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The trophic ecology of marine catfishes in south-eastern Brazil

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Original Article

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Abstract

The stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) and total mercury concentrations (THg) of the three marine catfish species *Aspistor luniscutis*, *Bagre bagre* and *Genidens genidens* were evaluated to understand their trophic relationship in northern Rio de Janeiro state, south-eastern Brazil. The $\delta^{13}C$ was similar among the three marine catfishes, whereas $\delta^{15}N$ was similar in *A. luniscutis* and *B. bagre* and lower in *G. genidens*. THg was higher in *G. genidens* and lower in *B. bagre*. The greater assimilation of Sciaenidae fishes and squids by *A. luniscutis* and *B. bagre* resulted in smaller isotopic niche areas and trophic diversity but higher isotopic niche overlap, trophic redundancy and evenness. For *G. genidens*, the similar assimilation of all prey items resulted in the broadest isotopic niche among the marine catfishes. The higher mercury content in *G. genidens* is consistent with an increased important contribution of prey with a higher Hg burden. The bioaccumulation process was indicated by significant correlations of $\delta^{15}N$ and THg with total length and total mass. Additionally, a significant correlation between THg and $\delta^{15}N$ reflected the biomagnification process through the food web.

Introduction

Food webs are models of trophic interactions among species, usually simplified into networks of species and energy links between them (Thompson *et al*., 2012). The trophic dynamic theory supports the understanding of food web structure and species interactions that ultimately shape modern marine ecosystem ecology, conservation and management (Treblico *et al*., 2013). Therefore, the analysis of diet to identify the role of each predator species on prey resource sharing relationships within the fish community is of great value (Svanbäck *et al*., 2015).

The coexistence of ecologically similar fishes in high abundance in an ecosystem is possible because of the development of strategies that allow not only spatial and/or temporal separation of the species (Azevedo *et al*., 1999) but also ecological variations in the use of available niches and/or partitioning of the available resources (Herder & Freyhof, 2006; Sandlund *et al*., 2010). On the other hand, the functional or morphological homology of sympatric species can potentially increase competition (Wootton, 1990). If the food resources are limited, this competition can result in exclusion of the less adapted species. Nevertheless, according to the principles of competitive exclusion, interspecific competition also favours trophic niche diversification or resource partitioning across species (Schluter, 1996; Svanbäck & Bolnick, 2008).

The isotopic niche concept proposed by Newsome *et al*. (2007), a refinement of Hutchinson's idea (Hutchinson, 1957, 1978), suggests the use of isotopic tools to assess the ecological characteristics of organisms that ecologists aim to investigate, such as coexistence and resource sharing. Stable isotopic signatures of carbon (C) and nitrogen (N) have been widely used in this sense (Jackson *et al*., 2011; Yasue *et al*., 2014; Gallagher *et al*., 2017; Jensen *et al*., 2017; Rader *et al*., 2017), as the values measured in the consumer's tissues are closely related to the values from its diet. Stable nitrogen isotope ratios in consumers are typically enriched in the heavier isotope (^{15}N) by 2–4‰ per trophic level (Minagawa & Wada, 1984; Peterson & Fry, 1987), making $\delta^{15}N$ values useful for the definition of trophic positions of consumers (Post, 2002). In contrast, the fractionation of carbon isotopes (^{13}C) is lower (0–1‰) and is typically used to define energy sources (De Niro & Epstein, 1978).

The determination of total mercury (THg) in organisms is a complementary tool for isotopic analysis that is widely used in trophic ecology investigations (Eagles-Smith *et al*., 2008; Fry & Chumchal, 2012; Pouilly *et al*., 2013). This tool has been used in ecological studies as a good indicator of the trophic level of organisms (Fry & Chumchal, 2012), but it can also be used to identify spatiotemporal patterns of fish bioaccumulation (Buckman *et al*., 2017; Liu *et al*., 2017) and biomagnification processes (Cresson *et al*., 2015; Chouvelon *et al*., 2018). Tropical estuaries are known as source of anthropogenic Hg for fish feeding in coastal areas (Le Croizier *et al*., 2019). In estuarine and coastal environments, it is estimated that 90% of the river-derived Hg is buried in sediments on ocean margins (Chester, 1990), highlighting the contribution of estuaries to the transport of Hg to coastal marine waters and, consequently, to the associated food webs.

In Brazil, the Ariidae family is represented by demersal marine catfishes usually found in coastal and estuarine ecosystems (Marceniuk & Menezes, 2007; Schmidt *et al.*, 2008; Denadai *et al.*, 2012; Pereyra *et al.*, 2016). Along the coast of São Paulo and Rio de Janeiro, their spatial distribution in estuarine systems is governed by salinity (Bizerril, 1999; Denadai *et al.*, 2012). They usually have wide trophic niches that, in general, overlap with each other's (Bruton, 1996; Denadai *et al.*, 2012) as many other sympatric fish species (Svanbäck *et al.*, 2015; Cachera *et al.*, 2017), and have been classified as generalist opportunistic omnivorous predators, with crustaceans, fishes, molluscs, annelids, detritus and algae commonly observed as the main groups of food items (Chaves & Vendel, 1996; Denadai *et al.*, 2012; Pinheiro-Sousa *et al.*, 2015; Tavares & Di Beneditto, 2017; Di Beneditto *et al.*, 2018; Di Beneditto & Tavares, 2019).

The amount of information generated by stomach assessments by scientists all over Brazil report the high importance of fishes and invertebrates (mainly crabs) as prey items of ariids (Chaves & Vendel, 1996; Denadai *et al.*, 2012; Tavares & Di Beneditto, 2017). To date, the trophic ecology of marine catfishes has been intensively studied over the last two decades (Chaves & Vendel, 1996; Bizerril, 1999; Denadai *et al.*, 2012; Pinheiro-Sousa *et al.*, 2015; Tavares & Di Beneditto, 2017; Di Beneditto *et al.*, 2018; Di Beneditto & Tavares, 2019). However, few studies off the Brazilian coast have focused on isotopic tracers (Giarrizzo *et al.*, 2011; Claudino *et al.*, 2015; Pereyra *et al.*, 2016; Di Beneditto *et al.*, 2018), and no data are available regarding stable isotopes coupled with Hg analyses in marine catfishes.

