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Trophic resource partitioning of two snook fish species (Centropomidae) in tropical estuaries in Brazil as evidenced by stable isotope analysis

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Abstract :

We investigated the trophic niches and the resource partitioning of two snook species, the common (Centropomus undecimalis) and the fat snook (C. parallelus), in four tropical estuaries of the northeastern Brazil, using stable isotope analyses of carbon (δ13C) and nitrogen (δ15N). Fish specimens, mainly juveniles, basal resources and a primary consumer were collected in 2015 during dry and rainy seasons in all estuaries, which exhibited differences in system size, geomorphologic shapes, levels of sea access and anthropic pressures. Potential effect of factors like fish body length, estuary and seasonality on isotope ratios were investigated. Positive relationships between the size of fish and δ15N values were found, regardless the species. Our results indicated that snooks can be characterized as secondary consumers and have close trophic niches in most estuaries. Trophic overlaps were more pronounced within the largest estuaries (Catuama and Santa Cruz), whereas smaller systems that have restricted connections to the sea presented low isotopic niche overlap between both species (Suape and Sirinhaém). Moreover, a higher variability of δ13C and δ15N values in snooks was found in larger estuaries undergoing stronger influences from coastal adjacent waters. Although we were not able to detect clear seasonal effects, greater isotopic overlaps were found during the rainy season. Despite the lack of intrinsic differences in life history traits, both species, dominated by juveniles, shared similar trophic niches in these environments.

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Highlights

► $\delta^{13}C$ and $\delta^{15}N$ of two Centropomidae were investigated in four estuaries in Brazil. ► Juveniles of *Centropomus undecimalis* and *C. parallelus* have close isotopic niches. ► Trophic overlaps were more pronounced in large estuaries. ► Resource partitioning process might reflects the resource availability in estuaries.

Keywords : Brackish water fish, Trophic relationships, Carbon, Nitrogen, *Centropomus*.

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1. Introduction

A theoretical niche is defined as the volume occupied by species in an *n*-dimensional space and predicts that two species cannot coexist when exhibiting the same fundamental niche (Hutchinson, 1957; Odum, 1976). Functionally related species thus tend to exhibit partitioning in resource use on a spatial, temporal or trophic axis to avoid competition and to optimize energy acquisition (Schoener 1974). The trophic niche of a species is one of the quantifiable dimensions of the many facets shaping the niche concept and is perhaps the most studied. Investigating the different resources consumed by different species along with associated levels of availability and accessibility allows for the comprehension of resource use in a fish community and reasons for varying degrees of niche overlapping (Losos, 2000) especially when dealing with important marine resources such as fish of the Centropomidae family (Figueiredo and Menezes, 1980; Muller et al., 2015) in tropical ecosystems.

Snooks (*Centropomus* spp.) are predators of great economic value used in recreational and commercial fisheries in tropical and subtropical estuaries throughout the American continent (Orrell, 2002; Muller et al., 2015). Among the six sympatric species occurring in the western Atlantic Ocean, the common (*Centropomus undecimalis* (Bloch, 1792)) and fat snook (*Centropomus parallelus* (Poey, 1986)) can be distinguished from other species from their greater economic value, larger size and broader and more abundant distributions along estuarine areas in Brazil (Figueiredo and Menezes, 1980; Rivas, 1986). Snooks are euryhaline and estuarine-dependent species that exhibit complex patterns of habitat shifting over their life cycle, forming a mosaic of estuarine and nearshore habitats (Barbour and Adams, 2012; Barbour et al., 2014; Dantas and Barletta, 2016; Daros et al., 2016). Juvenile snooks of both species usually inhabit mangrove creeks and move to deeper brackish waters as they grow (standard lengths of 150 to 300 mm) (Stevens et al., 2007; Blewett et al., 2009). In addition, despite differences in the maximum lengths of *C. undecimalis* (1300 mm; Orrel, 2002) and *C. parallelus* (600 mm; Figueiredo and Menezes, 1980), they become adults at very similar sizes (*i.e.*, ≥ 330 mm for *C. undecimalis* (Peters et al., 1998) and ≥ 280 mm for *C. parallelus* (Rorigues et al., 2006)). Both species mainly feed on crustaceans and smaller fish (Blewett et al., 2006; Contente et al., 2009; Dutka-Gianelli, 2014; Lira et al., 2017), though fish have been reported to constitute the main source of food for *C. undecimalis* while crustaceans prevail in the *C. parallelus* diet (Aliaume et al., 2005; Lira et al., 2017). The similarities in their habitats

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and feeding habits especially during juvenile stages can lead to resource competition and trophic niche overlapping that may alter the growth of individuals (Aliaume et al., 2005; Dutka-Gianelli, 2014).

The coexistence of the two snook species in tropical estuaries is a natural process, though it is still poorly documented (Dutka-Gianelli, 2014). Studies on Brazilian estuaries are currently restricted to a focus on only a few systems throughout the country and particularly in southern Brazil (Blaber and Barletta, 2016). Further, information regarding the ecological processes of fish often rely on studies conducted at a local scale, and comparisons drawn across sites may thus offer a stronger understanding of habitat use by species in complex environments like estuaries (Stevens et al., 2018). The estuaries addressed in this study exhibit different characteristics in terms of shapes, sizes, food web structures and anthropogenic impacts, which result in differences in how species use resources. For instance, morphological features of estuarine areas (*e.g.*, system size and structural heterogeneity) have been associated with resource availability (Abrantes et al., 2013; Bouillon et al., 2004), fish species diversity and food web composition (França et al., 2012; Vasconcelos et al., 2015), food chain length (Doi et al., 2009) as well as with interspecific processes between functionally related predators (Young, 2001; Mariani et al., 2011). Habitat changes caused by recurrent anthropogenic activities can also influence the environmental boundaries of estuarine systems and their role as migratory corridors for amphidromous species such as snooks (Cianciotto et al., 2019). These changes may affect numerous ecological processes such as the availability of prey from adjacent habitats, species distributions and interspecific processes observed among estuarine predators (Adams et al. 2009; Boucek and Rehage, 2013; Cianciotto et al., 2019). Understanding the coexistence of sympatric predators will help improve ongoing conservation measures and initiate an investigation of potential effects of climate change on the displacement and abundance of estuarine fish (*e.g.*, Araújo et al., 2018).

Trophic niche overlaps can be characterized with stomach content data coupled with other descriptive indexes such as those for diversity and evenness (Bearhop et al., 2004). However, methods for tracing organic matter flux through the food web such as the stable isotope analysis (SIA) method used in this study have provided insightful information on the use and partitioning of resources in fish assemblages (Newsome et al., 2007). Carbon and nitrogen stable isotope analyses offer the advantage of providing time integrated measures on food assimilated by an organism (DeNiro and Epstein, 1978; Herzka, 2005), which may vary from weeks to months (Herzka, 2005; Elsdon et al., 2010), rather than a common snapshot as provided by a dietary analysis (Pinnegar and Polunin, 2000). $\delta^{15}N$ exhibits a

considerable degree of enrichment per trophic level, allowing, with appropriate isotopic baselines and trophic fractionation, for the estimation of the trophic positioning of an organism (Post, 2002; Martínez del Rio et al., 2009). On the other hand, $\delta^{13}C$ outlines the origins of organic matter (Fry, 2006) when it presents low levels of enrichment across the food web and considerable variability between primary producers (*e.g.*, C3 and C4 plants) (Degens et al., 1968; Smith and Epstein, 1971; Post, 2002).

In this study, we evaluated resource partitioning between *C. undecimalis* and *C. parallelus* in four tropical estuaries of Brazil. Trophic niches were investigated via carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analyses to verify whether the use of resources by snook species is affected by estuaries with different morphological and biological features.

