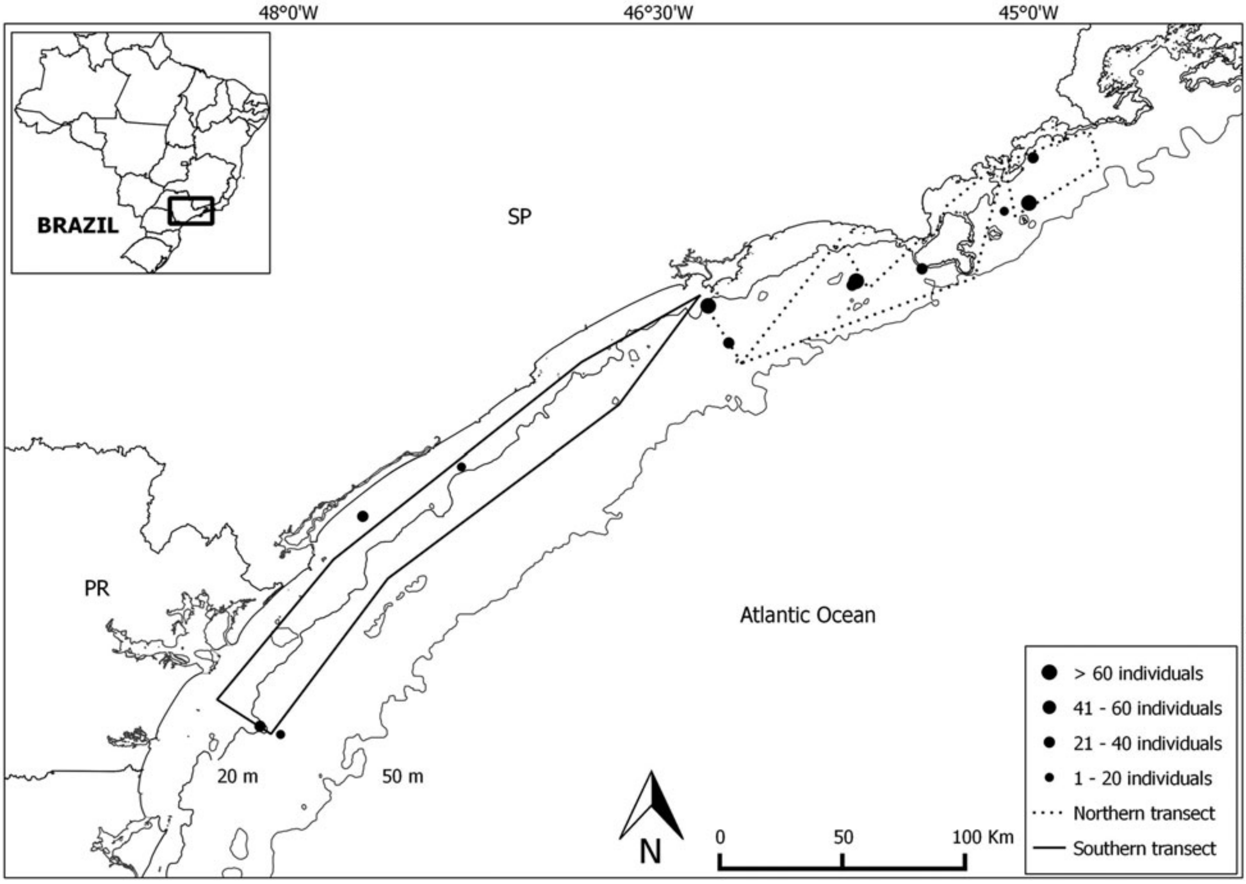

Fig. 1. Map of the study area showing the covered transects and the geographic position where groups of bottlenose dolphins (*Tursiops truncatus*) were sighted between 2012 and 2015 along the south-eastern coast of Brazil. SP, São Paulo state; PR, Paraná state.

Rosso, 2008). Darwin software was used to model photographs (see Stewman *et al*., 2006), and all matches were manually checked. Individual movements were analysed using estimated Euclidean distances within ArcGIS (ESRI, USA), following the shoreline whenever physical barriers such as islands were found in the middle of the path.

Gender of biopsied individuals

Skin samples were used to sex the sampled individuals following the methodology described in Rosel (2003). These analyses were conducted at the Departamento de Genética, Evolução e Bioagentes at Universidade Estadual Paulista (UNICAMP), São Paulo State, Brazil.

Stable isotope analyses

We collected 35 skin samples from bottlenose dolphins: 11 in the southern sector and 24 in the northern one. In the laboratory, samples were dried in an oven at 60°C for 48 h. Lipids were extracted from samples with a solution with chloroform and methanol (2:1) for 24 h as they may influence the values of δ^{13}C (Folch *et al*., 1957). Giménez *et al*. (2017a, 2017b) tested the effects of lipid extraction from the skin of bottlenose dolphins, showing that effects were not significantly present due to low lipid content indicated by C:N ratios. Although there is no consensus among other studies on the need for extraction, we proceeded with lipid extraction as it is recommended in most cases (Newsome *et al*., 2010). However, studies by Liden *et al*. (1995) and Pinnegar & Polunin (1999) suggested that compounds used in the extraction may affect the δ^{15}N values. Therefore, analyses in duplicate/triplicate were performed to avoid bias in the results. The elemental composition of carbon and nitrogen was used to calculate sample C:N ratios, with a C:N < 3.5 considered indicative of an efficient lipid extraction (Post *et al*., 2007).