The present study used isotopic tracers of carbon (^{13}C) and nitrogen (^{15}N) coupled with mercury (Hg) to understand the trophic relationships among three marine catfishes *Aspistor luniscutis* (Valenciennes, 1840), *Bagre bagre* (Linnaeus, 1766) and *Genidens genidens* (Cuvier, 1829) in south-eastern Brazil, leading to an improvement in the knowledge of their trophic dynamics in Brazilian shallow waters. The questions to be answered are as follows: (1) Do the isotopic niches of these catfish species overlap? (2) Are there any spatial and/or temporal patterns in habitat usage among these sympatric marine catfishes? and (3) Do these catfish species compete for the same resource items?

Materials and methods

Study site and sampling

Samples were collected off Manguinhos Beach (21°29′S 41°01′W), District of São Francisco do Itabapoana, at ∼10 m depth (Figure 1). This area is under the influence of the Itabapoana (north) and Paraíba do Sul (south) rivers. The shelf is naturally depleted of rock substratum or other hard substrates, and it is covered by extensive sandy beaches with variable amounts of mud and calcareous nodules, such as rhodolites (Zalmon *et al.*, 2002).

The marine catfishes *Aspistor luniscutis*, *Bagre bagre* and *Genidens genidens* and their potential prey groups were collected every three months between April 2010 and January 2011. The captured ariid specimens were classified as adults from 180 mm total length for both sexes of *A. luniscutis* (Froese & Pauly, 2019), from 159 and 212 mm total length for females and males, respectively, of *B. bagre* (Véras & Almeida, 2016), and from 55 and 85 mm total length for females and males, respectively, of *G. genidens* (Mazzoni *et al.*, 2000).

Fishes were sampled at 13 randomized sampling points with bottom gillnets (n = 78), measuring 25 m in length and 3 m in height and mesh sizes of 20 mm (n = 18), 30 mm (n = 42) and 40 mm (n = 18), measured between adjacent nodes, submerged for 24 h.

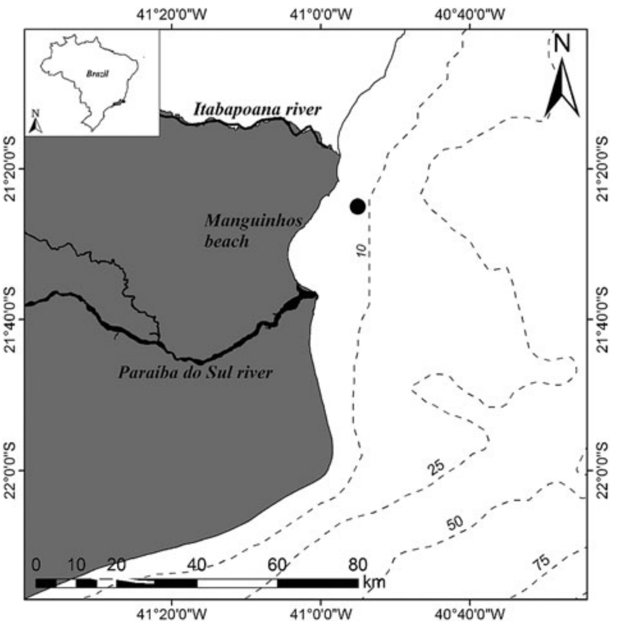

Fig. 1. Study area and sampling location (●) off Manguinhos Beach, northern Rio de Janeiro state, south-eastern Brazil.

Potential food resources identified based on previous stomach content studies of ariids (Chaves & Vendel, 1996; Denadai *et al.*, 2012; Tavares & Di Beneditto, 2017; Di Beneditto & Tavares, 2019) off the south-eastern Brazilian coast were also sampled in their natural habitat in the same sampling area. Corers (15 cm diameter, 20 cm height) were used to collect sediment and invertebrates. Phytoplankton and zooplankton were captured by surface trawl nets (30 cm mouth, 1.10 m length and of 20 and 70 µm mesh sizes, respectively) to sample local pelagic trophic end members.

All megafauna (fishes and invertebrates) collected were identified to the lowest taxonomic level, counted, measured (total length) and weighed (total body mass). Dorsal muscle tissues of fish, mantles of cephalopods and pieces of soft tissues (avoiding gastric tracts) of crustaceans as well as total organic matter in the sediment (SOM) and phytoplankton and zooplankton were dried and homogenized for stable isotope and THg analysis. All laboratory analyses were performed at the Laboratório de Ciências Ambientais from Universidade Estadual do Norte Fluminense Darcy Ribeiro.

Stable isotope analysis – δ^{13}C and δ^{15}N

All samples were stored in clean transparent plastic bags in iceboxes and then transported to the laboratory where they were kept frozen (−18°C) in dry sterile vials prior to analysis. Freeze-dried samples were ground with a mortar and pestle to a homogeneous fine powder. Approximately 0.5–1 mg of animal and phytoplankton tissues and 10 mg of sediment were used in the analysis.

For the elemental composition of carbon and nitrogen as well for δ^{13}C and δ^{15}N of sediment, ∼10 mg was weighed in silver capsules, followed by acidification through the addition of HCl (2 M) to remove inorganic carbon (Kennedy *et al.*, 2005; Brodie *et al.*, 2011).

The elemental and isotopic composition of all samples were determined using a Flash 2000 Elemental Analyzer with a

CONFLO IV interface coupled to a Delta V Advantage isotope ratio mass spectrometer (Thermo Scientific, Germany) in Laboratório de Ciências Ambientais. Samples were analysed using analytical blanks and urea analytical standards (IVA Analysentechnik-330802174; CH4N2O Mw = 60, C = 20%, N = 46%) using certified isotopic compositions ($\delta^{13}C = -39.89‰$ and $\delta^{15}N = -0.73‰$). For biota samples, analytical control was performed for every 10 samples using certified isotopic standards (Elemental Microanalysis Protein Standard OAS: 46.5 ± 0.78% for C; 13.32 ± 0.40% for N; −26.98 ± 0.13‰ for $\delta^{13}C$; + 5.94 ± 0.08‰ for $\delta^{15}N$). The accuracy of the sediment analysis verified using the Elemental Microanalysis Low Organic Soil Standard (1.52 ± 0.02% for C; 0.13 ± 0.02% for N; −27.46 ± 0.11‰ for $\delta^{13}C$; + 6.70 ± 0.15‰ for $\delta^{15}N$).

