

Historic foraging ecology of the endangered Lahille's bottlenose dolphin (*Tursiops truncatus gephyreus*) inferred by stable isotopes

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Highlights

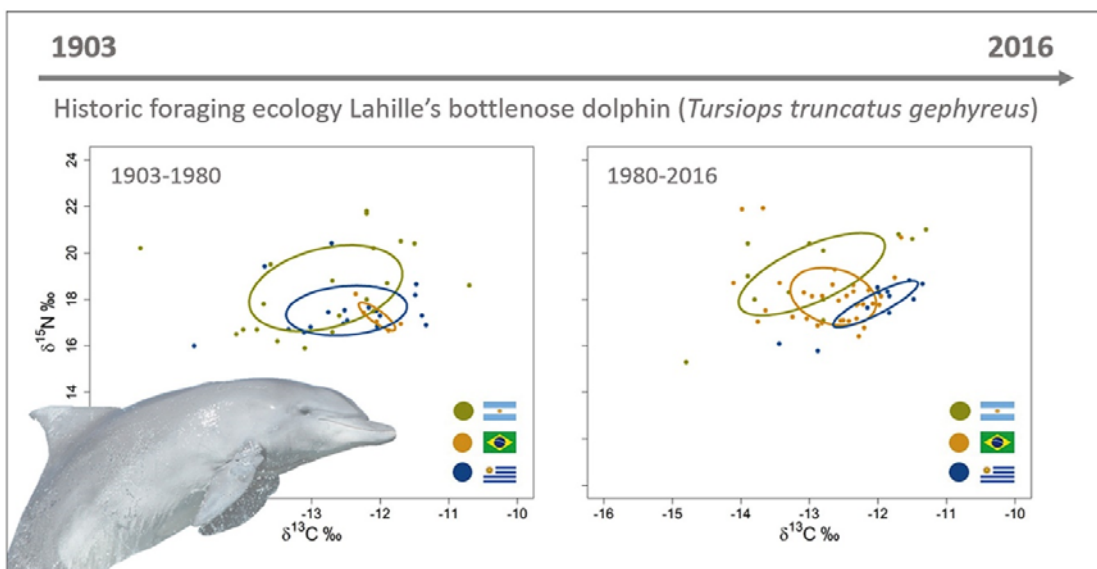
- Lahille's bottlenose dolphins from ARG maintained a broad isotopic niche along decades
- In UY and ARG the species seemed to forage upon demersal prey from the Atlantic coastal marine area
- Lower $\delta^{13}\text{C}$ values in UY historic samples reflected the past use of the estuary
- Isotopic niche segregation of ARG and UY showed a spatial and ecological structuring
- BR and UY, with a high overlap in isotopic niches, are probably an ecological unit

Abstract

The main aim of this work was to evaluate historical changes in the foraging ecology of Lahille's bottlenose dolphin (*Tursiops truncatus gephyreus*) along its distributional range. Stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) were analyzed in bone samples from specimens deposited in scientific institutions from Brazil (BR), Uruguay (UY) and Argentina (ARG), collected in periods PI (1903–1980) and PII (1981–2016). The isotopic values of ARG dolphins were different from UY and BR in both periods, reflecting variations in the composition of the diet and/or basal isotopic values. The considerably broad isotopic niche of the ARG dolphins was maintained in PII, following the trend of stable carbon and nitrogen

isotopic values along the decades. In this area, mixing models showed a diet with a high proportion of demersal prey, mainly from coastal marine waters. Lahille's bottlenose dolphins from UY showed a stability in nitrogen isotopic values but increasing carbon isotope values through decades. This increasing trend was consistent with a lower use of the Río de la Plata estuarine waters by the species reported for the last decades. In these areas, the species also showed a high proportion of demersal fish species. Finally, ARG and UY dolphins showed a partial and a total isotopic niche segregation during Periods I and II, respectively, probably reflecting a spatial/ecological structuring in this region. BR and UY samples, on the other hand, were not statistically different, probably forming an ecological unit. The retrospective analysis of the Lahille's bottlenose dolphin diet contributed to the knowledge of the ecological structure and feeding behavior of this poorly-known subspecies.

Graphical abstract



Keywords: Carbon; Nitrogen; Diet; *Tursiops truncatus gephyreus*; Western south Atlantic ocean

1. Introduction

Large marine predators are of particular interest as indicators of changes in the ecosystem due to their high trophic position in the food chain and normally long-life cycles (Sergio et al., 2008). Changes in trophic ecology (trophic level, foraging location) have been implicated as important regulators of population size and the distribution of marine organisms (Österblom et al., 2008). Cetaceans are large and highly mobile animals that live in dynamic environments, being considered important predators in marine ecosystems (Savenkoff et al., 2008). Therefore, understanding trophic interactions and trophic position that these organisms occupy in the food webs, contributes to reveal the functioning, structure and energy flow of marine ecosystems (Pauly et al., 1998).

The common bottlenose dolphin (*Tursiops truncatus*) occurs in almost all oceans, except in polar regions, and can be found exploring a variety of habitats along the coast and in deep waters in the open ocean (Wells and Scott, 2009). As it is common for widely distributed

species, a variety of forms have been observed for common bottlenose dolphins living in contrasting environments across its range. The coastal (or inshore) and pelagic (or offshore) ecotypes are the most commonly reported forms globally. These ecotypes differ in a number of morphological, ecological and genetic characteristics (e.g. Mead and Potter, 1995; Tezanos-Pinto et al., 2009; Perrin et al., 2011), albeit potentially subject to different degrees of divergence across ocean basins (e.g. Louis et al., 2014; Fruet et al., 2017). In the Southwestern Atlantic Ocean (SWAO), coastal and pelagic bottlenose dolphins occur in parapatry (Costa et al., 2016, 2019) and differ prominently on external morphology (Vermeulen and Cammareri, 2009; Fruet et al., 2017; Simões-Lopes et al., 2019), skull and spine characters (Barreto, 2000; Costa et al., 2016; Wickert et al., 2016; Hohl et al., 2020), sound emissions (Lima et al., 2020) and genetics, suggesting incipient evolution (Fruet et al., 2017; Costa et al., 2019; Oliveira et al., 2019). These divergence levels across multiple lines of evidence, particularly morphology and genetics, lead the Society for Marine Mammalogy's Committee on Taxonomy (2018) to recognize the SWAO coastal ecotype as a different subspecies (as proposed by Costa et al., 2016), the Lahille's bottlenose dolphin (*Tursiops truncatus gephyreus*).

