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ORIGINAL ARTICLE

Long-term and gender-related variation in the feeding ecology of common bottlenose dolphins inhabiting a subtropical estuary and the adjacent marine coast in the western South Atlantic

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ABSTRACT
We combined stomach content analysis and stable isotopes to investigate long-term changes in the feeding ecology of common bottlenose dolphins (*Tursiops truncatus*) from the Patos Lagoon estuary and adjacent marine coast, southern Brazil, during the past 35 years. Stomach contents of bottlenose dolphins collected between 2002 and 2012 (Period II) were compared to those previously described for this population (1977–1980, Period I), and δ^{13}C and δ^{15}N values in tooth dentine from specimens collected between 1977 and 2012 were used to assess temporal changes in contribution of the main prey to the diet of dolphins over time. Additionally, these data were used to verify the magnitude of trophic overlap between males and females from Period II. Bottlenose dolphins consumed a wide variety of prey. Demersal and demersal–pelagic teleost fish predominated. These results show that bottlenose dolphins from the Patos Lagoon estuary are opportunistic feeders and confirm the plasticity of the species, which preys upon the most available prey. Differences in diet were found between seasons and periods. Stable isotopes and stomach contents detected a significant long-term change in the proportions of their main prey. The contribution of *Micropogonias furnieri* and *Menticirrhus* sp. decreased after 1990 while a significant increase in the importance of *Trichiurus lepturus* was observed. Males consumed a significantly higher proportion of *T. lepturus* while *Mugil liza* was the main prey for females. These changes might be due to fishing-related changes in fish abundance.

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Introduction

Evaluating the feeding habits of marine mammals is important to determine their position in the food chain and define their ecological role in the ecosystem (Pauly et al. 1998). However, these ecological traits vary within components of the population due to different resource utilization. Plasticity in diet brings advantages to the predator by minimizing both intraspecific and interspecific effects of competition and by allowing adaptation to a changing environment (e.g. Schoener 1974; Saulitis et al. 2000; Bizzarro et al. 2007). Prey availability may vary naturally due to stochastic effects on survival and reproductive rates, and hence on recruitment, or due to human-related causes such as overfishing. Competition between marine mammals and fisheries is well documented and overfishing can affect marine mammals by reducing the availability of their prey (e.g. Plagányi & Butterworth 2005).

The subtropical Patos Lagoon estuary (PLE), southern Brazil, is an important spawning and nursing habitat of several fish and crustaceans (Castello & Möller 1978; Chao et al. 1985; Vieira & Castello 1997) that sustain commercial fisheries and top predators on the adjacent continental shelf (Pinedo 1997; Vooren 1997; Haimovici et al. 2006). Nevertheless, some species have already shown signs of collapse or overexploitation due to long-term fishing pressure in this area (e.g. Vasconcellos & Haimovici 2006; Vasconcellos et al. 2006; Odebrecht et al. 2010; Lemos et al. 2014). This estuary is home to a resident population of common bottlenose dolphins (*Tursiops truncatus* (Montagu, 1821) – referred to as the bottlenose dolphin), recently estimated at ca. 80–90 individuals (Fruet et al. 2011, 2015). The bottlenose dolphin is a wide-ranging cetacean inhabiting both coastal and oceanic areas of tropical and temperate zones of all oceans, sometimes

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The supplementary material for this article (Tables SI–SVI) is available at http://dx.doi.org/10.1080/17451000.2016.1213398

entering estuaries and rivers (Wells & Scott 2009). In the western South Atlantic, the species occurs from tropical to cold temperate waters and includes coastal and offshore ecotypes (Costa et al. 2016). The population that inhabits PLE is part of a metapopulation that includes groups occurring along the adjacent marine coastal zones (Fruet et al. 2014). The sex ratio of the estuary-resident population is female-biased (2:1), while the sex distribution of dolphins washed ashore along the coast is highly skewed towards males, mostly juveniles (Fruet et al. 2012, 2014). This suggests that some degree of habitat partitioning is likely to exist, which could be a strategy to minimize trophic overlap with conspecifics or to increase gene flow with adjacent populations to reduce inbreeding.

The bottlenose dolphin is defined as a generalist, but a particular diet has been observed in different places, reflecting some degree of plasticity in feeding habits according to spatial and temporal patterns of prey availability (e.g. Barros & Wells 1998). Furthermore, ontogenetic and gender-related differences in diet have been observed (Cockcroft & Ross 1990; Blanco et al. 2001; Pate & McFee 2012). Although the ontogenetic or gender-related variation in diet might exist because of differences either in energetic demands or physiological fitness/behavioural skills to catch some sorts of prey, it is probable that all components of the predator population will benefit by minimizing both intra- and interspecific trophic overlap (Begon et al. 2006). Likewise, temporal differences in diet, due to seasonal variation of energetic demand or prey availability, might represent an optimal niche adaptation to maximize local resource utilization.

In the PLE region it has been demonstrated through stomach content analysis (SCA) of carcasses washed ashore that bottlenose dolphins feed exclusively on teleost demersal fish (Pinedo 1982; Lopez 2013). SCA can yield direct information on the diet as well as insight on prey availability and variation. However, this information is often biased owing to different digestion rates or the secondary ingestion of prey (Barros & Clarke 2002). Some of these limitations can be minimized by increasing sample size over an appropriate time length. In the case of small populations, however, large sample size is an exception rather than a rule. An alternative to overcome these constraints is the stable isotope analysis (SIA) of key elements, such as carbon and nitrogen, as complementary methods for studies on feeding ecology and patterns of habitat use in aquatic vertebrates. Stable isotope values in animal tissues reflect those in the food webs where they feed and are useful particularly for determining trophic levels, identifying major food sources, and assessing foraging habitats (e.g. Rubenstein & Hobson 2004; Graham et al. 2010). Nitrogen isotope values increase considerably (ca. 3–5‰) and in a predictable fashion between trophic levels, hence reflecting trophic position (De Niro & Epstein 1981; Cabana & Rasmussen 1996). Although $\delta^{13}C$ values also increase with trophic levels, it happens at a much lower rate (ca. 1‰) (De Niro & Epstein 1978; Peterson & Fry 1987; McCutchan et al. 2003). Therefore, carbon isotope values are often used as an indicator of the sources at the base of the food web where predators feed (Hobson 1999; Graham et al. 2010). Teeth are a particularly informative tissue for tracking the diet of cetaceans over their lifetimes, as they provide a permanent dietary record for an individual because, under normal conditions, growth layers in teeth do not resorb or modify (Walker & Macko 1999; Niño-Torres et al. 2006). Therefore, temporal changes in the diet can be investigated by analysing the stable isotope composition in teeth of these long-lived predators.

