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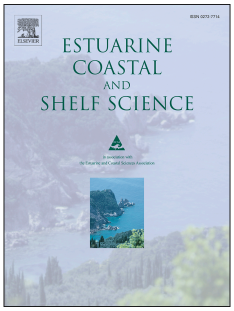

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Trophic ecology of the juveniles of two jack species (*Caranx latus* and *C. hippos*) in contrasted tropical estuaries.

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Abstract

Jacks are highly prized tropical marine fish. Most of them complete their whole life cycle at sea but some use estuaries at the juvenile stage before moving back to coastal waters and joining the adult exploited stocks. Little is known about jacks' trophic ecology in estuaries, although their juveniles' ability to successfully exploit available resources in these productive environments may strongly affect stock recruitment success in the species concerned. In this study, stomach content and stable isotope analyses were combined to investigate diet and food niche overlap of juveniles from two sympatric species of jacks (*Caranx latus* and *C. hippos*) in three contrasted estuaries (Suape, Sirinhaém and Santa Cruz) spread along the northeastern Brazilian coast. Overall, although the juveniles of *C. latus* exhibited a more piscivorous diet than those of *C. hippos*, the two species had very similar isotopic niches, with mean δ^{13}C and δ^{15}N values of -19.35 ± 2.10‰ and 11.03 ± 1.11‰ and of -19.10 ± 1.82‰ and 10.21 ± 1.21‰, for *C. hippos* and *C. latus* respectively. In all the estuaries sampled, both species mostly ate fish (N_i = 20.1 - 46.2%, W_i = 60.1 - 75.1%, essentially Gobiidae and Clupeidae) and crustaceans (N_i = 26.0 - 65.9%, W_i = 23.3 - 38.2%, mainly Penaeidae shrimps). As a result, the overlap between their global estuarine isotopic niches was >68%. However, diet composition for the two species varied among estuaries, indicating that their juveniles partly adapt their food preferences to local prey availability. Notably, prey preferences differed significantly between the two species only in the Santa Cruz estuary, where δ^{15}N values were the highest for both species. Conversely, interspecific differences in δ^{13}C ratios were greater in the Suape and the Sirinhaém estuaries, likely reflecting a wider diversity in the carbon sources sustaining local food webs. Thus, combined differences in juvenile diet and food web structure at each location resulted in much-reduced local isotopic niche overlaps between the two species (from 27% in Suape to 57% in Santa Cruz). These results have important implications for resource and ecosystem management in northeastern Brazil and call for systematic cross-site comparisons when evaluating fish ecology and resource partitioning within estuarine systems.

Keywords: Marine fish, Trophic relationships, Stomach content, Stable isotope analysis, Carbon, Nitrogen.

1. Introduction

Estuaries are highly exploited ecosystems a host a high number of fish species (Blaber 1997; Vasconcelos et al., 2015), many of which colonize them during the juvenile stage seeking for protection and favorable growth conditions (Nagelkerken et al., 2000; Beck et al., 2001; Dahlgren et al., 2006). Although knowledge on the use of estuaries by tropical fishes has significantly grown in recent years (Blaber, 2013), the information available concerns only a few estuarine systems so further research is needed to assess the actual value of tropical estuaries as fish juvenile habitats (Blaber and Barletta, 2016). Indeed, a variety of biological and physical factors might affect the physiology of fish and their resource use in estuaries (Blaber, 2007). For instance, estuaries' morphology and spatiotemporal dynamics modulate not only fish diversity (França et al., 2012; Vasconcelos et al., 2015), but also food web structure and composition (Harrison and Whitfield, 2006, 2012; Silva-Júnior et al., 2017), resource availability (Doi et al., 2009; Hoeinghaus et al., 2011; Boucek and Rehage, 2013) and seascape connectivity (Sheaves, 2009; Ogden et al., 2014). The degree to which each species benefits from available food resources in these complex environments may also influence the survival and fitness of fish juveniles (Le Pape and Bonhommeau, 2015; Yeung and Yang, 2017; Hiraoka et al., 2019). Therefore, investigating species' resource use in contrasted estuarine juvenile habitats can not only improve the knowledge and understanding of their ecology (*e.g.* Stevens et al., 2018) but also help defining local management strategies (Sheaves et al., 2015). This is particularly true in tropical regions where the socio-economic demand for coastal fish resources is growing (Barlow et al., 2018; FAO, 2018) and where environmental awareness is only just emerging (Mitra and Zaman, 2016).

Species ecological niches play a central role in defining available resource use and interspecific interactions at the community level (Van Valen, 1965; Ross, 1986). Among the many facets of the ecological niche, the trophic niche is perhaps the easiest to evaluate (Ross, 1986). It can be studied using empirical methods like stomach content analysis (SCA), which provides a snapshot of the items ingested by the individuals (Hyslop, 1980; Pinnegar and Polunin, 2000), or through the use of natural tags such as stable isotope analysis (SIA). This later approach, usually combines nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopic ratios (Fry, 2006) to provide an integrated image of the food resources assimilated by the individuals over periods of time ranging from a few weeks to a few months (Herzka, 2005). The method relies on the assumption that the isotope ratios of an organism reflect, in a predictive way, those of its food sources (Fry, 2006). In general, the $\delta^{15}N$ is used as a proxy for organisms' trophic position in the food chain (Post, 2002; Martínez Del Rio et al., 2009), while the $\delta^{13}C$ allows identifying the main organic matter source(s) supporting their growth (Fry, 2006; Layman, 2007). Combining SIA and SCA enables better resolution of dietary patterns and accurate identification of the food sources sustaining animal growth (Silveira et al., 2020). In this study, we applied these complementary methods to describe variations in diet and compare strategies of estuary resource use in the juveniles of two sympatric species of jacks along the northeastern coast of Brazil.

Jacks (*Caranx* spp.) are marine fish found both in inshore and offshore coastal environments (Figueiredo and Menezes, 1980; Smith-Vaniz, 2002). Although these large predators are neritic and reef associated when adult, some of them may use a mosaic of habitats along their life cycle and colonize inshore estuaries as juveniles (Smith-Vaniz, 2002). This is the case for both the horse-eye jack (*Caranx latus*, Agassiz 1831) and the crevalle jack (*Caranx hippos*, Linnaeus 1766), two highly exploited species with a widespread distribution in the Atlantic Ocean (Figueiredo and Menezes, 1980). In Brazil, *C. latus* and *C. hippos* represent almost 75% of the national landings for jacks, with more than 6.000 tons fished annually between 2009 and 2011 (MPA, 2011). Yet, little is known about their life cycle and their ecology at the juvenile stage. The yearlings of the two species are found in a broad range of inshore and coastal habitats along the Brazilian coast (Figueiredo and Menezes, 1980; Paiva and Araújo, 2010), and information regarding their trophic ecology in estuaries is particularly scarce (*e.g.* Vasconcelos Filho et al., 2010; Medeiros et al., 2017).

Differences in resource use among juvenile habitats may affect fish early growth and body condition (*e.g*. Isnard et al. 2015) and modulate recruitment success in exploited species (Gillanders et al., 2015). To avoid competition for food and optimize energy acquisition, sympatric species usually tend to partition resources at multiple scales (Schoener, 1974; Losos, 2000). However, *C. latus* and *C. hippos* not only have similar body shapes and lengths, but they are also both reported to feed mainly on fish and crustaceans (Hofling et al., 1998; Smith-Vaniz, 2002; Vasconcelos Filho et al., 2010). Therefore, they might have similar uses of estuarine resources and their co-occurrence in certain estuaries might result in an interspecific competition for food, with potentially high consequences in terms of local fisheries production. To investigate this, we assessed variations in the diets and isotopic niches of their juveniles among three neighboring Brazilian estuaries with contrasted morphological and biological features, and where the relative densities for the juveniles of the two species differ markedly (Paiva and Araújo, 2010;

Silva-Júnior et al., 2017), which allowed exploring whether their feeding strategies change under different degrees of potential competition.