The Lahille's bottlenose dolphin occurs only in a small portion of the SWAO, between the state of Parana in southern Brazil in the North (approximately 25°S; Costa et al., 2016; Wickert et al., 2016) and the province of Chubut in Argentina in the South (approximately 46°S; Coscarella et al., 2012), a distributional range of approximately 3500 km of coastline (Vermeulen et al., 2019). Two main populations are currently recognized: southern Brazil/Uruguay, composed of multiple local populations, and a single one placed in Argentina (Fruet et al., 2014). Local populations are small (<100 individuals) (see Fruet et al., 2016 for review) and preferably occur in coastal and estuarine areas, in shallow waters, with depths below 20 m (Di Tullio et al., 2016).

Lahille's bottlenose dolphin is considered a generalist consumer (see Laporta et al., 2016 for review). In southern Brazil, the species is preferably ichthyophagous, consuming mainly pelagic-demersal and demersal sciaenid fishes (Pinedo, 1982; Secchi et al., 2016; Machado et al., 2020). However, it presents some degree of plasticity in foraging habits and in feeding according to spatial and temporal patterns of prey availability (Secchi et al., 2016; Genoves et al., 2020). Temporal changes in the contribution of the main prey of Lahille's bottlenose dolphin have been observed, possibly due to the lower availability of the same prey caused by overexploitation by commercial fishing (Secchi et al., 2016). On the other hand, both in Uruguay and Argentina, data on this specie's diet are very scarce, limited to the description of prey found in the stomach contents of a reduced number of individuals (Mermoz, 1977; Moreno et al., 1984; reviewed in Laporta et al., 2016). Nevertheless, the available information on prey consumed by the subspecies in those two countries coincides with their neighboring populations in southern Brazil, indicating a diet based mainly on demersal fish - a consistent feeding habit among coastal populations of *Tursiops* around the world (Wells and Scott, 2009).

The conservation status of the Lahille's bottlenose dolphin was recently assessed and is currently listed as “Vulnerable” by the IUCN under criterion D1 (Vermeulen et al., 2019) and regionally listed as Endangered in the National Red List of Brazil (2019), the Red List of Mammalian Species of Argentina (Vermeulen et al., 2019) and in the list of Conservation Priority Species in Uruguay (Soutullo et al., 2013). Its inshore distribution makes the subspecies more susceptible to anthropogenic impacts, mainly due to the negative effects of direct (bycatch) or indirect (competition) interactions with fisheries (Fruet et al., 2012; Secchi

et al., 2016). In Argentina and Uruguay, the subspecies was formerly common along coastal regions of the Río de la Plata estuary during the 1960s–1980s (Lázaro and Praderi, 2000; Vermeulen et al., 2017). However, sighting data has decreased notably since the 1990s in this region and currently the species distribution reduced to some portions of its original range (Lodi et al., 2016; Vermeulen et al., 2017). The causes for narrowing its original distribution in Argentina and Uruguay are not well understood, but suggest that some kind of pressure must have played a role at population or ecosystem level (Bastida and Rodríguez, 2003; Coscarella et al., 2012; Cappozzo et al., 2013; Vermeulen et al., 2017).

Stable isotope analyses (SIA) have been commonly applied to reconstruct the historical diet of marine megafauna (e.g. Riofrío-Lazo and Auriolés-Gamboa, 2013; Drago et al., 2017; Artecona et al., 2019). This method is particularly useful for determining trophic level, identifying major food sources, and assessing foraging habitats of these predators (Das et al., 2003; Krahn et al., 2007; Pinela et al., 2010; Riccialdelli et al., 2010). This information can refer to different time scales through the analysis of tissues with different turnover rates. Those tissues with low turnover rates (e.g., bone, Newsome et al., 2007), allow the access to long-term dietary information (Riccialdelli et al., 2010; Drago et al., 2017). Carbon stable isotopes ($\delta^{13}\text{C}$) can provide information on the sources of primary productivity (e.g. seagrass, salt marsh, phytoplankton, France, 1995; Walker et al., 1999; Graham et al., 2010), while nitrogen ($\delta^{15}\text{N}$) is useful to infer the trophic level and nutrient sources of the food web where the predator forages (Post, 2002; Graham et al., 2010). Thus, combining the information derived from these tracers it is possible to provide insights on the foraging ecology of a species. Furthermore, the isotopic niche, as proxy of the ecological niche, can be defined by using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data as its scenopoetic and bionomic axes, respectively (Bearhop et al., 2004; Newsome et al., 2007).

In this study, we analyze the carbon and nitrogen stable isotopes composition of bone collagen from Lahille's bottlenose dolphin skeletal material deposited in collections which encompass a time period of more than a century and from locations throughout almost the entire range of the subspecies. These analyses aimed to evaluate the temporal and spatial variation in isotopic compositions along the south of Brazil, Uruguay and north of Argentina, and particularly estimate the diet of the subspecies in Uruguay and Argentina. The retrieval of historical information about the ecology of this species will help to understand the historical and current factors that could be associated with the decline of their populations along their distribution.

2. Materials and methods

2.1. Study area

The coastal ecosystems of the SWAO are highly influenced by interactions among climatic conditions, continental discharges and oceanographic conditions (Kjerfve et al., 2001). In this region, a subtropical convergence originates from the confluence of cold waters from the Malvinas current and the warm waters of the Brazilian current. The coastal region is influenced by two main estuarine systems: the Río de la Plata and the Patos Lagoon estuaries (Seeliger and Odebrecht, 2010). The Río de la Plata is a large estuary that also supports a high productivity, being important areas for the reproduction and breeding of several species of fish such as sciaenids, clupeids and mugilids (Jaureguizar et al., 2003; Defeo et al., 2009; Botto et al., 2011). The Patos Lagoon, located in the extreme south of Brazil, forms an estuarine region of approximately 1000 km² whose connection with the Atlantic Ocean

occurs through a narrow channel. This estuary is an important spawning and nursing habitat of several fish and crustaceans (Castello and Möller, 1978; Chao et al., 1985; Vieira and Castello, 1997), thus, commercial fisheries and top predators inhabiting its adjacent coastal region are sustained by this production (Pinedo, 1997; Vooren, 1997; Haimovici et al., 2006) (Fig. 1).



Fig. 1. Map of the study area. The colored line indicates the sampling area of Lahille's bottlenose dolphins.

2.2. Sampling

Bone fragments were extracted from 103 Lahille's bottlenose dolphin specimens deposited in scientific collections of different institutions from Brazil (BR), Uruguay (UY) and Argentina (ARG). The specimens were assigned to this subspecies by carefully inspecting the

morphology of the skull in order to identify cranial diagnostic characters described in Barreto (2000), Costa et al. (2016) and Wickert et al. (2016). The specimens were collected between 1903 and 2016 along the coasts of Rio Grande do Sul, in southern Brazil, Uruguay and northern Argentina (Fig. 1). Only animals considered to be adults were used. Sex was available only for a few specimens, especially in the case of the older individuals. We only included animals classified as physically mature based on the fusion of the maxillae to the cranium (Ross and Cockcroft, 1990), as no teeth were available for age estimation for most of the specimens. We removed small bone fragments from the inner part of the occipital bone of the skull in order to not interfere with its morphometric measurements.