The objective of this study was to investigate long-term changes in the feeding ecology of a high-trophic-level predator inhabiting the PLE and adjacent marine coast. The hypotheses to be tested were that: (i) there are seasonal differences in the diet of bottlenose dolphins, (ii) sex-biased distribution minimizes trophic overlap between adult male and female bottlenose dolphins and (iii) a temporal change has occurred in the diet composition of the dolphins.

Materials and methods

Sample acquisition

The samples used in this work were collected from stranded carcasses of bottlenose dolphins washed ashore along the southern portion of Rio Grande do Sul state, southern Brazil between 1977 and 2012. This portion of the coast is characterized by a 355 km long sandy beach interrupted by the mouth of PLE and bounded to the north by the Lagoa do Peixe bar (31°21′S–51°02′W) and to the south by the Chui river (33°45′S–53°22′W), on the border with Uruguay (Figure 1). Nevertheless, all carcasses were collected adjacent to the estuary (61% were found up to 45 km to the north and 39% up to 65 km to the south of the estuary mouth). Furthermore, nearly 70% of those were within 20 km of the entrance of the PLE. The occurrence of carcasses decreased as distance from the estuary increased (Fruet et al. 2012; Prado et al. 2016). The lower estuary is the main concentration area for this population to feed, rest and reproduce (e.g. Matos et al. 2007; Di Tullio et al. 2015; Fruet

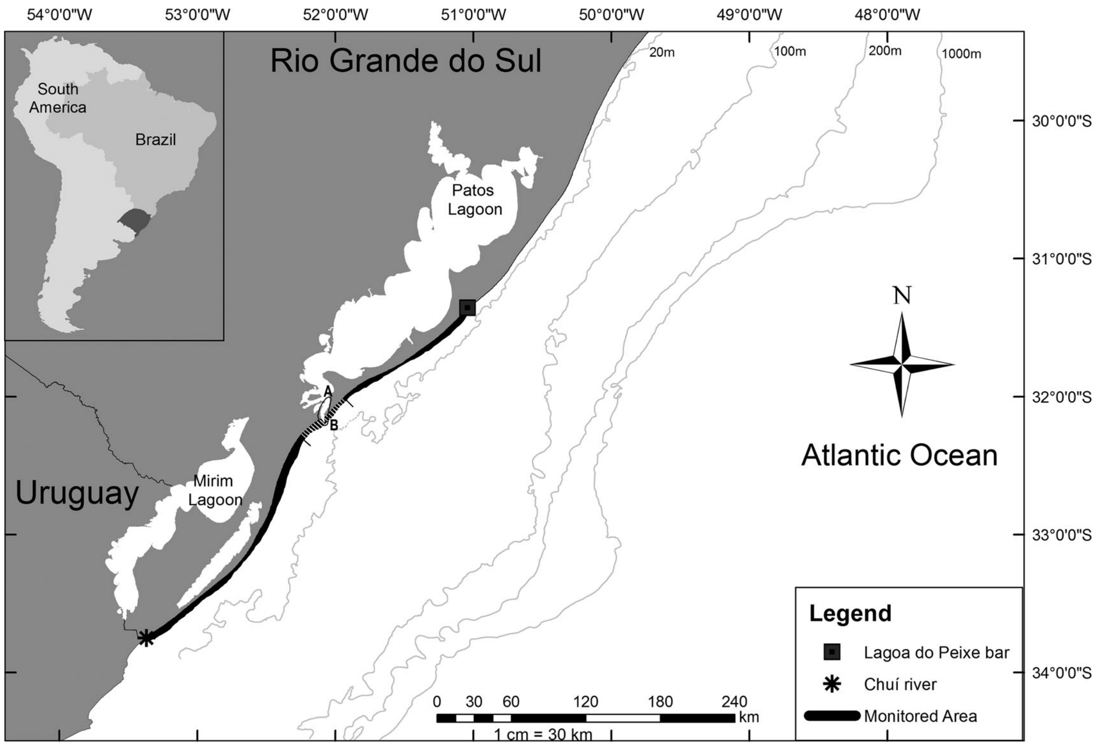

Figure 1. Study area comprises a 350 km long stretch of a sandy beach from Chui river to Lagoa do Peixe bar, southern Brazil. The main usage areas by estuary-dependent (A) and coastal dolphins (B) are indicated.

et al. 2015). The higher incidence of carcasses in the vicinity of the estuary is probably because it coincides with the area where the overlap between dolphins and gillnet fisheries is highest (Di Tullio et al. 2015). The total length of the dolphins, measured as a straight line from the tip of the rostrum to the notch of the fluke tail (Norris 1961), was recorded and the sex was determined whenever possible. Teeth were obtained from all specimens for age determination and SIA, and the stomachs were collected from those carcasses with a decomposition state up to code 4 *sensu* Geraci & Lounsbury (2005).

Teeth from 87 individuals (41 males, 25 females and 21 of undetermined sex), collected between 1977 and 2012, were used for SIA. For SCA, the stomachs of 46 dolphins (29 males, 14 females and three of unknown sex), collected between 2002 and 2012 (Period II), were analysed. Additionally, previously published prey data (Pinedo 1982) of 12 individuals (five males, three females and four undetermined), collected between 1976 and 1980 (Period I), were considered for temporal comparison purposes.

Prey samples for isotopic mixing models were selected based on fish species identified in the stomachs. Specimens of each species that were within the size range consumed by bottlenose dolphins were obtained during research expeditions or from local fishing industries between 2011 and 2015. The limitation of this approach is that it is assumed that the isotope signal of the dolphin's prey did not change throughout the study period. White dorsal muscle was sampled from each fish and stored in a freezer at −20°C until processing for SIA.

Stomach content analysis

Stomach contents were gently washed with running water over a 200 µm mesh size sieve. Otoliths were separated, washed, dried and stored. Cephalopod beaks and crustaceans were preserved in 70% alcohol. Otoliths and beaks were separated into right and left and upper and lower, respectively. For each stomach, the maximum number of right or left otoliths and upper or lower beaks was considered as the minimum number of fish and cephalopods consumed (Barros & Odell 1990). All otoliths and beaks were identified under a stereoscopic microscope and compared with the reference collection of the Demersal Resources and Cephalopods Laboratory (Federal University of Rio Grande, LRDC/FURG). In order to minimize underestimation of size and biomass of consumed prey, measurements were taken only for whole or minimally worn otoliths. Worn or broken otoliths had their measurements assigned based on length of entire or slightly worn otoliths of the same species randomly sampled within the same stomach (Barros & Odell

1990). No measure was considered for very worn or broken otoliths when there was no other otolith of the same species in the same stomach that could be measured. Otolith total length was measured as the longest longitudinal distance. In the case of otoliths with broken ends, the width, defined as the greatest distance perpendicular to the longitudinal axis, was used instead. All measurements were taken using a digital calliper, with resolution of 0.005–0.01 mm.

