Temporal and individual variation in the diet of the Neotropical otter, Lontra longicaudis *(Olfers, 1818) (Carnivora, Mustelidae), as revealed by stable isotope analysis of vibrissae*

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ORIGINAL ARTICLE

Temporal and individual variation in the diet of the Neotropical otter, *Lontra longicaudis* (Olfers, 1818) (Carnivora, Mustelidae), as revealed by stable isotope analysis of vibrissae

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Abstract

The Neotropical otter, *Lontra longicaudis*, is a semiaquatic mustelid that preys upon fish, amphibians, and crustaceans, in variable proportions according to habitat and/or season. Due to the difficulty of observing this species in the wild, information on its ecology is typically obtained through vestiges, such as feces, which usually do not provide data at the individual level. Thus, this study aimed to assess temporal and individual variation in the diet of the Neotropical otter through chronologically ordered carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes data, as a proxy for dietary variation. For this purpose, isotopic values of 127 fragments of vibrissae collected from 21 individuals found dead along three coastal regions of southern Brazil were analyzed. Values ranged between − 24.0 and − 12.9‰ for $\delta^{13}C$ and from 10.6 to 18.4‰ for $\delta^{15}N$. Vibrissae isotopic longitudinal data were variable, indicating individual changes in the proportion of food items consumed and in foraging sites that spanned from freshwater to marine environments. Most of the populational variation in isotopic composition resulted from differences between individuals. The results of this study revealed temporal and individual variation in resource and habitat use by the Neotropical otter in three coastal ecosystems, and suggest that a high individual foraging specialization may occur in this species.

Keywords Carbon · Feeding habits · Habitat use · Individual specialization · Nitrogen

Introduction

Information on the ecology of most otter species is provided by vestiges such as feces, which are often easy to find and reveal valuable information (e.g., Kanchanasaka and Duplaix 2011; Brzeski et al. 2013; Buzzell et al. 2014; Martínez-Abraín et al. 2020; Sittenthaler et al. 2020). This is also the

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case for the Neotropical otter, *Lontra longicaudis*, for which almost all information, especially regarding feeding habits, was obtained through these methods. For instance, Trinca et al. (2013) analyzed fecal DNA from a population of this species inhabiting an Atlantic forest in Brazil and revealed that females are philopatric, whereas males are dispersive. Dietary studies performed with scat content indicate that the main prey group for the Neotropical otter is fish, followed by crustaceans and amphibians (Quadros and Monteiro-Filho 2001; Alarcon and Simões-Lopes 2004; Quintela et al. 2008; Carvalho-Junior et al. 2010; Rheingantz et al. 2011; Costa-Braga et al. 2019). Trophic diversity is typically high in coastal areas due to the availability of alternative prey (Rheingantz et al. 2017) as both marine and freshwater environments are accessible (e.g., Alarcon and Simões-Lopes 2003; Carvalho-Junior et al. 2012; Andrade et al. 2019). In addition to spatial differences, the proportion of consumed items in the diet of the Neotropical otter may vary seasonally, according to main prey availability (Rheingantz et al. 2011; Quintela et al. 2012a; Costa-Braga et al. 2019). However, except for fecal DNA analysis, it is impossible to identify individuals and thus assess individual patterns in diet.

An important ecological concept is that of individual specialization (Bolnick et al. 2003), which states that conspecific individuals are not ecologically identical or equivalent and each one may rely on a subset of resources used by the overall population. This variation is not related to either ontogenetic niche shifts or ecological sexual dimorphism, being observed among individuals of a given sex and age. The degree of individual specialization relies on factors such as intra- and interspecific competition, ecological opportunity, and predation pressure (Araújo et al. 2011). Besides that, in contrast to specialist populations, generalist populations tend to be ecologically variable and may be composed of relatively specialized individuals (Bolnick et al. 2007). In turn, an individual specialist has a restricted diet concerning its population's diet, while the feeding habits of a generalist individual comprise its majority (Bolnick et al. 2003).

Individual foraging specialization can be assessed through stable isotope analysis of continuous growing and inert tissues, such as vibrissae (e.g., Kernaléguen et al. 2012), dentin (e.g., Rossman et al. 2015), baleen plates (e.g., Eisenmann et al. 2016), and scutes of carapaces (e.g., Vander Zanden et al. 2013). In the case of studies with otters, the individual specialization can be assessed by analyzing the vibrissae, as demonstrated for the sea otter, *Enhydra lutris* (e.g., Newsome et al. 2009, 2015; Smith et al. 2015). Stable isotope analysis is based on the premise that the isotopic composition of consumer's tissues reflects the food digested and assimilated, with predictable changes due to the loss of light isotopes, following the biogeochemical processes of the trophic web (Peterson and Fry 1987). Carbon isotopic values ($\delta^{13}C$) are especially useful to infer preferred habitats of consumers, since $\delta^{13}C$ values are related to the fractionation of carbon during the photosynthetic process (Kelly 2000), and, thus, are distinctive between environments dominated by producers with different physiologies in both terrestrial and aquatic ecosystems (DeNiro and Epstein 1978). Nitrogen isotopic values ($\delta^{15}N$) are also affected by the physiological mechanisms of the producers, as well as by the external nitrogen source (Evans 2001). However, there is a marked enrichment in the heavy isotope along with the trophic web, so the values of $\delta^{15}N$ tend to reflect the trophic position of the consumers (Post 2002). Thus, although stable isotopes do not usually provide taxonomic information regarding prey consumed, it can offer a useful proxy of dietary variation and habitat use over time and it is especially efficient for studying populations where temporal data series of individuals would, otherwise, be challenging to acquire (Newsome et al. 2009).

In addition to studies with the sea otter, individual specialization has already been investigated in the African clawless otter, *Aonyx capensis*, and in the spotted-necked otter, *Hydrictis maculicollis* (Jordaan et al. 2019, 2020), through isotopic composition along vibrissae. The African clawless otter, as the Neotropical otter, may use both freshwater and marine habitats, presenting substantial behavioral and dietary plasticity (Jordaan et al. 2019). Differences in individual carbon and nitrogen isotopic ratios of the spotted-necked otter feeding on freshwater sources are also evident (Jordaan et al. 2020). Recently, Carrasco et al. (2019) analyzed the stable isotope composition of carbon and nitrogen in tooth dentin of Neotropical otter samples from coastal aquatic ecosystems in southern Brazil. Results revealed a wide trophic diversity, which might be a consequence of individual variation in generalist populations. However, the methodology employed by the authors did not allow the testing of this hypothesis.

Therefore, the present study expands the knowledge reported in Carrasco et al. (2019) by assessing individual and temporal variation in the diet of the Neotropical otter through carbon and nitrogen stable isotopes of vibrissae.

Materials and methods

Study sites and sampling

Neotropical otter samples ($n = 21$) were collected opportunistically from carcasses by plucking out the vibrissae from the muzzle. These samples were obtained by different institutions, between 1998 and 2017, along three coastal regions of southern Brazil: Santa Catarina Island (27°35′S, 48°28′W), Tramandaí River Basin (29°48′S, 50°11′W), and Taim Wetland (32°44′S, 52°34′W) (Table 1, Fig. 1). Considering that the Neotropical otter usually exhibits relatively

Table 1 Age class, sex, date of collection, study area, sampling institution, vibrissae length, and number of fragments analyzed of Neotropical otters from the present study. Mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values (‰) of the vibrissae are also shown