The diet of the Lahille's bottlenose dolphins from BR was previously reported by Secchi et al. (2016) based on stomach content and stable isotopes analyses. Therefore, in order to investigate the diet of the species in the remaining locations (UY and ARG) we searched for stable isotope values of the described main prey for the species in those areas. In the case of UY, previous studies on the diet of other marine mammal species provided data of prey species common to the Lahille's bottlenose dolphin (e.g. Franco-Trecu et al., 2012; Franco-Trecu et al., 2013). In the case of Argentina, due to the scarce isotopic data on coastal fish species, we collected muscle tissue of fish species considered as prey for the Lahille's bottlenose dolphins based on previous reports (Bastida and Lichtschein, 1984; Moreno et al., 1984; Laporta et al., 2016; Vermeulen et al., 2019) and personal observations (R. Bastida, personal observation) both in estuarine and marine coastal waters of Buenos Aires (between 36° and 38° S).

2.3. Stable isotope analyses

Bone samples were cleaned with distilled water and sanded with a Dremel® tool to eliminate external impurities. Lipids were removed using a Soxhlet and a chloroform methanol solution (2:1) for 8 h. The bone fragments were then macerated to a powder and acidified to remove inorganic carbon by using HCl 2% with replacement of the acid solution every 24 h (two cycles), washed with successive rinses of deionized water and dried at 60 °C. Prey muscle samples were washed with distilled water, dried in an oven at 60 °C and powdered with mortar and pestle. Approximately 0.7–1 mg of each powdered sample was weighed and stored in tin capsules until isotopic analysis. No lipid extraction was performed on prey tissues as they showed atomic CN values compatible with pure protein content (i.e. CN > 3.5, Post et al., 2007).

Stable isotope analysis was performed using an elemental analyzer coupled to a Thermo Scientific Delta V isotope ratio mass spectrometer at the University of New Mexico Center for Stable Isotopes (UNM–CSI). The isotopic ratios are expressed as delta (δ) values

following the equation:
$$\delta_{sample} = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) * 1000$$
, where R_{sample} and $R_{standard}$ are the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratios of the sample and standard, respectively. The internationally accepted standards are Vienna Peedee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen. Delta values were calculated using multiple-point normalization. The internal laboratory standards used were soy protein, whey protein, casein, tuna, IAEA-N1, IAEA-N2, USGS-4 and USGS-43. Analytical precision (SD) of these internal standards was measured to be < 0.2‰ for $\delta^{15}\text{N}$ and < 0.04‰ in the case of $\delta^{13}\text{C}$. We measured the C:N ratios of each sample, and their mean value (3.0) was in the expected range for pure protein (Ambrose, 1990).

2.4. Statistical analyses

Carbon isotopic values were corrected for the Sues effect following Cullen et al. (2001) using a correction of 0.005‰ for samples before 1960 (Eq. (1)) and 0.022‰ for data after 1960 (Eq. (2)) as follows:

$$\delta^{13}\text{C}_{corr} = \delta^{13}\text{C} - \text{number of years to 1960} \cdot 0.005 - \text{number of years since 1960} \cdot 0.22 \quad \text{Eq.1}$$

$$\delta^{13}\text{C}_{corr} = \delta^{13}\text{C} - \text{number of years since 1960} \cdot 0.022 \quad \text{Eq.2}$$

Temporal trends in isotopic values within each area were evaluated through a linear regression analysis. For this analysis samples were assigned to decades according to their collection year or to their most probable collection decade. This last approach was necessary because some samples, especially those from the beginning of the twentieth century, did not have exact year of collection.

Furthermore, in order to test for regional and temporal differences in isotopic values, samples were divided in two periods: I)1903–1980 and II)1981–2016. The first period (hereafter, Period I) represents the previous stage to the large development of the bottom trawl industrial fishery along south Brazil, Uruguay and Argentina after 1967 (Yesaki and Bager, 1975; Defeo et al., 2009; Haimovici and Cardoso, 2017; Marcovecchio et al., 2019; Muniz et al., 2019). This development resulted in a substantial decrease in the industrial demersal landings in the following decades, when some of the main target species (i.e. *Micropogonias furnieri*, *Cynoscion guatucupa*, *Macrodon atricauda*, *Paralichthys brasiliensis*) started to show signs of overexploitation (Gianelli and Defeo, 2017; Haimovici and Cardoso, 2017; Marcovecchio et al., 2019). Therefore, the second period (hereafter, Period II) considered samples collected during the decades after this increase in fishing effort, that potentially might affect coastal ecosystems along these countries.

Two-way factorial ANOVAs, followed by Tukey post-hoc tests were used to analyze the effects of the sampling area (BR, UY and ARG) and the period (I and II) and their interaction on the isotope values of the dolphins.

We used the package SIBER (Stable Isotope Bayesian Ellipses in R, Jackson et al., 2011) to estimate the isotopic niche for the dolphins. Standard Ellipse Areas corrected for small samples (SEAc) and Bayesian standard ellipse areas (SEAB) with their respective 95% credibility intervals were generated for each period and area. Additionally, we calculated overlap area between paired SEAc and SEAB (between periods within each area and among areas within each period) using maximum-likelihood estimations and Bayesian inferences with 100,000 posterior draws, respectively (Jackson et al., 2011). The percentage of the ellipse area occupied by the overlap area was calculated for each group.

In order to calculate the most probable diet proportions for Lahille's bottlenose dolphins from UY and ARG we ran Bayesian stable isotope mixing models, implemented in the MixSIAR package (Stock and Semmens, 2016). Models were run only for dolphins collected in Period II in order to minimize potential temporal differences in prey isotopic values. We estimated dietary proportions without informative prior distributions as no information on the relative importance of prey to the diet was available for these areas. Prey isotopic values were

included as mean and standard deviation. In the case of Argentina, isotopic results of prey samples collected (present study) were used in the models (Table S2). Almost no information is available for the diet composition of Lahille's bottlenose dolphins from Uruguay. However, based on recognized movements between Uruguay and southern Brazil (Laporta et al., 2016) and the similarity of the fish fauna between these areas, the known prey composition of Lahille's bottlenose dolphins from BR (Secchi et al., 2016) was used to select sources for the mixing models. Therefore, published prey isotopic data from samples collected in UY were used (Bergamino et al., 2011; Franco-Trecu et al., 2012, 2013) (Table S1).