Stable isotope analysis

To prevent the influence of the lactation signal on the isotopic composition of teeth, only individuals >3 years were used for SIA. Ages were estimated by counting dentinal and/or cemental incremental layers or growth layer groups (GLGs) (Perrin & Myrick 1980). Teeth were processed for age estimation following Hohn et al. (1989). GLG counting was performed without reference to biological data, such as length or sex. Each GLG was considered to represent one year of age (Hohn et al. 1989). If the age estimation was missing, individuals were considered as adult males and females if their total length was >318 cm or 278 cm, respectively (Fruet et al. 2012).

SIA of teeth was performed following the protocol described in Knoff et al. (2008). Teeth were dried for 3–4 days in a 60°C oven and cleaned of outer soft tissue with a carbide burr attached to a drill. A low-speed saw with a diamond-embedded blade was used to cut through the centre of the tooth in the longitudinal buccal–lingual axis in order to expose the GLGs. The exposed dentine was sampled with a small drill bit, ensuring that all GLGs were sampled so that the resulting powder would represent the entire life of the individual. The powder was acidified with 30% hydrochloric acid (HCl) to remove biogenic carbonates, which could alter the organic $\delta^{13}C$ measurements, and then dried again for 1 h in a 60°C oven. Muscle samples from prey were thawed, dried in a stove at 60°C for 48 h and ground to fine powder using a mortar and pestle. No lipid extraction was performed because mean C:N ratios from all samples were < 3.5 (mean teeth C:N = 3.2 and mean prey muscle C:N = 3.4), indicating low fat content (Post et al. 2007).

Samples of approximately 1 mg of residual acidified tooth or 0.7 mg of powdered muscle were weighed in tin capsules and analysed through an elemental analyser (ECS 4010, Costech Analytical, Valencia, CA) coupled to a continuous-flow isotope ratio mass spectrometer (Delta Plus XP, Thermo Finnigan Bremen) (Stable Isotope Core Laboratory, Washington State University). The natural abundance of stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) is expressed in a delta notation (δ) as per mill variations (‰) when compared with international standards (e.g. Vienna Pee Dee Belemnite, VPDB, for carbon and atmospheric N_2 for nitrogen). Results were expressed as:

$$dX = [R_{sample}/R_{standard} - 1]$$

where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. Repeated analysis of an internal standard yielded a within-run standard deviation of 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. Stable isotopic values of carbon were corrected for 0.022‰ per year to account for changes in the $\delta^{13}C$ of atmospheric CO_2 due to the burning of fossil fuels (the Suess effect) (Francey et al. 1999; Indermühle et al. 1999). All corrections of $\delta^{13}C$ values were referenced to 2012. Suess-corrected carbon isotope values were referred to as $\delta^{13}C_{Suess}$.

Data analysis

The values obtained for the dimensions of the otoliths and beaks were used to estimate the total length (TL) of teleost, mantle length (ML) of cephalopods and their biomass, using specific regression equations (available at the LRDC/FURG). Empty stomachs were excluded from the analyses. For each prey, the following indicators were calculated: the frequency of occurrence (%FO), number of stomachs in which a particular taxon occurs divided by the total number of stomachs with food items; numerical frequency (%N), total number of individuals of a taxon divided by the total number of prey consumed; biomass (%W), contribution of each prey biomass divided by total biomass. The Index of Relative Importance (IRI) was calculated as: IRI = (%N + %W) %FO (Pinkas et al. 1971). Intra-annual variation in the diet was evaluated by referring months to cold and warm seasons according to mean PLE surface water temperature measured from 2002 to 2011, which ranged from 13–19°C (May to October) to 20–26°C (November to April).

The existence of intraspecific dietary overlap between sexes, seasons and periods were evaluated with the Specific Overlap Index (SO) and the General Overlap Index (GO) (Petraitis 1979; Ludwig & Reynolds 1988). Values for both indices vary between 0 and 1. SO can be described as the probability of one curve of niche utilization being explained by the other. In this case, it is tested whether the utilization curve of a subgroup (males, for example) completely overlaps with the utilization curve of another subgroup (females), and vice versa. Because they are asymmetrical curves, it means that curve 1 may explain curve 2, but curve

2 does not necessarily explain curve 1 (Petraitis 1979). The null hypothesis of complete specific overlap of curve 1 on curve 2 (SO 1) was tested through the U test which follows a chi-square distribution with r − 1 degrees of freedom (Ludwig & Reynolds 1988). The GO evaluated the probability of obtaining the utilization curve of each subgroup from the common utilization curve of all groups (Petraitis 1979). The hypothesis of complete general overlap between subgroups (GO 1) was verified by the V test, which follows a chi-square distribution with degrees of freedom (s − 1) × (r − 1) (Ludwig & Reynolds 1988). Both U and V tests are equivalent to the G test as described in Zar (1999). In order to calculate the GO and SO, the number of occurrences of prey species (r) in the different subgroups (s) is required (see Ludwig & Reynolds 1988). Only prey species with IRI > 1% in the pooled sample were considered (e.g. Koen-Alonso et al. 2002).

Stable isotopic compositions of bottlenose dolphin's tooth collagen were compared among decades using ANOVA, followed by a post-hoc Tukey's test for pairwise comparisons. δ^{13}C and δ^{15}N values of male and females collected during Period II were compared through Student's *t*-tests. No test could be performed for Period I due to small samples sizes. Normality and homogeneity of variances were assessed using Shapiro–Wilks and Cochran tests, respectively (Zar 1999).