Sample ID	Sampling date	Institution	Sex	Age class	Vibrissa length (cm)	Number of fragments	$\delta^{13}C$	$\delta^{15}N$
Santa Catarina Island								
910	04/14/1998	UFSC	M	Adult	5.4	7	−20.7 ± 1.1	13.3 ± 1.3
2792	08/03/1999	UFSC	M	Adult	7.8	12	−20.8 ± 1.3	12.3 ± 0.5
3090	11/25/2002	UFSC	M	Cub	3.0	3	−13.0 ± 0.2	18.2 ± 0.3
3390	08/09/2004	UFSC	F	Adult	6.9	10	−21.0 ± 0.5	12.5 ± 0.5
158		UFSC	M	Cub	6.0	8	−18.5 ± 0.9	13.0 ± 0.7
Tramandaí River Basin								
1483	05/27/2004	GEMARS	M	Adult	3.4	4	−21.8 ± 0.3	11.6 ± 0.1
1405	05/15/2010	GEMARS	F	Adult	4.6	3	−23.9 ± 0.3	11.8 ± 0.5
1481	11/21/2011	GEMARS	M	Adult	10.1	8	−14.2 ± 0.3	13.7 ± 0.4
1631	08/21/2012	GEMARS	F	Cub	3.5	3	−22.9 ± 0.3	13.8 ± 0.7
1629	12/31/2012	GEMARS	M	Adult	6.3	7	−21.9 ± 0.9	12.5 ± 0.8
1632	02/18/2013	GEMARS	M	Adult	5.5	6	−22.3 ± 0.8	11.8 ± 0.9
1666	10/10/2013	GEMARS	F	Adult	5.9	5	−21.9 ± 0.9	12.2 ± 0.5
1677	02/27/2014	GEMARS	M	Adult	6.7	7	−21.2 ± 0.7	13.1 ± 0.6
1702	07/09/2014	GEMARS	M	Juvenile	5.2	4	−23.5 ± 0.6	13.1 ± 0.4
1701	08/23/2016	GEMARS	M	Adult	5.4	6	−22.8 ± 0.6	12.7 ± 0.3
Taim Wetland								
66550	06/06/2013	FURG	F	Adult	5.4	3	−20.5 ± 0.6	10.7 ± 0.1
353	09/05/2016	FURG	M	Adult	5.2	8	−22.2 ± 0.5	11.5 ± 0.9
960	09/22/2016	NEMA	M	Adult	6.0	7	−15.7 ± 0.9	16.5 ± 0.5
998	10/14/2016	FURG	M	Adult	6.0	7	−22.1 ± 0.2	13.4 ± 0.2
338	12/16/2016	FURG	M	Adult	1.2	1	−22.5	13.1
521	06/28/2017	FURG	M	Adult	6.6	8	−21.3 ± 0.6	12.5 ± 1.1

Date of sampling of the individual 158 is unknown. Legend: UFSC (Universidade Federal de Santa Catarina), GEMARS (Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul), FURG (Universidade Federal do Rio Grande), and NEMA (Núcleo de Educação e Monitoramento Ambiental)

small home range (Trinca et al. 2013), we assume that the vibrissae isotopic signals reflect those assimilated at the proximities of the study sites where the animals were found.

Both Santa Catarina Island and Tramandaí River Basin have a subtropical climate, with rainfalls distributed throughout the year and temperatures around 23 °C in summer and 16 °C in winter. Taim Wetland has a temperate climate, with climatic conditions in summer similar to the former study areas, but showing lower temperatures in winter, around 11 °C (Wrege et al. 2012).

Santa Catarina Island is part of the central coast of Santa Catarina State, separated from the continent by a narrow channel of approximately 500 m. It is inserted in the Atlantic rain forest biome and presents a great variety of ecosystems, including forests, lagoons, coastal dunes (i.e., foredunes), and beaches (Steiner et al. 2006). The lagoons primary producers' community is mainly dominated by cyanobacterium (e.g., *Cylindrospermopsis raciborskii*) (Hennemann and Petrucio 2011) and dense vegetation surrounding it predominantly formed by sedges, *Schoenoplectus californicus* (Ferreira et al. 2016). The coast is bedrock-dominated with dune fields (Klein et al. 2016). Foredune vegetation is mainly composed of *Spartina ciliata* (Silva et al. 2008). In the marine environment, there are several species of red algae, mostly of Ceramiales order (Bouzon et al. 2006).

The Tramandaí River Basin is located in the northern coastal plain of Rio Grande do Sul State. It consists of a system of medium-sized lagoons interconnected by small channels and by the Tramandaí River with the estuary of Tramandaí Lagoon, which flows to the Southwestern Atlantic Ocean (Villwock 2009; Loitzenbauer and Mendes 2012). Along the margins of the estuary, it is possible to see banks of coastal marsh plants, such as *Schoenoplectus americanus*. The submerged vegetation is mainly composed of the widgeon grass *Ruppia maritima* and green alga *Enteromorpha* sp. (Hoeinghaus et al. 2011). Due to the connection with the ocean, there is also a diversity of marine algae (e.g., *Operculodinium* sp. and *Dictyocha* sp.) (Medeanic et al. 2010). The margins of freshwater lagoons are covered predominantly by emerging aquatic macrophytes (e.g., *Typha domingensis*

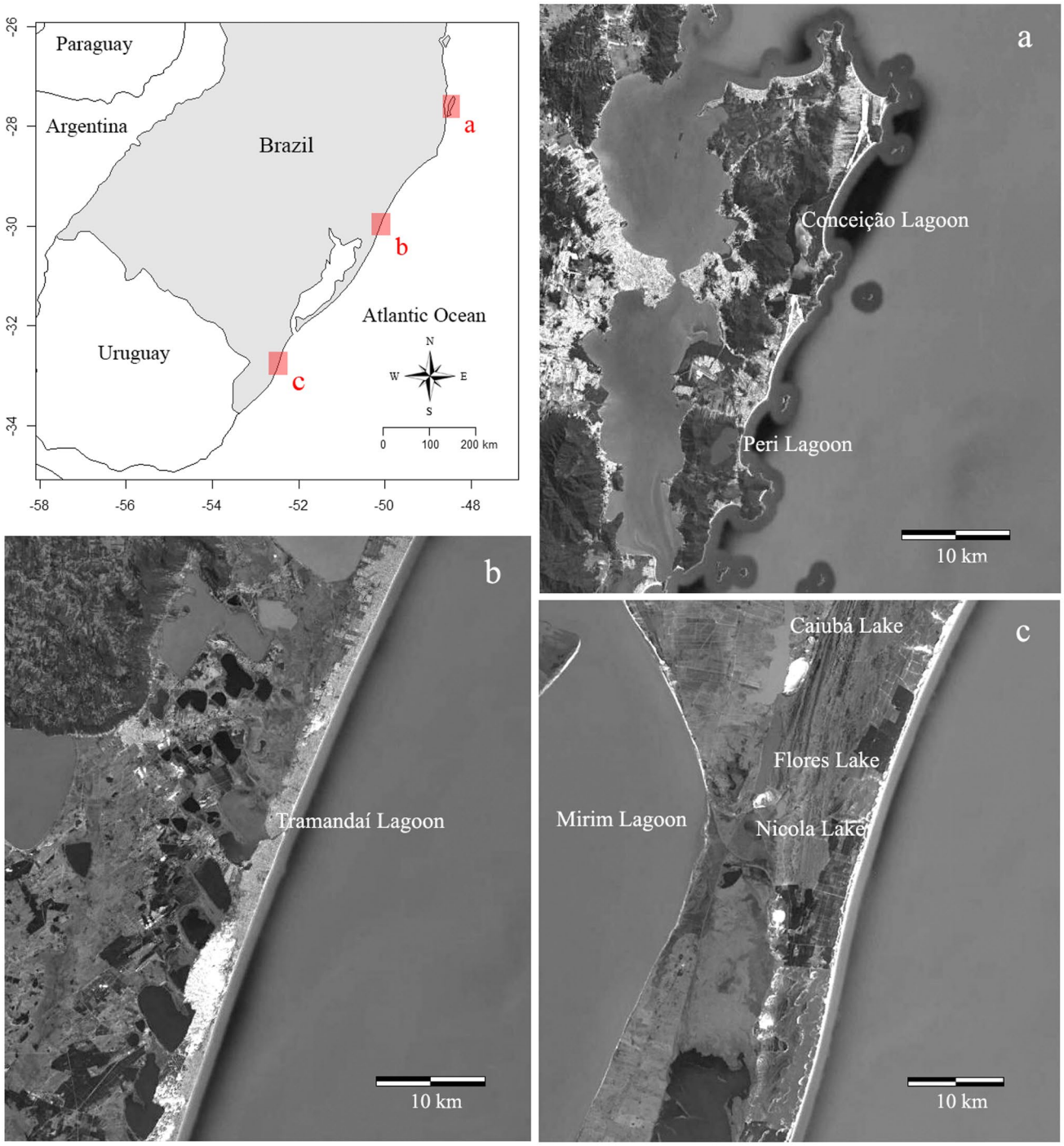

Fig. 1 Study area in southern Brazil showing the three sampling locations: **a** Santa Catarina Island, **b** Tramandaí River Basin, and **c** Taim Wetland. The most important water bodies from each location are indicated

and *S. californicus*). In these aquatic bodies, there are also floating aquatic and submerged macrophytes (*Eichhornia* sp. and *Potamogeton* sp., respectively), as well as green algae (*Chara* sp. and *Nitella* sp.) (Prado 2009).