No diet-to-bone collagen trophic discrimination factors (TDFs) obtained under experimentally controlled conditions are available for any cetacean, however, some indirect approaches were applied in order to estimate suitable TDFs for this tissue. Borrell et al. (2012) reported diet-to-bone collagen TDFs for fin whales (*Balaenoptera physalus*) calculated from the difference between krill (*Meganyctiphanes norvegica*) and fin whale bone collagen isotopic values ($\Delta^{13}\text{C} = 3.11 \pm 0.27\text{‰}$ and $\Delta^{15}\text{N} = 2.03 \pm 0.71\text{‰}$). Teixeira et al. (2020) used experimentally-derived TDFs for skin from bottlenose dolphins (Gimenez et al., 2016) corrected by the offset between skin and bone collagen isotopic values obtained from paired samples from franciscana dolphins (*Pontoporia blainvillei*) ($\Delta^{13}\text{C} = 3.6\text{‰} \pm 0.4\text{‰}$ and $\Delta^{15}\text{N} = 2.1\text{‰} \pm 0.5\text{‰}$). Therefore, the adequacy of the prey groups and the two sets of TDF values to each mixing model were tested using mixing polygons (Smith et al., 2013). These models provided a quantitative basis for model acceptance or rejection based on a frequentist probability that the proposed mixing model can correctly calculate source contributions to explain the isotopic value of dolphins. All analyses were performed in R version 3.6.0 (R Core Team, 2019).

Table 1. Mean and SD values of $\delta^{13}\text{C}$ and $\delta^{13}\text{C}$ values corrected by the Suess effect ($\delta^{13}\text{C}_{\text{corr}}$) and $\delta^{15}\text{N}$ (in ‰) in bone collagen of *Tursiops truncatus gephyreus* sampled between 1903 and 2016 in Brazil, Uruguay and Argentina. The values for samples collected in Periods I (1903–1980) and II (1981–2016) in each area are also shown.

	Mean \pm SD $\delta^{13}\text{C}$	Mean \pm SD $\delta^{13}\text{C}_{\text{corr}}$	Mean \pm SD $\delta^{15}\text{N}$	n
<i>Brazil</i>				
Period I	-11.2 \pm 0.2	-12.1 \pm 0.3	17.3 \pm 0.6	5
Period II	-12.3 \pm 0.6	-12.7 \pm 0.6	18.1 \pm 1.2	36
All periods	-12.2 \pm 0.7	-12.6 \pm 0.6	18.0 \pm 1.2	41
<i>Uruguay</i>				
Period I	-11.4 \pm 0.7	-12.5 \pm 0.9	17.5 \pm 1.1	18
Period II	-11.9 \pm 0.7	-12.0 \pm 0.6	17.8 \pm 1.0	11
All periods	-11.6 \pm 0.7	-12.3 \pm 0.8	17.6 \pm 1.0	29
<i>Argentina</i>				
Period I	-12.2 \pm 1.1	-12.8 \pm 1.1	18.5 \pm 1.9	20
Period II	-12.7 \pm 1.1	-13.0 \pm 1.1	19.1 \pm 1.8	12
All periods	-12.4 \pm 1.1	-12.9 \pm 1.1	18.7 \pm 1.8	32

3. Results

Mean nitrogen isotope values were significantly different among areas (2-way ANOVA, $F_{2, 4.85}$ $p = 0.01$, Table 1), but the period and the interaction term were not significant ($F_{1, 0.2.88}$, $p = 0.09$ and $F_{2,0.25}$, $p = 0.78$, respectively). Tukey's post hoc test revealed that mean ARG $\delta^{15}\text{N}$ values were higher than those of samples from UY ($p = 0.008$). Significant differences were found for $\delta^{13}\text{C}_{\text{corr}}$ values between areas (2-way ANOVA, $F_{2,3.22}$, $p = 0.04$), but periods ($F_{1,0.5}$, $p = 0.82$) and the interaction term were not significant ($F_{2,2.26}$, $p = 0.11$). Tukey's post

hoc test showed that mean UY $\delta^{15}\text{N}$ values were higher than those of samples from ARG ($p = 0.034$) (Table 1).

No temporal trend was observed in $\delta^{15}\text{N}$ values of dolphins collected in any of the three areas (ARG, $R^2 = 0.022$, $p = 0.29$; BR, $R^2 = 0.003$, $p = 0.88$; UY, $R^2 = 0.066$, $p = 0.84$). In the case of $\delta^{13}\text{C}_{\text{corr}}$ values, a positive temporal trend was observed in the case of UY samples ($R^2 = 0.22$, $p = 0.026$), but no significant trend was observed in the case of ARG ($R^2 = 0.000$, $p = 0.21$) or BR ($R^2 = 0.007$, $p = 0.74$) (Fig. 2).