A Bayesian mixing model for stable isotope data (SIAR, Stable Isotope Analysis in R; Parnell et al. 2010), a package developed for the statistical environment R (R Development Core Team 2011), was used to calculate the relative contribution of potential prey species to the diet of bottlenose dolphins. Separate runs were performed for isotopic data of each decade (1970, 1980, 1990, 2000 and 2010) and for males and females from Period II. Mean and standard deviation of isotopic data of prey species that accounted for > 95% of the IRI (based on results from the stomach content analysis performed here) were included in the model. No available diet-to-dentine trophic enrichment factors (TEFs) are available for cetaceans, and thus the conservative TEFs of 5.0% (0.5% SD) and 3.4% (0.5% SD) for δ^{13}C and δ^{15}N, respectively, were used in the model (Minagawa & Wada 1984; Newsome et al. 2010; Riccialdelli et al. 2013). Furthermore, the mean and standard deviation of prey elemental concentration (C and N) were also used as the input of the model in order to improve the discrimination of prey. SIAR model outcomes were presented as a mean percentage (%) of total prey composition with the 95% credibility interval (CI$_{95}$). Normality of data was assessed through Shapiro–Wilks tests as required for SIAR (Parnell et al. 2010).

Finally, two sets of standard ellipses were constructed using the SIBER routine (Jackson et al. 2011), included in SIAR (Parnell et al. 2013), in order to examine the variation in δ^{13}C and δ^{15}N values and to estimate the isotopic niche space. One set of standard ellipses, corrected for small sample sizes (SEAc), was plotted for Periods I (N 15) and II (N 49). In order to increase the sample size for Period I, we added data from animals > 10 years old sampled in the 1980s. This procedure was made assuming that a significant part of their average isotopic composition would be from dentine deposited during the 1970s or before. The other set was developed from males (N 25) and females (N 12) sampled in Period II. Niche area and overlap were estimated for each set of ellipses.

Results

Stomach content analysis

Food remains were found in only 31 stomachs and included otoliths of at least 587 teleosts (10 of which could not be identified due to advanced wear), structures of one cephalopod and three crustaceans (Table SI, supplementary material). Fish found in dolphin stomachs represented at least 13 taxa, seven of which (53.8%) belonged to bottom-dwelling fish of the family Sciaenidae (Table SI). *Micropogonias furnieri* (Desmarest, 1823) and *Paralonchurus brasiliensis* (Steindachner, 1875) were the most important prey in number (35.3%, 19.9%) and IRI (70.5%, 8.9%). *Micropogonias furnieri* and *Menticirrhus* sp. were the most frequent (54.8%, 35.4%), while in terms of biomass, *M. furnieri* (68.7%) and *Trichiurus lepturus* Linnaeus, 1758 (14.0%) were the most representative (Table SI).

Twenty males and 10 females had identifiable prey remains in their stomachs. Sixteen taxa were found in male stomachs, while nine were found in females. For males, *M. furnieri* and *P. brasiliensis* were the most important prey by number (32.6%, 24.0%), frequency of occurrence (55.0%, 35.0%) and IRI (70.3%, 12.2%). The greatest contribution in biomass came from *M. furnieri* (67.2%) and *T. lepturus* (17.2%) (Table SII). For females, on the other hand, *M. furnieri* and *Menticirrhus* sp. were the most important prey in number (43.8%, 26.7%) and frequency of occurrence (60.0% for both). The most representative prey by weight was *M. furnieri* (78.8%), followed by *Mugil liza* Valenciennes, 1836 (9.2%) and *Menticirrhus* sp. (8.9%). According to IRI, *M. furnieri* (67.4%) and *Menticirrhus* sp. (20.4%) were the most relevant species (Table SII). There was no significant difference in the mean length of the ingested main prey species between male and female bottlenose dolphins (ANOVA, $p > 0.05$ for all comparisons).

Most stomach samples were collected from stranded carcasses during warm months (N 35; 12 were empty), while only 11 were gathered in cold months (three were empty). Sixteen and 12 prey species were recorded in stomachs from warm and cold months, respectively (Table SIII). In warm months, the most ingested prey were *M. furnieri* (41.0%) and Engraulidae (18.1%), and the most frequently ingested were *M. furnieri* (65.2%) followed by *T. lepturus* and *M. liza* (34.7% for both). These three species were also the most important prey in biomass (72.1%, 13.8% and 8.4%) and relative importance (77.4%, 8.6% and 5.7%). On the other hand, during cold months, *Menticirrhus* sp. and *P. brasiliensis* were the most important prey by number (23.3%, 37.9%), occurrence (50.0%, 37.5%) and IRI (48.5%, 28.5%), and *Menticirrhus* sp. (41.3%) and *T. lepturus* (16.1%) by weight (Table SIII). No differences were found between males and females for both GO and SO (Table I). There were no differences in the diet of dolphins between the two seasons and periods, according to the GO. However, the null hypothesis of complete overlap in resource utilization was rejected according to the SO for seasonal comparison (warm–cold months) and periods (Period I–Period II; Period II–Period I), indicating some seasonal and interdecadal differences in the diet of bottlenose dolphins inhabiting the PLE and the adjacent marine coast (Table I). A decline in frequency of occurrence of *M. furnieri* and an increase of some species such as *T. lepturus* and *P. brasiliensis* were observed between periods. Moreover, *Menticirrhus* sp. was absent in the first period, while in period II it appears as an important prey species (Figure 2).

Table I. Diet overlap analyses between the major sources of variation in the sample studied.

General overlap index

Source of variation	GO	V	df	P
Sex	0.98	2.33	4	0.68
Period of the year	0.97	3.98	4	0.41
Periods	0.95	8.29	4	0.08

Specific overlap index

Source of variation	i	k	SO	U	df	P
Sex	Males	Females	0.92	6.02	4	0.20
	Females	Males	0.91	3.89	4	0.42
Period of the year	Warm	Cold	0.80	19.90	4	<0.001
	Cold	Warm	0.90	5.06	4	0.28
Periods	Period I	Period II	0.07	10.10	4	0.04
	Period II	Period I	0.04	368.09	4	<0.0001

GO, general overlap index; V, statistic to test the null hypothesis that GO = 1; df, degrees of freedom; *P*, probability of the statistic; SO_{ik}, specific overlap of group i onto group k; U, statistic to test the null hypothesis that $SO_{ik} = 1$.