The Taim Wetland is the southernmost study area, located in the extreme south of Brazil, also inserted in the coastal plain of Rio Grande do Sul. It comprises mostly flooded portions of land and lakes. Consequently, there is a predominance of macrophytes (*Zizaniopsis bonariensis*, *S. californicus,* and *Myriophyllum aquaticum*) and phytoplankton as primary producers (Marques et al. 2013). In elevated land portions, less prone to flooding, there is the development

of palustrine forests composed by trees such as *Erythrina crista-galli*, *Ficus organensis*, *Blepharocalyx salicifolius*, *Eugenia uruguayensis,* and *Sebastiania brasiliensis* (Waechter and Jarenkow 1998). The coastal region is characterized by the presence of foredunes sparsely covered by herbaceous plants (e.g., *Androtrichum trigynum*) (Gomes and Krause 1982; Seeliger et al. 1998). In the marine environment, the main primary producers are phytoplankton (diatoms and dinoflagellates algae) (Odebrecht and Garcia 1998) and benthic algae (e.g., *Bryopsis plumosa* and *Gymnogongrus griffithsiae*) (Cordazzo and Seeliger 1995).

Stable isotope analysis

Vibrissae were cleaned with a 2:1 chloroform:methanol solution to remove surface contaminants and lipids. After cleaning, vibrissae were subsampled into fragments of 0.6 cm using a nail clipper. Then, each fragment was sealed into tin capsules. When the subsample weight was insufficient for isotopic analysis (< 0.5 mg), it was packed with the next fragment. Thus, the number of samples per individual varied according to vibrissae length and weight, ranging from 1 to 12. The carbon and nitrogen isotopic compositions were determined at the University of New Mexico Center for Stable Isotopes (UNM–CSI, Albuquerque, NM) through a Costech 4010 (Costech, Valencia, CA) elemental analyzer coupled to a Thermo Scientific Delta V (Thermo Scientific, Bremen, Germany) isotope ratio mass spectrometer. The natural isotopic ratios (R) of each element ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in Neotropical otter vibrissae segments are reported by the heavier form (X) expressed by delta notation (δ) in parts per thousand (‰) relative to the standards V-PDB (Vienna Pee Dee Belemnite limestone) for $\delta^{13}C$ and atmospheric nitrogen (N_2) for $\delta^{15}N$, following the equation:

$$\delta X = \left[\left(R_{Sample}/R_{Standard}\right) - 1\right]$$

Analytical precision was monitored through internal laboratory standards at UNM–CSI (soy protein, whey protein, casein, tuna, IAEA-N1, IAEA-N2, USGS-4, and USGS-43), and it was measured to be < 0.2‰ for $\delta^{15}N$ and < 0.04‰ for $\delta^{13}C$.

Data analysis

Temporal variation in the individuals' diet was assessed by a longitudinal analysis of $\delta^{13}C$ and $\delta^{15}N$ values along vibrissae. For this purpose, we relied on the vibrissae linear growth rates reported for the sea otter: 7.7 cm/year for adults and 15.8 cm/year for cubs (Tyrrell et al. 2013). Based on these values, a single fragment of a Neotropical otter adult vibrissae (0.6 cm) may encompass a time window of approximately one month, while a fragment of cub vibrissae would encompass two weeks. Then, according to the growth rate and date of sampling, we assigned each subsample to a season of the year. The date of sampling of #158, an individual from Santa Catarina Island, is unknown, so it was not possible to associate the fragments to seasons for this individual. All vibrissae fragments, from base to the tip, were included in the analysis.

The individuals were classified as cub, juvenile, or adult according to the morphological characteristics of the skull, followed by the read of growth layer groups of canine cement (for more information, see Carrasco et al. 2019). When the skull and teeth were not available, the individuals had their ages estimated by total body length, since the average size of adult animals is around 120 cm (Cimardi 1996). Therefore, the individuals #1631 (54 cm), #998 (121 cm), and #338 (119 cm) were classified as cub and adults, respectively.

To estimate the relative isotopic contribution of food sources to the Neotropical otter diet, we applied Bayesian Stable Isotope Mixing Models in R (SIMMR) package version 0.4.1 (Parnell and Inger 2016). We ran models for each individual separately using $\delta^{13}C$ and $\delta^{15}N$ values of otter vibrissae and muscle of potential prey. The food items included in the model were selected from previous dietary information according to fecal analysis (F. Barbieri, personal communication; Colares and Waldemarin 2000; Quadros and Monteiro-Filho 2001; Alarcon and Simões-Lopes 2004; Kasper et al. 2004; Carvalho-Junior et al. 2010; Santos 2011; Quintela et al. 2012a; Sousa et al. 2013; Peres 2014) and Bayesian models (Carrasco et al. 2019). In both Santa Catarina Island and Taim Wetland, potential prey was selected from freshwater and marine environments, while in Tramandaí River Basin, sources were selected from freshwater and estuarine environments, based on the otters' dietary preferences for each region. The values of potential prey muscle were obtained from the literature (Silva-Costa and Bugoni 2013; Britto and Bugoni 2015; Carrasco et al. 2019). Most of the isotopic signatures of prey items included in the model are from animals sampled in both summer and winter austral seasons (Carrasco et al. 2019). Sources were aggregated into groups according to ecological and isotopic similarities (Table S1) to increase the discriminatory power of mixing models (Phillips et al. 2014). The values used as trophic discrimination factors (i.e., predictable differences between the isotopic ratios of the consumer and its diet) were $+2.2 \pm 0.7$‰ for $\delta^{13}C$ and $+3.5 \pm 0.6$‰ for $\delta^{15}N$, as reported for sea otter vibrissae (Newsome et al. 2010a). The models were evaluated a priori through simulated mixing polygons (Smith et al. 2013; Fig. S1).

The degree of individual specialization for adult males was measured through the Within-Individual Component/Trophic Niche Width (WIC/TNW) index for continuous data of $\delta^{13}C$ and $\delta^{15}N$ values, using the R Individual Specialization (RInSp) package version 1.2.4 (Zaccarelli et al. 2013).

The WIC/TNW index (based on Roughgarden 1974) compares the individual's niche to its population, ranging from zero, when individuals are specialists and each one uses only a small fraction of the population niche, to one, when there is no specialization and all individuals use the same subset of resources. We standardized the number of samples for each individual to make them contribute equally to the analysis. We applied the WIC/TNW index only for Taim Wetland ($n=4$, seven subsamples per individual) and Tramandaí River Basin ($n=6$, four subsamples per individual) males. It was not possible to evaluate the individual specialization for females from Taim Wetland and Tramandaí River Basin and either for both sexes from Santa Catarina Island due to an insufficient number of samples. In addition, we excluded juveniles and cubs to avoid the possible effects of ontogenetic differences.

To compare spatial isotopic differences in otters' $\delta^{13}C$ values between study areas, we applied a one-way analysis of variance (ANOVA). $\delta^{15}N$ values were compared using the non-parametric Kruskal–Wallis test, because the samples were not normally distributed according to the Shapiro–Wilk test. To compare stable isotope signatures of food sources from distinct environments (freshwater vs. marine/estuarine), we applied a Wilcoxon unpaired test using individual values of potential prey according to the habitat for Santa Catarina Island and Tramandaí River Basin. It was not possible to test for differences in the environments for Taim Wetland as we had access to marine prey mean values only (Silva-Costa and Bugoni 2013). We also tested for differences in isotopic values between winter and summer through Wilcoxon unpaired test using $\delta^{13}C$ and $\delta^{15}N$ values of species that had at least three samples per season.