Carbon and nitrogen contents were expressed as per cent elements (%) and the detection limits were 0.05% and 0.02%, respectively. Carbon and nitrogen isotope ratios were expressed in δ notation as ‰ relative to Pee Dee Belemnite (PDB) and atmospheric nitrogen, respectively, and were calculated using the following equation:

$$\delta = (\mathrm{Rsample}/\mathrm{Rstandard}) \times 10^3$$

where $\delta = \delta^{13}C$ or $\delta^{15}N$ and $R = \delta^{13}C{:}\delta^{12}C$ or $\delta^{15}N{:}\delta^{14}N$. Analytical reproducibility was based on triplicates for every 10 samples: ± 0.3‰ for $\delta^{15}N$ and ± 0.2‰ for $\delta^{13}C$. There was no prior lipid extraction from the fish muscle samples, but the C/N ratios were lower than 3.5, indicating a low lipid level that did not compromise the carbon isotope results and their interpretation (Post *et al*., 2007).

Total mercury analysis – THg

Dry muscle samples were digested according to Bastos *et al.* (1998). Briefly, the digestion of tissue samples was performed in a digestion block (60°C, 4 h) with a mixture of 3 ml HNO_3: H_2SO_4 (1:1) and 1 ml of concentrated H_2O_2 and allowed to stand overnight. The addition of 5 ml of 5% $KnMnO_4$ and subsequent 30 min of heating were followed by titration with hydroxylamine hydrochloride ($NH_3OHCl + NaCl$ 12%). THg was determined with a QuickTrace M-7500 CETAC (CV-AAS). The detection limit was 0.25 ng g^{-1}. The analytical control of the method was determined and monitored using replicate analysis, blank solutions, and certified reference material from the National Research Council-Canada (DORM-2 dogfish *Squalus acanthias* muscle sample). The analytical coefficient of variation between replicates was less than 10%, and the recovery of THg was in agreement with certified values (higher than 90%). Our results are expressed in ng g^{-1} dry weight (dw).

Data treatment and analysis

The differences between species regarding total length and $\delta^{15}N$ were assessed via one-way parametric ANOVA followed by Tukey's HSD *post hoc* test. For total mass, $\delta^{13}C$, C/N and THg, normality (Shapiro–Wilk test) and homoscedasticity (Levene test) were not achieved, and therefore non-parametric analysis of variance (Kruskal–Wallis) was applied followed by Dunn's *post hoc* test. Linear regressions were performed to check for possible relationships between variables (total length and $\delta^{15}N$, total mass and $\delta^{15}N$, total length and $\log_{10}$THg and total mass and $\log_{10}$THg). Correlation between $\delta^{15}N$ and $\log_{10}$THg was also used with the organisms that compose the food web. Results were considered significant at $P < 0.05$.

Isotopic niche breadth was quantified for each marine catfish using the standard ellipse area corrected for small sample sizes (SEAc), calculated with the Stable Isotope Bayesian Ellipses tool in R (SIBER) (Jackson *et al*., 2011). To evaluate the relative contribution of the different prey, *Xiphopenaeus kroyeri* (Heller, 1862), *Callinectes* sp., *Doryteuthis sanpaulensis* (Brakoniecki, 1984), *Porichthys porosissimus* (Cuvier, 1829) and Sciaenidae, that represent a pool of species composed by *Isopisthus parvipinnis* (Cuvier, 1830), *Paralonchurus brasiliensis* (Steindachner, 1875) and *Stellifer rastrifer* (Jordan, 1889), were used in the Bayesian stable isotope mixing model in the software package SIAR (Stable Isotope Analysis in R) (Parnell & Jackson, 2013), which allows the inclusion of isotopic signatures and fractionation together with the uncertainty of these values within the model. To reduce the uncertainty in the interpretation of the mixing model, the potential prey were reduced/grouped to a total of five sources, similarly to the previous study of Di Beneditto *et al.* (2018).

The trophic enrichment factors (TEFs) are key parameters in isotopic mixing models, representing the isotopic differences between consumers' tissues and their prey items after they reached equilibrium (Parnell *et al*., 2010). In the absence of species-specific TEF values from controlled diet experiments, these values can be obtained in meta-analyses for phylogenetically related species, considering the same tissue (Newsome *et al*., 2007). In this sense, we calculated $TEF^{15}N$ and $TEF^{13}C$ based on equations from a meta-analysis of isotopic studies that considered muscle of fish species (Caut *et al*., 2009) ($\Delta^{15}N = -0.281\ \delta^{15}N + 5.879$ and $\Delta^{13}C = -0.248\ \delta^{13}C - 3.4770$). The calculated values for our data were + 1.8 ± 0.2‰ for $TEF^{15}N$ and + 0.5 ± 0.2‰ for $TEF^{13}C$, similar to those of marine catfishes of the same region (Di Beneditto *et al*., 2018).

The isotopic niche metrics that relate the characteristics of the isotopic space filled by each marine catfish species in this study were calculated and consisted of the following: NR (maximum $\delta^{15}N$ range – larger range suggests more trophic levels and greater degree of trophic diversity); CR (maximum $\delta^{13}C$ range – increased range suggests higher diversity of basal sources); TA (total area of isotopic niche – representing the total amount of niche space occupied); SEAc (corrected standard ellipses area for small sample size – isotopic niche width); CD (mean Euclidean distance from the centroid – higher distances suggests high average degree of trophic diversity within the food web); NND (mean Euclidean distance to the nearest neighbour – similar trophic ecology will exhibit small NND); and SDNND (standard deviation of NND – low values suggests more even distribution of trophic niche) (Layman *et al*., 2007).

One-way ANOVAs were also used to evaluate differences and interactions between species considering CD and MNND, because they involve comparisons of means. The statistic SDNND, being a standard deviation, was compared between groups by an F-ratio test. The *P* values were interpreted as strengths of evidence towards null hypotheses rather than on the dichotomic scale of significance testing (Hurlbert & Lombardi, 2009).

All statistics and models were fitted using R version 3.5.2 (2018–12–20, 'Eggshell Igloo') for Linux in the RStudio software (Version 1.1.436) (R Core Team, 2018).