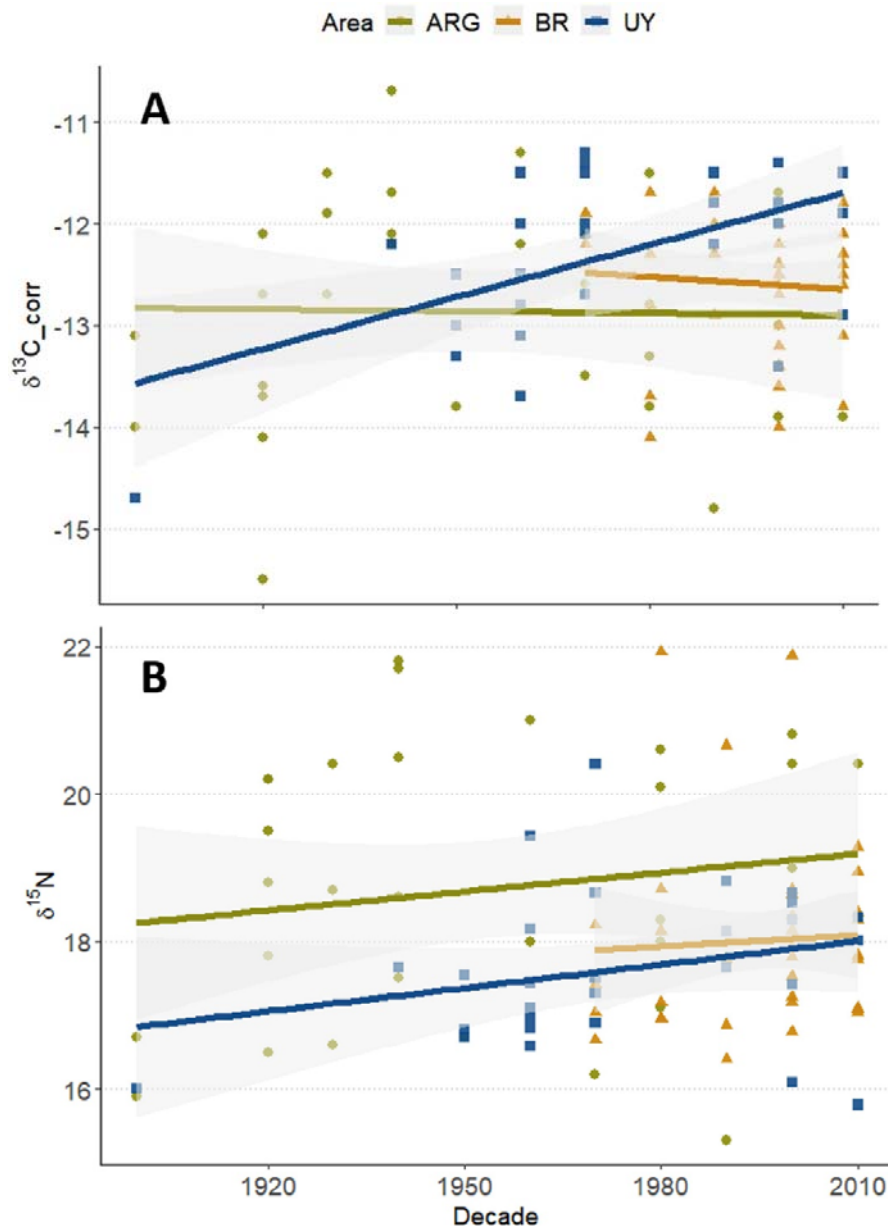


Fig. 2. Temporal trends in $\delta^{13}\text{C}_{\text{corr}}$ ($\delta^{13}\text{C}$ values corrected for isotopic baseline shifts) (A) and $\delta^{15}\text{N}$ values (B) in bone collagen of Lahille's bottlenose dolphins (*Tursiops truncatus gephyreus*) from Argentina (ARG, green dots and regression line) Brazil (BR, orange triangles and regression line) Uruguay (UY, blue squares and regression line) collected from 1903 to 2017. Each point represents individual isotopic compositions. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.1. Isotopic niche areas

The isotopic niche areas of the individuals sampled in the different periods showed different patterns of overlap among the areas. During the first period, ARG ellipse area was considerably larger than that of UY, and ellipse area from BR was the smallest. There was a considerable overlap, mainly between BR and UY, covering 80.0% and 10.3.% of their isotopic areas, respectively. ARG and BR ellipses also showed an overlap that included 2% and 32.5% of their respective ellipse areas. The overlap between ARG and UY isotopic areas, represented 33.9% and 71% of their respective areas. In the second period, ARG and UY dolphins showed a complete segregation of their isotopic niches, while BR ellipse area was partially overlapped with that of ARG (representing 25.0% of the ARG and 50.0% of BR areas) and UY (covering 20.8% and 45.5% of BR and UY areas, respectively) (Table 2, S3, S4, Fig. 3).

Table 2. Values of standard ellipse areas for small sample sizes ($SEAc$) and Bayesian ellipse areas (SEA_B) with their respective credibility intervals (CI 95%) from $\delta^{13}C_{corr}$ ($\delta^{13}C$ values corrected by the Suess effect) and $\delta^{15}N$ values of Lahille's bottlenose dolphin (*Tursiops truncatus gephyreus*) from Brazil (BR), Uruguay (UY) and Argentina (ARG) sampled during Periods I (1903–1980) and II (1981–2016). All metrics are in (‰^2).

	Period I			Period II		
	BR	UY	ARG	BR	UY	ARG
$SEAc$	0.4	3.1	6.5	2.4	1.1	4.8
SEA_B	0.3	2.8	6.0	2.3	1.0	4.4
$CI_{95\%}$	0.1–1.0	1.7–4.6	3.7–9.4	1.7–3.3	0.6–2.1	2.4–8.2

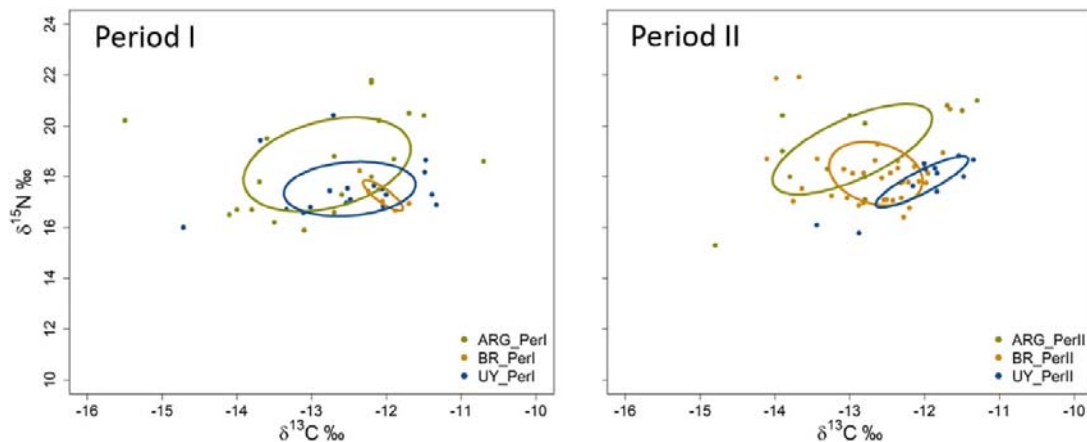


Fig. 3. Biplot of $\delta^{13}C_{corr}$ ($\delta^{13}C$ values corrected for isotopic baseline shifts) and $\delta^{15}N$ values of Lahille's bottlenose dolphin (*Tursiops truncatus gephyreus*) from Brazil (BR) Uruguay (UY) and Argentina (ARG) sampled during Periods I (1900–1980) and II (1981–2017). Each point represents the individual isotopic composition. Standard ellipse areas corrected for small sample sizes ($SEAc$) representing the isotopic niche of dolphins collected in different areas and periods are shown.