All statistical analyses were performed in the R statistical environment version 3.6.1 (R Core Team 2019). The significance level for two-sided tests was $\alpha=0.05$.

Results

A total of 127 fragments from 21 vibrissae of the Neotropical otter were analyzed for stable isotopes: 5 vibrissae from Santa Catarina Island (mean 8.0 ± 3.4 subsamples per individual), 10 from Tramandaí River Basin (mean 5.3 ± 1.8 subsamples per individual), and 6 from Taim Wetland (mean 5.7 ± 2.9 subsamples per individual) (Table 1). The isotopic values of the otters did not differ significantly between areas in both carbon (ANOVA; $p=0.06$) and nitrogen (Kruskal–Wallis; $p=1.0$). Temporal data series are represented in Figs. 2, 3, and 4.

In subsamples from Santa Catarina Island, the isotopic values ranged from -22.3 to -12.9‰ and from 11.2 to 18.4‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. An adult male (individual #910) showed a wide range of values for both isotopes, with a difference between maximum and minimum values of 3.1‰ for $\delta^{13}C$ and 3.3‰ for $\delta^{15}N$. Values were more enriched in the heavier isotopes during spring and depleted in autumn. Another adult male (#2792) also showed great variation for $\delta^{13}C$ (4.4‰), with a peak in winter, but low changes in $\delta^{15}N$ values, which varied only by 1.4‰. $\delta^{15}N$ and $\delta^{13}C$ values varied, respectively, by 2.2 and 3.2‰ in a male cub (#158). The lowest variation (0.3‰ for $\delta^{13}C$; 0.5‰ for $\delta^{15}N$) and more enriched values (mean -13.0 ± 0.2 and 18.2 ± 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively) were also observed in a male cub (#3090) (Fig. 2).

The results found for Tramandaí River Basin vibrissae fragments ranged from -24.0 to -13.8‰ for $\delta^{13}C$ and from 11.3 to 14.8‰ for $\delta^{15}N$. The greatest longitudinal variation was observed in two males: #1629 (2.7‰ for $\delta^{13}C$, 1.9‰ for $\delta^{15}N$) and #1632 (2.7‰ for $\delta^{13}C$, 1.9‰ for $\delta^{15}N$), followed by an adult female (#1666) (2.5‰ for $\delta^{13}C$, 1.5‰ for $\delta^{15}N$), that showed more enriched values during the summer (Fig. 3).

Carbon and nitrogen isotopic ratios ranged from -22.7 to -15.0‰ and from 10.6 to 17.1‰, respectively, for vibrissae fragments of individuals sampled from Taim Wetland. Males from this region also showed wide isotopic variation. $\delta^{15}N$ varied 3.1‰ for the individual #521, with a peak in spring followed by a decrease in summer, while $\delta^{13}C$ did not vary considerably. A peak in spring was also observed for the individual #960, with a variation of 2.1‰ in $\delta^{13}C$ and only 1.5‰ in $\delta^{15}N$ along the vibrissa (Fig. 4).

The isospace biplot, representing the individual isotopic ratios of consumers and their potential prey, corrected by the trophic discrimination factors indicated that potential prey from different environments are isotopically distinct (e.g., marine vs. freshwater, with the latter presenting more ^{13}C- and ^{15}N-depleted isotopic values) for all studied regions (Fig. 5). Statistical analyses confirmed this pattern. In Santa Catarina Island, marine prey was isotopically distinct from freshwater ones (Wilcoxon test; $\delta^{13}C$, $p<0.001$, $\delta^{15}N$, $p<0.001$). Similarly, in Tramandaí River Basin, freshwater sources were different in $\delta^{13}C$ (Wilcoxon test; $p<0.001$), but no differences were found in $\delta^{15}N$ (Wilcoxon test; $p=0.07$). Most of the prey species tested for isotopic seasonal effects showed no differences in $\delta^{13}C$ and $\delta^{15}N$ values between winter and summer seasons (Table S2).

The isotopic signal of individuals from Santa Catarina Island was similar to freshwater prey, except for a male cub (#3090). Indeed, the mixing model shows that freshwater herbivorous fish and freshwater omnivorous fish were the most important prey for two adult males (#910 and #2792), an adult female (#3390) and a cub male (#158), while marine carnivorous fish was more important for individual #3090 (Fig. 6).

The most important prey for the Neotropical otter in Tramandaí River Basin was freshwater carnivorous fish

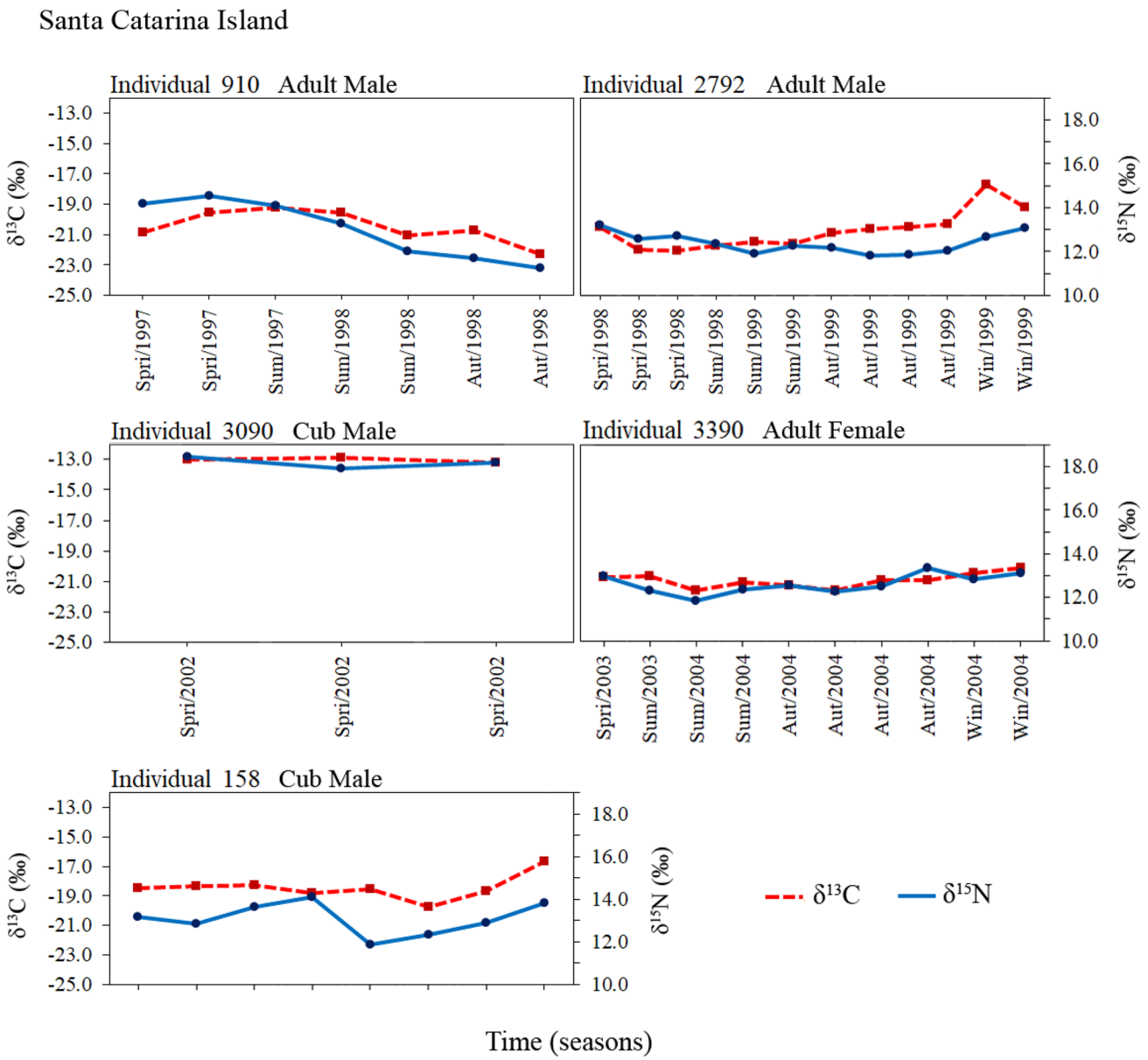

Fig. 2 Variability in $\delta^{13}C$ and $\delta^{15}N$ vibrissae values through time (expressed in austral seasons) for each individual of Neotropical otter sampled in Santa Catarina Island

followed by freshwater omnivorous fish. In this region, one adult male (#1481) presented an isotopic signal consistent with a diet based on estuarine herbivorous fish (Fig. 7).