2. Material and Methods

2.1. Study area

The three tropical estuarine systems selected for this work (Santa Cruz, Suape and Sirinhaém, Fig. 1) are located in the western South Atlantic Ocean, along the coast of the Pernambuco state, on the northeastern coast of Brazil. In this area, the climate is sub-tropical, with annual temperatures ranging from 18 to 32ºC, around an annual mean of 24ºC (CPRH, 2003; 2003a). Rainfalls occur all year round along the shore but they are more intense in the late autumn and winter (May to August). The driest period of the year is late spring and early summer (from October to December) due to the northward displacement of the Intertropical Convergence Zone (ICTZ) in the Atlantic and the occurrence of stronger southeast trade winds (CPRH, 2003; 2003a; Hounsou-gbo, et al. 2015). The local climate is influenced both by seasonal (displacement of the ICTZ) and by inter-annual (*e.g.* El Niño Southern Oscillation – ENSO) meteorological phenomena, which results in a highly variable weather and precipitation patterns among years (Hastenrath, 2012).

Although relatively close to each other, the Santa Cruz, Suape and Sirinhaém estuaries exhibit distinct morphological and biological features and are subject to different freshwater inputs and degrees of anthropogenic pressures (Table 1). Located in the north of the Pernambuco state, the estuarine complex of Santa Cruz is the largest estuary of the three, and one of the most important fishery ground of the state (Medeiros et al., 2001). It consists in a shallow U-shape channel that receives continental inputs from six rivers (draining three hydrological basins) and is connected to the sea by two large entrances (Silva et al., 2011). Because the seawater inflow is high, the estuary is under a strong marine influence (Flores Montes et al., 1998; Figueiredo et al., 2006). Furthermore, the reduced current velocity in the inner part of the main channel results in a predominance of muddy substrates along the estuary (CPRH, 2003), where hypersaline conditions prevail during the driest months of the year (Medeiros and Kjerfve, 1993). The local fauna comprises a large number of marine and estuarine invertebrates and fish that use this estuary at different stages of their life (Vasconcelos-Filho and Oliveira, 1999). The fish assemblage is diverse, with numerous species with distinct morphologies, as illustrated by the presence of bottom-associated species like gobies (Silva-Júnior et al., 2017; Ferreira et al., 2019).

The estuaries of Suape and Sirinhaém, both situated in the south of the Pernambuco state, are smaller (Table 1). Because the annual rainfall in the state increases southwards (CPRH, 2003a), they receive higher freshwater inputs, especially Sirinhaém (Table 1). The Suape estuary is formed by two rivers, which flow into a shallow brackish lagoon with limited connection to the sea. It can be classified as euryhaline and exhibits the lowest primary productivity of the three estuaries studied (Silva et al., 2019; Table 1). The estuary of Sirinhaém is the smallest estuary studied, but that with the highest percentage of mangrove cover (Table 1). Located within two marine protected areas (CPRH, 2003a), it gathers a variety of interconnected lagoons and channels that spread on the shallow flood plain around the main bed of the Sirinhaém river, which constitutes its sole connection to the sea (CPRH, 2003a). This particular configuration intensifies the effects of the watershed dynamics, with salinities ranging from nearly 0 at low tide to up to 30 at high tide (Silva et al., 2009). The fish assemblages of the Sirinhaém and Suape estuaries are similar, with a common dominance of pelagic species (Bezerra Junior et al., 2011). Moreover, both estuaries exhibit much lower densities of *C. hippos* than those observed in Santa-Cruz (Silva-Júnior et al., 2017).

2.2. Fish sampling and diet composition

The *Caranx latus* and *C. hippos* juveniles used for this work were captured over five successive years (2015-2019), using both beach seines (20 x 1.9 m, mesh 20 mm), trawled along the river banks, and block nets (350 x 2.9 m, mesh 70 mm) set close to mangrove creeks. Although sampling design was not even among years and estuaries, sampling surveys in each estuary were carried out for all months and always included the same locations (Fig. 1). To account for potential changes in feeding habitat preferences according to the season or increasing fish size, juvenile jacks were systematically sampled in all the main types of habitat they occupy in each estuary. These habitat types were determined according to local fishermen's knowledge on *Caranx* sp. occurrence in the estuaries and confirmed by prior exploratory surveys. They comprise main foraging grounds for the two species, within and outside the shore-fringed mangroves that predominate in the three estuaries. In all three estuaries, both the mudbanks below fringing mangrove and the adjacent river banks, of maximum 1.5 m depth, were sampled at low tide. However, in the larger and deeper Santa Cruz estuary, juvenile jacks were also systematically collected within the central channel of the estuary, where water depth remains above 5 m at low tide. On the river banks and in the Santa Cruz central channel, sediments are composed of a mix of thin sand and silt, and mangrove litter and macroalgae occasionally found on the bottom. Depending on the size and geomorphology of the estuary, fish juveniles were collected at 2 to 5 sites per habitat type for each sampling date. This allowed covering most of the spatiotemporal variability in juvenile distribution, and associated diet variation, between and within estuaries for the two species.

Upon collection, all juveniles were identified following specific literature (Figueiredo and Menezes, 1980; Smith-Vaniz, 2002)**,** measured (standard length – SL in mm) and stored frozen until further analysis. Their stomach contents were assessed under a stereomicroscope until 70 non-empty stomachs per species and estuary could be gathered. As densities for the two jack species are rather low in estuaries during the wetter months of the year (Vilar et al., 2011; Silva-Júnior et al., 2017; da Silva et al., 2018), fish from different years had to be pooled to reach a minimum number of 10 non-empty stomachs for both the dry (September to March) and the rainy (April to August) seasons in the area (CPRH, 2003; 2003a), and a maximum of 30 individuals per year for each estuary. Prey items in all stomachs were identified to the lowest taxonomic level possible, depending on their degree of digestion. All identified prey items were counted and weighed (g) and well-preserved ones, *i.e.* those only slightly digested, were measured (total length, in mm).

For both species, global diet composition was characterized using the frequency of occurrence (F_i) and the relative percentage in number (N_i) and in weight (W_i) of each prey item. F_i corresponds to the number of individual stomachs containing the prey item i divided by the total number of stomachs containing food. N_i and W_i represent the relative number or weight of the prey item i divided by the total number or total weight of prey in the stomachs, respectively. In order to account for the uncertainty associated to these indexes and provide a confidence interval (95%) for each prey item, a bootstrap procedure based on 5000 re-sampling trials was used (Tirasin and Jorgensen, 1999). The importance of each prey item in the diet was estimated using the alimentary coefficient (Q) proposed by Hureau (1970):

$$Q = N_i \times W_i.$$

According to Hureau (1970), prey items should be considered preferential when $Q \geq 200$, secondary when $20 \leq Q < 200$, and occasional ($Q < 20$). All dietary indexes were calculated both using major taxonomic groups (*e.g.* Teleostei) and applying the lowest possible identification levels, down to family.