Results

The potential basal sources and prey groups are presented in Table 1. The lowest values of $\delta^{13}C$ and $\delta^{15}N$ were observed for particulate organic matter in sediment (SOM) and phytoplankton, respectively, while the highest values were found for Sciaenidae and *Doryteuthis sanpaulensis*, respectively. THg

Table 1. Potential basal sources and prey group size range (mm), mean ± standard deviation (SD) of $\delta^{13}C$ (‰), $\delta^{15}N$ (‰) and THg (ng g^{-1} dw) sampled in northern Rio de Janeiro state, south-eastern Brazil

Basal sources/Prey group	Size range[a]	$\delta^{13}C$	$\delta^{15}N$	THg
SOM	–	−20.67 ± 0.93	9.03 ± 2.66	–
Phytoplankton[b]	–	−19.02	7.50	0.02
Zooplankton[b]	–	−17.68 ± 0.74	8.44 ± 0.12	0.04
X. kroyeri	30.00–70.00	−17.19 ± 0.40	11.96 ± 0.21	3.06 ± 1.37
Callinectes sp.	88.00–162.00	−16.32 ± 1.44	11.91 ± 0.39	1087.20 ± 290.00
D. sanpaulensis	–	−17.33 ± 0.31	13.25 ± 0.55	2.48 ± 1.17
P. porosissimus[c]	180.00	−18.00 ± 0.80	10.60 ± 0.50	630.00
Sciaenidae	125.00–175.00	−15.77 ± 0.86	13.20 ± 0.32	171.60 ± 64.65

[a]For fish species, the size range is standard length; for *X. kroyeri*, the size range is total length; for *Callinectes* sp., the size range is carapace width.
[b]Composite sample.
[c]One single specimen.

Table 2. Number of individuals (n), mean ± standard deviation (SD) of total length (mm), total mass (kg), $\delta^{13}C$ (‰), $\delta^{15}N$ (‰), C/N (%) and THg (ng g^{-1} dw) of the marine catfishes *Aspistor luniscutis*, *Bagre bagre* and *Genidens genidens* in northern Rio de Janeiro state, south-eastern Brazil

	Aspistor luniscutis	*Bagre bagre*	*Genidens genidens*
n	25	21	19
Total length	269.85 ± 48.70[a]	354.74 ± 49.63[b]	353.35 ± 26.65[b]
Total length (min – max)	200–343	282–424	302–393
Total mass	0.229 ± 0.138[a]	0.313.83 ± 0.148[b]	0.454 ± 0.147[c]
Total mass (min – max)	0.070–0.550	0.127–0.550	0.132–0.700
$\delta^{13}C$	−15.89 ± 0.71[a]	−16.16 ± 0.40[a]	−15.91 ± 0.45[a]
$\delta^{15}N$	14.62 ± 0.28[a]	14.62 ± 0.46[a]	13.84 ± 0.71[b]
C/N	3.18 ± 0.06[a]	3.20 ± 0.04[a]	3.17 ± 0.06[a]
THg	524.58 ± 191.58[a]	310.00 ± 175.50[b]	693.33 ± 269.07[c]

Letters indicate significant differences ($P < 0.05$).

concentrations were lowest for phytoplankton and highest for *Callinectes* sp.

Overall, 65 muscle samples were analysed for $\delta^{13}C$, $\delta^{15}N$ and THg representing the three ariid species in the present study. For *Aspistor luniscutis*, *Bagre bagre* and *Genidens genidens* similar $\delta^{13}C$ values (Kruskal–Wallis, $\chi^2 = 4.545$, $P > 0.05$) and C/N ratios (Kruskal–Wallis, $\chi^2 = 4.029$, $P > 0.05$) were observed (Table 2). The species *A. luniscutis* is the smallest (total length – ANOVA, $F = 26.962$, $P < 0.001$) and lightest (mass – Kruskal–Wallis, $\chi^2 = 17.610$, $P < 0.001$) catfish. Nitrogen isotope signatures ($\delta^{15}N$) were similar for *A. luniscutis* and *B. bagre*, while a lower value ($\delta^{15}N$ – ANOVA, $F = 18.089$, $P < 0.001$) was found for *G. genidens*. Total mercury (THg) was significantly different (Kruskal–Wallis, $\chi^2 = 21.892$, $P < 0.001$) for all three species, with the highest concentrations in *G. genidens* and lowest concentrations in *B. bagre*.

The $\delta^{13}C$ and $\delta^{15}N$ values of the invertebrates *Doryteuthis sanpaulensis*, *Callinectes* sp., *Xiphopenaeus kroyeri* and of the bony fishes *Porichthys porosissimus* and Sciaenidae, all prey items for marine catfishes, ranged from −18.00 ± 0.80‰ for *P. porosissimus* to −15.77 ± 1.44‰ for Sciaenidae and 10.60 ± 0.60‰ for *P. porosissimus* to 13.25 ± 0.55‰ for *D. sanpaulensis*, respectively. The $\delta^{13}C$ of organic matter (OM) basal sources (SOM and phytoplankton) and zooplankton ranged from −20.67 ± 0.93‰ for SOM to −17.68 ± 0.75‰ for zooplankton while $\delta^{15}N$ values ranged from 7.05‰ for phytoplankton to 9.03 ± 2.66‰ for SOM (Figure 2).

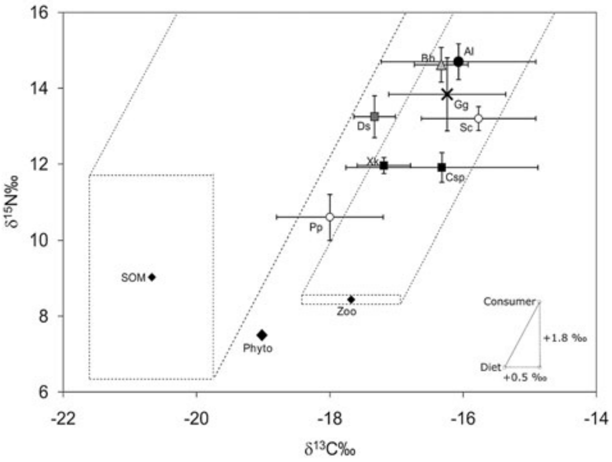

Fig. 2. Relationship between $\delta^{13}C$ and $\delta^{15}N$ considering *Aspistor luniscutis* (Al), *Bagre bagre* (Bb), *Genidens genidens* (Gg), *Doryteuthis sanpaulensis* (Ds), *Xiphopenaeus kroyeri* (Xk), *Callinectes* sp. (Csp), Sciaenidae (Sc), *Porichthys porosissimus* (Pp), zooplankton (Zoo), phytoplankton (phyto) and organic matter in sediment (SOM) in northern Rio de Janeiro state, south-eastern Brazil. The range of isotopic ratios measured for the potential SOM and phytoplankton (through zooplankton) sources is represented by small hatched squares. Hatched zones represent the zone influenced by the OM sources.