2. Material and methods

2.1. Study area and sampling procedures

Located along the west coast of the South Atlantic Ocean, the study area includes four estuarine systems positioned along the coast of Pernambuco state, northeastern Brazil (Fig. 1), which exhibits distinct morphologic and physicochemical characteristics subject to different anthropogenic pressures (Table 1). The largest estuarine complex in Pernambuco is the Santa Cruz Channel system located along the northern coast, which is characterized as a U-shape channel that connects to the sea through two entrances (Silva et al., 2011). Due to its size and morphological variations (Medeiros and Kjerfve, 1993), the Santa Cruz Channel complex was subdivided in two smaller systems, (1) the estuary of Catuama (Fig. 1a) and (2) the Santa Cruz Channel (Fig. 1b), which are associated with the northern and southern entrances, respectively. The estuaries of (3) Suape and (4) Sirinhaém are distinct in size and shape when compared to those along the northern coast. Suape, located 40 km from the state capital (Recife), is composed of two main rivers that flow into a large brackish lagoon (CPRH, 2001) (Fig. 1c). In addition to its limited depth and restricted connection to the ocean, the estuary hosts an important industrial harbor in its marine portion. Sirinhaém, located in the southern part of Pernambuco, is the smallest estuary of the four (Table 1). The system serves as a shallow and narrow connection to the ocean, including a small collection of lagoons and flooded plains (CPRH, 2001) (Fig. 1d).

Sampling surveys were carried out within each estuary from January to April and from August to September of 2015, which represent the local dry and rainy seasons, respectively (Medeiros et al., 2001). Block nets set close to mangrove creeks (350 x 2.9 m, mesh 70 mm) and beach seine trawls (20 x 1.9 m, mesh 20 mm) were deployed to collect *C. undecimalis* and *C. parallelus* individuals. All specimens were

identified from a specific reference (Figueiredo and Menezes, 1980), stored in ice, measured (standard length - SL) and then processed for isotopic analysis.

To identify background isotope ratios for the base of the food web of the studied environment, a long-lived primary consumer (mangrove oyster *Crassostrea rhizophorae*) and four representative sources of organic matter in estuaries were collected in each survey. Organic matter sources included a few primary producers such as mangrove trees (rotten leaves from *Rhizophora mangle*) and macroalgae (*Sargassum* sp. and *Ulva* sp.) as well as suspended particulate organic matter (POM) and particulate organic matter in sediment (SOM). Oysters and samples of mangrove leaves and macroalgae were collected by hand during low tide periods. POM was sampled while collecting snook specimens by filtering water through fiberglass filters (0.75 µm) while SOM was collected from the top 2 mm layer of sediment.

2.2. Stable isotope analysis

White muscle from each fish specimen and the adductor muscles of oysters were extracted, rinsed with distilled water to remove exogenous materials (*e.g.*, remaining scales or bones), and dried in an oven at 60°C for 48 hours. The whole sample of basal sources was used for the analysis. Dried samples were ground into a fine powder with a mortar and pestle. POM and SOM samples were duplicated. One subsample was acidified to remove inorganic carbon prior to the $\delta^{13}C$ analysis. The other subsample was used for our $\delta^{15}N$ analysis (Pinnegar and Polunin, 1999). Likewise, lipid extraction was performed on mangrove oyster samples using a procedure adapted from Kojadinovic et al. (2008). Oyster samples were processed in duplicate with one subsample dedicated to $\delta^{13}C$ and with the other used for lipid extraction for $\delta^{15}N$ measurement. Each sample weighed between 0.35 and 0.45 mg and was analyzed for carbon and nitrogen isotope ratios with a mass spectrometer (Thermo Delta V+) coupled to an element analyzer (Thermo Flash 2000, interface Thermo ConFio IV) at the Pôle de Spectrométrie Océan (PSO - IUEM, Plouzané, France).

Results for carbon and nitrogen are reported as $\delta^{13}C$ and $\delta^{15}N$ values, respectively, and are derived from the relation between the isotopic value for the sample and a known standard of $\delta^{13}C$ or $\delta^{15}N$ = $[(R_{sample} / R_{standard}) -1] \times 10^3$ where R corresponds to ratio $^{13}C/^{12}C$ or ratio $^{15}N/^{14}N$. Standards used for $\delta^{13}C$ and $\delta^{15}N$ included PeeDee Belemnite (PDB) limestone and atmospheric nitrogen, respectively. The analytical precision of the analysis monitored from a known standard (Thermo – Acétanilide) every six samples was defined as ± 0.11‰ (standard error) and ± 0.07‰ for carbon and nitrogen, respectively.

2.3. Data analysis

Due to the broad range of sizes of the snook specimens, we first assessed the relationships between stable isotope values and fish size (SL) using covariance analyses (ANCOVA). We then investigated potential effects of species (*C. undecimalis* / *C. parallelus*), estuaries (Catuama / Santa Cruz / Suape / Sirinhaém) and seasons (dry / rainy) using two linear models applying fish length as a continuous explanatory variable and with $\delta^{15}N$ and $\delta^{13}C$ as used dependent variables, respectively. Model selection was performed using classical statistical inference (test F) combined with an automated stepwise selection method based on the Akaike Information Criterion (AIC) (Akaike, 1974). Main effects and first order interactions were evaluated to find the more parsimonious model. Moreover, $\delta^{13}C$ and $\delta^{15}N$ values of oyster and basal sources were tested across the estuaries and seasons using separate non-parametric Kruskal Wallis tests to verify whether differences in isotope ratios observed among the sites are associated with food webs.

Resource partitioning was investigated by analyzing overlaps between the isotopic niches. Isotopic niches of both snook species for each estuary and season were computed with the standard ellipses area method and from $\delta^{13}C$ and $\delta^{15}N$ values. The standard ellipses area (SEA) represents the mean core of the isotopic niche and covers approximately 40% of the available data (Jackson et al., 2011). This method is less sensitive to sample sizes than other conventional methods (*e.g.*, convex hull area) (Jackson et al., 2011; Syväranta et al., 2013). To address biases that can emerge from comparisons drawn between groups of unequal sample sizes (*i.e.*, underestimation of the population's SEA for small samples), Jackson et al. (2011) proposed a corrected standard ellipse area (SEA_C) that maintains the same geometric features but with a slight increase in the ellipse area for smaller sample sizes. In addition, for comparative purposes, the isotopic space was standardized following Cucherousset and Villéger (2015). Finally, to overcome the effect of fish size for nitrogen isotopes, we predicted $\delta^{15}N$ values from the selected linear model by fixing fish size at 200 mm SL, roughly representing the mean and mode of the specimens analyzed. The variability in $\delta^{15}N$ among individuals was determined by adding the model's residuals for the given length of each specimen to the predicted $\delta^{15}N$ calculated for a fish size of 200 mm. For example, when a residual of 0.25 (positive) was calculated for a 150 mm (SL) fish of one species for a given estuary and month and when predictions for the same species, estuary and month for a fixed fish size of 200 mm were measured as 10‰, the final predicted $\delta^{15}N$ value was defined as 10.25‰ (10‰+0.25‰). Therefore,

predicted $\delta^{15}N$ and raw $\delta^{13}C$ values were used to compute standard ellipses, as fish size was not found to have a significant effect on carbon values.

The trophic positioning of snooks across estuaries and seasons was determined using the following formula developed by Post (2002):

$$TP_{SIA} = \lfloor(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/TDF\rfloor + TP_{baseline}$$

where $\delta^{15}N_{consumer}$ and $\delta^{15}N_{baseline}$ are the $\delta^{15}N$ values for the target consumer and baseline, respectively; TDF is the trophic discrimination factor and $TP_{baseline}$ is the trophic position of the baseline. The trophic position estimate is influenced by the baseline's representativeness of the target consumer food chain (Post, 2002). Therefore, we propose two alternatives approaches to TP_{SIA} estimation based on distinct baselines: (i.) TP_{SIA1} – a long-lived filter feeder as a baseline (*Crassostrea rhizophorae;* $TP_{baseline} = 2$); (ii.) TP_{SIA2} – $\delta^{15}N$ the values of all available basal resources of each site as a baseline ($TP_{baseline} = 1$). To account for uncertainty associated with the index, a Bayesian model was applied in the calculation of TP_{SIA} using predicted $\delta^{15}N$ values of snooks and a TDF of 2.30 ± 1.60‰ (mean ± standard deviation, McCutchan Jr et al. (2003)).