2.3. Stable isotope analyses (SIA)

For each species, 10 to 30 juveniles from each estuary were selected for SIA. As the minimum size for both species in our samples was 35 mm SL, these fish were chosen to measure at least 60 mm in size (SL) to ensure that the isotopic compositions from their local prey were incorporated within the tissue at the time of capture (Herzka 2005). Fish were collected in 2015, 2018 and 2019 during both the dry and the rainy seasons (APAC, 2019), so their isotopic ratios should accurately reflect the temporal (inter and intra-annual) variabilities in fish diet and food web composition at each estuary. Basal estuarine organic matter sources, *i.e.* the main benthic algae (*Sargassum* spp., *Ulva* spp., *Gracilaria cervicornis*), the microphytobenthos, the mangrove trees (rotten leaves from *Rhizophorae mangle*), and the organic matter present in the surface sediment (SOM) and in the water column (POM), were collected in each estuary in 2015, both during the dry (January to March) and the rainy (July to September) seasons (APAC, 2019). Mangrove tree leaves and algae were collected manually at low tide. POM was obtained by filtering water (0.5 – 1 L) on precombusted fiberglass filters (0.75 µm), whereas SOM was sampled from the 2 mm surface layer of the sediment. Benthic microphytobenthos was collected from the sediment surface at low tide and extracted in the laboratory following Riera and Richard (1996). Other potential organic matter sources for the three estuaries studied, such as marine POM and SOM from the adjacent coastal zone were also collected, at two locations: one near the entrance of the Santa Cruz estuary and one further south, near the mouths of the Sirinhaém and Suape estuaries.

For fish specimens, white muscle was extracted and rinsed with distilled water while, for organic matter sources, samples were analyzed whole. Samples were dried in an oven at 60°C for 48 hours and ground into a fine powder with a mortar and pestle. For all POM and SOM samples, a subsample was acidified to remove the inorganic carbon prior $\delta^{13}C$ analysis, while the remaining material was used directly for $\delta^{15}N$ analyses (Pinnegar and Polunin, 1999). Carbon and nitrogen isotope ratios were analyzed 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). Carbon and nitrogen isotopic ratios are reported as $\delta^{13}C$ and $\delta^{15}N$ values (in ‰), respectively, derived from the formula:

$$\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 10^3$$

where δX corresponds to $\delta^{13}C$ or $\delta^{15}N$ and R to the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and a known standard, for carbon or nitrogen, respectively. The standards used for $\delta^{13}C$ and $\delta^{15}N$ were the Pee Dee Belemnite (PDB) limestone and atmospheric nitrogen, respectively. The analytical precisions of the analyses, monitored through the repeated analysis (every six samples) of an internal standard (Thermo – Acétanilide), was of 0.10‰ and 0.07‰ for carbon and nitrogen isotopes, respectively.

2.3. Data analysis

All statistical analyses were made with the R software (R Core Team, 2019), using the packages *vegan* (Oksanen *et al.*, 2017), *boot* (Canty and Ripley, 2020) and *SIBER* ("Stable Isotope Bayesian Ellipses in R" (Jackson and Parnell, 2016)). Only the prey items observed more than once within the stomachs analyzed were kept for SCA data analyses.

Because body size modulates the type and size of the prey consumed by an organism (Shelton et al., 1977), potential differences in the size (SL in mm) of the fish used for SCA were investigated, among estuaries and between species. Kruskal-Wallis tests were used for this, as the assumptions of data normality and homoscedasticity were not met. Then, the relationship between fish size and prey length was assessed for each species using covariance analyses (ANCOVA). Differences in prey length according to the species and the sampling location were also tested, using Kruskal-Wallis tests as data did not meet the assumptions of normality and homoscedasticity. Lastly, differences in diet composition according to fish size were evaluated for both *C. latus* and *C. hippos*, using two non-parametric permutational multivariate analyses of variance (PERMANOVA), one per species. The PERMANOVA procedure performs a sequential test of terms based on distance matrices and allows for hypotheses testing between predictor variables (Anderson, 2001).

PERMANOVA tests were also applied to investigate differences in diet composition between species (*C. latus*/ *C. hippos*), among estuaries (Santa Cruz/ Suape/ Sirinhaém) and between the two species in each estuary. *Post-hoc* comparisons were applied only for variables with a significant effect on the diet ($p < 0.05$). The distance matrices were based on Bray-Curtis dissimilarity computed from $log(x+1)$ transformed data of prey relative weight for each individual fish. In addition, two dietary matrixes were used separately to assess the effect of prey identification on the analyses: one including all prey items and the other with only the prey items identified at least to the order level.

Potential differences in the size (SL in mm) of the juveniles used for SIA and in their isotopic ratios (both for carbon and for nitrogen, separately) were tested between locations and fish species using separate ANOVA models. *Post-hoc* Tukey's tests were applied on variables with significant effects in the isotopic composition of jacks ($p < 0.05$). The trophic positions of the juveniles of the two jack species were compared by evaluating the areas occupied by their isotopic niches, computed using the corrected standard ellipses area (SEA_C) method, which measures the space occupied by a species in a bi-dimensional plane, here $\delta^{13}C$ *vs.* $\delta^{15}N$ (Jackson et al., 2011). This approach is less sensitive to variations in sample size than other conventional metrics (Jackson et al., 2011; Syväranta et al., 2013), and provides insightful information on predators' resource use by incorporating both the variance in the isotopic ratios of local basal food sources and the difference in the energy pathways that their prey rely on (Bearhop et al., 2004). Indeed, although a considerable part of the variation in predator isotopic niches can be attributed to diet, it may also reflect differences in prey isotope ratios and in the organic matter sources sustaining food webs (Newsome et al., 2007; Flaherty and Ben-David, 2010). Therefore, the percentage of overlap between the isotopic niches (SEA_C) of the two species was used to measure the degree to which they may rely on similar food resources. In order to account for the uncertainty associated to SEA_C overlaps, a Bayesian approach was applied to assess the mean and 95% credible intervals ($CI_{95\%}$) of isotopic niche overlaps between the two species (Jackson et al., 2011).

3. Results

Although the total sample of juvenile jacks gathered over the five years of survey was more than satisfactory (n = 439 of SL = 35 - 157 mm), the numbers and the sizes of the juveniles varied between species and estuaries. For example, while total abundances were comparable at all locations for *C. latus*, *C. hippos* juveniles were 2- to 3-fold less common in Sirinhaém and Suape (Fig. 2). As a result, the total number of juveniles collected was higher for *C. latus* (n = 266) than for *C. hippos* (n= 173). In turn, although the juveniles of *C. latus* (SL = 105 ± 25 mm) were consistently bigger ($p < 0.001$) than those of *C. hippos* (SL = 88 ± 26 mm), patterns of size variation between estuaries were similar for the two species, with consistently bigger juveniles ($p < 0.001$) in Suape and smaller ones ($p < 0.001$) in Sirinhaém (Fig. 2). These differences were considered during fish sub-sampling for both stomach content analysis and SIA, in order to reduce bias in our conclusions and provide a realistic overview of the global trophic ecology of the two species.

Among the 394 fish selected for stomach content analysis, few had empty stomachs (33% for *C. latus* and 6% for *C. hippos*). Relative numbers and size distributions in the 338 remaining ones (207 *C. latus* and 131 *C. hippos*) were similar to those observed in the total catches, with slightly higher mean SL values for *C. latus* than for *C. hippos* in every estuary, and larger juvenile sizes in Suape for both species (Table 2). Muscle samples from 112 juvenile fish (60 *C. latus* and 52 *C. hippos*) were analyzed in SIA (Table 2). To allow for muscle signature to reflect the diet in the estuaries, the minimum size of the fish selected for the SIA was 65 mm (SL). Altogether, the distribution of SIA juvenile sizes was similar for the two species ($p = 0.905$), however it varied between estuaries ($p < 0.001$), reflecting the differences in sizes observed in the field. As for SCA, this sub-sample contained a larger number of individuals from Santa Cruz in order to reflect the higher abundance of juvenile jacks at this estuary.