Stable isotope analysis

The 87 bottlenose dolphins included in the SIA were collected over 35 years starting in the late 1970s. The mean age of the animals varied from 10.3 (SD 7.5) in the 2000s to 18.2 (SD 16.7) in the 2010s (Table II). Non-significant differences were observed in $\delta^{13}C_{Suess}$ values among decades (ANOVA, $p = 0.78$), while $\delta^{15}N$ values were statistically different (ANOVA, $p < 0.01$). Mean $\delta^{15}N$ values were higher in 1990 than 2000 (Tukey's HSD, $p < 0.01$) (Figure 3). Mean stable isotope compositions of main prey varied from −17.2 ± 0.7‰ to −14.8 ± 1.2‰ for $\delta^{13}C$ and from 12.0 ± 0.7‰ to 15.7 ± 0.4‰ for $\delta^{15}N$ (Table SIV, Figure 3). Stable isotope mixing models showed different patterns of relative importance of prey across decades. *M. furnieri* and *Menticirrhus* sp. were important prey to the bottlenose dolphin during the first three decades. However, the contribution of these two species declined in the 2000s and 2010s. On the other hand, *T. lepturus*, whose relative importance was considered low during the first three decades, increased its contribution from 2000 onwards (Table SV, Figure 4), becoming the most important prey for bottlenose dolphins in the 2010s. The importance of *M. liza* (except for the 1990s) and *P. brasiliensis* remained almost constant through the decades with slight oscillations. Differences in mean stable isotope compositions between males and females were non-significant (Student's *t*, $p = 0.20$ and $p = 0.53$, for $\delta^{13}C_{Suess}$ and $\delta^{15}N$ values, respectively). When only Period II (2002–2012) is considered, however, *T. lepturus* was

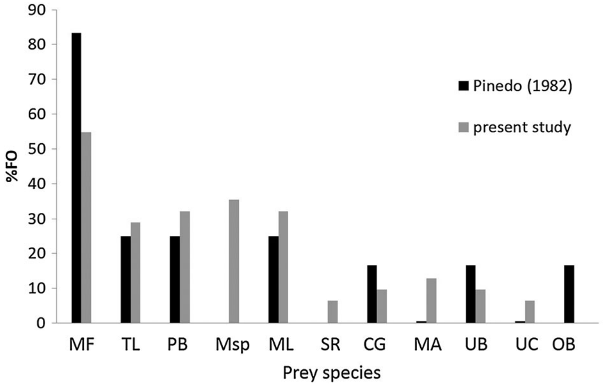

Figure 2. Comparison of frequencies of occurrence of the main prey species of bottlenose dolphins from the PLE and adjacent marine coast, southern Brazil, as observed in this study (2002–2012) and in Pinedo (1982) (1976–1980). MF, *Micropogonias furnieri*; TL, *Trichiurus lepturus*; PB, *Paralonchurus brasiliensis*; Msp, *Menticirrhus* sp.; ML, *Mugil liza*; SR, *Stellifer rastrifer*; CG, *Cynoscion guatucupa*; MA, *Macrodon atricauda*; UB, *Urophycis brasiliensis*; UC, *Umbrina canosai*; OB, *Odonthestes bonaerensis*.

Table II. Mean (± SD) $\delta^{13}C$, $\delta^{13}C_{Suess}$ (corrected for Suess effect) and $\delta^{15}N$ values in teeth collagen of bottlenose dolphins found dead along the southern coast of Brazil from 1977 to 2012, with their respective samples sizes (*N*).

Decade	Mean age (SD; *N*)	$\delta^{13}C$ (‰)	$\delta^{13}C_{Suess}$ (‰)	$\delta^{15}N$ (‰)	*N*
1970					
Males		−10.7	−11.4	17.8	1
Females		−11.0 ± 0.3	−11.7 ± 0.3	17.4 ± 1.3	2
All	17.8 (3.3; 4)	−10.5 ± 0.6	−11.2 ± 0.6	18.0 ± 1.0	5
1980					
Males		−10.5 ± 0.6	−11.0 ± 0.6	17.9 ± 1.4	6
Females		−10.7 ± 0.6	−11.3 ± 0.6	18.6 ± 0.8	9
All	11.2 (6.5; 19)	−10.5 ± 0.6	−11.1 ± 0.6	18.2 ± 1.1	20
1990					
Males		−10.7 ± 0.5	−11.1 ± 0.5	18.9 ± 0.8	6
Females		−9.7	−10.1	18.2	1
All	12.0 (9.9; 4)	−10.6 ± 0.7	−11.0 ± 0.7	19.0 ± 0.8	9
2000					
Males		−11.0 ± 0.4	−11.1 ± 0.4	17.8 ± 0.8	20
Females		−10.6 ± 0.7	−10.7 ± 0.7	17.5 ± 0.7	10
All	10.3 (7.5; 28)	−10.9 ± 0.5	−11.0 ± 0.5	17.9 ± 0.8	40
2010					
Males		−11.3 ± 0.3	−11.3 ± 0.3	18.4 ± 0.6	8
Females		−10.5 ± 0.8	−10.6 ± 0.8	17.6 ± 0.7	3
All	18.2 (16.7; 9)	−11.2 ± 0.7	−11.2 ± 0.7	18.2 ± 0.7	13

Mean (± SD; *N*) age of analysed dolphins in each decade is also provided (column 2).

by far the most important prey for males, followed by *M. furnieri* and *M. liza*, while the latter was the main prey for females followed by *T. lepturus* (Table SVI, Figure 5). Males showed a smaller isotopic niche area (1.0) than females (1.5). The overlapping area between their ellipses (0.6) represents, respectively, 56% and 38% of the isotopic niche for males and females (Figure 6).

Discussion

Despite sampling biases towards juveniles and adult males and towards warm months, which is consistent with the bottlenose dolphin stranding patterns in the area (Fruet et al. 2012), and the inherent methodological constraints of SCA and SIA, the combination of the two approaches allowed a first characterization of the feeding ecology of bottlenose dolphins in the PLE and adjacent marine coast to be given. On one hand, SIA of inert tissues such as teeth incorporates the information of the animals' entire life, and hence the averaging process of determining the importance of some prey throughout a long period loses resolution. It was assumed here that sampled dolphins within each decadal period depicted the pattern of temporal variation in diet and that the isotopic signal of the prey did not change over time. Although this can be seen as a caveat of this study, the mean age of dolphins is similar among the three intermediate decades. Much older animals were sampled in the extreme periods (1970s and 2010s); hence, this difference is unlikely to influence the general observed patterns. Conversely, SCA only informs about the animal's last meal and does not reflect what is being assimilated in a longer term. Nevertheless, temporal (seasonal and interdecadal) patterns as well as gender-related differences were mostly consistent between the two approaches (see below).

The bottlenose dolphins from PLE and the adjacent marine coast appear to be preferentially ichthyophagous, preying largely upon demersal and demersal–pelagic sciaenid fish from the coastal zone. These results corroborate previous studies conducted in the region (Pinedo 1982; Lopez 2013). The prevalence of sciaenids can be explained by their high availability in the area (Haimovici et al. 1996). Fish of this family are important resources for regional fisheries and *Micropogonias furnieri* (the most important prey) is one of the most abundant and commercially important in southern and southeastern Brazil (Haimovici et al. 2006; Vasconcellos & Haimovici 2006). The high importance of sciaenids as prey, including the genus *Micropogonias*, seems to be a norm for coastal bottlenose dolphins worldwide (e.g. Barros & Odell 1990; Wells & Scott 2009).