In Taim Wetland, the feeding habits of the Neotropical otter were more diverse, with a high contribution of amphibians, followed by freshwater invertebrates and omnivorous fish. As in the other areas, we identified an individual (#960, adult male) with a marine diet (Fig. 8).

The WIC/TNW index, used to infer the degree of individual specialization, was 0.01 and 0.09 for carbon and nitrogen stable isotopes, respectively, for males from Tramandaí River Basin. Males from Taim Wetland showed a WIC/TNW equal to 0.04 for $\delta^{13}C$ and 0.09 for $\delta^{15}N$. All values were significant against the null hypothesis that all individuals are generalists (i.e., WIC/TNW = 1). The results of total niche width (TNW), the sum of within-individual component (WIC), and between-individual component (BIC), used to calculate the index, are shown in Table 2.

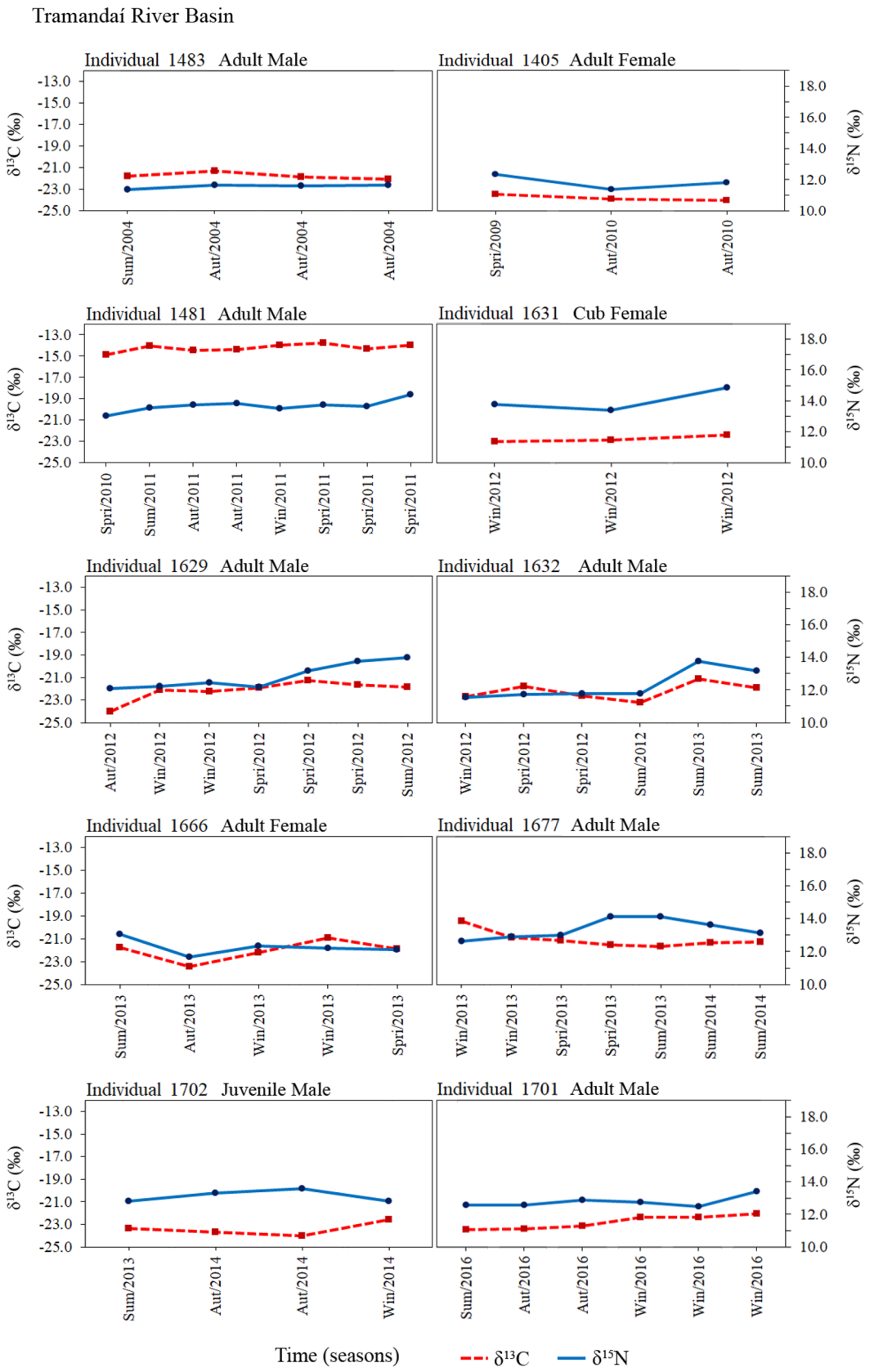

Fig. 3 Variability in $\delta^{13}C$ and $\delta^{15}N$ vibrissae values through time (expressed in austral seasons) for each individual of Neotropical otter sampled in Tramandaí River Basin