Samples of ~0.3–0.7 mg of residual skin were encapsulated in tin capsules and sent to the Stable Isotope Core Laboratory (Washington State, USA) for isotopic analyses. Analyses were performed using a GV Instruments Isoprime mass spectrometer interfacing with a Costech elemental analyser. The analytical precision was ±0.3 for δ^{13}C and ±0.5 for δ^{15}N. The δ^{13}C and δ^{15}N values were calculated using the equation proposed by Peterson & Fry (1987):

$$\delta = \frac{\delta\ \text{sample}}{\delta\ \text{standard}} - \times 1000$$

where δ sample and δ standard are the isotopic values of the sample and standard, respectively. The standards used were the Pee Dee Belemnite (PDB) and atmospheric nitrogen (N_2) for carbon and nitrogen isotopic signatures, respectively.

Isotopic data treatment

δ^{13}C and δ^{15}N values were initially compared between the two main surveyed sectors (northern and southern) to evaluate possible spatial segregation. The São Paulo state coast is influenced by different environmental and oceanographic processes depending on the sector (see Besnard, 1951; Castro-Filho *et al*., 1987; Castro & Miranda, 1998; Castro *et al*., 2006). Therefore, these processes may affect the distribution and the composition of bottlenose dolphins' prey (e.g. Ballance, 1992), influencing their

Table 1. Collected data on sightings of bottlenose dolphins (*Tursiops truncatus*) after 21 oceanographic cruises conducted between 2012 and 2015 along the south-eastern coast of Brazil

Date	Sector	Group size (N)	Biopsies (N)	Depth (m)	Temperature (°C)	Salinity (psu)
04/14/2012	N	70	0	30	–	–
12/06/2012	N	12	0	34	28.1	–
01/19/2013	N	35	0	30.5	26	–
08/10/2013	S	30	5	15.5	19.3	39
02/10/2014	S	15	1	20.7	32.7	30
02/26/2014	S	40	0	23.3	29.9	40
05/08/2014	N	80	11	36.7	25.3	35
08/20/2014	S	17	0	32	21.9	40
08/21/2014	S	55	6	15.6	21.1	27
11/11/2014	N	26	3	35	24.5	38
12/17/2014	N	65	6	25.5	24.9	30
12/19/2015	N	35	4	43	26	37
06/09/2015	N	25	0	25	25	35

Date (MM/DD/YYYY), investigated sector (north – N and south – S), environmental parameters (water depth, temperature and salinity), group size, and number (N) of collected biopsies are presented.

trophic ecology in the surveyed sectors. The isotopic signatures were compared between male and female bottlenose dolphins of both sectors. These comparisons were also useful to evaluate the existence of sexual segregation in the study area, because energy demands may vary between genders (e.g. Rossman *et al.*, 2015; Secchi *et al.*, 2017). Data were tested for normality and homoscedasticity using the Shapiro–Wilk and Bartlett tests, respectively. A Student's *t*-test was then applied using averages of the δ^{13}C and δ^{15}N values to compare patterns in habitat use and trophic ecology between the sectors. For gender comparisons, a Welch *t*-test was used with the same intentions. All statistical analyses were performed using R 3.5.3 (R Development Core Team, 2019). Results are shown using mean ± SD when applicable. P<0.05 was chosen to indicate statistical significance.

The isotopic niche width was estimated between sectors and sexes using Stable Isotope Bayesian Ellipses through the SIBER package in R (see Jackson *et al.*, 2011). The standard ellipse area (SEA) for each group was estimated, as well as SEA corrected for small sample size (SEA$_C$). In addition, Bayesian SEA (SEA$_B$) based on 100,000 posterior draws was computed. The probability (P) that two isotopic niche areas differed from each other was determined using Bayesian inference based on these posterior draws (i.e. the probability that the isotopic niche area of group 1 is greater than group 2 is the proportion of group 1 standard ellipses that are greater than group 2 standard ellipses, based on 100,000 replicates). The per cent overlap between the isotopic niches was calculated using the SEA$_C$ (with 100% as the upper limit). For these estimations, a prediction interval (p-interval) of 40% was considered (see Jackson *et al.*, 2011).

Results

Observation effort, photo-ID and individual movements

The 21 oceanographic cruises conducted between 2012 and 2015 resulted in sightings of 13 groups of bottlenose dolphins (~62% of the surveys). From these sightings, eight groups were observed in the northern sector and five in the southern sector (Figure 1). The number of individuals per group ranged from 12 to 80 (39 ± 22 individuals, mean ± SD; N = 13) and sightings were reported in waters with bottom depths ranging from 15.5–43 m (28 ± 8 m, mean ± SD; N = 13), with surface water temperatures ranging from 19.3–32.7°C (28 ± 8°C, mean ± SD; N = 12), and water salinity ranging between 27–40 psu (35 ± 4 psu, mean ± SD; N = 10) (Table 1).