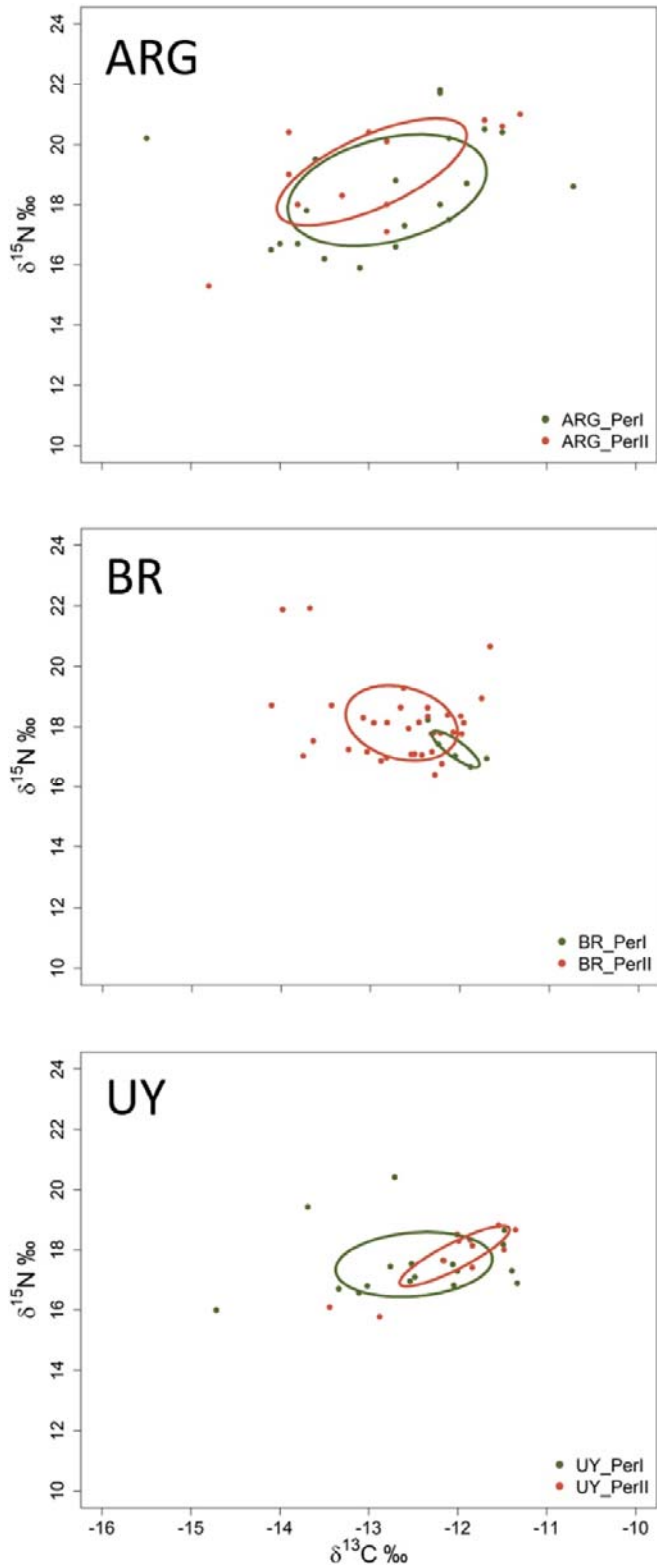


Fig. 4. Biplot of $\delta^{13}\text{C}_{\text{corr}}$ ($\delta^{13}\text{C}$ values corrected for isotopic baseline shifts) and $\delta^{15}\text{N}$ values of Lahille's bottlenose dolphin (*Tursiops truncatus gephyreus*) from Brazil (BR) Uruguay (UY) and Argentina (ARG) sampled during Periods I (1900–1980) and II (1981–2017). Each point represents the individual isotopic composition. Standard ellipse areas corrected for small sample sizes (SEAc) representing the isotopic niche of dolphins collected in different areas and periods are shown.

The comparison between isotopic ellipses between periods within each area, showed a decrease in the isotopic niche areas from Period I to Period II for ARG and UY, and an increase in the niche area for BR. A high overlap between the ellipses representing these two periods for ARG and UY. In ARG the overlap area covered 60.0% and 81.2% of the Period I and Period II niche areas, respectively. In UY, the overlap area covered 25.8% and 72.7% of the Period I and Period II areas, respectively. For BR periods, the overlap area was smaller and it represented 50.0% of the Period I area and 8.3% of the Period II area (Table 2 and S4, Fig. 4).

3.2. Diet composition of dolphins from Argentina and Uruguay

Mixing polygons showed that almost all ARG and all UY individuals, were within the 95% mixing region formed by the TDF-corrected isotopic values of their respective prey when using the set of TDF values from Giménez et al. (2016) modified by Teixeira et al. (2020) (Fig. S1). In the case of polygons generated by correcting prey isotopic values using Borrell et al. (2012) TDFs 50% of the individuals were outside the outermost contour in the case of ARG. In the case of UY, even though all individuals were within the outermost polygon, most of them were located in the outermost contours, showing a worse performance with respect to the previous model. Therefore, MixSIAR models for ARG and UY were run using Giménez et al. (2016) modified by Teixeira et al. (2020) TDFs.

MixSIAR models showed that for Period II ARG dolphins, *Pagrus pagrus* and *Percophis brasiliensis*, followed by *Cynoscion guatucupa* were the most important prey items. *Micropogonias furnieri* had a lower contribution, while the remaining fishes (*Brevoortia aurea*, *Macrodon atricauda*, *Mugil liza* and *Odonthestes* sp.) showed a minimal contribution to the diet of these dolphins (Fig. 5).

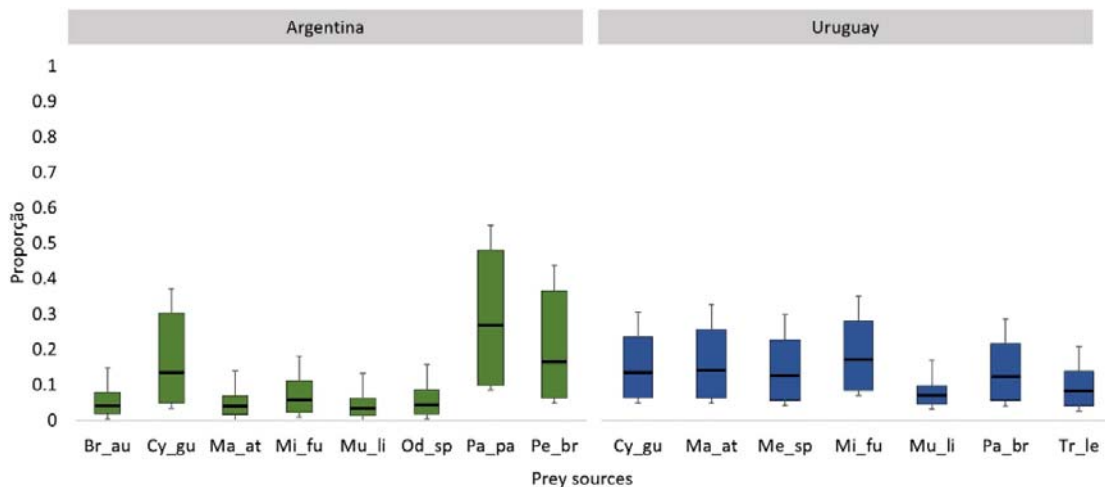


Fig. 5. Relative contribution of prey sources to the diet of Lahille's bottlenose dolphins (*Tursiops truncatus gephyreus*) from Argentina and Uruguay collected in Period II (1981–2017) according to MixSIAR models. Sources: *Brevoortia aurea* (Br_au), *Cynoscion guatucupa* (Cy_gu), *Macrodon atricauda* (Ma_at), *Micropogonias furnieri* (Mi_fu), *Mugil liza* (Mu_li), *Odonthestes* sp. (Od_sp), *Pagrus pagrus* (Pa_pa), *Percophis brasiliensis* (Pe_br), *Menticirrhus* sp. (Me_sp), *Paralonchurus brasiliensis* (Pa_br), *Trichiurus lepturus* (Tr_le).