The $\delta^{15}N$ was significantly correlated with total length and total mass only for *B. bagre* (Figure 3A, B). THg also showed correlations, but with total length, for both *B. bagre* and *G. genidens*,

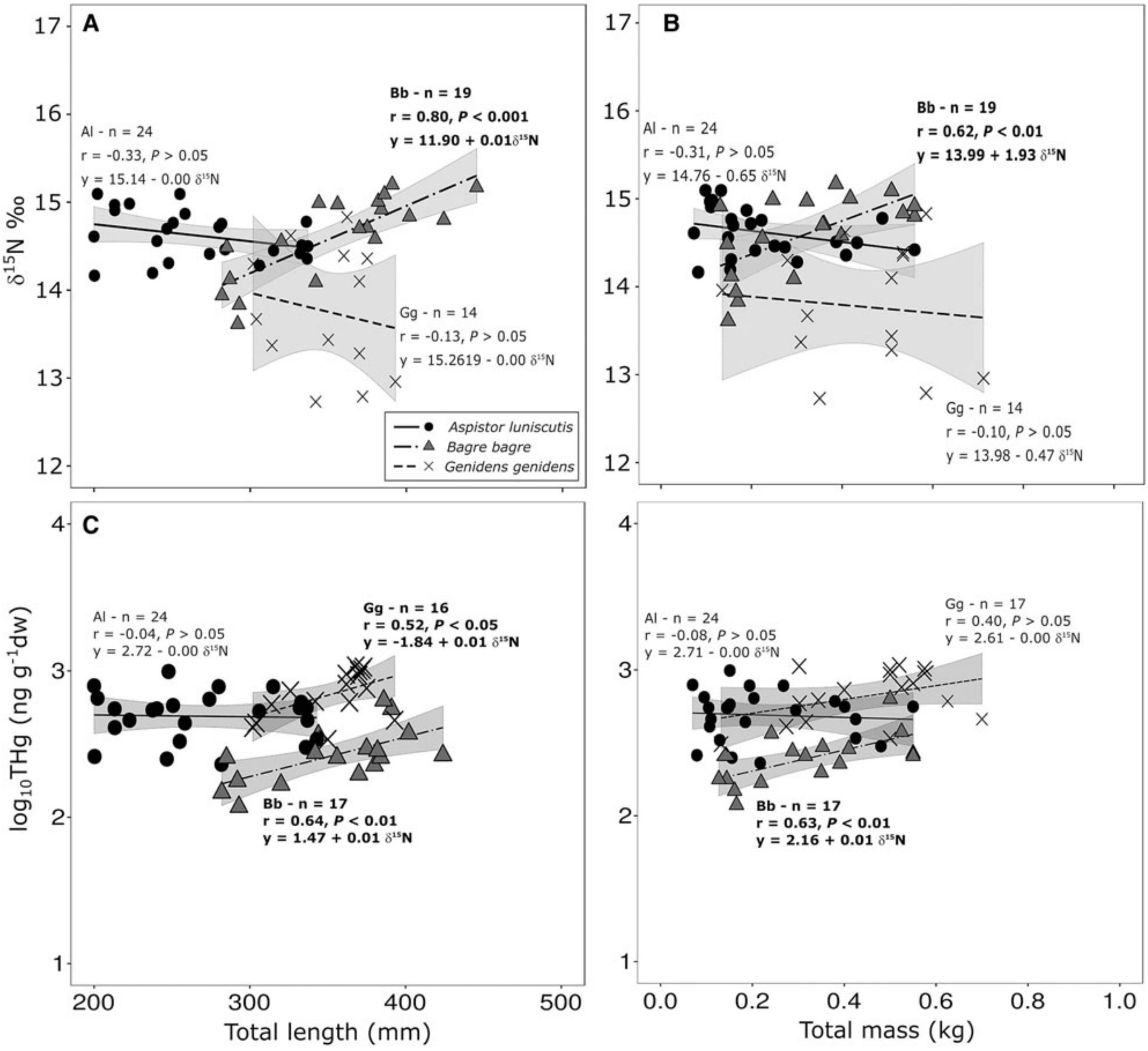

Fig. 3. Relationships between: (A) $\delta^{15}N$ (‰) and total length (mm), (B) $\delta^{15}N$ (‰) and total mass (kg), (C) log-transformed total mercury (THg) and total length (mm) and (D) log-transformed total mercury (THg) and total mass (kg) of the three marine catfishes *Aspistor luniscutis* (Al), *Bagre bagre* (Bb) and *Genidens genidens* (Gg) in northern Rio de Janeiro state, south-eastern Brazil. The results from the linear models (lines + 95% confidence interval grey polygons) are plotted on observed log-transformed data. The r and *P*-values of the Pearson correlation as well as the equations of the lines (derived from linear model output) are indicated. Bold values indicate significant ($P < 0.05$) relationships.

and with total mass, for *B. bagre* only (Figure 3C, D). No correlations between variables were observed for *A. luniscutis*.

The relationship between $\delta^{15}N$ and THg was highly significant. The slope was 0.34, indicating biomagnification of Hg over the increase in $\delta^{15}N$ in this marine food web (Figure 4).

The isotopic niche area represented by SEAc revealed a broader trophic niche for *G. genidens* (1.88‰^{2}) than for *A. luniscutis* (0.55‰^{2}) and *B. bagre* (0.47‰^{2}) (Figure 5). The greatest isotopic niche overlap was observed for the ellipses of *B. bagre* on *A. luniscutis*, followed by *A. luniscutis* overlapping the ellipse of *B. bagre*, covering an area of 0.29‰^{2}. The lowest SIBER ellipse overlaps were observed for *G. genidens* on *A. luniscutis* and *B. bagre*, with overlapping areas of 0.21 and 0.15‰^{2}, respectively (Figure 5, Table 3).

Table 4 presents the quantitative metrics to estimate the isotopic niche breadth for the three marine catfishes. The highest values of food web length (NR), variability of food resources (CR), total occupied niche area (TA) and small sample size corrected standard ellipse area (SEAc) were observed for *G. genidens*. Additionally, trophic diversity within the demersal food web (CD – ANOVA, $F = 7.515$, $P = 0.001$), trophic redundancy (MNND – ANOVA, $F = 6.842$, $P = 0.001$) and evenness (SDNND – F-ratio test, $P < 0.001$) were higher for *G. genidens* than for *A. luniscutis* and *B. bagre*. Similar to *G. genidens*, the species *A. luniscutis* also presented elevated variability of food resources compared with *B. bagre*.