A total of 11,572 photos yielded the identification of 177 unique individuals, with 24 sighted more than once. The discovery curve of new individuals (Figure 2) did not reach a plateau. This could be due to low survey effort relative to the abundance of the species or their mobility in the study area. Re-sightings occurred in intervals that varied between 82 and 979 days (368 ± 194 days, N = 24) and at distances ranging from 7–179 km (25.9 ± 55 km, N = 24). Movements of re-sighted individuals are shown in Figure 3, considering 22 individuals sighted on two occasions and two individuals sighted on three occasions. These two bottlenose dolphins were only sighted in the southern sector. Their first and second sightings were closely spaced (7 km apart) over an interval of 345 days. These dolphins were sighted together with 15 other catalogued individuals. Their third sighting was reported 82 days and 177 km away from the second one. These results suggest upon first impression the existence of a possible spatial segregation. During the four years of investigation, re-sighted bottlenose dolphins were not observed using both sectors.

Stable isotope analyses

Skin samples of bottlenose dolphins were collected in seven from 12 sightings totalling 35 individuals (Table 1). Considering the results of SIA, δ^{13}C and δ^{15}N values ranged from −16.79 to −12.39‰ (−14.82 ± 1.07, N = 35) and from 14.94–18.57‰ (17.22 ± 0.88, N = 35), respectively. The mean values and variability of the data for sectors and genders by sectors are shown in Table 2 and Figure 4. For the two isotopic values, the differences for the means were not significant between sectors (δ^{13}C: P = 0.30; δ^{15}N: P = 0.91). Regarding the comparisons between genders, males sampled in the south sector presented δ^{13}C values more enriched than the southern females, northern males and northern females. In contrast, southern females, northern males and northern females did not differ in relation to their carbon signatures. Similarly, there were no differences in the δ^{15}N values

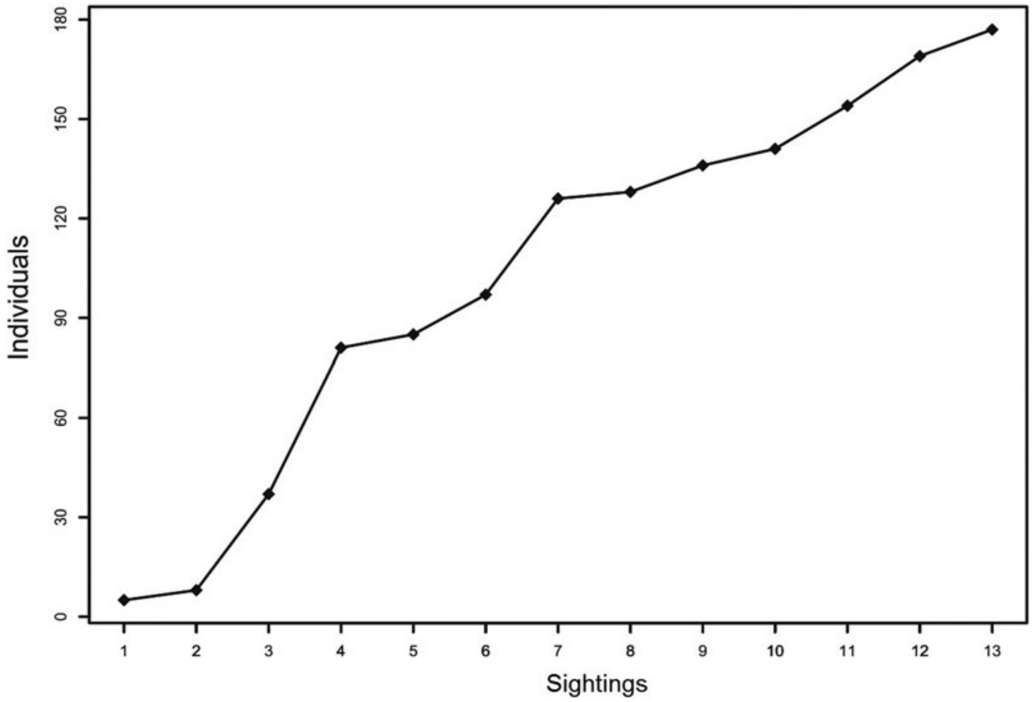

Fig. 2. Discovery curve of individual identifications of bottlenose dolphins (*Tursiops truncatus*) sampled in oceanographic cruises conducted between 2012 and 2015 along the south-eastern coast of Brazil.

between males and females of the same sector and between different sectors. The results of the statistical tests are presented in Table 3.

Isotopic niche width was estimated and varied between sectors and genders (Figure 5). Bottlenose dolphins sampled in the northern sector had a larger niche when compared with the southern ones (3.20 and 1.56‰^{2}, respectively; $P = 96\%$). For gender comparisons, the SEA$_B$ of the northern males was greater than the northern females (3.77 and 2.89‰^{2}, respectively; $P = 74\%$). In contrast, the southern females presented a larger isotopic niche than the southern males (1.19 and 0.46‰^{2}, respectively; $P = 94\%$). Regarding gender comparisons between distinct sectors, the ellipses of the northern males and females were larger than the southern ones in almost 100% of the total Bayesian estimates.