3.1. Diet composition

Overall, diet composition was not significantly different between the two jack species ($p = 0.089$) which both mainly ate fish and crustaceans (Q > 1205, Table 3). All other prey items were found to be occasional ($Q < 20$), irrespective of the species (Table 3). However, when considering only the prey items identified to at least the order level, the two species did show significant differences in diet composition ($p = 0.010$). Although fish remains in the stomachs were often too digested to be identified, fish prey belonged to at least nine different families for *C. latus*; six for *C. hippos* (Table 3). Fish (Teleostei) were the main prey of the juveniles of *C. latus* ($Q = 3252$), whereas *C. hippos* fed on fish ($Q = 1205$) and crustaceans ($Q = 2537$) in similar proportions (Table 3). Fish dominated the diet of both species in terms of occurrence and weight, but crustaceans prevailed in number in the diet of *C. hippos* (Table 3). For both species, most of the fish prey identified were Gobiidae ($F_{\mathrm{i}} = 19.0$ to 23.6; $N_{\mathrm{i}} = 4.3$ to 7.5; $W_{\mathrm{i}} = 33.2$ to 39.9%), but their consumption was higher in *C. latus* ($F_{\mathrm{i}} = 23.6$; $N_{\mathrm{i}} = 7.5$; $W_{\mathrm{i}} = 39.9\%$). Decapods, in particular Penaeidae shrimps, were the main crustacean prey found in the stomachs of the juveniles of the two species (Table 3). However, mysids also contributed significantly to their diet, especially for *C. hippos*, in which they were the most abundant crustacean prey ($N_{\mathrm{i}} = 36.6\%$).

Overall diet composition was found to be similar across the full size-range of the juveniles studied irrespective of the species (*C. latus*: $p = 0.089$; *C. hippos*: $p = 0.193$) and, when considering only the prey items identified to at least the order level, significant differences in diet according to fish size were found solely for *C. latus* ($p = 0.034$). Even then, only a slightly higher contribution in weight of fish prey was observed in *C. latus* juveniles larger than 60 mm (SL). The standard length of the juveniles did not have any significant effect on the sizes of their two main prey, namely fish (adjusted $r^2 = 0.01$, $p = 0.591$) and shrimps (adjusted $r^2 < 0.01$, $p = 0.376$). The size of these later were similar in all estuaries (Fish, $p =$

0.292; Shrimps, $p = 0.839$) and for both jack species (Fish, $p = 0.184$; Shrimps, $p = 0.515$) (Supplementary Fig. S1).

The diet of both species varied according to the estuary, regardless the level of prey identification applied ($p < 0.002$). Specifically, differences between estuaries were found only for Suape (Suape – Santa Cruz: $p < 0.015$; Suape – Sirinhaém: $p < 0.027$). In this estuary, *C. hippos* presented the most different diet, composed mainly of fish prey ($F_i = 60.0$; $N_i = 33.8$; $W_i = 81.4\%$). The diets of the two species were similar between Santa Cruz and Sirinhaém, either when considering all prey items ($p = 0.060$) or only those identified to at lowest taxonomic level ($p = 0.204$). Moreover, interspecific differences in diet composition were only significant in Santa Cruz, independently of the level of prey identification applied ($p < 0.025$). In this estuary, Gobiidae fish prevailed in the diet of *C. latus* and decapod shrimps in that of *C. hippos* (Supplementary Table S1). Although the two species had similar overall diets in the two remaining estuaries (Suape: $p > 0.236$; Sirinhaém: $p > 0.113$), they presented slight spatial variations in their prey preferences. In Suape, the diet of the two species only differed in terms of the type of fish consumed, with higher contributions of Clupeidae and Engraulidae for *C. hippos*, and of Gobiidae and Gerreidae for *C. latus* (Supplementary Table S2) while, in Sirinhaém, significantly higher proportions of crustaceans (Penaeidae shrimps) were found in the diet of *C. hippos* than in that of *C. latus* (Supplementary Table S3).

3.2. Stable isotopes analysis

The juveniles from the two species had very variable $\delta^{13}C$ and $\delta^{15}N$ values irrespective of their estuary of capture, ranging from -24.36 to -15.73‰ and from 8.00 to 13.66‰, respectively (Table 2; Fig. 3). Due to this variability, $\delta^{13}C$ values were not significantly different among estuaries ($p = 0.088$) nor between species, with average values of -19.10 ± 1.82‰ for *C. latus* and -19.35 ± 2.10‰ for *C. hippos*. Differences in $\delta^{13}C$ values between the two species were not significant either within each given estuary ($p = 0.147$). Conversely, significant differences in $\delta^{15}N$ were found according to both the estuary ($p < 0.001$) and the species ($p < 0.001$). Indeed, although $\delta^{15}N$ values for both species did not differ significantly between Suape and Sirinhaém ($p = 0.790$; Fig. 3), they were consistently higher in Santa Cruz ($p < 0.001$). Similarly, although the $\delta^{15}N$ values of the two species were similar within each estuary ($p = 0.804$; Fig. 4), the juveniles of *C. hippos* exhibited higher $\delta^{15}N$ values in overall (11.03 ± 1.10‰) than those of *C. latus* (10.21 ± 1.21‰) due to differences in spatial distribution among them.

The global trophic (isotopic) niches of the two species were similar in size, with areas (SEA_C) of 7.3 and 7.0 ‰² for *C. latus* and *C. hippos* respectively. They largely overlapped, with 68.4% ($CI_{95\%}$ 54.1 – 82.6%) of their total area in common. However, both the SEA_C sizes and their overlaps varied according to the estuary (Fig. 3). Juvenile *C. latus* exhibited slightly wider isotopic niches than *C. hippos* in both Santa Cruz (SEA_C = 5.6‰² for *C. latus* and 4.5‰² for *C. hippos*) and Sirinhaém (SEA_C = 7.9‰² for *C. latus* and 7.1 ‰² for *C. hippos*), with high isotopic niche overlaps at both sites (57.5%, $CI_{95\%}$ 40.1 – 73.8%, in Santa Cruz and 54.3%, $CI_{95\%}$ 32.3 – 77.4%, in Sirinhaém). Conversely, in Suape, where the two species had the most different isotopic niches, niche area was much wider in *C. hippos* (SEA_C =9.5 ‰²) than in *C. latus* (SEA_C =2.7 ‰²). At this particular site, juvenile niche overlap between the two species was only of 27.13% ($CI_{95\%}$ 11.5 – 45.0%), but the isotopic niche area (SEA_C) of *C. hippos* covered up to 94.6% of that of *C. latus*. In the two remaining estuaries (Santa Cruz and Sirinhaém), the two species shared between 63 to 87% of their isotopic niche areas.

$\delta^{13}C$ and $\delta^{15}N$ values for the organic matter sources at the base of the food webs ranged from -29.25 to -14.50‰ and from -1.03 to 10.11‰, respectively, in the estuaries studied (Supplementary Table S4, Fig. 4). However, the variability in C and N isotopic ratios in the estuarine food webs depended greatly on the location: for example, the range in $\delta^{15}N$ values for organic matter source was the widest, but that in $\delta^{13}C$ values the lowest, in Santa Cruz (Fig. 4).

4. Discussion

While differences in resource use within estuarine fish assemblages are thought to be largely modulated by species' functional traits (Albouy et al., 2011), closely related species are expected to display contrasted diets to allow their populations to co-exist in the wild (Ross, 1986). However, very few cross-sites comparisons were carry out so far to investigate diet plasticity for closely related fish species co-occurring in diverse biotic and environmental settings (*e.g.*, Mariani et al. 2011). Our results bring new insights on this matter, by revealing site-related variations in the trophic ecology of the juveniles of two commercially important species from the *Caranx* genus with similar ecological features. Indeed, *Caranx latus* and *C. hippos* not only have similar shapes and growth trajectories (Viana et al., 2016), but also reproduce on deep reefs along the shelf (Heyman and Kjerfve, 2008), and mostly colonize estuaries as juveniles, before moving to deeper waters when adults (Smith-Vaniz, 2002). In the estuaries, their juveniles have been similarly reported to feed on a broad diversity of fish and crustaceans (Vasconcelos

Filho et al., 2010; Medeiros et al., 2017), including key species in estuarine food webs (Ferreira, 2018; Lira et al., 2018). The present study however showed that, although gobies and decapod shrimps are the main food items ingested by both species, *C. latus* juveniles have a more piscivorous diet than those of *C. hippos*. These benthic prey represent a substantial part of the diet of juvenile jack species in general (Blaber and Cyrus, 1983; Smith and Parrish, 2002; Figueiredo and Pessanha, 2015; Medeiros et al., 2017) and are commonly eaten by other estuarine fish (Blaber, 1986; Vasconcelos Filho et al., 2003; Lira et al., 2017). The juveniles of the two species were also found to largely prey on pelagic fish like engraulids and clupeids in the three estuaries studied, as already reported from visual census studies in these ecosystems (Cermak, 2002). This indicates that, at least in estuaries, *C. latus* and *C. hippos* juveniles forage both at mid-water and directly above the substrate, feeding on a mix of pelagic and benthic prey.