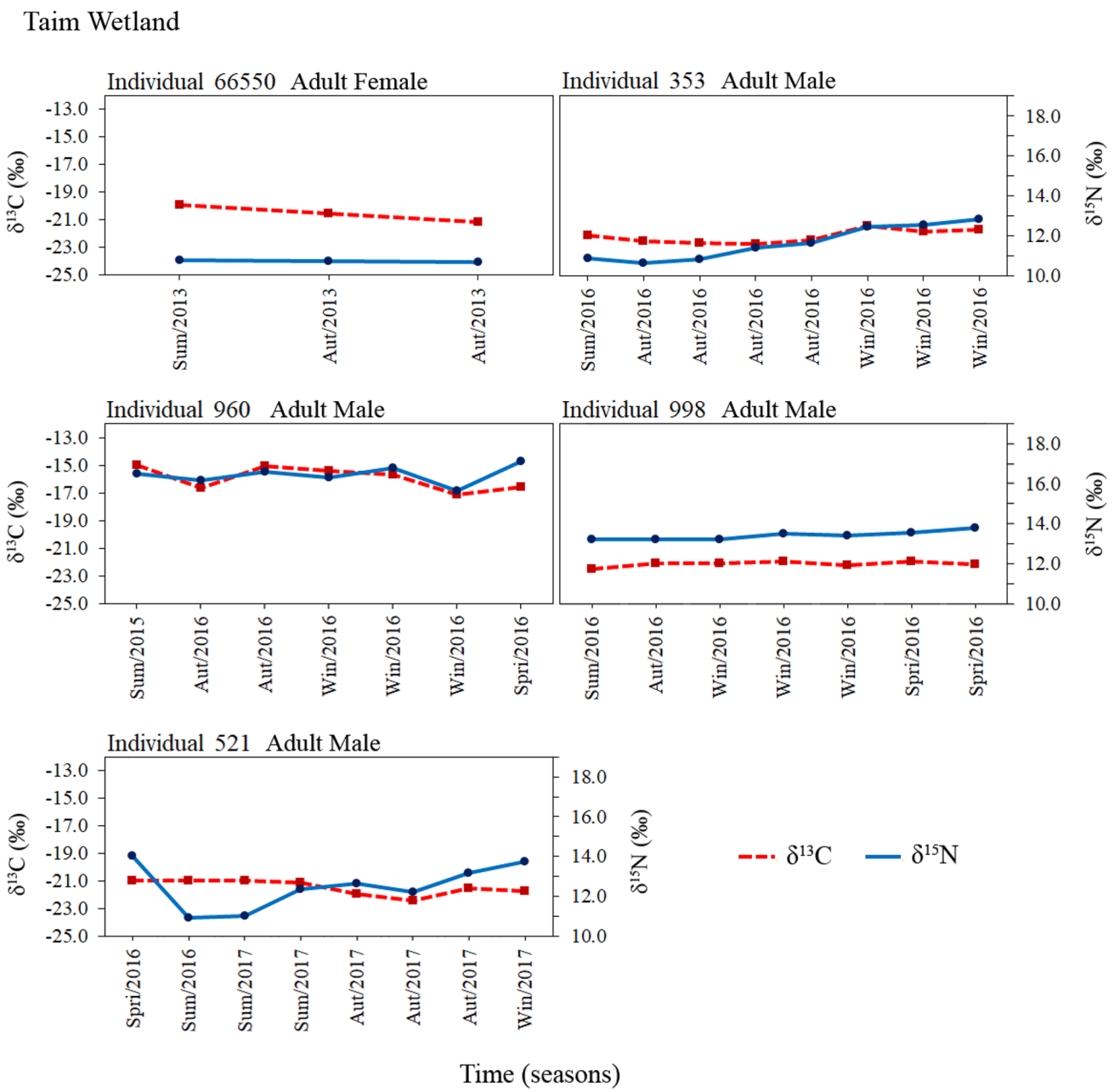

Fig. 4 Variability in $\delta^{13}C$ and $\delta^{15}N$ vibrissae values through time (expressed in austral seasons) for each individual of Neotropical otter sampled in Taim Wetland

Discussion

In this study, we assessed individual foraging history of the Neotropical otter through stable isotope analysis of longitudinal sections of their vibrissae. The results revealed temporal and individual variation in resource and habitat use by this species in three coastal ecosystems, which may reflect a high individual specialization, at least in males.

The isotopic differences found along vibrissae follow shifts in diet, as observed in other aquatic mammals (Newsome et al. 2010b; Kernaléguen et al. 2015a). Furthermore, habitat shifts could also be detected, since marine-derived nutrients are characterized by enriched heavier carbon and nitrogen isotopes (Schoeninger and DeNiro 1984) as we noticed in some individuals' vibrissae. Thus, we have assumed that the baseline isotopic composition did not vary seasonally and fluctuations observed along vibrissae were explained by changes in diet/habitat only.

In Santa Catarina Island, both adult males showed a high variation in isotopic ratios related to shifts in the

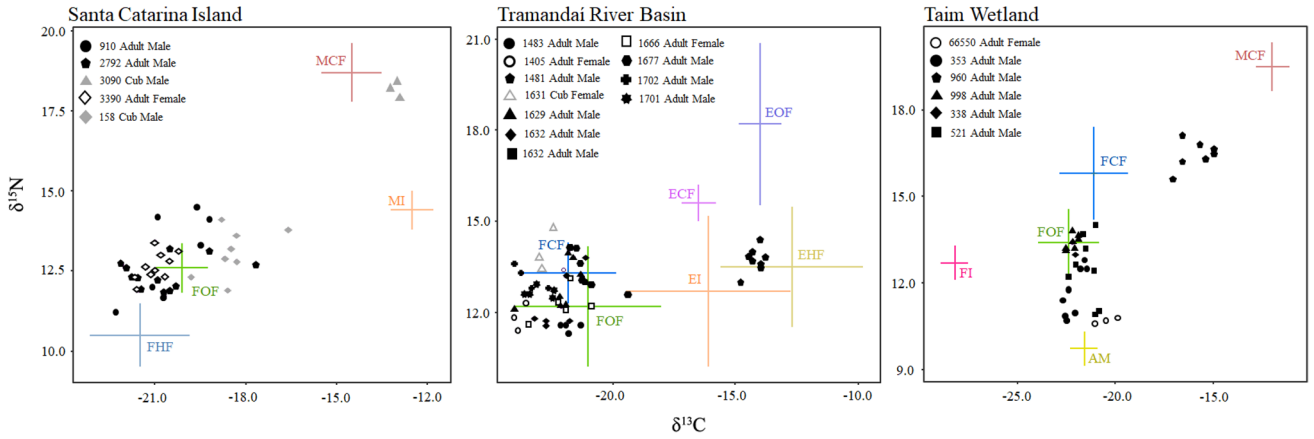

Fig. 5 $\delta^{13}C$ and $\delta^{15}N$ bivariate plots of individual Neotropical otter (*Lontra longicaudis*) vibrissae (solid and open geometric shapes), and mean isotopic values of dietary sources corrected for trophic discrimination factors: freshwater herbivorous fish (FHF), freshwater omnivorous fish (FOF), freshwater carnivorous fish (FCF), freshwater invertebrates (FI), amphibians (AM), estuarine herbivorous fish (EHF), estuarine omnivorous fish (EOF), estuarine carnivorous fish (ECF), estuarine invertebrates (EI), marine carnivorous fish (MCF), and marine invertebrates (MI)

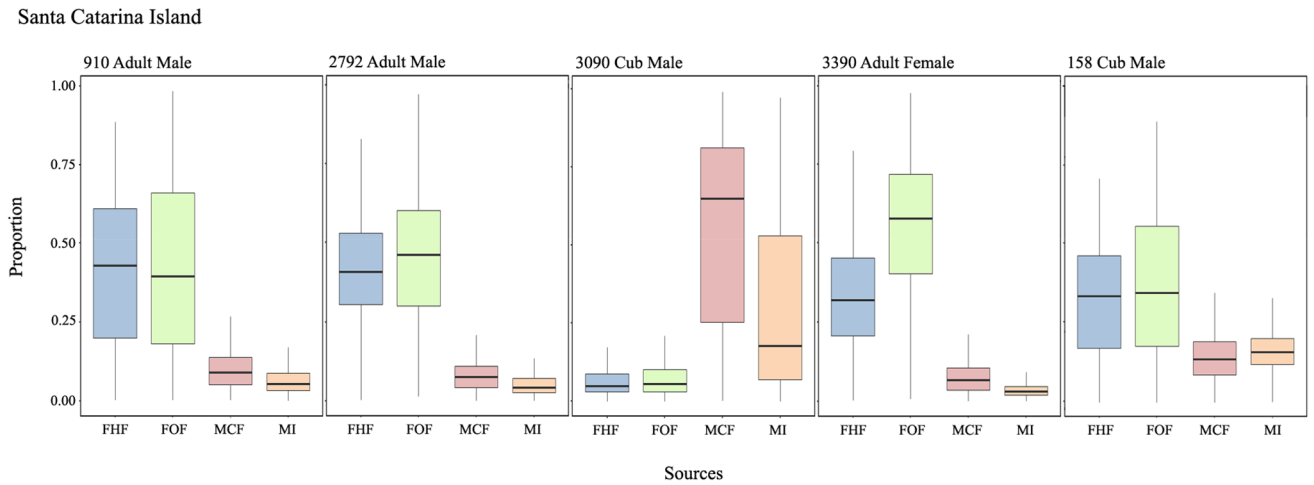

Fig. 6 Dietary proportions for each individual from Santa Catarina Island according to SIMMR Bayesian models. Sources: freshwater herbivorous fish (FHF), freshwater omnivorous fish (FOF), marine carnivorous fish (MCF), and marine invertebrates (MI)

consumption of different freshwater prey. The only female analyzed varied less throughout the year, which suggests consistent feeding habits and philopatric behavior. Only one male cub showed high carbon and nitrogen isotopic values, suggesting a marine diet. Carrasco et al. (2019) obtained similar results for this individual by analyzing the isotopic ratios of its dentin collagen. Another male cub analyzed presented freshwater signature; however, it is possible to observe an abrupt fall in $\delta^{15}N$ values, while $\delta^{13}C$ values remained constant, followed by a little increase of both isotopes. The most likely explanation for this pattern is that the vibrissa encompassed the nursing period, followed by weaning, and an habitat shifts from freshwater to marine environment. This abrupt $\delta^{15}N$ decrease has been associated to weaning, since offspring, while nursing, are a trophic level higher than their mothers, reflected in $\delta^{15}N$ values, whereas $\delta^{13}C$ values would remain unaffected due to milk lipid composition (Jenkins et al. 2001; Cherel et al. 2015; Drago et al. 2015). In addition, this cub was also found in a rocky shore region, supporting the recent incorporation of marine nutrients. According to vibrissae growth rates (Tyrrell et al. 2013), the nursing period would have comprised approximately 2–3 months for this cub, as reported by Kruuk (2006) for otter species. Nevertheless, it is important to note that we are not considering the intrauterine period of vibrissae synthesis and that we have relied on sea otter vibrissa growth for our analysis, which may differ from actual rates for our studied species.