The overlap between the SEA$_C$ of the northern and southern individuals was 41 and 79%, respectively (Figure 6). Regarding gender comparisons, the overlaps varied from 14.33 and 97.72%, with the smallest overlap being found between southern and northern males, and the largest one between northern males and females. Small overlaps were also calculated between southern males and northern females (~14.50%). Besides that, larger overlaps were also calculated between northern and southern males (95%), northern males and southern females (~90%), northern females and southern males (~74%), northern and southern females (~92%) and northern females and males (~76%). Finally, intermediate values were found between southern females and northern males (~35%) and between southern and northern females (~47%). No overlap was found between the SEAc of southern males and females. All percentages are shown in Table 4 and presented in Figure 7.

Discussion

The bottlenose dolphin was sighted over almost the entire studied area in depths ranging from 15.5–43 m. Lodi *et al.* (2016) suggested that the species has a continuous distribution along the Brazilian coast, which varies in depth from 1.6–50 m, as reported by Laporta *et al.* (2016). The group sizes detected in the present work (mean 39 ± 22 individuals, N = 13) were higher than those previously observed in other regions of the Brazilian coast. Lodi & Monteiro-Neto (2012) reported groups of bottlenose dolphins of up to 30 individuals off the coast of Rio de Janeiro. Additionally, small groups of up to nine individuals were found in estuarine waters of southern Brazil (see Simões-Lopes & Fabian, 1999; Fruet *et al.*, 2011; Daura-Jorge & Simões-Lopes, 2016; Giacomo & Ott, 2016). According to Norris & Dohl (1980) and Gygax (2002), social groups of toothed whales have the tendency to be larger and as they are found further away from the coast, that may help them to optimize location and capture of patchy food resources in a vast area, as well as to protect their congeners from predators. For bottlenose dolphins, differences in group size are possibly related to ethological and ecological drivers such as the flexible and highly adaptable behaviour of the species, their social patterns that may vary by region and the distribution of prey and predators (Shane *et al.*, 1986; Defran & Weller, 1999; Connor *et al.*, 2000).

Movements of bottlenose dolphins may vary consistently when comparing coastal and oceanic populations. For example, coastal groups observed along the Florida coast showed short movements up to 40 km (see Durden *et al.*, 2019). In contrast, Robinson *et al.* (2012) estimated distances up to 1277 km for eight coastal bottlenose dolphins sampled on Irish and UK coasts, which presented a new record for European waters, where the species usually show site fidelity and movements less than a few hundred km. Regarding the oceanic dolphins, Wells *et al.* (1999b) and Klatsky *et al.* (2007) reported travelled distances from 1300 and 4200 km, respectively. Here, we identified short-range movements of up to 179 km for bottlenose dolphins using photo-identification in south-eastern Brazil. In northern waters from the surveyed area, Lodi *et al.* (2008) showed that eight individually marked coastal bottlenose dolphins moved up to 100 km. In contrast, off southern Brazil, Simões-Lopes & Fabian (1999) observed movements of bottlenose dolphins that reached 314 km.