4.1. Variation in food sources during juvenile life

Body size plays a central role in determining the type and size of the prey consumed by fish (Shelton et al., 1977), particularly in species like jacks that display schooling behaviors (Figueiredo and Menezes, 1980; Graham and Castellanos, 2005). Although a marked increase in piscivory has been reported for jacks at sizes above 200 mm SL (Blaber and Cyprus, 1983; Sudekum et al., 1991; Smith and Parrish, 2002), in this study, significant changes in diet composition due to increasing body size were only found for juvenile *C. latus*, and only consisted in small differences in the prey species ingested. The relatively low taxonomic precision for prey identification in the stomachs (particularly for small fish prey) may have hampered the power of our analysis. Yet, for both species, juvenile fish size did not seem to significantly be related to the size of the prey ingested. The diet of the two species thus seems to be fairly stable over the size range studied here (35 – 157 mm SL). However, as major morphological changes in fish take place between the post-larval and juvenile stages (Nunn et al., 2012), dietary shifts in the two species might occur in smaller fish, *i.e.* before and during estuary colonization (Cocheret de la Morinière et al., 2003; Usmar, 2012). These dietary shifts can reflect either an increase in fish foraging ability as they grow, or changes in prey availability (Nunn et al., 2012). They probably also take place in larger fish, when they move towards offshore habitats (Cocheret de la Morinière et al., 2003).

Differences in environmental characteristics are also a major source of variation in the diet of fish, as they influences both the type and the availability of local food resources (Dineen et al., 2007; Jensen et al., 2008; Evangelista et al., 2014). Given the differences in food web structure and fish assemblages among the three estuaries studied, we expected the juveniles of the two species to display different food preferences and isotopic ratios among locations (Merigot et al., 2017; Silva-Júnior et al., 2017). However, although their prey preferences and isotopic niches varied from one estuary to the other, spatial differences in diet composition were surprisingly small, with only a greater consumption of fish (particularly of the Clupeidae and Engraulidae families) by *C. hippos* in Suape. As fish from different years and seasons were pooled in this work and because inter and intra-annual variations in food web composition and food availability may be significant in estuaries (*e.g.* Garcia et al. (2012) and Boucek and Rehage (2013)), seasonal processes might partly bias the results presented here, especially regarding the average isotopic compositions of jacks at each location. However, the $\delta^{13}C$ and $\delta^{15}N$ values observed are within the ranges reported in other tropical estuaries, both for primary producers and for juvenile jacks (Abrantes et al., 2014; Claudino et al., 2015; Dolbeth et al., 2016). Their high variabilities suggest that the amplitude in $\delta^{13}C$ and $\delta^{15}N$ isotopic compositions of the jacks at each estuary largely reflects those at the base of local food chains. Thus, in Suape and Sirinhaém, the wide range of $\delta^{13}C$ values observed for organic matter sources is reflected in a greater range of $\delta^{13}C$ values for the two jack species. Similarly, the higher $\delta^{15}N$ ratios of the juvenile jacks in Santa Cruz may partly reflect the incorporation of enriched ^{15}N organic matter from coastal marine sources into the food web in this estuary, which has important connections with the marine realm (Flores Montes et al., 1998), although we cannot rule out this could indicate slightly higher trophic levels. Other sources may contribute to the local ^{15}N enrichments such as agricultural and domestic wastes (Morris et al., 2015) given the proximity in the region of highly urbanized areas (CPRH, 2003).

Potential biases in diet composition obtained from SCA may arise from the caveats inherent to the technique. In particular, differences in digestion rates among prey and the difficulty to identify some of them when partly digested can lead to an over-estimation of the contribution of the food items with low digestion rates and to greater proportions of unidentified prey in the diet of carnivorous species (Hyslop, 1980). This could partly be the case in our study, as fish and crustaceans (*i.e.* relatively big prey with hard skeletons) are less easily digested than soft-bodied organisms (Buckland, et al., 2017). Moreover, sampling for SCA requires to match predators' local feeding strategies across time and space in order to produce a realistic image of their diets. Although this is yet to be demonstrated, feeding in juvenile jacks might also take place at times of the day not sampled during our survey. This would explain the high level of prey digestion in some of the stomachs analyzed and might have contributed to bias our results, by further precluding identification of the prey items with high digestibility. Within estuarine systems, the types and abundances of the prey available for foraging fish strongly vary according to habitat type (Svanbäck and Eklöv, 2002; Lecomte and Dodson, 2005; Cardozo et al., 2020), which partly contributes to diet changes in the predators exhibiting seasonal or size-related shifts in habitat use (Stevens et al., 2007; Ferreira et al., 2016; 2019). However, juvenile jacks are highly mobile within estuaries, using a wide diversity of estuarine habitats irrespective of their age (Medeiros et al., 2017). Moreover, the sampling design in this study attempted to capture most of the spatial and temporal variation in habitat use by the two species, by capturing juvenile jacks in all their main estuarine habitats (*e.g.* mangrove creeks, river banks) at each date, over multiple seasons and years. Because our sub-sampling strategy for SCA accounted for spatiotemporal differences in the abundances of the two species, among and within locations, the image of the global diet provided here should be rather realistic. Indeed, it reflects their habitat use but also the inter-annual and inter-seasonal variations in food source availability and food web structure in the three estuaries sampled, which are also likely to modulate fish diet composition (Boucek and Rehage, 2013; Garcia et al., 2017; Possamai et al., 2018).

4.2. Possibility for trophic competition

In estuaries, physico-chemical gradients (*e.g.* in salinity) drive food web structure and determine habitat suitability for fish (Barletta et al., 2008; da Silva et al., 2018). However, food abundance also modulates interactions between potential competitors (Sánchez-Hernández et al., 2017; Costa-Pereira et al., 2019). As a result, co-existing species tend to either share abundant food resources or differ in one or more dimensions of their environmental niche (Ross, 1986). One major caveat when evaluating resource partitioning between coexisting species is the measurement of only one dimension of their ecological niche (Costa-Pereira et al., 2019). With this regard, stable isotope analysis is a valuable complementary approach to common dietary methods (Silveira et al., 2020), calculating the isotopic niche as a proxy of the trophic niche (Newsome et al., 2007). However, although the position and the size of the isotopic niche of a species are primarily driven by variations in its diet, they can be influenced by its biology and physiology (Gorokhova, 2018; Karlson et al., 2018), and by habitat-driven differences in the isotope ratios of local food webs (Flaherty and Ben-David, 2010). In this study, SCA and SIA presented opposing results, especially in the Santa Cruz estuary where the greater difference in diet between the two species did not result in a reduction in their isotopic niche overlap. Moreover, the variability in δ^{13}C values for both species at each site largely followed that of the organic matter sources present in the estuary. This suggests that the position and size of the isotopic niches for juvenile jacks in our study area largely reflect local variation in the isotopic signatures of their prey caused by local differences in food web structure. This confirms that the isotopic niche approach should be interpreted with caution, and does not necessarily provide accurate information to evaluate food partitioning between co-existing species (Flaherty and Ben-David, 2010; Petta et al, 2020; Shipley and Matich, 2020). Because tropical estuaries often exhibit a wide variety of organic matter sources and consumers, isotopic signals may be mixed along their food webs (Layman, 2007). Therefore, the isotopic niche approach might prove less valuable in these complex environments than in lakes or on land, where its application has been successful in elucidating biological processes at inter and intraspecific scales within food webs (Pettitt-Wade et al., 2015; Mumby et al., 2018; Sheppard et al., 2018; Costa-Pereira et al., 2019).