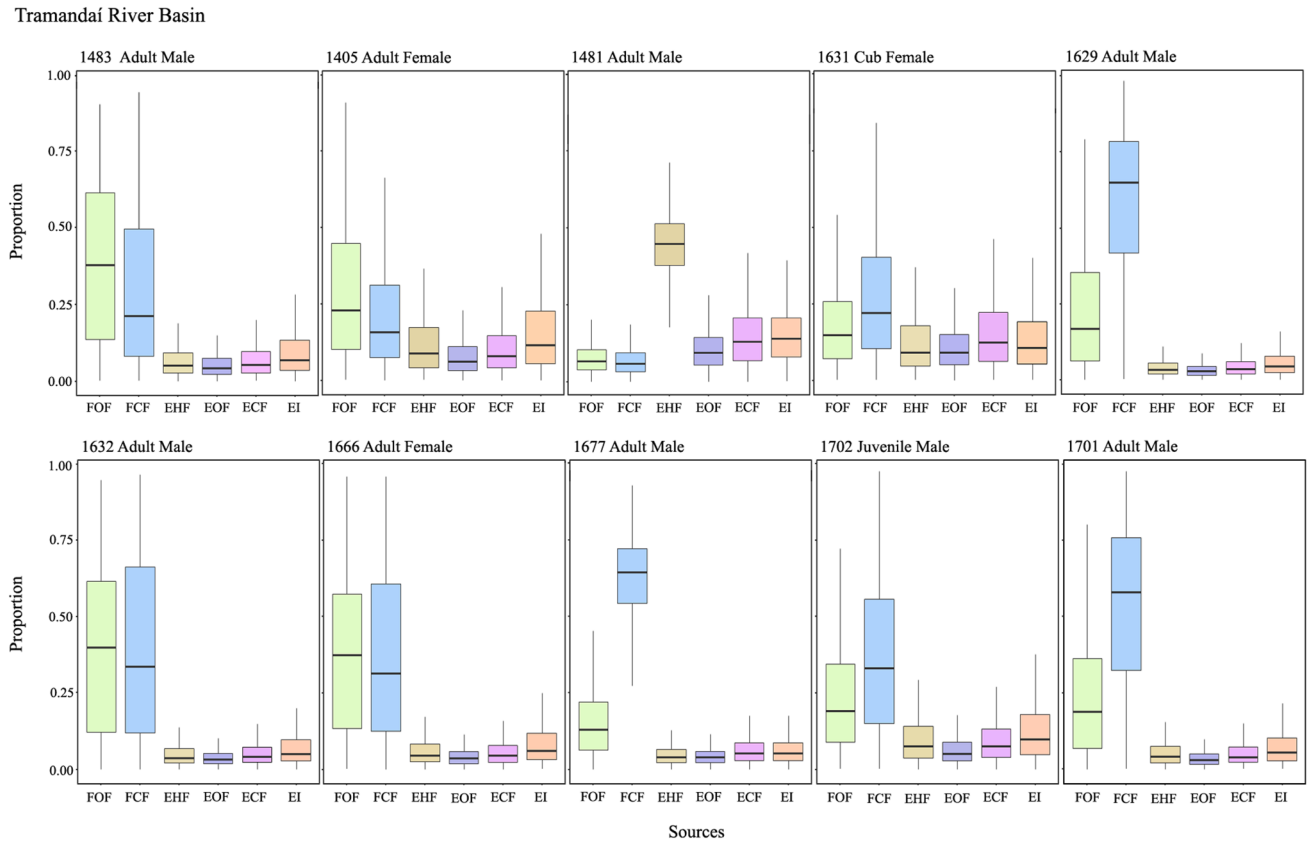

Fig. 7 Dietary proportions for each individual from Tramandaí River Basin according to SIMMR Bayesian models. Sources: freshwater omnivorous fish (FOF), freshwater carnivorous fish (FCF), estuarine herbivorous fish (EHF), estuarine omnivorous fish (EOF), estuarine carnivorous fish (ECF), and estuarine invertebrates (EI)

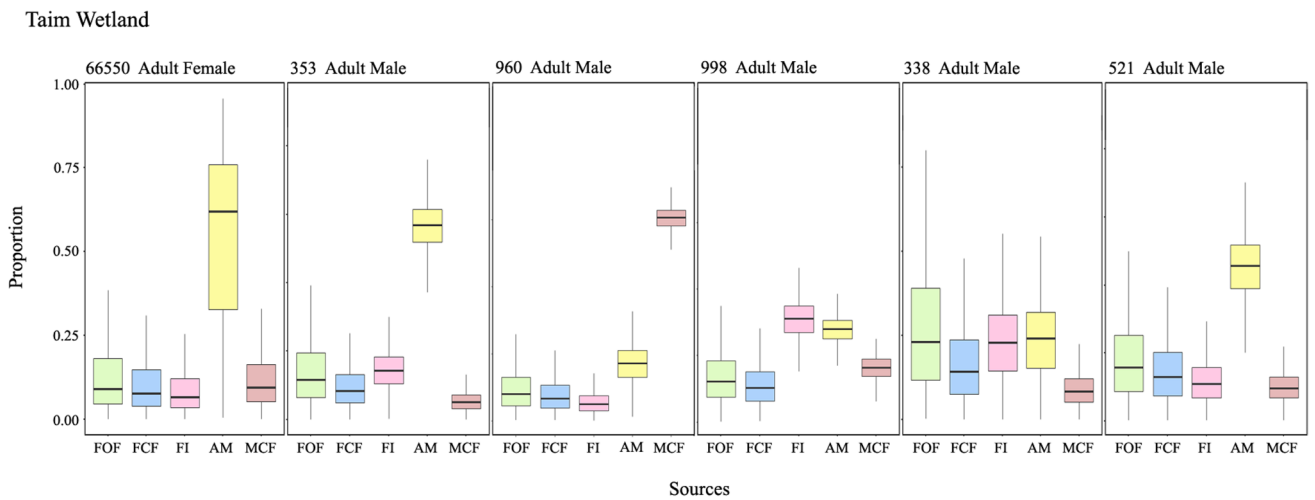

Fig. 8 Dietary proportions for each individual from Taim Wetland according to SIMMR Bayesian models. Sources: freshwater omnivorous fish (FOF), freshwater carnivorous fish (FCF), freshwater invertebrates (FI), amphibians (AM), and marine carnivorous fish (MCF)

Previous studies have also reported the use of both freshwater and marine habitats by the Neotropical otter near Santa Catarina Island (e.g., Alarcon and Simões-Lopes 2003; Carvalho-Junior et al. 2012). Due to the geological characteristics of this region, there are several rocky structures along with the surroundings of the aquatic environments

Table 2 Isotopic niche breadth (Total Niche Width—TNW), and intraindividual (Within-Individual Component—WIC), and interindividual (Between-Individual Component—BIC) variation in $\delta^{13}C$ and $\delta^{15}N$ values of males from Tramandaí River Basin and Taim Wetland

	TNW	WIC	BIC	WIC/TNW	*p* value
Tramandaí River Basin					
$\delta^{13}C$	9.0	0.1	8.9	0.01	0.001
$\delta^{15}N$	0.7	0.06	0.6	0.09	0.001
Taim Wetland					
$\delta^{13}C$	6.8	0.3	6.5	0.04	0.001
$\delta^{15}N$	3.9	0.4	3.6	0.09	0.001

WIC/TNW index spans from 0, when individuals are specialists, to 1, when all individuals are generalists

which form semi-closed compartments mainly used by the Neotropical otter as shelters. These internal compartments protect the otter against weather conditions, retaining the heat during winter, and are cooler in summer (Carvalho-Junior et al. 2006). Therefore, the occurrence of the species in coastal beaches is expected due to the presence of rocky shores (Carvalho-Junior et al. 2006, 2012). Although we only have registered a marine signal in cubs in this area, it is likely that females were using these environments as well, as parental care in otters is restricted to females and lasts for about a year (Kruuk 2006).