Dolphins from UY showed a high proportion of *Micropogonias furnieri* in their diets during Period II. Other demersal fish species (*Cynoscion guatucupa*, *Macrodon atricauda*,

Menticirrhus sp. and *Paralonchurus brasiliensis*) had a similar contribution to their diet during this period, with the exception of *Mugil liza* that showed the lowest proportion (Fig. 5).

4. Discussion

The temporal and spatial variations in the trophic ecology of the Lahille's bottlenose dolphin were analyzed by means of stable isotope analysis of historical and contemporary bone samples. Our findings represent the first information about the foraging ecology of this endemic dolphin for the coasts of Argentina and Uruguay, showing a diet mainly based on demersal fish for both areas, as reported for populations from southern Brazil (Secchi et al., 2016; Machado et al., 2020). The temporal trend in isotopic values of carbon and nitrogen in the three areas, can be interpreted as a considerable stability in the feeding patterns of the species, at least for BR and ARG. In the case of UY, an increase in carbon isotopic values added to a decrease in the isotopic niche area between historical (Period I) and recent (Period II) samples, indicates that a potential change in the feeding patterns of this species might have occurred within the last decades. In UY, lower stable isotopic values are found in predators that use the estuarine waters of the Río de la Plata (e.g. franciscana dolphins, *Pontoporia blainvillei*), compared to those foraging in the adjacent coastal marine waters (e.g. South American sea lion, *Otaria flavescens* and franciscanas inhabiting marine waters) (Franco-Trecu et al., 2017; Artecona et al., 2019). Therefore, this shift in isotopic values towards more ^{13}C -enriched carbon isotopic values is may be related to a recent reduction in the use of the estuarine waters as a foraging ground by the Lahille's bottlenose dolphin in UY. Indeed, the species used to be seen in the UY estuarine coasts, in front of Montevideo and other coastal cities and now it is rarely seen in those areas, being mainly concentrated in the Atlantic section of the coast of this country (Lodi et al., 2016).

Lahille's bottlenose dolphins from Argentina showed a remarkable consistent isotopic niche area. This result was not expected considering the long period represented by the samples (1903–2010) and the important changes in the distribution patterns of the species in this country (Lodi et al., 2016; Vermeulen et al., 2017). Lahille's bottlenose dolphins used to occupy the estuarine waters of Río de la Plata and Bahía Samborombón and the marine coastal waters of Buenos Aires until the early 2000s. Specimens collected from Period I virtually covered the entire range of the historical distributional area of the Lahille's bottlenose dolphin in ARG, ranging from the Río de la Plata down to northern Patagonia coast (Vermeulen et al., 2017). However, the species is currently only seen in the southern coast of the Buenos Aires province and northern Patagonia (Lodi et al., 2016; Vermeulen et al., 2017); the causes of this reduction are still unknown (Vermeulen et al., 2017). According to mixing models, Period II dolphins relied mostly on *Pagrus pagrus*, *Percophis brasiliensis* and *Cynoscion guatucupa* as their main prey, followed by *Micropogonias furnieri* and *Odonthestes* sp. *Micropogonias furnieri* is the main demersal fish target for the Argentinian coastal fleet, operating in Río de la Plata, being the most important prey for estuarine franciscanas dolphins inhabiting this estuary (Rodríguez et al., 2002). On the other hand, *M. furnieri*, *C. guatucupa* and *P. pagrus* are more commonly caught along the marine coasts of Buenos Aires (Marcovecchio et al., 2019) where *C. guatucupa* is the most important prey of the marine franciscana dolphin within this area (Rodríguez et al., 2002; Paso-Viola et al., 2014). Therefore, the high proportion of *P. pagrus*, *P. brasiliensis* and *C. guatucupa* in the diet of Period II dolphins can be interpreted as an indication of a mostly marine feeding habit, considering the recognized opportunistic habit of the species. Although a similar isotopic niche area and a high overlap among ellipses for Periods I and II samples should point to a

conservative diet throughout the last century and the first decade of the present century, temporal changes at the base of food webs (Drago et al., 2017) or in the isotopic compositions of the prey cannot be ruled out as potential confounding factor that influenced the homogenization of the isotopic signal along this period. Unfortunately, no information about the feeding habits is available for Period I dolphins preventing a more accurate assessment of changes in the diet composition of this species in this part of its distribution.

In the case of Lahille's bottlenose dolphins from Uruguay the increasing trend in $\delta^{13}\text{C}_{\text{corr}}$ values accompanied by a reduction in the isotopic niche area from Period I to Period II, was interpreted as a change in the habitat use of the species. However, nitrogen isotopic values appeared to remain stable along the decades. Although no correction was performed for baseline modification in nitrogen stable isotopic values, this trend does not seem to have been affected by the baseline decreasing trend in $\delta^{15}\text{N}$ values of blue mussel (*Mytilus edulis*) shell samples reported in Drago et al. (2017). Similar results were found by Artecona et al. (2019) for franciscanas and South American sea lions inhabiting the same area, that did not show significant differences in $\delta^{15}\text{N}$ between historical and modern samples.

Mixing models used to infer dietary proportions for Lahille's bottlenose dolphins from Period II in UY, showed a high proportion of demersal fishes such as *M. furnieri*, *Macrodon ancylodon*, *C. guatucupa*, *Paralanchurus brasiliensis* and *Menticirrhus* sp., while *Trichiurus lepturus* and *M. liza* had a minimal contribution to their diet. *M. furnieri* is the most important prey species in the artisanal UY fleet and, although it is now showing signs of overexploitation, it still constitutes the main fish landed in the estuarine region, together with *C. guatucupa* and *M. ancylodon* (Defeo et al., 2009). In this context, the shift in the isotopic niche area observed for Period II dolphins might be related to a reduction in their use of the estuarine waters, probably related to the increased fishing effort, and the intense competition with fisheries along the Río de la Plata estuary.