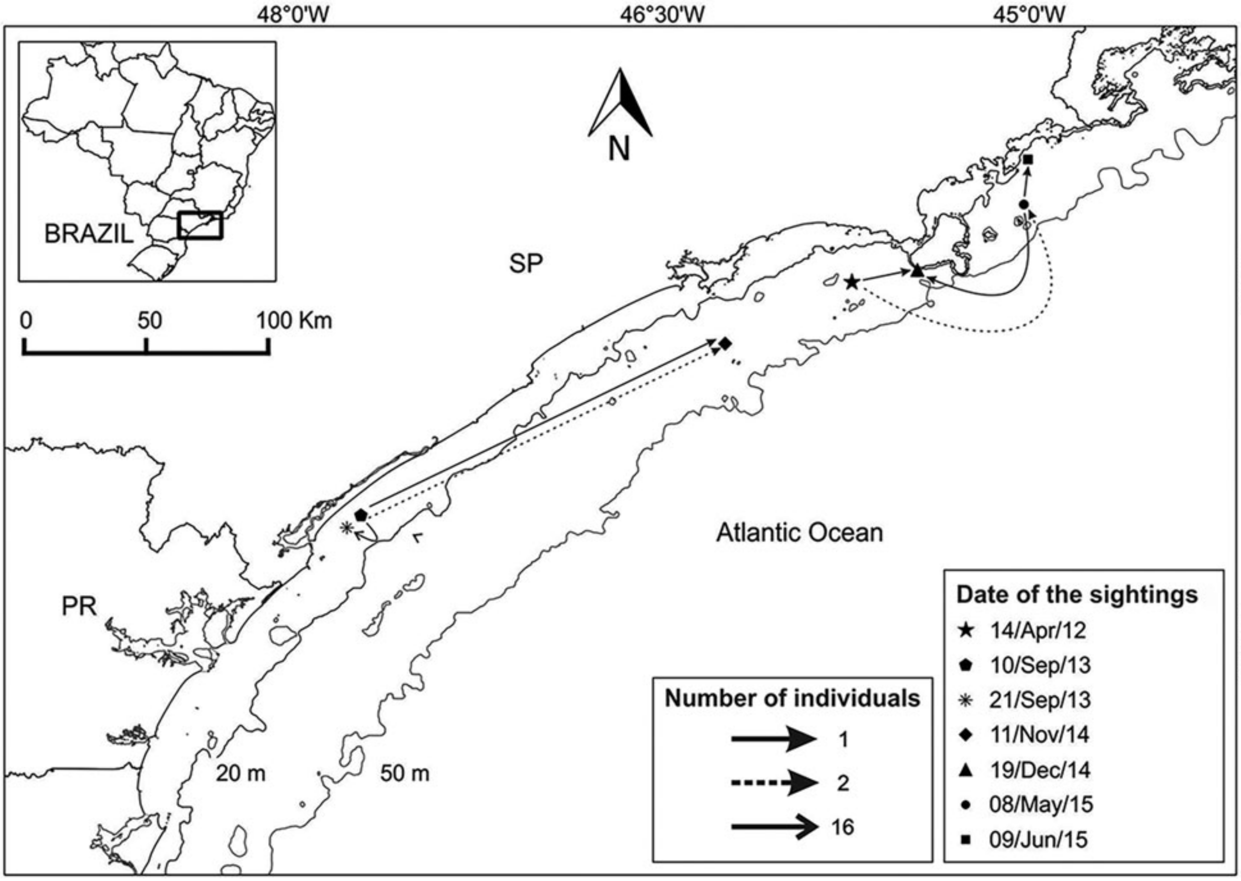

Fig. 3. Sightings and re-sightings of bottlenose dolphins (*Tursiops truncatus*) along the south-eastern coast of Brazil between 2012 and 2015. The start of each arrow indicates the first sightings and the arrowhead indicates the direction of the re-sightings. The format of the arrows indicates the number of individuals re-sighted between the sightings. SP, São Paulo state; PR, Paraná state.

Table 2. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios (mean ± SD) and ranges (minimum and maximum) of bottlenose dolphins (*Tursiops truncatus*) sampled along the south-eastern coastal waters of Brazil between 2012 and 2015

	Sector/Gender	N	Mean ± DP	Minimum	Maximum
$\delta^{13}C$ (‰)	North	24	−15.22 ± 0.96	−16.79	−13.72
	South	11	−14.64 ± 1.08	−16.50	−12.39
	Northern male	13	−14.86 ± 0.32	−16.79	−12.89
	Northern female	11	−14.94 ± 0.35	−16.50	−12.39
	Southern male	6	−13.98 ± 0.10	−14.41	−13.72
	Southern female	5	−15.45 ± 0.29	−16.02	−14.37
$\delta^{15}N$ (‰)	North	24	17.43 ± 0.88	16.02	18.29
	South	11	17.20 ± 0.97	14.94	18.57
	Northern male	13	17.23 ± 0.30	14.94	18.46
	Northern female	11	17.21 ± 0.25	15.86	18.57
	Southern male	6	17.12 ± 0.28	16.00	18.15
	Southern female	5	17.26 ± 0.29	16.60	18.29

The values are separated by the sectors (north and south) and genders by sector (southern males and females, and northern males and females).

Movements may occur for a diversity of reasons, such as feeding, searching for mates and protection from predators (Stern, 2009). Simões-Lopes & Fabian (1999) suggested the movements of bottlenose dolphins in southern Brazil were probably related to mullet (*Mugil* sp.) migration, an important prey for the species diet in that region. Besides that, the same authors argued that those movements could also be related to the dispersion of genes among social groups of different areas. Few stomach content studies of bottlenose dolphins have been conducted in south-eastern Brazil (e.g. Di Beneditto *et al.*, 2001; Santos *et al.*, 2002; Melo *et al.*, 2010; Moura *et al.*, 2016), with only 14 stomachs analysed so far. These samples suggested an ichthyophagous feeding

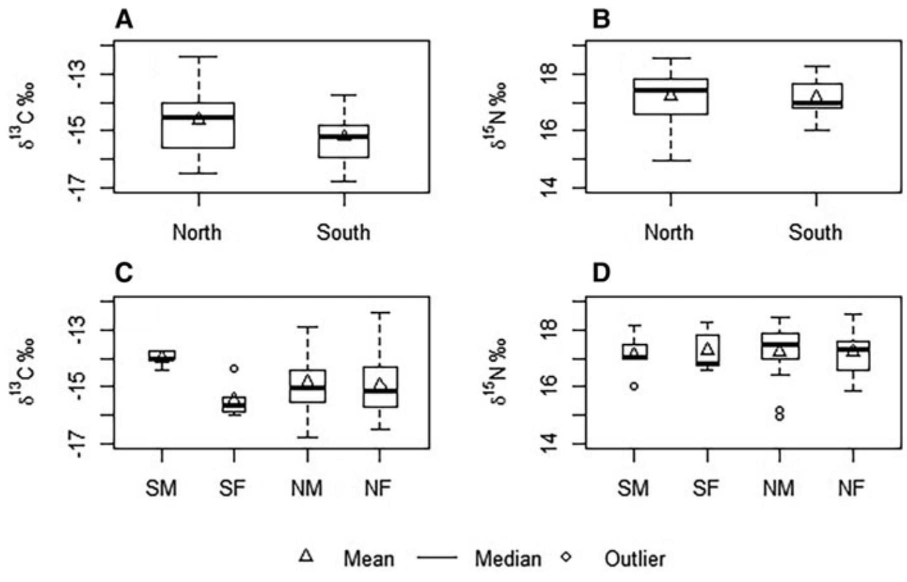

Fig. 4. Box plots of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic ratios for bottlenose dolphins (*Tursiops truncatus*) sampled along the south-eastern coast of Brazil between 2012 and 2015 in relation to the northern and southern sectors (A and B) and considering genders by sectors (C and D). Whiskers represent maximum and minimum values. An observation beyond 1.5 times the spread is considered an outlier. SM, southern males; SF, southern females; NM, northern males; NF, northern females.