Individuals from Tramandaí River Basin preyed mainly on fishes from freshwater environments throughout the seasons, with slight changes in feeding habits, probably related to a variation in the proportions of consumed prey, as evidenced by longitudinal isotopic oscillations. In this region, we detected a male with an isotopic signature along vibrissa compatible with the estuary environment of Tramandaí Lagoon. Surprisingly, dentin collagen of the same individual showed isotopic ratios consistent with the freshwater environment (Carrasco et al. 2019). These differences are probably due to distinct turnover rates between tissues. Tooth dentin is deposited continuously and, thus, can provide information from years to decades (Newsome et al. 2010b; Bocherens and Drucker 2013). According to canine cement growth layer groups, this otter was 6 years old (Carrasco et al. 2019), and dentin isotopic composition may reflect the same period. Vibrissae fragments, in contrast, are estimated to encompass about a month in adult otters (Tyrrell et al. 2013) and, in this individual case, vibrissa may have been synthesized during the last year only. Therefore, the analysis of different tissues of the same animal was able to detect patterns in distinct temporal scales.

Negative interactions between the Neotropical otter and fishery activities have been reported in Tramandaí Lagoon. Local artisanal fishermen from this region have complained that the Neotropical otter frequently consumes catfishes (*Genidens* spp.) and mullets (*Mugil* sp.) caught in their gillnets inside the estuary (Barbieri et al. 2012). In the present study, we found a male that has used the estuary as a foraging area for at least 1 year, preying mainly on mullets, a fish that is an important resource for local fishermen (Klippel et al. 2005). F. Barbieri (personal communication) reported that the Neotropical otter also preys on whitemouth croakers (*Micropogonias furnieri*), and blue crabs (*Callinectes* spp.) in this area. Thus, the results of the present study corroborate the use of the estuarine environment of Tramandaí Lagoon by the Neotropical otter and that it could compete with artisanal fishery for resources.

In the Taim Wetland region, similar to Tramandaí River Basin, some individuals presented different isotopic values according to the analyzed tissue. The only female in our sample presented depleted values for both $\delta^{15}N$ and $\delta^{13}C$ along the vibrissa. However, this female had enriched carbon and nitrogen ratios in the dentin collagen (Carrasco et al. 2019). This means that this individual spent most part of its life feeding on the coast (as reflected by the enriched isotopic dentin ratios) and occasionally preying upon freshwater prey, mainly amphibians, in the wetland (evidenced by depleted isotopic ratios of vibrissa). An adult male, in contrast, presented enriched carbon and nitrogen ratios in the vibrissa and depleted ratios in the dentin collagen (Carrasco et al. 2019), also indicating a shift in habitat and diet. It is possible that in coastal habitats of the Taim Wetland region, the Neotropical otter feeds on fish entering up coastal streams, as reported by Quintela et al. (2012a) through a fecal analysis. In flooded portions, on the other hand, amphibians seem to be an important prey.

It was suggested that the Neotropical otter contributes to the flow of matter and energy between marine and freshwater environments (Carrasco et al. 2019). Although long isotopic temporal windows may indicate continuous use of marine or estuarine environment during months or even years, on smaller time scales, these animals need to access freshwater sources to avoid physiological stress related to salinity (see Kruuk 2006). Thus, based on the physiology of this species, associated with the results found in the present study and by Carrasco et al. (2019), it is possible to confirm that at least some individuals alternate between marine and freshwater environments, transporting nutrients from one food web to another.

Differences in the home range are known to exist between sexes of the Neotropical otter, as males perform longer displacement movements than females (see Trinca et al. 2013). Here, we provide evidence that both males and females may move from a marine to a freshwater habitat, which suggests that females can also move around, probably following resource availability. Nevertheless, we were able to sample more males than females, which may be a consequence of their dispersive pattern. Perhaps, animals with dispersive

behavior are more susceptible to negative anthropic interactions. In southern Brazil, the mortality of otters is mainly associated with roadkill, followed by hunting and agonistic interactions with domestic animals, such as dogs (Quintela et al. 2012b). The cause of death for most of the otters used in this study was roadkill.

Sexual variation in resource specialization has been reported in several species of marine mammals, mainly related to differences in home ranges and reproductive investment. Males of fur seals, genus *Arctocephalus*, for example, exploited a greater diversity of foraging habitats than females (Kernaléguen et al. 2012, 2015b). This pattern was also observed in the present study for the Neotropical otter, since males showed greater isotopic variation, which can be related to a higher ecological opportunity (i.e., diversity of foraging habitats and prey). While for sea otters, the lower trophic diversity in females reflects a greater degree of specialization, due to their small range and greater intraspecific competition, which leads to trophic segregation between them (Smith et al. 2015).

There has been some contrasting information regarding the feeding habits of the Neotropical otter. Several authors reported the species as generalist (e.g., Chemes et al. 2010; Muanis and Oliveira 2011; Duque-Dávila et al. 2013; Vezzosi et al. 2014), while others have classified it as specialist (e.g., Quadros and Monteiro-Filho 2001; Carvalho-Junior et al. 2012; Rheingantz et al. 2012). Considering the ecological plasticity demonstrated in the present study, our results suggest that individuals use only a fraction of the total niche occupied by the species. In other words, specialist individuals compose a generalist population. This evaluation was only possible through the analysis of temporal data series on individuals' vibrissae. For future studies, we recommend that individual specialization analysis should include females, as their foraging strategies can differ from males due to differential reproductive investment and spatial ecology, as reported for other mammalian species (e.g., Kernaléguen et al. 2012, 2015b; Smith et al. 2015). Also, it is important to analyze a larger sample of males, since, in the present study, the WIC/TNW index was calculated to a limited number of adult males. Furthermore, we recommend that the degree of individual specialization should be measured across distinct environments. It is known that individual specialization can be dependent on habitat characteristics and the trophic structure (Newsome et al. 2015). The behavior of the Neotropical otter can also vary according to the region (Quadros and Monteiro-Filho 2001).

Stable isotopes are a useful tool to identify ecological patterns in species that are difficult to observe in nature, such as the Neotropical otter, as the technique has the potential to reveal information that would not be obtained otherwise. However, it is important to consider the limitations of this approach, especially regarding Bayesian mixing models. For instance, mixing models are sensitive to the lack of important sources (Phillips et al. 2014). Since dietary population variability can be high, especially in coastal areas (Rheingantz et al. 2017), it is possible that we did not include some important sources to the diet of the Neotropical otter in the mixing models, especially for Santa Catarina Island. Despite that the main prey of the Neotropical otter in this area is fish, crustaceans can comprise part of its diet in the freshwater environment (Carvalho-Junior et al. 2013), which were not analyzed due to sampling difficulties. Besides incorporating all potential prey into the model, it is important to account for seasonal effects. Isotopic signals of potential prey tissues should reflect the time period over which they were consumed (Phillips et al. 2014). In the present study, however, seasonality did not significantly affect $\delta^{13}C$ and $\delta^{15}N$ values for most prey items, while a few could not be tested due to small sample sizes, which may not be representative of the group. Regardless of the mentioned caveats, we were able to detect clear isotopic gradients across the Neotropical otter feeding areas (e.g., freshwater vs. marine) which enlightens our understanding about the feeding ecology of this species.

Conclusions

This was the first study to assess individual time-series patterns in the diet of the Neotropical otter through stable isotope analysis, contributing to the understanding of the feeding ecology of the species. The resource and habitat use by the Neotropical otter varies temporally and individually in different coastal ecosystems. The temporal variation reflects changes in the proportion of consumed freshwater prey or dietary shifts related to a change from marine to freshwater environments. In addition, intraspecific variation in isotopic ratios along vibrissae may reflect a high degree of individual specialization in this species. We recommend further research to assess individual specialization in a larger sample to confirm the pattern reported here, especially for females.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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