The diet composition of these dolphins reflects their main distribution patterns, which corresponds to the lower estuary and along the adjacent marine coast, within 2 km from shore (Di Tullio et al. 2015). The dominance of bottom-dweller fish is consistent with feeding habits observed elsewhere in the western South Atlantic and worldwide (for a review see Wells & Scott 2009). A higher importance of pelagic prey can be observed in the diet of the offshore ecotypes (e.g. Barros et al. 2010). In southern Brazil, differences in the diet between offshore and inshore ecotypes were also suggested based on stable isotope data (Botta et al. 2012).

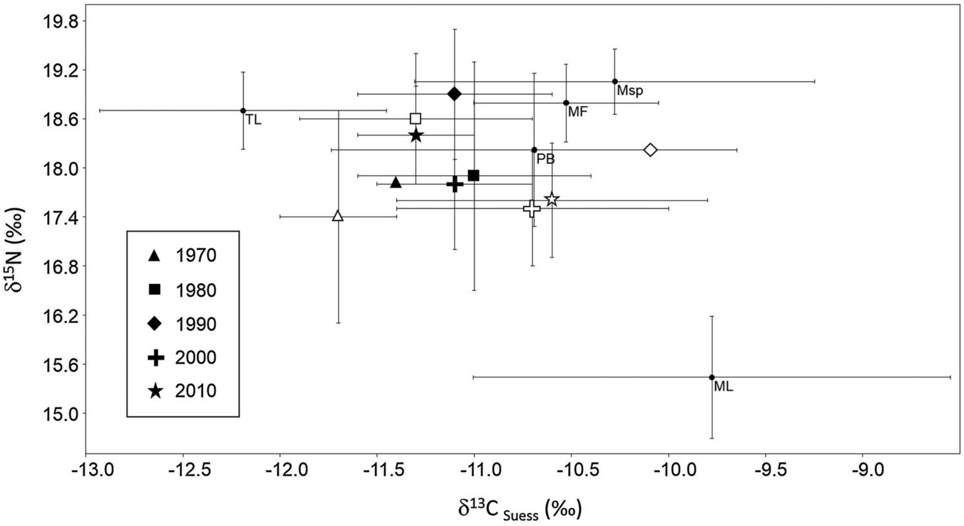

Figure 3. Dentine collagen mean $\delta^{13}C_{Suess}$ and $\delta^{15}N$ values (± SD) of male (closed symbols) and female (open symbols) bottlenose dolphins from the PLE and adjacent marine coast, southern Brazil in the last five decades and mean muscle $\delta^{13}C$ and $\delta^{15}N$ values (± SD) of their main prey species. Prey values have been corrected for trophic discrimination by adding 0.5‰ and 3.4‰ to $\delta^{13}C_{Suess}$ and $\delta^{15}N$ values, respectively. Msp, *Menticirrhus* sp.; MF, *Micropogonias furnieri*; ML, *Mugil liza*; PB, *Paralonchurus brasiliensis*; TL, *Trichiurus lepturus*.

Gender-related differences

The hypothesis that sex-biased distribution minimizes trophic overlap between adult male and female bottlenose dolphins cannot be fully supported by the data. No differences were found regarding the GO and the SO. This lack of variation in utilization of resources between sexes indicates that resource sharing or potential competition might exist between males and females. Nevertheless, SCA showed that *Micropogonias furnieri*, *Paralonchurus brasiliensis* and *Trichiurus lepturus* were the most important prey for males. For females, *M. furnieri* was also the most important prey, though, followed by *Menticirrhus* sp. and *Mugil liza*. When only Period II (2002–2012) is considered, however, *T. lepturus* was by far the most important prey for males, while *M. liza* was the main prey for females. SIA confirmed the importance of *M. liza* for females and that *T. lepturus* was an important prey for males. This variation in diet might be due the differences in habitat use patterns. Females are twice as likely to be found in the sheltered and more productive waters of the PLE than males based on random sampling for genetic sex ratio (Fruet et al. 2014). The wider ellipse of the isotopic niche of females suggests that they use, predominantly, an environment with a stronger variation in its physical–chemical conditions (estuary) than males (adjacent marine coast). In estuarial systems salinity, water temperature and other physical-chemical conditions are much more variable than on the adjacent coast due to the influence of both fresh and salt water. This variation promotes changes in the biota (including the primary producers), hence the much wider (carbon axis) ellipses. These results indicate that some level of habitat partitioning and trophic segregation exists. The observed patterns benefit females, which is to be expected from the evolutionary point of view, as they represent the component of the population with a higher reproductive value (Caughley 1977). Strategies to minimize intraspecific competition were also observed in other coastal bottlenose dolphin populations. Cockcroft & Ross (1990) found that adult males consume a greater proportion of larger fish than did adult females. Santos et al. (2007) observed that larger animals consume larger fish of certain species. Blanco et al. (2001) found that adult bottlenose dolphins feed upon a greater variety of prey sizes than do juveniles. On the other hand, Pate & McFee (2012) found that immature males preyed predominantly upon schooling fish. A trend towards greater consumption of squid by mature females was observed in some regions (e.g. Blanco et al. 2001; Pate & McFee 2012). The requirement of a higher-quality diet in mature females might be related to the energetic costs of reproduction. In fact, pregnant and lactating females do feed upon prey with higher nutritional value as observed in pantropical spotted dolphins, *Stenella attenuata* (Gray, 1846) (Bernard & Hohn 1989) and Atlantic spotted dolphins, *Stenella frontalis* (Cuvier, 1829) (Malinowski & Herzing 2015).