Table 3. Results of the Student's and Welch *t*-test for comparisons of carbon ($\delta^{13}C$ – lower-left) and nitrogen ($\delta^{15}N$ – upper-right) isotope ratios from male and female bottlenose dolphins (*Tursiops truncatus*) sampled in the south and north sector of the study area between 2012 and 2015 along the south-eastern coast of Brazil

	Southern male	Southern female	Northern male	Northern female
Southern male		0.76	0.83	0.82
Southern female	**0.005**		0.95	0.91
Northern male	**0.02**	0.19		0.97
Northern female	**0.02**	0.29	0.85	

The numbers represent the *P*-values. The bold *P*-values represent the ones which are statistically significant.

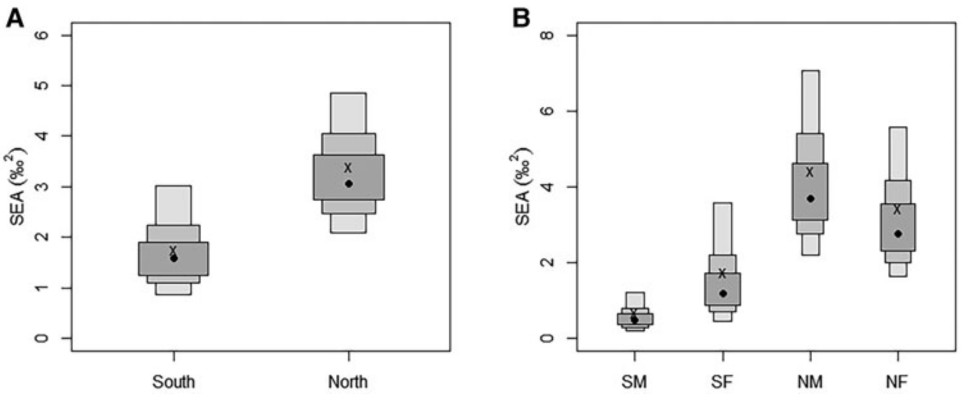

Fig. 5. Density plot of Bayesian standard ellipse areas (SEA_B) for bottlenose dolphins (*Tursiops truncatus*) sampled along the south-eastern coast of Brazil between 2012 and 2015 in relation to the northern and southern sectors (A) and considering genders by sector (B). The black dots represent the mode of posterior distribution of SEA_B values with grey boxes presenting the 50, 75 and 95% credibility intervals (from dark to light grey, respectively). The black 'X' represents the mean standard ellipse area correct for small sample numbers (SEA_C). SM, southern males; SF, southern females; NM, northern males; NF, northern females.

strategy, but the small sample size does not allow us to reach further conclusions regarding the influence of prey preferences on movement patterns in the surveyed area. Besides that, potential predators such as killer whales (Santos *et al.*, 2010) and great sharks (Santos & Gadig, 2009) were previously reported in the surveyed area and closer vicinities, but no interactions with bottlenose dolphins have been observed. Therefore, additional investigation of such parameters should be addressed in the surveyed area to better understand the described local movements.

Only 13.6% of the catalogued bottlenose dolphins were re-sighted. This fact could be related to the small number of cruises in comparison to the abundance of the species in the study area. We showed that re-sightings occurred within both the northern and southern sectors. However, in the southern re-sightings, 17 individuals were seen in two different sightings with 345 days and 6.5 km of distance between them, which may indicate site fidelity and a preference of use of the southern area. Besides that, no re-sighted bottlenose dolphin was seen moving in both sectors, which could be showing a spatial segregation of individuals in the southern and northern part of the study area. Thus, we tested for differences in stable isotopes signatures of bottlenose dolphins found in the two areas to evaluate whether they were ecologically segregated.