Resource partitioning has been reported for many fish species, and in diverse types of estuaries, including tropical ones (Pimentel and Joyeux, 2010; Le Loc'h et al., 2015; Moulton et al., 2017; Stevens et al., 2020). In the three estuaries studied here, although the two jack species had very similar prey and isotopic niches in overall, they exhibited slight spatial differences in their diet composition, which contributed to reduce the actual overlap in their niches at each studied location. This supports the idea that juvenile jacks adapt their feeding strategies to local food resources' availability in order to reduce trophic competition among them. This seems to occur in different ways though, depending on local environmental conditions. Indeed, although prey abundance was never directly assessed in any of the three estuaries studied, previous work concluded that Santa Cruz is that with the greatest fauna biodiversity in the area (Silva-Júnior et al., 2017). In particular, it sustains a wide variety of secondary consumers (Vasconcelos Filho et al., 2010; Ferreira, 2018), many of which are prey for juvenile jacks. In this rich environment, both *C. latus* and *C. hippos* juveniles occur at higher densities than in other estuaries (Paiva and Araújo, 2010, Silva-Júnior et al., 2017). They exhibit the most contrasting diets, but surprisingly also the most similar isotopic niches. Because the high diversity of secondary consumers in Santa Cruz allows many carnivores to feed upon both pelagic and benthic prey (Vasconcelos Filho et al., 2003), the local similarity in juvenile jacks' isotopic niches likely reflects the isotopic ratios of their fish and crustacean prey, as most of these are small predators feeding on both food chains. Thus, it appears that, when the diversity and availability of food is high like in Santa-Cruz, the juveniles of the two species avoid trophic competition by exploiting different prey, matching their respective diet preferences. Nonetheless, they apparently have to adapt these later and partially compete for food in less favorable environments. Indeed, in the Suape and Sirinhaém estuaries, where the diversity of available prey is limited, the two species focus on the same food resources. The greatest variability in their $\delta^{13}C$ ratios at these sites indicates that they rely on a broader number of food chains though, including those based on allochthonous sources of organic matter, like freshwater inputs (Abrantes and Sheaves, 2010). This diversification of carbon sources can be seen as an ecological response to reduce competition between species (Lecomte and Dodson, 2005). It might allow *C. latus* and *C. hippos* to co-exist in Suape and Sirinhaém in spite of their similarities in diet. The fact that the abundances of both *C. latus* and *C. hippos* juveniles are lower in these two estuaries suggests that the higher trophic niche overlap observed at these sites result in an increased competition for food among them. However, further information on the temporal fluctuations in prey abundance and the timing of their consumption is needed before one can conclude about the actual intensity of this phenomenon. First, trophic competition between fish species with similar global diets can be reduced when these later largely reflect an opportunistic use of seasonal peaks in the abundances of the most shared prey (Lucena et al., 2000; Boucek and Rehage, 2013). This might very well be the case here, especially as this kind of opportunistic feeding behavior would explain the variability in $\delta^{13}C$ ratios observed for both species. Differences in feeding rhythms between *C. latus* and *C. hippos* may also reduce the intensity of the trophic competition among their juveniles at the daily scale, as already observed for other jack species (Blaber and Cyrus, 1983). Lastly, competition for food is also often avoided through differences in the periods for juvenile occurrence in the estuaries, as observed in local snook species with similar diets but distinct spawning periods (Stevens et al., 2020). However, this does not really apply here as *C. latus* and *C. hippos* in northeastern Brazil both are expected to spawn from April to June (Heyman and Kjerfve, 2008), and their juveniles are mostly fished in local estuaries during the late summer (McBride and McKown, 2000; Vilar et al., 2011; da Silva et al., 2018).

Conclusion

This study contributes to better understanding the drivers of juvenile trophic ecology and its variation in tropical estuaries. Although the two close species of jacks studied here apparently globally rely on similar prey during their juvenile estuarine life, our results revealed some plasticity in their resource use, supporting the idea that resource partitioning processes between sympatric species are locally dependent (Costa-Pereira et al., 2019). Such plasticity in resource use according to local food web structure may not only favor the coexistence of a larger number of species but also provide greater stability for estuarine food webs (Kondoh, 2003). In order to evaluate it, cross-sites comparisons should be systematically undertaken when investigating the trophic ecology of sympatric fish species, particularly in tropical estuaries that show a high diversity of food sources (Layman, 2007). As spatial variation in the trophic ecology of predators like *C. latus* and *C. hippos* may not only influence the growth and survival of their juveniles, but also modulate their respective roles in the functioning of estuarine food webs, such cross-sites comparisons could be key for evaluating the implications of different co-existence scenarios, not only on the maintenance of coastal fish stocks but also on the composition and functioning of estuarine systems. This should be undertaken keeping in mind that both anthropic pressures and Climate Change may displace the environmental boundaries of estuaries or alter the composition and productivity of their food webs (Araújo et al. 2016, Chevillot et al. 2019), thereby affecting the way fish species exploit estuarine resources and modifying their roles in food webs.

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Figure Captions

Fig 1 Study area in northeastern Brazil, showing sampling locations within the Santa Cruz (a.), Suape (b.) and Sirinhaém (c.) estuaries (black dots). For each estuary, mangrove cover is indicated in dark grey.

Fig 2 Number of individuals (*n*) and length frequency distributions of the *Caranx latus* and *C. hippos* juveniles sampled in the estuaries of Santa Cruz, Suape and Sirinhaém.

Fig 3 Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of the two jack species, *Caranx latus* and *C. hippos*, in three contrasted estuaries of northeastern Brazil (Santa Cruz, Suape and Sirinhaém). Ellipses represent the isotopic niche (SEAc) for both species. Pie charts present the global diet of each species based on prey relative weights (W_i, see Table 3).

Fig 4 Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios (mean ± standard deviation) of *Caranx latus* and *C. hippos* and the main available organic matter sources in three contrasted estuaries of northeastern Brazil (Santa Cruz, Suape and Sirinhaém). Isotopic signatures for the organic matter sources sampled in the estuaries and in adjacent coastal zones are represented by black and grey squares, respectively. Light grey polygons show the range of isotopic ratios of all estuarine organic matter sources except mangrove trees (*R. mangle*). Arrows in the bottom left corner of each panel illustrate the average isotopic enrichment per trophic level (+ 0.47 ± 1.23 ‰ for $\delta^{13}C$ and + 2.54 ± 0.11 ‰ for $\delta^{15}N$) usually applied in aquatic environments (Vander Zanden and Rasmussen, 2001; Vanderklift and Ponsard, 2003). Pie charts present the local diets of each species based on prey relative weights (W_i, see Supplementary Tables S1, S2 and S3).