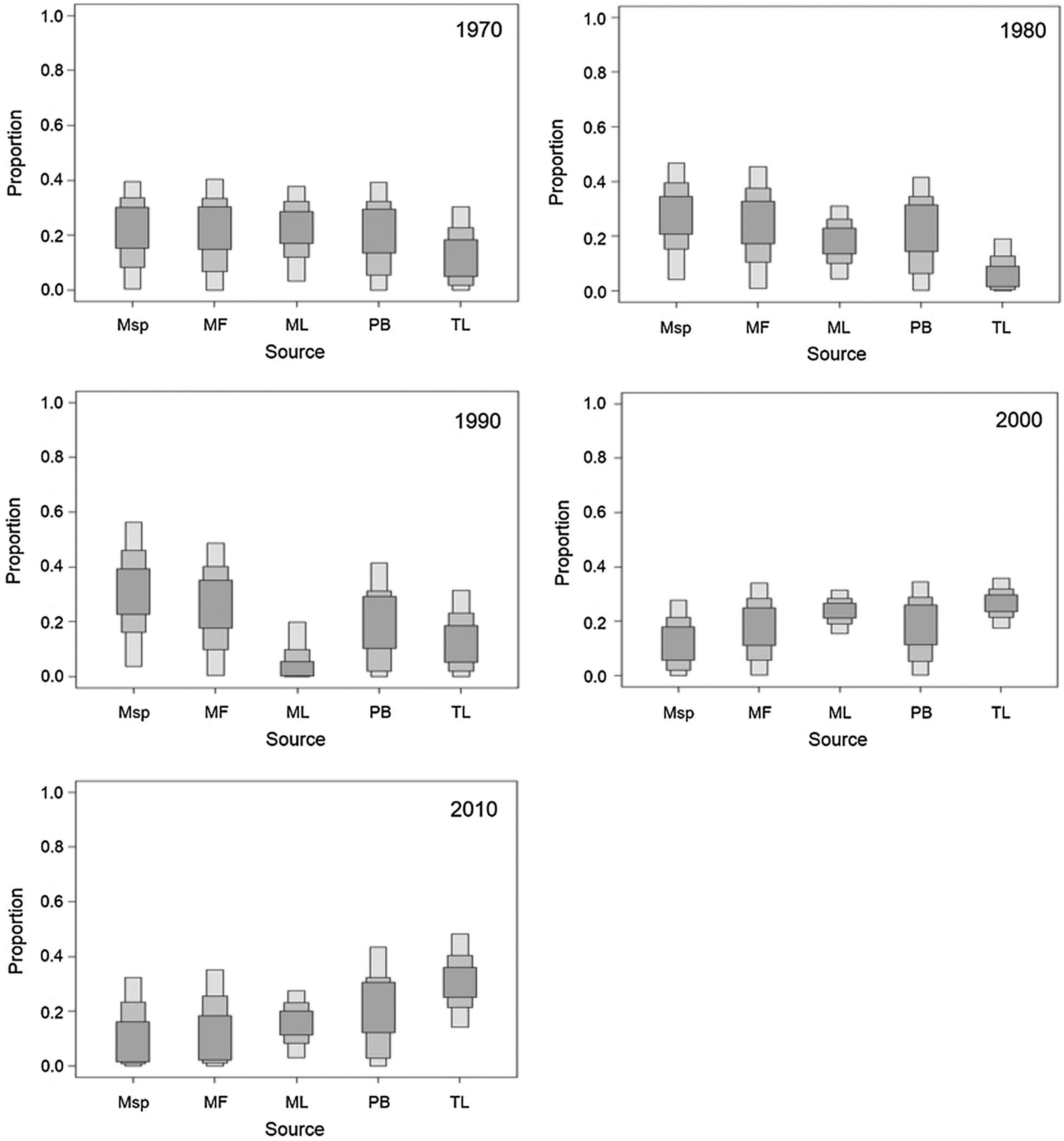

Figure 4. Relative contribution of prey sources to the diet of bottlenose dolphins from PLE and the adjacent marine coast, southern Brazil, in the last five decades. The proportion of each fish species is shown as box plots showing the 50%, 75% and 95% credibility intervals (CI): CI_{50} dark grey; CI_{75} medium grey; CI_{95} light grey. Msp, *Menticirrhus* sp.; MF, *Micropogonias furnieri*; ML, *Mugil liza*; PB, *Paralonchurus brasiliensis*; TL, *Trichiurus lepturus*.

Temporal variation

Seasonal

Data on stomach content analysis confirmed the hypothesis that seasonal differences in the diet of bottlenose dolphins exist. Although the mean number of ingested prey was similar between seasons, the biomass ingested by dolphins during the warm months was significantly greater than in cold months. This might be explained by the greater biomass of *Mugil liza* and *Micropogonias furnieri* (probably mature fish), which were consumed more often during this period. It is probably advantageous to the predator to consume larger prey if the trade-off between chasing cost and energy return compensates, especially during the breeding period when cost for reproduction

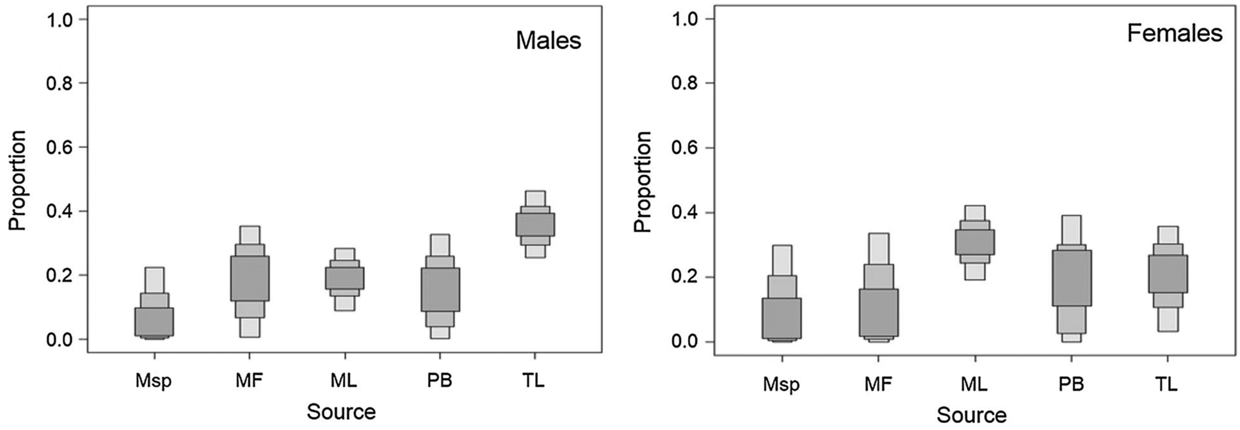

Figure 5. Relative contribution of prey sources to the diet of male and female bottlenose dolphins from PLE and the adjacent marine coast, southern Brazil, between 2002 and 2012. The proportion of each fish species is shown as box plots showing the 50%, 75% and 95% credibility intervals (CI): CI_{50} dark grey; CI_{75} medium grey; CI_{95} light grey. Msp, *Menticirrhus* sp.; MF, *Micropogonias furnieri*; ML, *Mugil liza*; PB, *Paralonchurus brasiliensis*; TL, *Trichiurus lepturus*.