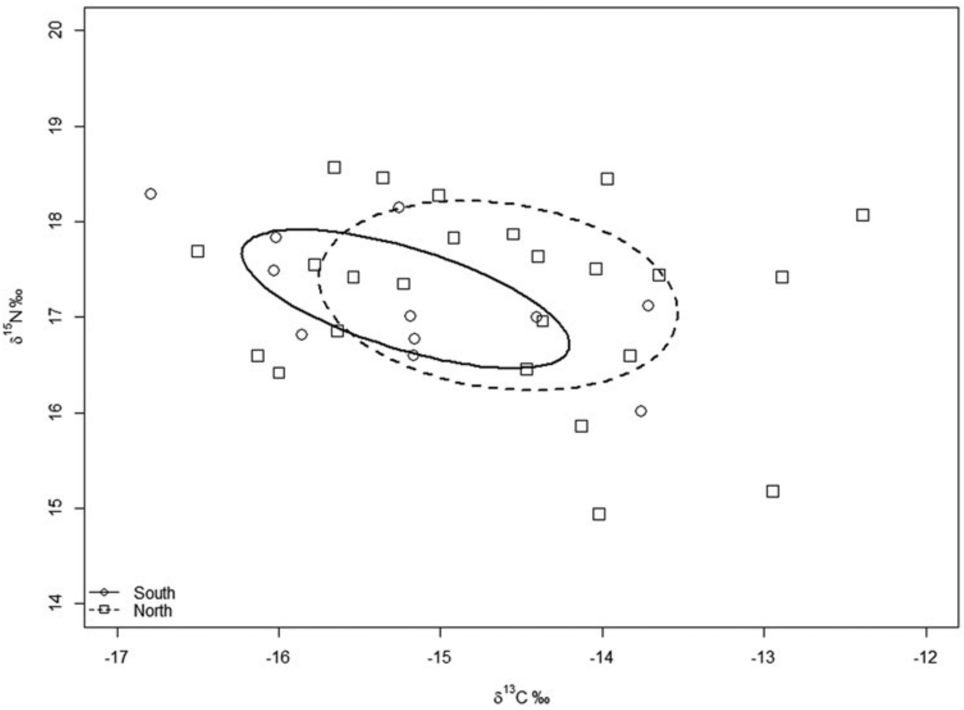

Fig. 6. Stable isotope values of bottlenose dolphins (*Tursiops truncatus*) sampled along the south-eastern coast of Brazil between 2012 and 2015 in relation to the northern and southern sectors. The lines depict the standard ellipse for corrected small sample size (SEA_C). The SEA_C represents the isotopic niche.

Table 4. Percentages of overlap calculated between the standard ellipses corrected for small sample sizes (SEA_C) estimated for male and female bottlenose dolphins (*Tursiops truncatus*) sampled in the southern and northern sector of the study area between 2012 and 2015 in the south-eastern coast of Brazil

	Southern males	Southern females	Northern males	Northern females
Southern males		0.00	14.33	14.43
Southern females	0.00		35.20	46.70
Northern males	95.00	89.70		97.72
Northern females	74.30	92.33	75.60	

The values represent the overlaps between the groups using the lines as reference.

Bottlenose dolphins sampled in the southern and northern regions of the study area did not present statistically significant differences between their isotopic signatures, which may indicate that dolphins of both sectors are influenced by similar carbon sources and occupy equivalent trophic levels. This fact is confirmed by the high overlaps found between the isotopic niches, indicating ecological similarities. In contrast, we found significant differences when splitting the dataset by sector and sex. First, southern males and females could be differentiated between their $\delta^{13}C$ values, which showed no overlap between their niches. This suggests a possible variation in the foraging environments and, consequently, a sexual segregation for the species in this region. Cockcroft & Ross (1990) has previously shown that males were consuming a greater proportion of larger fish than females in South Africa. Similarly, Secchi *et al.* (2017) revealed sexual differences in the prey preferences from the southern coast of Brazil, which was attributed to distinct habitat use. In contrast to the southern sector, bottlenose dolphins may not be isotopically segregated by gender in the northern sector, suggesting a similar feeding ecology which is reinforced by the great overlap between their isotopic niche. According to Riccialdelli & Goodall (2015), an absence of niche segregation between individuals of distinct sexes might be a result of a cooperation in feeding activities, which is known for other populations of the species (see Wells & Scott, 1999, 2017). It is important to note that similar isotopic signatures can be produced by distinct prey that are bound to analogous carbon sources and trophic levels (Bearhop *et al.*, 2004; Browning *et al.*, 2014). Therefore, northern males and females could be using different prey that are not distinguishable in their carbon and nitrogen isotopic signatures. However, it is important to note the limited sample size for the isotopic analyses, mainly when we consider the division of the dataset by area and sex. Thus, complementary studies to improve our knowledge of the social patterns and diet of *T. truncatus* in the south-eastern Brazilian coast are important for a better understanding of this result.

We found the isotopic niche width was significantly greater for the northern sector than for the southern one (3.20 and 1.56‰^{2}, respectively). Such divergence may be related to the temporal variability of oceanographic conditions in the study area that can influence the diversity and availability of prey and, therefore, the habitat use by bottlenose dolphins. The southern sector is highly affected by the Cananéia-Iguape estuarine complex basin, which drains organic matter to the coast (Besnard, 1951), and also functions as a nursery area for many fish species (Schaeffer-Novelli *et al.*, 1990). In contrast, the northern sector is characterized by rocky shores with no influence of discharges from estuaries or large riverine tributaries (Besnard, 1951), but