To draw comparisons, trophic positions were also estimated using stomach content data (TP_{SCA}) from Lira et al. (2017), who studied the feeding habits of snooks of the Santa Cruz and Sirinhaém estuaries. TP_{SCA} was determined based on the dietary features of individuals of 150 to 250 mm (SL, Supplementary Table S1) applying the following formula:

$$TP_{SCA} = \sum(W_i T_i) + 1$$

where W_i and T_i are the relative weight and the trophic positioning of the *i*th prey item, respectively (adapted from Winemiller (1990)). W_i is the weight of prey *i* divided by the total weight of prey items. Trophic positions of prey items were obtained from major functional groups (*e.g.*, primary producers = 1; omnivorous =2.5) based on a dietary analysis (Supplementary Table S2). Items with less accurate taxonomic identification (*e.g.*, decapod crustaceans) were considered omnivorous due the diverse feeding habits of each group (Fauchald and Jumars, 1979; Brusca and Brusca, 2007). Fish items were classified by their functional trophic guilds according to Elliott et al. (2007).

All statistical analyses were performed with R version 3.4.4 (R Core Team, 2018) using packages *SIAR* ("Stable Isotope Analysis in R" (Parnell and Jackson, 2015)) and *SIBER* ("Stable Isotope Bayesian Ellipses in R" (Jackson and Parnell, 2016)) for the estimation of isotopic niche areas and overlaps, and the

tRophicPosition ("tRophicPosition: Bayesian Trophic Position Calculation with Stable Isotopes" package (Quezada-Romegialli et al., 2017)) was used for trophic positioning calculations.

3. Results

A total of 138 fish specimens (62 *C. undecimalis* and 76 *C. parallelus*), 25 mangrove oysters (*Crassostrea rhizophorae*) and 85 samples of basal sources (22 samples of *Rhizophorae mangle*, 9 *Sargassum* sp., 9 *Ulva* sp., 21 POM and 24 SOM) were collected for stable isotope analyses. Fish sizes ranged from 57 to 392 mm (SL) with a predominance of juveniles of size classes 150 to 250 mm (Fig. 2). Stable isotope ratios of the snooks covered a broad range of $\delta^{13}C$ (-25.38 to -14.22‰) and $\delta^{15}N$ values (6.93 to 13.63‰) across the sites and seasons (Table 2). Stable isotope ratios of oysters and basal resources ranged from -29.24 to -14.50‰ and from -1.03 to 10.11‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively (Supplementary Table S3).

While we find no strong evidence for rejecting the fact that the medians of $\delta^{13}C$ ratios from basal sources were similar between the studied locations (Kruskal-Wallis: χ^2 = 1.471, *p*-value = 0.688) and seasons (Kruskal-Wallis: χ^2 = 0.793, *p*-value = 0.373), Sirinhaém and Suape exhibited broader levels of variability for $\delta^{13}C$ than Catuama and Santa Cruz. Mangrove trees and macroalgae were found to be responsible for depleted and enriched $\delta^{13}C$ values, respectively (Supplementary Table S3). The medians of carbon values for mangrove oysters were found to be similar between seasons (Kruskal-Wallis: χ^2 = 0.665, *p*-value = 0.414) but not between estuaries (Kruskal-Wallis: χ^2 = 15.726, *p*-value = 0.001). Conversely, oyster mean $\delta^{15}N$ values showed significant differences between seasons (Kruskal-Wallis: χ^2 = 14.086, *p*-value < 0.001) but not between locations (Kruskal-Wallis: χ^2 = 4.795, *p*-value = 0.187). No significant differences were found in medians of $\delta^{15}N$ values from basal resources across the studied locations (Kruskal-Wallis: χ^2 = 1.167, *p*-value = 0.760) and seasons (Kruskal-Wallis: χ^2 = 0.044, *p*-value = 0.832). Stable isotope ratios of POM and macroalgae presented the highest values of $\delta^{15}N$ for the studied locations and exhibited notably high $\delta^{15}N$ means in Suape during the dry season.

The results of the ANCOVA model for snook $\delta^{15}N$ values show a significant effect of fish length (adjusted r^2 = 0.32, F = 22.45, p < 0.001) with no separate slopes (t test, t = 0.376, p = 0.707) or distinct intercepts (t test, t = -1.054, p = 0.294) for the interaction between length and species. Conversely, fish body length did not influence $\delta^{13}C$ values (adjusted r^2 = 0.00, F = 1.364, p = 0.256) (Fig. 3).

The more parsimonious linear model selected for snook $\delta^{15}N$ considered species, estuaries, seasons, the covariate size, and interactions between species and estuaries (adjusted r^2 = 0.53, F = 18.69,

$p < 0.001$; Supplementary Table S4). Residuals were graphically checked for statistical adequacy (Supplementary Fig. S1). Species within each estuary and for a given season showed overall distinct predicted $\delta^{15}N$ means with differences ranging from 0.20 to 1.33‰. The two snook species exhibited similar predicted $\delta^{15}N$ means for Catuama while differences by species were higher in Suape (0.95 and 1.05‰ during the dry and rainy seasons, respectively) and Sirinhaém (0.85 and 0.41‰) (Fig. 4). In Santa Cruz, differences in predicted $\delta^{15}N$ means were mainly identified by species (1.23 and 1.33‰ during dry and rainy seasons, respectively), but snooks also presented more variability and degrees of overlap in predicted $\delta^{15}N$ values in this estuary. Differences in predicted $\delta^{15}N$ means across seasons were found to be higher for Sirinhaém (0.64 and 1.08‰ for *C. undecimalis* and *C. parallelus*, respectively) (Fig. 4). Furthermore, predicted $\delta^{15}N$ means were higher during the dry season, and *C. parallelus* presented higher predicted $\delta^{15}N$ means than *C. undecimalis* in every estuary other than that in Suape.

Variability in snook $\delta^{13}C$ values was found to be high, but estuaries were the only significant factor selected under the more parsimonious linear model (adjusted $r^2 = 0.17$, $F = 10.53$, $p < 0.001$; Supplementary Table S4). No pattern was observed between the two species or across seasons (Fig. 4). Overall, mean $\delta^{13}C$ values for snooks were more depleted in Sirinhaém, and $\delta^{13}C$ value ranges were found to be greater in Santa Cruz and Catuama (Fig. 4).

The isotopic niches of both snook species were found to vary across areas and seasons (Supplementary Table S5). The estimated standard ellipse area (SEA_C) of snook communities is larger in the northern areas (Santa Cruz and Catuama) than in the southern estuaries (Sirinhaém and Suape) (Fig. 5). Northern estuaries also show more pronounced overlapping patterns than the other systems (Supplementary Table S5). SEA_C overlaps between species were found in all estuaries but that in Suape. No overlap was observed for Sirinhaém for the dry season. Overlaps were found to be more pronounced during the rainy season (Supplementary Table S5, Fig. 5). The SEA_C of *C. undecimalis* in Suape for the rainy season was not computed due to its small sample size (n = 3).

Overall, snook species were classified across the third and fourth trophic positions (Table 3). Minor differences were found between species within the sites where *C. parallelus* presented higher TP_{SIA} values in all estuaries except in the case of Suape. *C. parallelus* present the highest TP_{SIA} values in Sirinhaém. Seasonal effects on TP_{SIA} were found to be weak yet present in Sirinhaém for TP_{SIA1} and in Catuama for TP_{SIA2} where snooks show decreasing values from the dry to rainy seasons (~ 0.8). TP_{SIA1} shows more pronounced and constant seasonal effects than TP_{SIA2}. TP_{SIA1} presents lower modes than

TP_{SIA2} except for Santa Cruz and Suape during the dry season. TP_{SCA} estimates exhibit similar values for snooks in Santa Cruz and Sirinhaém, characterizing snooks as secondary consumers (Table 3).

4. Discussion

Trophic niche width and resource partitioning can be expressed with gut content analyses, but stable isotope ratios of nitrogen and carbon are also an efficient tool for elucidating trophic interactions occurring in food webs and between species in competitive environments (*e.g.*, Newsome et al., 2007). We thus attempt to examine hypotheses supported by our results while applying a complementary stable isotope and stomach content methods.