The SIAR analysis revealed similar relative contributions of all prey items in *A. luniscutis* and *B. bagre*, highlighting higher assimilations of Sciaenidae fishes and *D. sanpaulensis* (73 and 70%, respectively) compared with *G. genidens*, which presented no preference for any prey (Figure 6).

Discussion

This study revealed the extent of sharing and segregating food resources of the three sympatric marine catfish species *Aspistor luniscutis*, *Bagre bagre* and *Genidens genidens* based on comparisons of food assimilation using SIAR, SIBER, isotopic niche

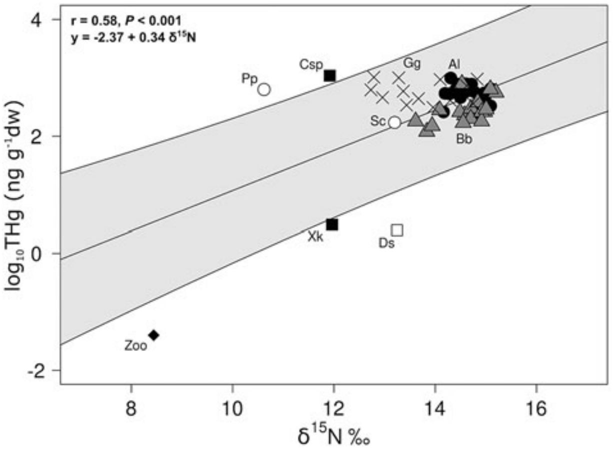

Fig. 4. Relationships between $\delta^{15}N$ (‰) and log-transformed THg considering *Aspistor luniscutis* (Al), *Bagre bagre* (Bb), *Genidens genidens* (Gg), *Doryteuthis sanpaulensis* (Ds), *Xiphopenaeus kroyeri* (Xk), *Callinectes* sp. (Csp), Sciaenidae (Sc), *Porichthys porosissimus* (Pp) and zooplankton (Zoo) in northern Rio de Janeiro state, south-eastern Brazil. The results from the linear model (lines + 95% confidence interval) are plotted on observed log-transformed data. The r and *P*-values of the Pearson correlation as well as the equation of the line (derived from linear model output) are indicated. Bold values indicate significant ($P < 0.05$) relationships.

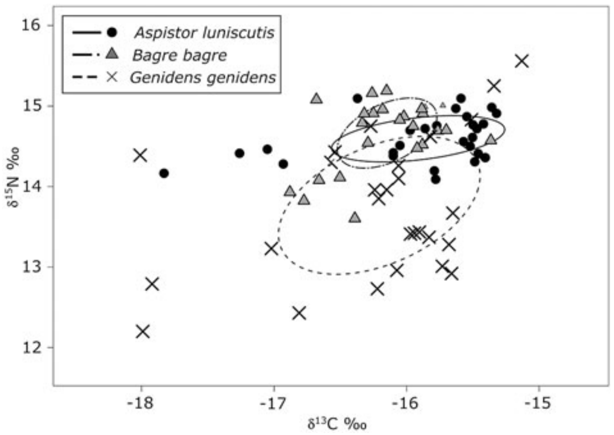

Fig. 5. The standard ellipse areas corrected for small sample size (SEAc) for the three marine catfishes *Aspistor luniscutis*, *Bagre bagre* and *Genidens genidens* in northern Rio de Janeiro state, south-eastern Brazil.

Table 3. Overlapping SEAc (%) between the three marine catfishes *Aspistor luniscutis*, *Bagre bagre* and *Genidens genidens* in northern Rio de Janeiro state, south-eastern Brazil

	A. luniscutis	*B. bagre*	*G. genidens*
A. luniscutis	–	63.0	10.9
B. bagre	53.3	–	7.7
G. genidens	37.2	31.3	–

breadth metrics and THg concentrations. Diet overlaps observed between the three marine catfish species were explained by proportions in the assimilation of Sciaenidae fishes (*Isopisthus parvipinnis*, *Paralonchurus brasiliensis* and *Stellifer rastrifer*), *Doryteuthis sanpaulensis*, *Xiphopenaeus kroyeri* and *Callinectes* sp.

The present study corroborated using a stable isotope approach to classify marine catfish trophic guilds as omnivorous, as previously determined by stomach contents and stable isotope studies (Chaves & Vendel, 1996; Denadai *et al.*, 2012; Tavares & Di Beneditto, 2017; Di Beneditto *et al.*, 2018; Di Beneditto & Tavares, 2019). In south-eastern Brazil, Denadai *et al.* (2012) analysed stomach contents and intestine remains in juveniles, sub-adults and adults, concluding that marine catfishes have wide trophic plasticity during their lifetimes. Juveniles feed mainly on soft and small food items, such as algae and molluscs; adults forage on harder and larger items, such as crustaceans, molluscs and fishes; and sub-adults feed on both prey types.

The SIBER analysis revealed overlaps between the isotopic niches of *A. luniscutis*, *B. bagre* and *G. genidens*. The greater overlaps (>53%) between the isotopic niches of *A. luniscutis* and *B. bagre* indicate that these two species rely on similar prey proportions of assimilation, specifically on Sciaenidae and *D. sanpaulensis*, as observed by SIAR analysis. The species *A. luniscutis* and *B. bagre* presented lower trophic diversity within the demersal food web (CD) and higher trophic redundancy (MNND) and evenness (SDNND) when compared with *G. genidens*, reinforcing its more restricted assimilation of prey resources. Based on isotopic niche metrics, *G. genidens* showed the broadest niche breadth among the catfishes, as evidenced by the highest isotopic niche metrics observed (NR, CR, TA, SEAc, CD, MNND, SDNND). Similar to what other authors found through stomach content analysis (Denadai *et al.*, 2012), the isotopic data suggest that diet of *G. genidens* is the most diversified, based on the higher proportion of assimilation of *Porichthys porosissimus* and *Callinectes* sp. in the Paraíba do Sul river (PSR) estuary compared with *A. luniscutis* and *B. bagre*.

The higher trophic plasticity of *G. genidens* and the similar isotopic niches of *A. luniscutis* and *B. bagre* may be a result of three situations, individually or combined: (1) the high abundance of shrimps, crabs and neritic squids in the study area; (2) different spatial habitat usage by catfishes in the estuarine system; and (3) foraging of other prey items to avoid competition.