leads to higher energetic requirements. In fact, these two prey species were mostly ingested by females. According to the SO (warm–cold months), there are some differences in the resource utilization by bottlenose dolphins inhabiting the PLE and the adjacent coast throughout the year. These differences are probably due to the higher occurrence of *M. furnieri*, *Trichiurus lepturus* and *M. liza* during warm months and *Menticirrhus* sp. and *Paralonchurus brasiliensis* during cold months. *Trichiurus lepturus* and *Umbrina canosai* Berg, 1895 (the latter has only been observed during warm months) are warm-water species; thus, their availability increases during this period (Haimovici et al. 1996; Martins 2000). The estuarine-dependent *Mugil liza* uses the PLE to develop until maturation and by April, large shoals of mullet concentrate at the mouth of estuaries prior to migration (Vieira & Scalabrin 1991). Its greatest abundance during the warm months in the diet can be explained by the greater abundance of mature individuals near the estuary mouth where dolphins concentrate (Di Tullio et al. 2015). Although *P. brasiliensis* and *M. furnieri* use the region throughout the year (Haimovici et al. 1996), the importance of the former increased during cold months, because the occurrence of the latter dropped in the stomachs of the dolphins. Seasonal differences in preferred prey and niche breadth are most likely driven by seasonal changes in oceanographic conditions that lead to variation in the abundance of species associated with warm and cold waters (Haimovici et al. 1996). These results show that bottlenose dolphins from PLE are opportunistic feeders and confirm the plasticity of the species, which preys upon the most available prey.

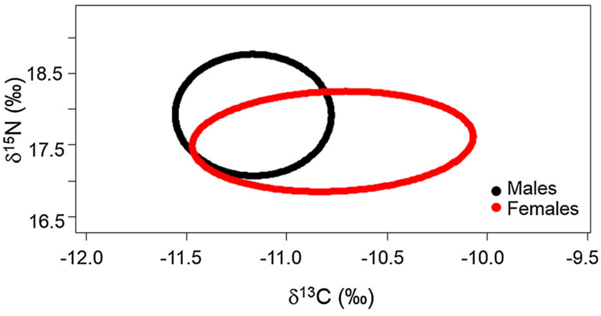

Figure 6. Standard ellipse area (SEAc) for each group was calculated using SIBER (Jackson et al. 2011).

Interdecadal analyses

The overall diet composition of bottlenose dolphins from PLE and the adjacent marine coast has remained broadly similar over 35 years. However, the hypothesis of a temporal change in dolphin diet composition is confirmed by SCA with some support by SIA (i.e. SIBER analysis). The frequency of occurrence and relative importance (SCA) and the estimated contribution (SIA) of the main prey have changed over time. The differences found in SO provide further evidence of this long-term change and is probably explained mostly by the decline of *Micropogonias furnieri* and an increase in the frequency of occurrence of *Trichiurus lepturus* and *Paralonchurus brasiliensis* in the stomachs between periods. Despite the inherent uncertainty associated with SIA, the proportional contribution of *M. furnieri*/*Menticirrhus* sp. (grouped here as they have similar isotopic values: Figure 3) has decreased in recent decades while the importance of *T. lepturus* increased (Figure 4). Whether the observed variation is due to climate- or fisheries-related changes is difficult to assess. The difficulty in disentangling these potentially synergetic effects increases as likely temporal changes in the baseline isotopic signature (e.g. Garcia et al. 2016) were not considered and are known to influence the dispersion of the isotopic values of the consumers (e.g. Newsome et al. 2007; Jackson et al. 2011). Nevertheless, the decreased occurrence of *M. furnieri*, *Macrodon atricauda* (Günther, 1880) and *Umbrina canosai* in the stomachs coincides with the period when there was a sharp decline in the landings and available biomass of the first two species in the region (Haimovici 1997; Haimovici et al. 1997; Vasconcellos & Haimovici 2006; Cardoso & Haimovici 2015). According to Haimovici et al. (1997), *M. furnieri* was overexploited in the 1980s and 1990s, while *P. brasiliensis* and *T. lepturus*, which are not important commercially, increased their contribution in the diet. The same trend of decrease in the occurrence of *M. furnieri* and *M. atricauda* and increased importance of *T. lepturus* was observed in the diet of the franciscana dolphin, *Pontoporia blainvillei* (Gervais & D'Orbigny, 1844) in this region (Secchi et al. 2003). This suggests that fluctuations in abundance of commercially important species affect the foraging ecology of local high-trophic-level marine mammal predators. Furthermore, bottlenose dolphins prey upon the target species of fisheries at both landed and discarded sizes (Figure 7), and hence some trophic and spatial overlap between the dolphins and the fishery is expected, raising concerns about the potential negative effect of uncontrolled fishing pressures on their feeding ecology and on the balance of this coastal ecosystem.

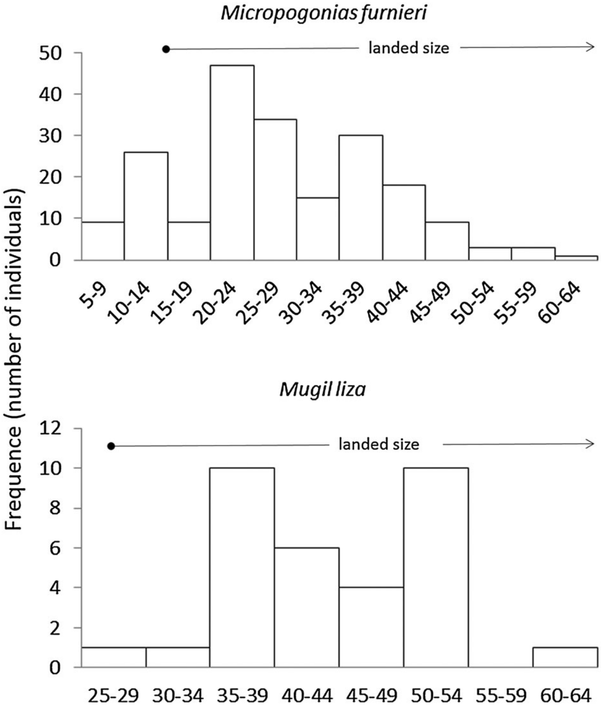

Figure 7. Regression-estimated size–frequency distribution of *M. furnieri* and *M. liza* consumed by bottlenose dolphins from PLE and the adjacent marine coast, southern Brazil (Period II, 2001–2012). The arrows indicate the landed size of the fishes (sources: Haimovici & Ignácio 2005; Miranda et al. 2006).

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