Body size plays a central role in predator-prey interactions (Shelton et al., 1977). The relationship between snook body length and $\delta^{15}N$ shows that *C. undecimalis* and *C. parallelus* feed on prey with higher $\delta^{15}N$ values as their body length and mouth's gap grow. On average, fish of 300 mm in length present $\delta^{15}N$ values 1.7‰ greater than those of specimens of 100 mm in length, which corresponds to almost one trophic level when assuming a trophic mean $\delta^{15}N$ fractionation value of 2.3‰ (McCutchan Jr et al., 2003). Our finding confirms previous stomach content and behavioral studies revealing an ontogenetic shift in snook diets (Blewett et al., 2006; Contente et al., 2009; Araújo et al., 2011). Moreover, we were not able to distinguish any species effect for $\delta^{15}N$ body length relationships, showing that both species exhibit the same feeding patterns for the size range studied even though *C. undecimalis* presents a faster body growth rate and reaches larger body sizes than *C. parallelus* (Orrel, 2002; Viana et al., 2016).

Snook $\delta^{13}C$ values were not found to be impacted by body length while values varied from -25.38‰ to -14.22‰. This great variability in $\delta^{13}C$ values may be due to the wide range of carbon sources in the studied estuaries (Layman, 2007), which may propagate along the food web to snook species. $\delta^{13}C$ values from basal sources collected in this study ranged from -29.25 to -14.50‰, which are similar to carbon source values reported for other Brazilian estuaries (Garcia et al., 2007; Giarrizzo et al., 2011; Hoeinghaus et al., 2011; Claudino et al., 2015).

The regression models show that the estuaries significantly differ in terms of carbon and nitrogen isotopes, though no differences in mean $\delta^{15}N$ and $\delta^{13}C$ values of basal sources were found between the locations. Thus, snooks exhibited different sources of primary production and feeding strategies that may be associated with differences in system sizes, geomorphologic shapes, levels of sea access and anthropic pressure levels among estuaries. The type of estuary considered and its underlying dynamics determine

nutrient availability (Bouillon et al., 2004; Lugendo et al., 2007; Hoeinghaus et al., 2011). For example, the estuarine complex of the Santa Cruz Channel (the Santa Cruz and Catuama estuaries) is influenced by marine inputs due to its broad connection to the sea (Flores Montes et al., 1998; Figueiredo et al., 2006). Indeed, marine basal sources often show ^{13}C-enriched values when compared to estuarine and freshwater environments (*e.g.*, marine phytoplankton δ^{13}C range: -17 to -23‰ (Bouillon et al., 2008)). Therefore, the broader connections of the Santa Cruz Channel compared to those of Sirinhaém and Suape (see Table 1) along with a stronger influence of adjacent coastal waters than that observed in Catuama (Flores Montes et al., 1998; Figueiredo et al., 2006) could explain the broader range of δ^{13}C snook values found in Santa Cruz. On the other hand, Sirinhaém presents depleted δ^{13}C values that may be due to the estuary's small size and to its narrow connection to the sea, which likely contributes to a low intake of marine water and to an increased assimilation of autochthon ^{13}C-depleted primary production (Bouillon et al., 2004). In the midterm, Suape is moderate in size among the estuaries studied with similar characteristics to those observed in Sirinhaém in terms of species diversity levels (Merigot et al., 2016) and morphology structures (Silva et al., 2011). However, the influence of marine water in Suape is more pronounced due to brackish lagoon formations (Paranaguá, 1986; Muniz et al., 2005). In addition, Suape is the area most heavily impacted by anthropic activities. Recurrent discharges of agriculture and industrial waste in Suape suggest a higher input of organic nutrients into the system (CPRH, 2001), which may be related to high δ^{15}N values observed in POM during the dry season (McClelland and Valiela, 1998; Morris et al., 2015).

In addition to intersite variability in δ^{13}C and δ^{15}N observed, differences in isotope ratios of snooks and basal sources across seasons were found to be more pronounced in Sirinhaém and in Suape to a lesser extent than in the northern estuaries. It is noteworthy that seasonal variations in tropical estuaries are frequently associated with changes in river runoff and with the contributions of terrestrial nutrients to food webs (*e.g.*, Lin et al., 2007; Abrantes et al., 2014), which usually present lower δ^{13}C values than estuarine sources (Smith and Epstein, 1971). The intensity of these effects can be mitigated by the morphological characteristics of each system and seems to reflect the balance of nutrients input into the estuary and their transport to the sea (Abrantes et al., 2013, 2014; Bouillon et al., 2004). The smaller systems of Sirinhaém and Suape with narrower connections to the sea may retain terrestrial nutrients in the estuarine area, allowing them to be incorporated into the food web during the rainy season, enhancing the potential importance of freshwater runoff in providing depleted δ^{13}C nutrients (terrestrial and C3 plant

input) (Smith and Epstein, 1971; Fry, 2006). Conversely, Santa Cruz and Catuama exhibit a well-mixed environment (Leite et al., 2008), and despite a clear seasonal trend reported for theses estuaries (Medeiros and Kjerfve, 1993; Medeiros et al., 2001), we were not able to identify any seasonal variations. Other studies have similarly observed minimal or absent seasonal variations in estuarine food webs (Akin and Winemiller, 2006; Baeta et al., 2009).

In the present study, the two snook species of *C. parallelus* and *C. undecimalis* were characterized as secondary consumers. These results corroborate previous studies focused on diet (Garcia and Giarrizzo, 2014), stable isotope (Giarrizzo et al., 2011; Winemiller et al., 2011) and ecosystem modeling (Rosado-Solórzano and Guzmán del Próo, 1998; Lira et al., 2018). Despite the differences observed in $\delta^{15}N$ levels among species within a given estuary, trophic positions presented similar values across species and estimate methods (stable isotopes and stomach content). It is worth noting that stomach content measures may overestimate TP values relative to TP_{SIA} due to difficulties associated with identifying digested prey items along with their respective TP and due to the contributions of indigestible parts (*e.g.,* decapods carapaces) particularly for piscivorous species such as *C. undecimalis* (Hyslop, 1980; Amezcua et al., 2015). On the other hand, TP_{SIA} is influenced by the baseline selected and by the use of an appropriate trophic discriminant factor (Post, 2002; Martínez del Rio et al., 2009). Although the use of a primary consumer as a baseline is recommended (Post, 2002; Mancinelli et al., 2013), in our case, available basal resources yielded results more similar to those of other studies (*i.e.,* TP values higher than 3 in most cases; ((Giarrizzo et al., 2011; Winemiller et al., 2011; Garcia and Giarrizzo, 2014; Lira et al., 2018)). Primary consumers examined in this study (*C. rhizophorae*) were carefully collected to form a representative baseline of the pelagic food web and to avoid the incorporation of pooled benthonic sources. In addition, our stomach contents analysis shows that snooks forage on prey associated with the substrate (Lira et al., 2018) and that this may not be directly linked to the pelagic food web in the studied estuaries. Pelagic food webs often exhibit higher $\delta^{15}N$ ratios than those of benthonic pathways as exemplified by the higher $\delta^{15}N$ values of POM observed here and can present underestimated TP_{SIA1} results. Thus, the use of a conjunct of basal resources as a baseline represents a mixture of pelagic and benthic pathways and may reflect the great diversity of sources available in tropical estuaries (Layman 2007). Nevertheless, this approach is centered on rough mean values of all available basal resources, and by selecting particular pool sources as baselines one can overestimate or underestimate the actual trophic positioning of a species. Basal resources also show high levels of interspecific variability and can obscure

spatial-temporal differences in the baseline when compared to primary consumers (Mancinelli et al., 2013), which may explain the similarities in TP_{SIA2} values observed between seasons. In addition to the inherent bias associated with TP_{SCA} and TP_{SIA} estimates, a joint approach adopting these methods can provide a more compelling account of the trophic positioning of organisms (*e.g.*, Amezcua et al., 2015).