Situation 1 can be sustained, as lolignid squids (*Doryteuthis plei* and *D. sanpaulensis*) have a strong association with the sea bottom and are considered abundant in the inner shelf from 10 to 50 m (Robin *et al.*, 2014; Costa *et al.*, 2015). A short distance south (100 km), in the Cabo Frio upwelling region, Soares *et al.* (2014) found similar $\delta^{15}N$ values (higher than for other invertebrates of the present study) of loliginid species (*D. plei* – 12.5‰ and *D. sanpaulensis* – 11.0‰) compared with our results (13.3‰). Shrimps (*Xiphopenaeus kroyeri*) and crabs (*Callinectes* sp.) are considered to be as abundant as squids on the northern coast off Rio de Janeiro (Di Beneditto *et al.*, 2010; Santos & Menegon, 2010; Fernandes *et al.*, 2014). Thus, the local abundance of prey is high to consumers. Nevertheless, the mean $\delta^{15}N$ values of decapods (*Callinectes* sp. and *X. kroyeri*) and

Table 4. Isotopic niche metrics of the marine catfishes *Aspistor luniscutis*, *Bagre bagre* and *Genidens genidens* in northern Rio de Janeiro state, south-eastern Brazil

	NR	CR	TA	SEAc	CD	MNND	SDNND
A. luniscutis	1.01	2.51	1.65	0.55	0.57^{a}	0.14^{a}	0.14^{a}
B. bagre	1.59	1.52	1.48	0.47	0.49^{a}	0.13^{a}	0.11^{a}
G. genidens	3.36	2.88	6.21	1.88	0.94^{b}	0.32^{b}	0.30^{b}

Letters indicate significant differences ($P < 0.05$).

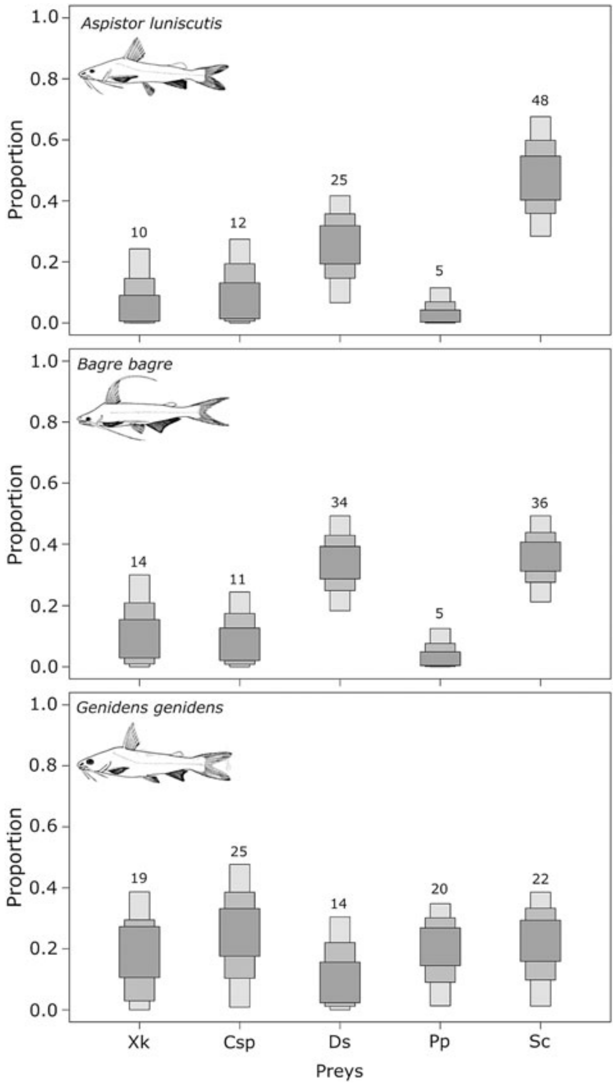

Fig. 6. Results of SIAR (Stable Isotope Analysis in R) showing 95% (dark grey), 75% (intermediate grey) and 25% (light grey) credibility intervals of prey items contributions to the diet of the catfishes *Aspistor luniscutis*, *Bagre bagre* and *Genidens genidens*. Xk, *Xiphopenaeus kroyeri*; Csp, *Callinectes* sp.; Ds, *Doryteuthis sanpaulensis*; Pp, *Porichthys porosissimus*; and Sc, Sciaenidae. Numbers above credibility intervals are the percentage of contribution of each prey to the respective predator.

D. sanpaulensis are higher than that of *P. porosissimus* (Table 2), reflecting the nitrogen isotope values of the consumers. In this sense, it is noteworthy that the δ^{15}N values of the catfishes represented differences in their prey isotopic values rather than in their trophic levels.

Denadai *et al.* (2012) observed a slight overlap between *A. luniscutis* and *G. genidens* because of crustacean fragments and fish scales in both diets and associated the small overlap (37.6%) with differences in spatial usage of the estuary. However, situation 2 may not be plausible. Pereyra *et al.* (2016) found that *G. genidens* adults consumed freshwater-derived carbon sources, and Bizerril (1999) also observed spatial differences governed by salinity in the habitat usage of marine catfishes, allowing their coexistence. The stable isotopes of the present study revealed no variation in habitat usage. The δ^{13}C results were similar among the three ariids, suggesting not only the absence of distinctions in basal OM assimilated sources but also similarity in habitat usage (Bouillon *et al.*, 2011). Nevertheless, our δ^{13}C values are in accordance with the previous study of Di Beneditto *et al.* (2018), reinforcing that marine catfishes are characteristically widespread in the coastal waters influenced by the PSR.

Although the focus of the present study was on trophic ecology rather than habitat usage variations, the THg concentrations observed in the present study coupled with previous knowledge of ariids suggesting different spatial usage in estuaries (Azevedo *et al.*, 1999; Bizerril, 1999; Schmidt *et al.*, 2008; Denadai *et al.*, 2012), can lead to misunderstandings about their spatial dynamics in the estuarine habitat. Regarding THg, a decrease in its concentration in fishes along the river–ocean gradient is expected (Liu *et al.*, 2017). As adult catfishes usually live in adjacent coastal waters influenced by estuaries (Mishima & Tanji, 1983; Denadai *et al.*, 2012) and only seek riverine waters during the spawning period (Schmidt *et al.*, 2008), the differences in THg concentrations between marine catfishes observed in the present study seem to be related to biological factors, not to spatial segregation.