In southern Brazil, Secchi et al. (2016) reported a decrease in the relative importance of *M. furnieri* and a rise in the proportion of *Trichiurus lepturus* and *P. brasiliensis* after the 1980s, which was probably related to the decline of *M. furnieri* due to overfishing (Haimovici and Cardoso, 2017). Isotopic niche areas for Period I was considerably smaller than that of Period II samples, which was probably related to the low sample size of the first period. Temporal trends in isotopic values showed a remarkable stability in both nitrogen and Suess-corrected carbon isotopic values. However, a more detailed analysis of the mean isotopic values in teeth collagen reported in Secchi et al. (2016) for dolphins from the same population, revealed some interdecadal differences in $\delta^{15}\text{N}$ values probably related to differences in the proportion of the main preys.

The comparison of the isotopic niche areas and mean isotopic niche values among areas and periods revealed some spatial patterns that could arise from an ecological structuring of the Lahille's bottlenose dolphin populations along its distribution. Nitrogen isotope values for samples collected along the coasts of Argentina were higher than those from Uruguay and southern Brazil, probably reflecting both a variation in diet composition and differences in the basal isotopic values among areas (Vales et al., 2013). This isotopic distinction of ARG dolphins can be considered as an additional line of evidence supporting the existence of an Evolutionarily Significant Unit (ESU) of Lahille's bottlenose dolphin in this area, isolated from Southern Brazil-Uruguay ESU (Fruet et al., 2014). In a temporal perspective, the analysis of samples covering more than a century also revealed that this ecological difference was consistent across decades, indicating that the large Río de la Plata estuary has probably

been acting as an important factor driving the ecological structuring of Lahille's bottlenose dolphin populations. In fact, the Río de la Plata estuary constitutes a biogeographic barrier for many taxa in both marine and terrestrial organisms and is hypothesized to constitute a significant biogeographic boundary to coastal ecosystems (Bisbal, 1995; Vales et al., 2013; Pereira et al., 2009). Abrupt environmental changes are known to have the potential to shape ecological patterns in the marine environment, even in high mobile species such as cetaceans. For example, franciscana dolphins inhabiting coastal waters at both sides of the Río de La Plata estuary show a fine-scale differentiation revealed by genetic data (Mendez et al., 2008, 2010; Costa-Urrutia et al., 2012; Gariboldi et al., 2016; Negri et al., 2016). This pattern is also supported by concomitant differences in the diet composition (Rodríguez et al., 2002) and morphometric parameters (Barbato et al., 2012). The application of stable isotope analysis to reveal population structure has been applied to support the genetic structuring observed in other cetaceans such as killer whales (*Orcinus orca*, Esteban et al., 2016), Atlantic spotted dolphins (*Stenella frontalis*, Méndez-Fernandez et al., 2020) and other *Tursiops truncatus* populations (e.g. Borrell et al., 2006; Brotons et al., 2008; Hohn et al., 2017; Giménez et al., 2018), even at a spatial fine-scale (Genoves et al., 2020). Furthermore, these ecological tracers can also provide clues to a potential population structuring when other tools are warranted (e.g. Troina et al., 2020). Although it was not the main purpose of this study, the ecological discontinuity observed between southern Brazil/Uruguay and Argentina Lahille's bottlenose dolphins, which matches with their genetic structuring patterns, seems to coincide with significant changes in ecological characteristics between these regions. This result is especially relevant in the context of the current geographic isolation of the Argentinian ESU of Lahille's bottlenose dolphin (Fruet et al., 2014) that points to the need of further research and monitoring towards its effective conservation.

Similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for dolphins sampled in southern Brazil and Uruguay were found. This result seems to be in line with the ecological characteristics of the region, where there are no evident environmental barriers acting in the coastal habitat, suggesting that dolphins from southern Brazil and Uruguay share similar resources and isotopic landscapes. Indeed, Fruet et al. (2014) proposed that dolphins from southern Brazil and Uruguay are split into at least five management units (MU's) functioning as a metapopulation, where exchange and/or movement of individuals between MU's can occur at different temporal and spatial scales. Photo-identification data conducted in La Coronilla, Uruguay, and in the Patos Lagoon estuary and adjacent coastal areas, southern Brazil, has revealed regular movement of dolphins between these two areas (Laporta et al., 2016). Every year, a great proportion of dolphins from Uruguay MU are observed feeding in the adjacencies of the Patos Lagoon estuary MU, especially during the cold months, but the inverse movement direction seems to be rare (Laporta et al., 2016). Therefore, the results presented here reinforce the ecological link between these two MUs, despite the fine scale genetic population structure.

The analysis of samples of the Lahille's bottlenose dolphin, including a large part of its distribution and a time series of more than a century, offered a unique opportunity to investigate trophic habits of this subspecies. However, caution is needed when interpreting the results obtained, mainly due to the small sample size in certain areas/periods. In addition, to apply isotope mixing models to investigate predator diets, some prior information about the composition of prey of the species is necessary (Phillips et al., 2014). The scarcity of previous studies on the species' diet in a large part of its distribution (i.e. Uruguay and Argentina) may have caused the inclusion of prey that are not part of the species' diet in those places, as well as the non-inclusion of a real dietary source. However, the inclusion of prey eventually reported as preferred dietary items and of fish species of common presence in the

studied areas, allows us to believe that the results obtained reflected a diet close to the real one. Still, one of the problems of using bone collagen, generally the most commonly available tissue in the case of historical samples of vertebrates, is the lack of specific isotopic discrimination factors for this type of tissue. However, we tried to control this caveat by testing the use of different trophic discrimination factors by means of mixing polygons.

5. Conclusions

Temporal trends in isotopic values of $\delta^{13}\text{C}_{\text{corr}}$ and $\delta^{15}\text{N}$ showed that no striking shifts in diet might have occurred in Lahille's bottlenose dolphins from ARG and BR between historical (Period I) and recent (Period II) periods. In the case of UY, a change in the habitat use might explain the increasing trends in $\delta^{13}\text{C}_{\text{corr}}$ values, supported by the current disappearing of the species from the estuarine waters of Río de la Plata. UY and ARG mixing models showed demersal fish species as the main prey for the species, which was in accordance to the diet reported for BR dolphins (Secchi et al., 2016) and for coastal *Tursiops* as a whole. Our findings showed a clear distinction in the isotopic values between dolphins from Brazil/Uruguay and those sampled in Argentina, which reinforces previously identified genetic distinction between these two evolutionary units (Fruet et al., 2014). In conclusion, the retrospective analysis by means of stable isotope compositions in archived bone collagen of Lahille's bottlenose dolphin contributed to the knowledge of feeding behavior and the ecological structure of this poorly known subspecies. These results provide an important contribution for future conservation strategies and management plans for this endangered cetacean subspecies, endemic of the southwestern Atlantic Ocean.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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