The isotopic niche approach can be used as a proxy for the diversity of isotopically distinct food sources assimilated by an organism (Newsome et al., 2007). In this study, larger SEA_C values were observed in Santa Cruz and to a lesser extent in Catuama. Such patterns can be attributed to the availability of resources in the studied locations. Coastal environments encompass a mosaic of habitats that are connected to one another through physical processes and through the movement of transient species (Sheaves, 2009). Broader connections to the sea observed in Santa Cruz and Catuama relative to Suape and Sirinhaém may facilitate connectivity to adjacent habitats and in turn enhance the availability of resources with distinct isotope ratios in these systems. Niche widths can also be influenced by interspecific processes occurring between coexisting species. In this case, we find a negative relationship between interspecific competition and niche breadth (niche variation hypothesis, Van Valen (1965)) where a reduction of interspecific processes is favored among individual variations in the use of resources (Bolnick et al., 2010). Wider isotopic niches observed in Santa Cruz than in Sirinhaém reveal similar trends as those reported by Lira et al. (2017) via stomach content analysis. Although resource availability was not directly examined, a stomach content analysis of snook species caught in Santa Cruz and Sirinhaém revealed that the diet of *C. parallelus* differs across estuaries with higher proportions of decapod crustaceans found in Sirinhaém and with fish and crustaceans prevailing in Santa Cruz (Lira et al., 2017). Such differences in diet and stable isotope analysis results reflect the opportunistic behaviors of *C. parallelus* in an environment with highly available food sources.

Overall, snooks exhibited similar trophic niches. Higher degrees of overlap evidenced from SEA_C values were observed for Santa Cruz and Catuama. Theoretically, the occurrence of functionally related species in an environment with limited resources leads to food partitioning processes (Losos, 2000). Conversely, when resources are abundant, niche overlap (*i.e.*, dietary overlap) between species may not configure interspecific competition but instead the sharing of prey (Delbeek and Williams, 1987; Lucena et al., 2000). Our findings support this hypothesis given similarities in the diets of snook species (Vasconcelos Filho et al., 2003; Lira et al., 2017) and the abundance of gobies (snooks' main prey) found in Santa Cruz (see Merigot et al., 2016; Silva-Júnior et al., 2016). Moreover, Santa Cruz and Catuama

estuaries show more abundant and taxonomically related fauna than Suape and Sirinhaém estuaries (Merigot et al., 2016) and support a wide range of fish species of the intermediate trophic levels (Vasconcelos Filho et al., 2003; Ferreira, 2018). Broader isotopic niches and greater overlaps observed in Santa Cruz and Catuama suggest that snooks feed on similar sources but also cover a broader food spectrum in these estuaries. By contrast, in smaller estuaries, *i.e.,* Sirinhaém and Suape estuaries, snooks exhibit more pronounced patterns of resource partitioning. Aliaume et al. (2005) reported that juvenile snooks exhibit similar feeding habits in estuarine areas of Porto Rico but are able to switch their prey to minimize competition with other species. Analogously, more pronounced SEA_C overlaps between snook species observed during the rainy season may be attributable to a broader availability of prey during this period. For instance, Silva et al. (2003) observed higher densities and less diversity in zooplankton communities in Santa Cruz during the rainy season. Seasonal effects of resource partitioning observed between consumers have also been reported for other fish species and often reflect peak levels of potential prey (*e.g.,* Delbeek and Williams, 1987; Lucena et al., 2000).

Our findings show that mostly juvenile *Centropomus parallelus* and *C. undecimalis* have similar trophic niches across the four estuaries studied, though the overall overlap in isotopic niches observed between species does not exceed 30%. Trophic partitioning between snooks was found to be greater in environments with restricted connection to the sea and with more mangrove area cover. The resource partitioning process observed between the two species likely reflects a relationship between morphologic features and resource availability within each system. Moreover, this potential sharing of resources does not represent a limiting factor for snook populations, as they constitute one of the most abundant species in estuaries of the area (Merigot et al., 2016). These results highlight the capacity for snooks to adapt to environments with different food web compositions, supporting the notion that these predators act as important species in estuarine environments (Lira et al., 2018).

Snooks are important marine resources for local fisherman as sources of income and food. However, in most regions of Brazil, conservation strategies for these species are focused strictly in their minimum catch sizes while the potential effects of habitat degradation on fish populations are often neglected. Habitat modification still remains a relevant threat to estuarine fish and especially for tropical ecosystems in developing countries, where population sizes and demand for resources are constantly increasing (Lotze et al., 2006; FAO, 2018). Indeed, over the last decades, estuaries have faced changes to their environmental features (*e.g.*, freshwater flows, mangrove cover levels, water temperatures,

sedimentation rates and salinity gradients) due to anthropogenic activities and climate change (Yang, 2015; Pelage et al., 2019). These modifications directly affect the food web dynamics and distribution of snooks species by regulating their accessibility to habitats and the availability of prey (Adams et al., 2009; Araújo et al., 2018; Cianciotto et al., 2019). For instance, human induced changes in the freshwater flow regimes of estuarine creeks in Florida have been shown to decrease the diversity of prey available to snooks (Adams et al., 2009). Moreover, the displacement of estuarine environmental boundaries due to climate change may enhance the coexistence and resource partitioning of snooks and other freshwater or marine species (*e.g.*, Boucek and Rehage (2013), Possamai et al. (2018)). Understanding how snooks use available resources under different scenarios (environmental settings) is of great importance to the evaluation of the ecological role of estuaries and to the elaboration of management policies based on an ecosystem approach rather than based on species-specific strategies for snooks. The results presented in this work exemplify plasticity in snook habitat use and resource partitioning across estuaries more accurately and can serve as a source of reference for future studies focused on the effects of climate change on estuarine fish ecology. While this study focused on juvenile fish, further studies on ontogenetic changes in habitat use by *Centropomus parallelus* and *C. undecimalis* might help elucidate patterns of resource partitioning occurring at different life stages among the two species.

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Figure Captions

Fig 1. Estuarine systems of Santa Cruz Channel (Catuama (a) and Santa Cruz (b)), Suape (c) and Sirinhaém (d) located in Pernambuco state, northeastern Brazil. Mangrove areas are shown in darker grey and sample locations on each site are represented by black dots.

Fig 2. Length frequency distributions of *Centropomus undecimalis* (a) and *C. parallelus* (b) sampled in four tropical estuaries, northeastern Brazil. Solid and dashed lines represent the size used for linear models and mean length of each species, respectively.

Fig 3. Relationship between nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope values and fish size (standard length) of *Centropomus undecimalis* (black points) and *C. parallelus* (grey points) sampled in four tropical estuaries, northeastern Brazil. Solid line shows significant linear regression with the shaded area representing the standard error.

Fig 4. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios (mean ± standard deviation in per mil) of snooks (*Centropomus undecimalis* and *C. parallelus;* FISH), a primary consumer (*Crassostrea rhizophorae*; INVTB) and sources of primary production (SOURCES) sampled in four tropical estuaries, northeastern Brazil, during dry and rainy seasons. Samples of snook species are presented with predicted $\delta^{15}N$ values. Species: 1. *C. undecimalis*; 2. *C. parallelus*; 3. *C. rhizophorae*; 4. POM, particulate organic matter; 5. SOM, sediment organic matter; 6. *Rhizophorae mangle*; 7. *Ulva* sp.; 8. *Sargassum* sp..

Fig 5. Scaled isotopic niches of *Centropomus undecimalis* and *C. parallelus* sampled in four tropical estuaries, northeastern Brazil, during dry and rainy seasons. Lines represent the corrected standard ellipses area (SEA_C) for each species, with scaled predicted $\delta^{15}N$ values (see subsection 2.3).