Previous studies developed along this area support the Hg assimilation related to predator–prey interactions (Carvalho *et al.*, 2008; Kehrig *et al.*, 2009; Di Beneditto *et al.*, 2012), suggesting that the past practices of gold-mining and the use of mercurial fungicides on sugarcane plantations in the PSR drainage basin are the main input sources of Hg in this fluvial ecosystem, which is largely exported to the adjacent marine areas, coupled with Hg atmospheric deposition (Lacerda *et al.*, 1993; Lacerda, 1996; Araujo *et al.*, 2017; Azevedo *et al.*, 2018). Reinfelder *et al.* (1998) indicated that the assimilation of dissolved Hg in the water column is an important route for bioaccumulation by aquatic organisms with small body sizes and greater surface areas. The input of Hg in food webs through phytoplankton and the successive increase in metal concentrations to the next trophic levels (Pickhardt *et al.*, 2002) were already observed in coastal areas influenced by PSR in other fish species (Di Beneditto *et al.*, 2012; Kehrig *et al.*, 2013).

The reasons for the elevated mean THg values observed in larger ariid individuals seem to be three-fold: first, it is related to the bioaccumulation of THg during the catfish lifespan, evidenced by the significant correlations ($P < 0.05$) between THg and total length and mass. The accumulation might occur in ariids in the adjacent marine waters of the PSR estuary in accordance with the findings of other authors that suggest that larger and/or older fish have higher THg concentrations due to longer exposure and the difficulty of eliminating mercury, as THg has a very slow excretion rate due to the metal's high affinity for thiol groups that constitute the protein fraction of the muscles (Nakao *et al.*, 2007). Second, the elevated assimilation of species closely related to the bottom sediment, that provides higher Hg bioavailability than the water column (Muto *et al.*, 2014; Le Croizier *et al.*, 2019), by *G. genidens* (*Callinectes* sp. – highest THg in prey and *P. porosissimus* – highest THg in prey fishes) and *A. luniscutis* (Sciaenidae fish) resulted in the higher THg than in *B. bagre*. Finally, the seasonality of the PSR discharge (input of Hg to the ocean) may also be an influencing factor. As observed by Rocha *et al.* (2015), at times of higher PSR discharge, *G. genidens* and *A. luniscutis* were more abundant, thus contributing to higher mean THg values for both species compared with *B. bagre*. At times of lower PSR discharge, *B. bagre* is more abundant; thus as suggested by authors worldwide and for the PSR estuary, during low river discharge the main source of Hg is the direct deposition of the contaminant from the atmosphere to surface waters, resulting in higher concentrations of THg in fish due to the rapid methylation and absorption by biota, thus becoming more bioavailable (Harris *et al.*, 2007; Mason *et al.*, 2012; Araujo *et al.*, 2017; Azevedo *et al.*, 2018).

Biomagnification was also indicated by the significant correlations of THg and δ^{15}N. Since diet is the main source of THg assimilation in fishes (Hall *et al.*, 1997), it might be occurring in this food web, as already observed for other fish species influenced by the PSR plume in the region (Bisi *et al.*, 2012;

Di Beneditto *et al.*, 2012; Kehrig *et al.*, 2013) and worldwide (Al-Reasi *et al.*, 2007; Liu *et al.*, 2017; Chouvelon *et al.*, 2018). In the present study, the slope of the linear regression between THg and δ^{15}N (0.34), used as measurement of biomagnification across food webs (Kidd *et al.*, 1995), was higher than those observed by Al-Reasi *et al.* (2007) in Gulf of Oman (0.07), Muto *et al.* (2014) in the Santos continental shelf (0.13), and Di Beneditto *et al.* (2012) (0.25) and Kehrig *et al.* (2013) (0.21) in the same region as our study. Although biomagnification studies in tropical marine ecosystems are limited, this range (0.07–0.34), already observed by Lavoie *et al.* (2013) in tropical marine food webs, reflects the different composition and vertical position in the water column (higher Hg bioavailability in the bottom sediment for benthic/demersal organisms) of the tropical food webs and/or differences in the growth rate of organisms (Muto *et al.*, 2014; Le Croizier *et al.*, 2019). It is already known that the biomagnification of Hg can vary greatly between marine ecosystems (Cossa *et al.*, 2012), or even between environments of the same ecosystem (Cresson *et al.*, 2015).

Competitive exclusion (situation 3) seems not to regulate the preference of Sciaenidae fishes and *D. sanpaulensis* by *A. luniscutis* and *B. bagre*. As mentioned above, Rocha *et al.* (2015) observed *A. luniscutis* and *G. genidens* in the region mainly during the rainy season (higher discharge of PSR – October to April), while *B. bagre* was observed during the dry season (lower discharge of PSR – May to September). In this sense, the elevated level of partitioning of resources between *A. luniscutis* and *B. bagre*, reflected by high isotopic niche overlaps, seems to exclude none of the species. Thus, based on the high abundance of prey coupled with the different seasonal abundances in the region of the catfishes, it seems they are not competing for the same resources, at the same time, in the same place, leading us to conclude that there is low evidence of interspecific resource competition.

In conclusion, we found that *G. genidens* has a broader trophic niche breadth, is considered generalist and is the most opportunistic marine catfish, due to assimilation of organisms in similar proportions and with lower δ^{15}N. The prey preference for Sciaenidae fishes and *D. sanpaulensis* was observed for *A. luniscutis* and *B. bagre*, resulting in the highest isotopic niche overlap and δ^{15}N signatures, answering the first question of the present study. The coexistence of these three sympatric marine catfishes is probably regulated by different temporal patterns in the coastal area influenced by the PSR plume (question 2) and the high abundance of prey items, leading to resource partitioning with no evidence of competition among the species (question 3). The THg highlighted the different proportions of assimilation of prey as well as the seasonality in the habitat usage by the species. Bioaccumulation of Hg was observed for *B. bagre* and *G. genidens* and Hg biomagnification also occurred in their food web. The understanding of the trophic dynamics of sympatric fishes enhances the knowledge of ecological and environmental forces driving their coexistence. More studies incorporating multiple tools are important for the advancement of knowledge of the trophic dynamics, life cycles, habitat usage and environmental role of marine catfishes in the continent–ocean interface.

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