Tables

Characteristics	Estuary		
	Santa Cruz	Suape	Sirinhaém
Type	Ria	Coastal lagoon	Coastal plain
Human pressures	Aquaculture, agricultural, industrial and domestic waste	Industrial harbour, industrial and agriculture waste	Industrial and domestic waste
Vegetated area (km²) †	48.0	23.1	17.0
Water surface area (km²) †	25.5	6.6	1.7
Mean depth (m)	3.0	3.1	2.6
Max. depth (m)	20	5	5
N of marine entrances	2	1	1
Width of marine entrances (km, mean and range) †	0.9 (0.5 - 1.3)	0.3	0.4
Pelagic productivity ($mgCm^{-3}h^{-1}$)	14.7	2.0	34.2
Temperature (°C, mean± SD) ‡	28.5 ± 1.1	27.1 ± 1.1	27.2 ± 2.4
Salinity (mean± SD) ‡	31.1 ± 2.9	17.7 ± 2.4	9.5 ± 3.6
Pluviometry (mm, mean± SD)	1517 ± 122	1869 ± 367	2053 ± 699
References	Medeiros and Kjerfve, 1993; Medeiros et al., 2001; Neuman-Leitão et al., 2001; CPRH, 2003, 2003a; Borges, 2011; Silva, 2009; Guimarães et al., 2010; Silva et al., 2011; APAC, 2019; Gonzalez et al., 2019; Silva et al., 2019		

Type, geomorphological classification on the type of estuary according to Pritchard's classification. Human pressure, existent anthropogenic activity with potential impact on the estuary. Vegetated area, area of mangrove cover vegetation. Max. depth, maximum depth during the high tide, usually near the estuary's entrance. N of marine entrances, number of connections to the sea. Pelagic productivity, mean annual phytoplankton productivity. Temperature, water surface temperature. Pluviometry, annual rainfall between 2014 and 2018.

Table 1 Summary of morphological characteristics, environmental settings and anthropogenic activities of the three estuaries (Santa Cruz, Suape and Sirinhaém) along the coast of Pernambuco, northeastern Brazil

Estuary	Species	Stomach content analysis†		Stable isotopes analysis			
		n	SL (mm)	n	SL (mm)	δ^{13}C (‰)	δ^{15}N (‰)
Santa Cruz	C. latus	70	98 ± 17 [50 – 135]	30	109 ± 18 [80 – 138]	-18.85 ± 1.59 [-23.4 – -16.5]	10.89 ± 1.09 [8.6 – 13.0]
	C. hippos	70	82 ± 24 [36 – 131]	30	111 ± 17 [82 – 142]	-18.94 ± 1.66 [-22.3 – -16.3]	11.61 ± 0.87 [10.4 – 13.7]
Suape	C. latus	67	129 ± 18 [82 – 157]	15	113 ± 16 [86 – 141]	-18.65 ± 1.45 [-21.9 – -16.6]	9.38 ± 0.73 [8.0 – 10.2]
	C. hippos	20	112 ± 29 [49 – 156]	10	114 ± 29 [65 – 145]	-20.25 ± 2.77 [-23.6 – -15.7]	10.28 ± 1.00 [8.8 – 12.0]
Sirinhaém	C. latus	70	79 ± 16 [35 – 116]	15	90 ± 20 [70 – 124]	-20.07 ± 1.08 [-24.4 – -15.9]	9.34 ± 1.16 [8.2 – 11.6]
	C. hippos	39	73 ± 12 [47 – 98]	12	87 ± 27 [65 – 138]	-19.64 ± 2.39 [-23.6 – -16.1]	10.22 ± 0.86 [8.7 – 11.7]

† Fish with non-empty stomachs only.

Table 2 Number of individuals (n), their mean standard length (SL ± S.D.) and isotopic ratio mean values (± S.D.) for carbon (δ^{13}C) and nitrogen (δ^{15}N) of *Caranx latus* and *C. hippos* analysed for stomach content and stable isotopes compositions, in the three estuaries (Santa Cruz, Suape and Sirinhaém). Minimum and maximum values of each variable are between brackets.

Item	Species							
	Caranx latus (*n* = 207; 102±27 mm)				*Caranx hippos* (*n* = 131; 84±25 mm)			
	F_i (%)	N_i (%)	W_i (%)	*Q*	F_i (%)	N_i (%)	W_i (%)	*Q*
ALGAE	**12.08** **[7.7 – 16.9]**	**4.19** **[2.4 – 6.6]**	**0.29** **[0.1 – 0.7]**	**0.82**	**2.90** **[0.8 – 6.1]**	**0.86** **[0.1 – 2.2]**	**0.18** **[0 – 0.6]**	**0.14**
Chlorophyta (Unidentified)	0.97 [0 – 2.4]	0.40 [0 – 1.1]	0.01 [0 – 0.1]	0.01	-	-	-	-
Unidentified Algae	11.11 [7.2 – 15.5]	4.87 [2.6 – 7.9]	0.28 [0.1 – 0.7]	1.36	3.05 [0.8 – 6.1]	1.00 [0.1 – 2.6]	0.18 [0 – 0.6]	0.18
FORAMINIFERA (Unidentified)	**0.48** **[0 – 1.4]**	**0.08** **[0 – 0.3]**	**<0.01**	**0.01**	**-**	**-**	**-**	**-**
	0.48 [0 – 1.4]	0.10 [0 – 0.3]	<0.01	0.01				
NEMATODA (Unidentified)	**5.31** **[2.4 – 8.7]**	**1.11** **[0.5 – 1.8]**	**<0.01**	**0.01**	**2.90** **[0.8 – 61]**	**0.48** **[0.1 – 1.1]**	**<0.01**	**0.01**
	5.31 [2.4 – 8.7]	1.39 [0.6 – 2.3]	<0.01	0.01	3.05 [0.8 – 6.1]	0.56 [0.1 – 1.3]	<0.01	0.01
BIVALVIA (Unidentified)	**0.48** **[0 – 1.4]**	**0.32** **[0 – 1.0]**	**<0.01**	**0.01**	**0.72** **[0 – 2.3]**	**0.10** **[0 – 0.4]**	**<0.01**	**0.01**
	0.48 [0 – 1.4]	0.40 [0 – 1.3]	<0.01	0.01	0.76 [0 – 2.3]	0.11 [0 – 0.4]	<0.01]	0.01
GASTROPODA (Unidentified)	**2.90** **[1.0 – 5.3]**	**1.26** **[0.3 – 2.6]**	**0.01** **[0 – 0.1]**	**0.01**	**-**	**-**	**-**	**-**
	2.90 [1.0 – 5.3]	1.59 [0.3 – 3.3]	0.01 [0 – 0.1]	0.01				

Table 3 Frequency of occurrence (F_i), relative abundance (N_i) and weight (W_i) and alimentary coefficient (*Q*) of prey items of *Caranx latus* and *Caranx hippos* in northeastern Brazil estuaries. Dietary indexes estimate for major taxonomic groups are shown in bold. Confidence interval estimates (95%) for dietary indexes are displayed between square brackets. The number of fish specimens (*n*) and their mean standard length (SL, ±SD) are presented for each species.