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Tables

Characteristics	Estuary			
	Estuarine Complex of Santa Cruz Channel		Suape	Sirinhaém
	Catuama	Santa Cruz		
Type	Ria	Ria	Coastal lagoon	Coastal plain
Estuary (km²) †	49.8	25.9	29.7	18.7
Vegetated area (km²) †	35.2	14.9	23.1	17.0
Water surface area (km²) †	14.6	10.9	6.6	1.7
Mean depth (m)	7.5	3.0	3.1	2.6
Max. depth (m)	20	7	5	5
Mouth width (km) †	1.3	0.5	0.3	0.4
Temperature (°C, mean± SD) ‡	26.62 ± 0.79	28.58 ± 1.18	27.13 ± 1.09	27.24 ± 2.47
Salinity (mean± SD) ‡	28.58 ± 1.18	31.16 ± 2.94	17.77 ± 2.43	9.57 ± 3.69
Activity	Aquaculture, industrial and domestic waste		Industrial harbour, industrial and agriculture waste	Industrial and domestic waste
Reference	Medeiros and Kjerfve, 1993; Medeiros et al., 2001; Guimarães et al., 2010; Silva et al., 2011		CPRH, 2001; Borges, 2011; Silva et al. 2011	CPRH, 2001; Silva, 2009; Silva et al., 2011

† Data obtained with the software ArcGis 10.1 based on satellite images from LANDSAT 7. ‡ Personal data collected during surveys in 2015. Type, geomorphological classification on the type of estuary according to Pritchard's classification. Estuary, the respective estuarine area; the estuary's area was consider as the sum of mangrove and water surface areas. Max. depth, maximum depth during the high tide, usually near the estuary's mouth. Temperature, sea surface temperature. Activity, existent anthropogenic activity with potential impact on the estuary. Reference, references used for the morphologic characteristics.

Table 1 Summary of morphological characteristics and anthropogenic activities of four estuaries along the coast of Pernambuco, Brazil.

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Estuary	Species	Season									
		Dry					Rainy				
		n	SL (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Pred. $\delta^{15}N$ (‰)	n	SL (mm)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Pred. $\delta^{15}N$ (‰)
Catuama (CAT)	*C. undecimalis*	6	202±36 [158 – 244]	-17.10±2.51 [-21.62 – -14.74]	10.30±0.96 [8.80 – 11.67]	10.27±0.81 [9.10 – 11.37]	9	199±27 [149 – 231]	-20.09±2.30 [-23.51 – -14.92]	10.07±0.51 [9.44 – 10.95]	10.08±0.48 [9.32 – 10.72]
	C. parallelus	8	91±35 [70 – 178]	-20.06±0.92 [-21.03 – -18.08]	9.55±0.56 [8.88 – 10.29]	10.47±0.73 [9.15 – 11.25]	8	140±29 [90 – 176]	-19.79±1.61 [-21.78 – -16.47]	9.91±0.92 [8.98 – 11.47]	10.40±0.86 [9.40 – 11.84]
Santa Cruz (STC)	*C. undecimalis*	10	227±21 [204 – 257]	-19.03±2.00 [-22.81 – -16.74]	10.89±0.95 [9.54 – 12.36]	10.67±0.92 [9.48 – 12.21]	8	310±102 [69 – 392]	-18.95±3.32 [-24.31 – -14.94]	10.94±1.88 [6.94 – 12.77]	10.02±1.36 [8.04 – 11.65]
	C. parallelus	5	239±26 [205 – 273]	-20.83±3.97 [-24.90 – -14.22]	12.23±1.25 [10.60 – 13.64]	11.90±1.09 [10.41 – 13.22]	8	165±23 [132 – 192]	-19.39±1.73 [-22.40 – -17.72]	11.05±1.12 [9.48 – 13.15]	11.35±1.08 [9.75 – 13.31]
Suape (SUA)	*C. undecimalis*	7	250±39 [213 -323]	-20.20±0.72 [-21.31 – -19.39]	11.86±0.43 [11.32 – 12.50]	11.43±0.15 [11.21 – 11.65]	3	169±69 [94 – 230]	-19.28±0.62 [-19.80 – -18.60]	10.88±1.02 [9.74 – 11.72]	11.13±0.44 [10.63 – 11.47]
	C. parallelus	14	175±61 [57 – 250]	-20.06±1.54 [-24.85 – -18.71]	10.27±0.79 [8.47 – 11.50]	10.48±0.76 [8.62 – 11.56]	11	132±23 [87 – 167]	-19.88±1.72 [-22.70 – -16.50]	9.52±0.38 [8.65 – 9.98]	10.08±0.38 [9.19 – 10.40]
Sirinhaém (SIR)	*C. undecimalis*	9	208±16 [184 – 243]	-21.58±1.16 [-23;48 – -20.18]	10.36±0.23 [9.97 – 10.71]	10.29±0.17 [9.91 – 10.49]	10	196±68 [150 – 386]	-22.09±0.88 [-23.34 – -20.79]	9.62±0.52 [8.77 – 10.66]	9.65±0.42 [8.93 – 10.27]
	C. parallelus	10	199±49 [119 – 289]	-20.25±2.31 [-25.38 – -16.62]	11.14±0.61 [10.24 – 12.10]	11.14±0.61 [10.19 – 12.16]	12	212±43 [151 – 290]	-22.37±0.90 [-23.43 – -20.13]	10.17±0.35 [9.64 – 10.77]	10.06±0.30 [9.47 – 10.55]

Table 2 Number of samples (n), mean fish standard length (SL; ± S.D.), isotopic means (± S.D.) of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$) and predicted $\delta^{15}N$ at 200 mm SL (see subsection 2.3) (± S.D.) of *Centropomus undecimalis* and *C. parallelus*, during dry and rainy seasons, sampled in four tropical estuaries, northeastern Brazil. Minimum and maximum values of each variable are shown in brackets

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Species	Season					
	Dry		Rainy			
	TP_{SIA1}	TP_{SIA2}	TP_{SIA1}	TP_{SIA2}	n	TP_{SCA}
Catuama (CAT)						
C. undecimalis	3.15 [2.32 – 5.18]	3.83 [3.07 – 5.19]	2.74 [2.45 – 3.37]	2.97 [2.35 – 4.01]		
C. parallelus	3.23 [2.41 – 5.47]	3.93 [3.21 – 5.25]	2.91 [2.46 – 3.94]	3.12 [2.42 – 4.25]		
Santa Cruz (STC)						
C. undecimalis	3.26 [2.75 – 4.10]	3.14 [2.34 – 4.36]	2.73 [2.18 – 3.68]	3.31 [2.49 – 4.61]	8	3.45
C. parallelus	3.79 [2.92 – 5.09]	3.66 [2.61 – 5.28]	3.15 [2.70 – 4.32]	3.88 [3.08 – 5.31]	10	3.47
Suape (SUA)						
C. undecimalis	3.85 [3.08 – 5.06]	3.43 [2.39 – 4.86]	3.35 [2.42 – 5.60]	3.87 [2.61 – 6.03]		
C. parallelus	3.46 [2.80 – 4.61]	2.96 [1.99 – 4.38]	2.89 [2.41 – 3.83]	3.45 [2.69 – 4.70]		
Sirinhaém (SIR)						
C. undecimalis	3.43 [2.57 – 6.57]	3.56 [2.71 – 5.03]	2.71 [2.31 – 3.59]	3.41 [2.73 – 4.59]	45	3.55
C. parallelus	3.80 [2.79 – 5.71]	3.97 [3.01 – 5.49]	2.89 [2.44 – 3.90]	3.60 [2.90 – 4.81]	30	3.54

Table 3: Trophic position estimates with stable isotopes (TP_{SIA}) and stomach content analysis (TP_{SCA}) of from two sympatric estuarine fishes (*Centropomus undecimalis* and *C. parallelus*) at four tropical estuaries, northeastern Brazil. TP_{SIA} is presented as the mode of Bayesian model results with 95% credibility intervals shown in brackets. TP_{SIA} was estimated using two distinct baselines: a long-lived primary consumer (TP_{SIA1}); and all available basal sources at each site (TP_{SIA2}).