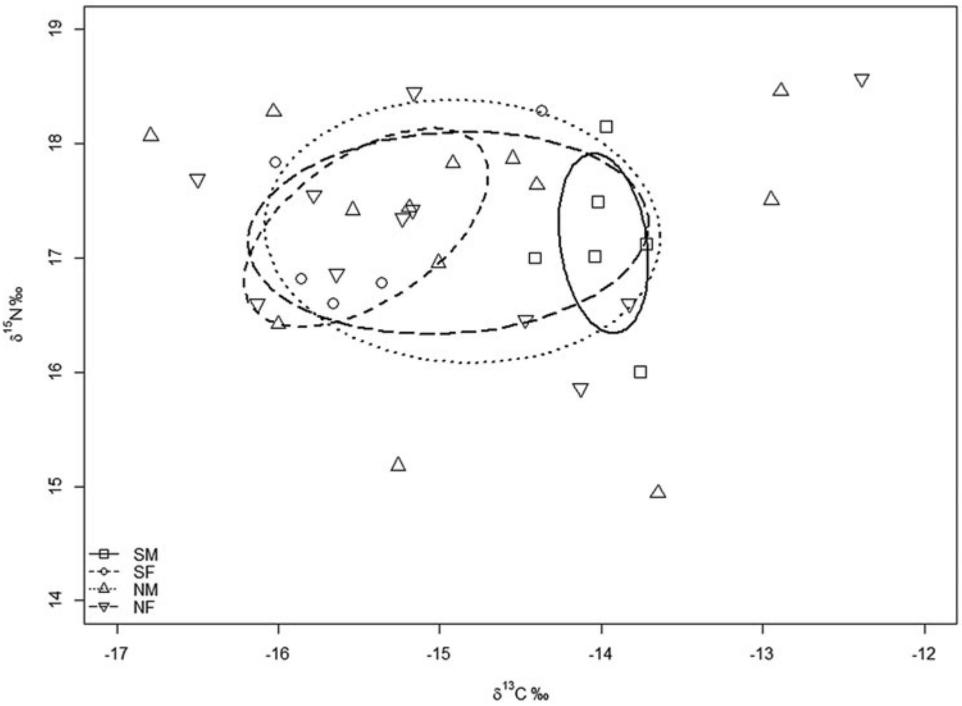

Fig. 7. Stable isotope values of the bottlenose dolphins (*Tursiops truncatus*) sampled along the south-eastern coast of Brazil between 2012 and 2015 considering genders by sector. The lines depict the standard ellipse for corrected small sample size (SEA_C). The SEA_C represents the isotopic niche. SM, southern males; SF, southern females; NM, northern males; NF, northern females.

is strongly influenced by coastal upwelling (Castro-Filho *et al.*, 1987; Castro *et al.*, 2006), which may also contribute to the local biological productivity (Matsuura, 1996). Therefore, it would be important to evaluate in detail the local prey diversity and abundance, since they could influence these patterns. Additionally, future studies on bottlenose dolphins' local diet should be considered to understand its variability in relation to distinct regions of the Brazilian south-eastern coast.

Despite the isotopic differences found between genders in the southern sector and the similarities for the northern one, males and females in both regions presented distinct isotopic niche width, which can be due to divergence in their home ranges. For example, male bottlenose dolphins may frequently exhibit a large home range (see Wells, 2003; Urian *et al.*, 2009), which could provide different resources and, consequently, a larger niche. However, they could specialize in certain types of prey, that may be related with their caloric requirements, as was suggested by Rossman *et al.* (2015) to explain the smaller isotopic niche found for male bottlenose dolphins in relation to females in Sarasota Bay. In contrast, females may present higher fidelity to some areas and consequently smaller home ranges (see Wells, 2003; Urian *et al.*, 2009), but they could specialize in a greater subset of resources that also provide a larger isotopic niche (e.g. Rossman *et al.*, 2015; Secchi *et al.*, 2017).

The present work revealed similar carbon isotopic signatures to other studies which sampled coastal ecotype individuals of *T. truncatus* in south-eastern Brazil (~23°S) (see Bisi *et al.*, 2013). However, in contrast, the values in our study differed from the ones from individuals belonging to the estuarine ecotype found in waters from southern Brazil (~28–33°S) (see Botta *et al.*, 2012; Secchi *et al.*, 2017). Although different tissues were analysed when comparing studies, the observed $\delta^{13}C$ values showed divergence possibly induced by the habitat use of the species in different regions of the Brazilian coast. Therefore, our results reinforce previous studies, which have described the existence of two stocks of bottlenose dolphins showing differences in their distribution, that are individuals in estuarine-shallow coastal waters south of 28°S and individuals in coastal-oceanic waters north of 28°S (see Costa *et al.*, 2019). However, there are no available investigations regarding isotopic values from latitudes lower than Rio de Janeiro state along the Brazilian coast. Thus, more studies with individuals of lower latitudes will be important to render a more complete description of the differences in area of use of bottlenose dolphins in that region.

The absence of re-sighted individuals moving across both surveyed sectors may be showing two different stocks with similar $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures in the study area. Besides that, this fact may indicate a certain degree of fidelity of bottlenose dolpins sampled in each sector, although we have limited photo-ID data to prove this completely. However, differences in the width of isotopic niches denote some important ecological variations. These results could be being influenced by local oceanographic factors, which may also contribute to differences in the feeding ecology and habitat use of males and females sampled in each sector, although it would be important to increase the number of samples to improve our conclusions about this finding. The present work is a preliminary evaluation that needs to be continued over the long term in the study area. Thus, we suggest that future local studies can combine photo-identification and SIA with other methods, such as stomach content analyses, genomics and telemetry that will be useful to better understand ecological aspects of *T. truncatus* off the south-eastern Brazilian coast. In further investigations it will be important to increase the amount of data for local bottlenose dolphin isotopic signatures, and also include other cetacean species with their potential prey to better understand the structure and their function in the local coastal ecosystem.

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