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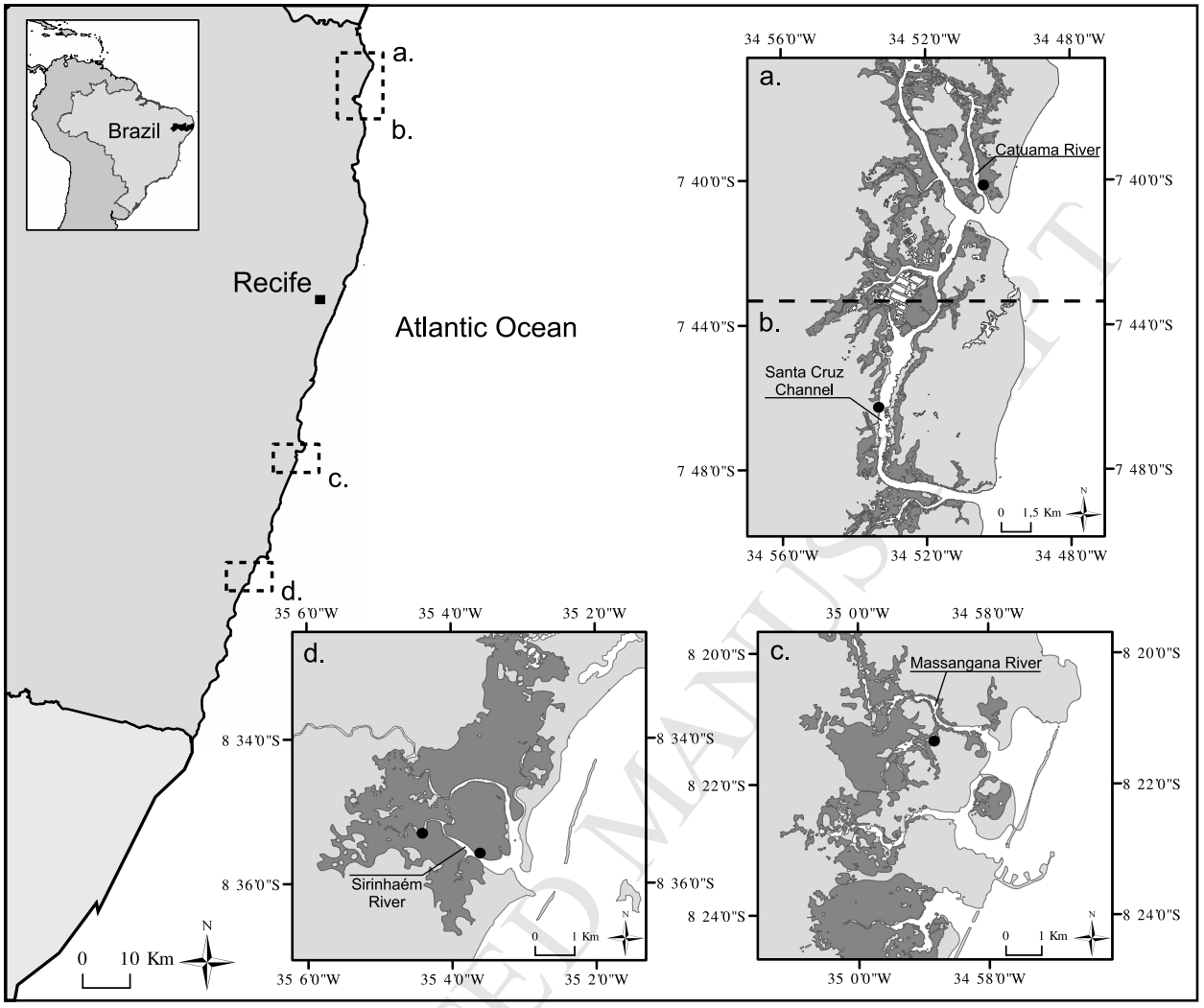

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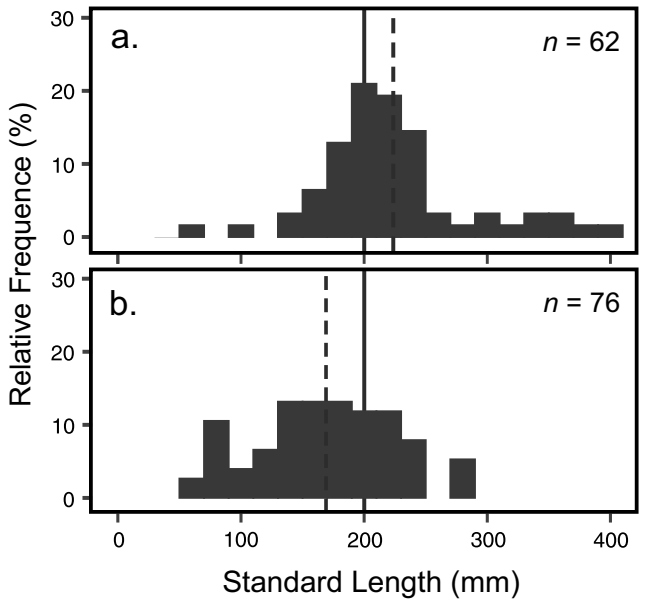

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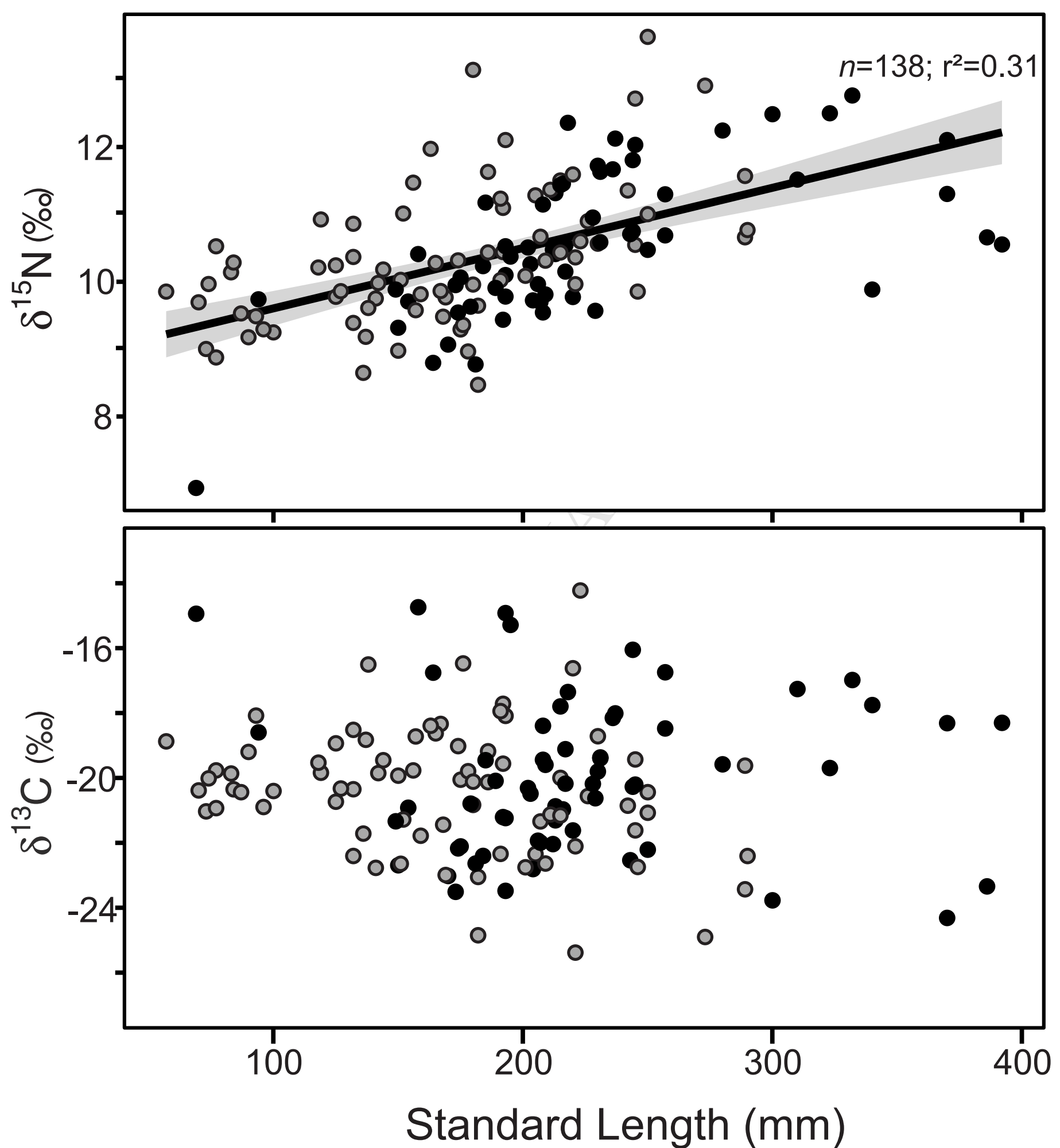
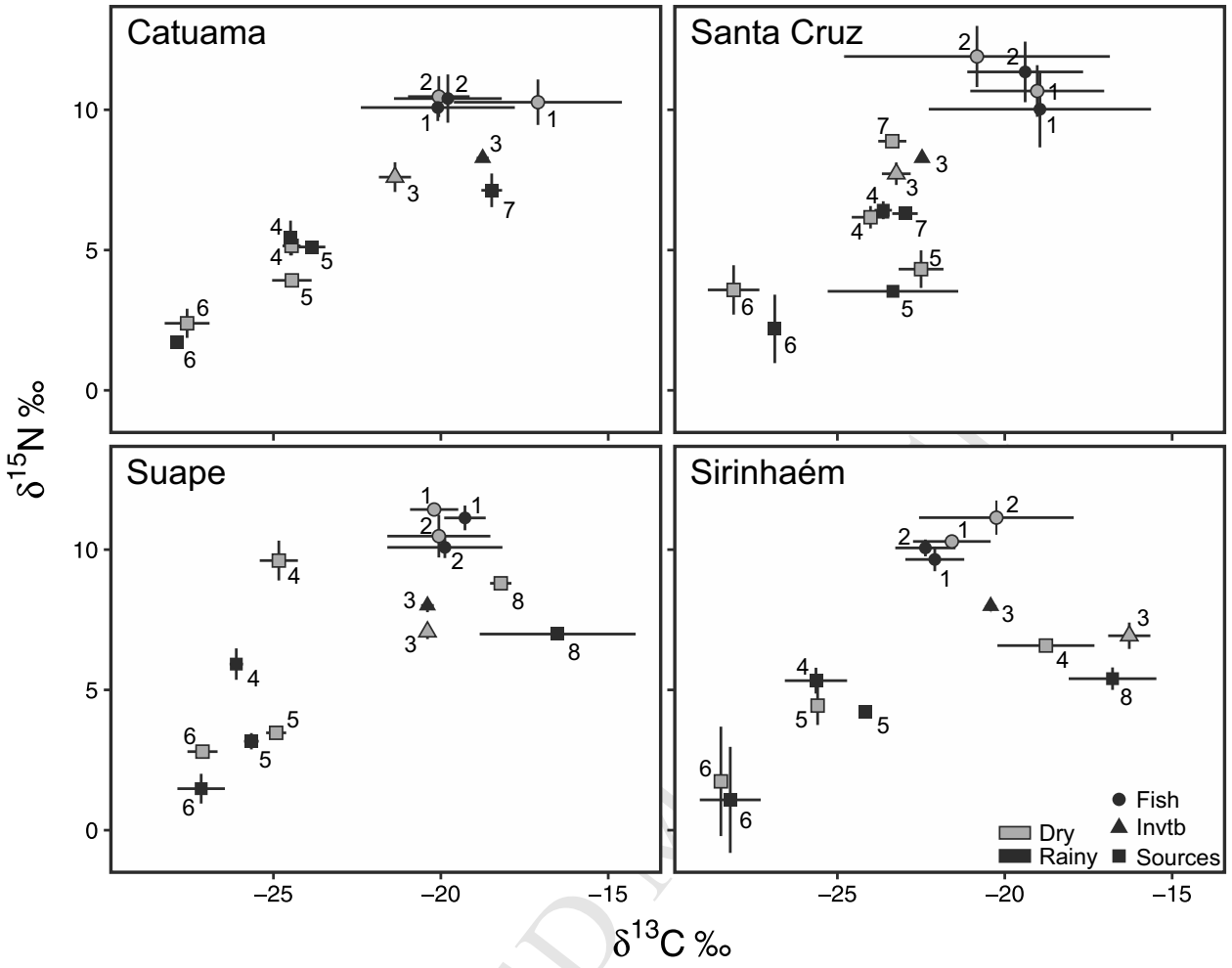

n=138; r²=0.31
δ15N (‰)
12
10
8
δ13C (‰)
-16
-20
-24
100
200
300
400
Standard Length (mm)


Catuama
Santa Cruz
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Dry
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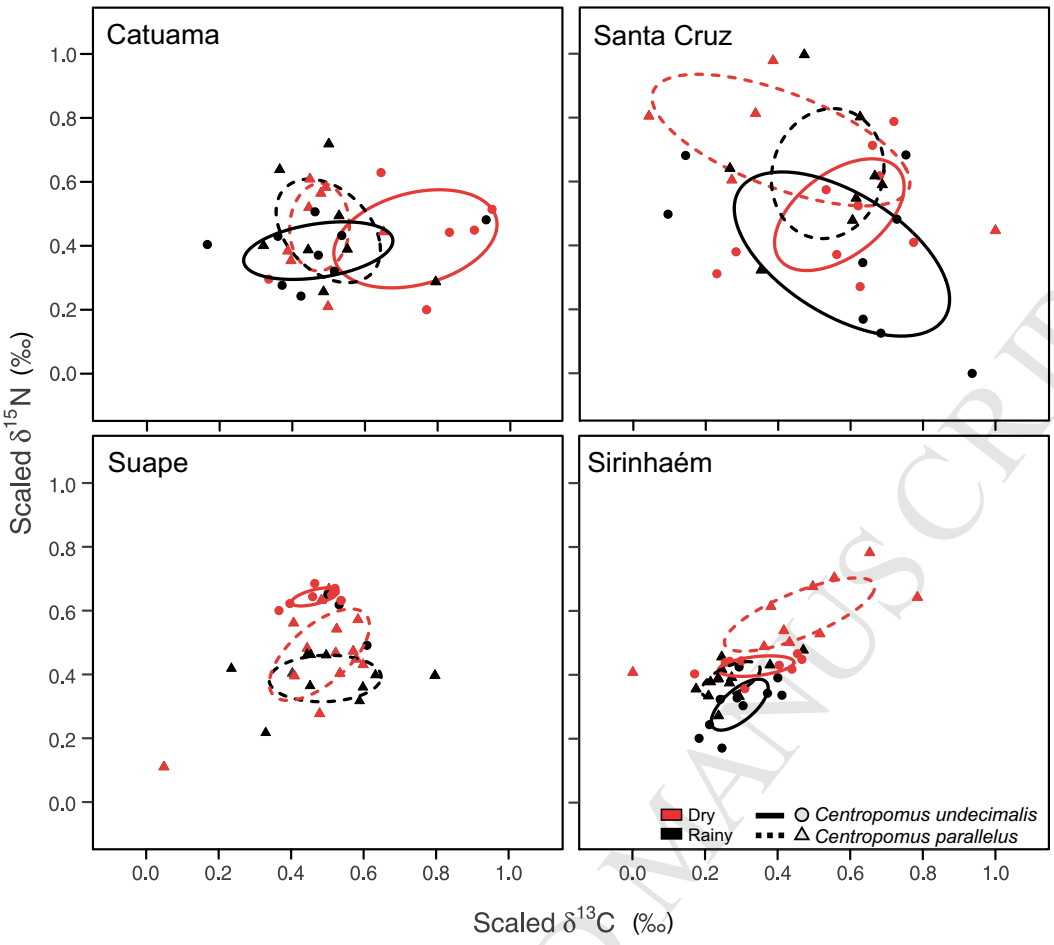

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Highlights

- $\delta^{13}C$ and $\delta^{15}N$ of two Centropomidae were investigated in four estuaries in Brazil
- Juveniles of *Centropomus undecimalis* and *C. parallelus* have close isotopic niches
- Trophic overlaps were more pronounced in large estuaries
- Resource partitioning process might reflects the resource availability in estuaries

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