POLYCHAETA (Unidentified)				**0.48** **[0 – 1.4]**	**0.08** **[0 – 0.3]**	**<0.01**	**0.01**	**1.45** **[0 – 3.8]**	**0.57** **[0 – 1.7]**	**0.01** **[0 – 0.1]**	**0.01**
				0.48 [0 – 1.4]	0.10 [0 – 0.3]	<0.01	0.01	1.53 [0 – 3.8]	0.67 [0 – 1.9]	0.01 [0 – 0.1]	0.01
OLIGOCHAETA (Unidentified)				**0.48** **[0 – 1.4]**	**0.08** **[0 – 0.3]**	**<0.01**	**0.01**	**2.17** **[0 – 17.1]**	**0.29** **[0 – 0.7]**	**<0.01**	**0.01**
				0.48 [0 – 1.4]	0.10 [0 – 0.3]	<0.01	0.01	2.29 [0 – 5.3]	0.33 [0 – 0.9]	<0.01	0.01
CRUSTACEA				**49.28** **[42.5 – 56.0]**	**26.07** **[19.7 – 33.3]**	**23.30** **[14.2 – 34.6]**	**705.34**	**60.87** **[51.9 – 68.7]**	**65.97** **[51.7 – 75.4]**	**38.22** **[22.8 – 60.3]**	**2537.20**
Cirripedia (Unidentified)				0.48 [0 – 1.4]	0.60 [0 – 2.0]	<0.01	0.01	0.76 [0 – 2.3]	0.78 [0 – 2.9]	<0.01	0.01
Copepoda (Unidentified)				1.45 [0 – 3.4]	1.79 [0 – 4.6]	<0.01	0.01	7.63 [3.1 – 12.2]	2.12 [0.8 – 2.1]	<0.01	0.01
Malacostraca	Decapoda	Brachyura	Portunidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.10 [0 – 0.4]	0.01	1.53 [0 – 3.8]	0.22 [0 – 0.6]	0.05 [0 – 0.2]	0.01
			Sesarmidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.05 [0 – 0.2]	0.01	-	-	-	-
			Unidentified Brachyura	0.97 [0 – 2.4]	0.70 [0 – 2.1]	0.14 [0 – 0.5]	0.09	1.53 [0 – 3.8]	0.33 [0 – 1.0]	0.32 [0 – 1.2]	0.10
		Caridea	Alpheidae	4.83 [1.9 – 8.2]	1.99 [0.7 – 3.9]	1.56 [0.1 – 4.7]	3.10	1.53 [0 – 3.8]	0.22 [0 – 0.6]	1.22 [0 – 4.8]	0.26
			Unidentified Caridea	2.90 [1.0 – 5.3]	0.99 [0.7 – 2.0]	1.38 [0.3 – 2.9]	1.36	-	-	-	-
		Dendrobranchiata	Aristeidae	0.48 [0 – 1.4]	0.20 [0 – 0.7]	0.06 [0 – 0.2]	0.01	-	-	-	-
			Penaeidae	11.59 [7.2 – 15.9]	4.87 [2.6 – 7.7]	14.60 [7.8 – 23.5]	71.10	20.61 [13.7 – 27.5]	8.37 [3.8 – 15.4]	19.26 [9.9 – 33.3]	161.20
		Unidentified Decapoda		15.46 [10.6 – 20.3]	8.84 [4.6 – 15.0]	4.86 [2.2 – 8.6]	42.96	23.66 [16.8 – 31.3]	15.07 [7.9 – 15.4]	10.56 [4.0 – 22.2]	159.13
	Isopoda (Unidentified)			2.90 [1.0 – 5.3]	0.79 [0.2 – 1.6]	0.01 [0 – 0.1]	0.01	3.82 [0.8 – 7.6]	0.56 [0.1 – 1.2]	0.06 [0 – 0.2]	0.03

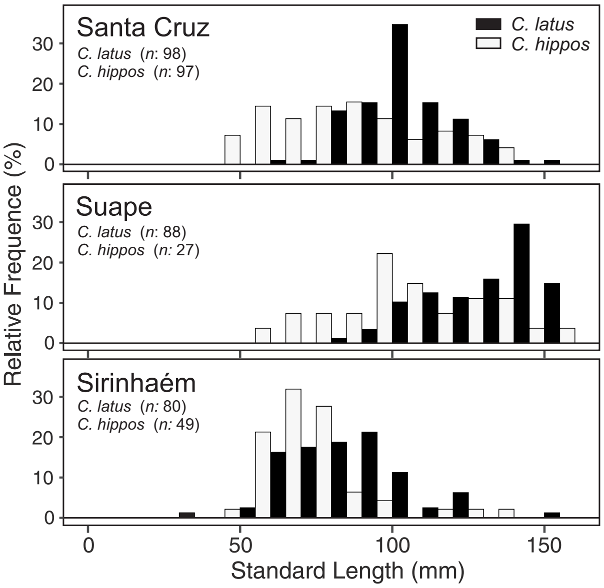
Table 3 Continued.

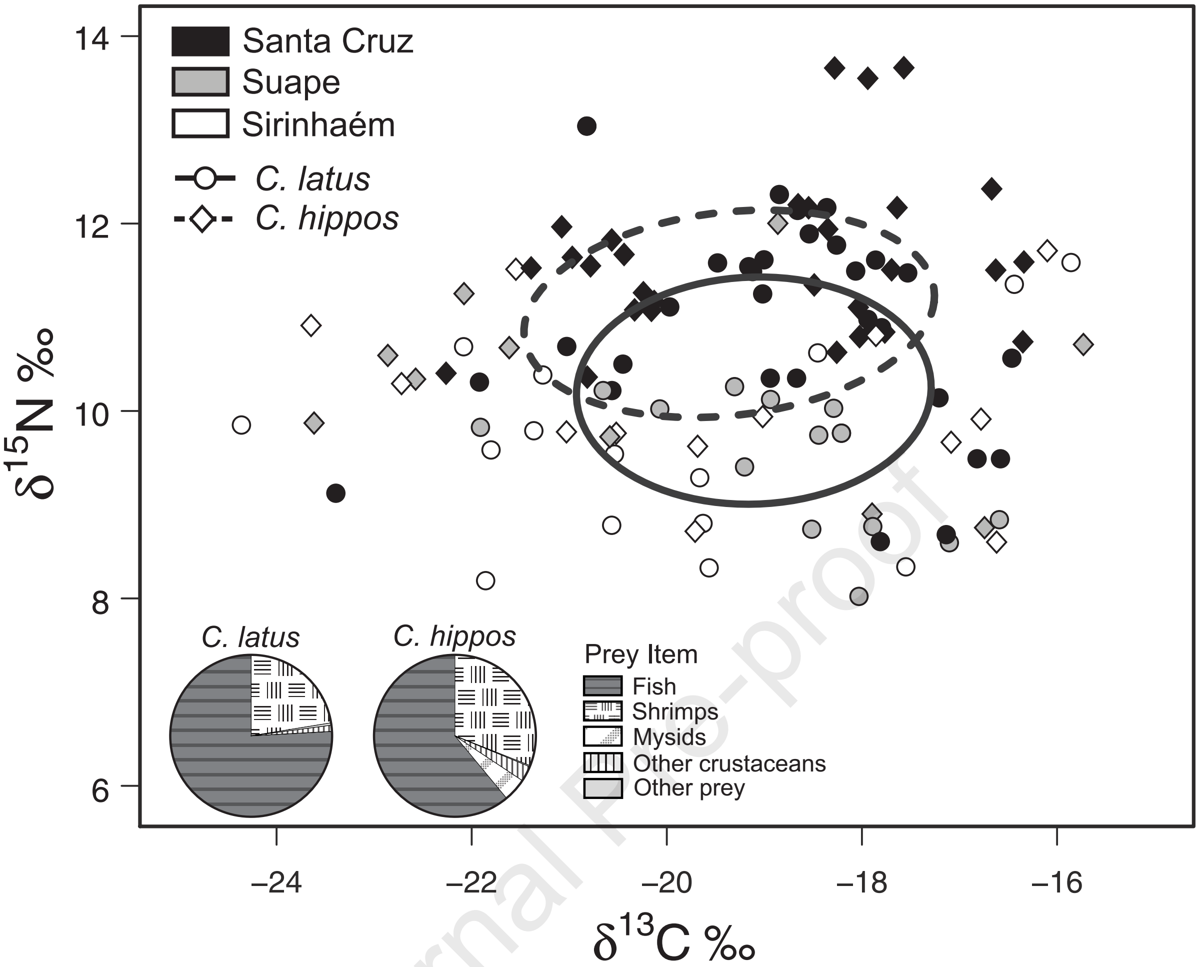
	Mysida (Unidentified)		1.93 [0.5 – 3.9]	0.79 [0.1 – 1.7]	0.01 [0 – 0.1]	0.01	7.63 [3.1 – 12.2]	36.61 [12.7 – 53.9]	4.67 [0.9 – 11.1]	170.96
	Stomatopoda (Unidentified)		-	-	-	-	0.76 [0 – 2.3]	0.11 [0 – 0.4]	0.03 [0 – 0.1]	0.01
Ostracoda (Unidentified)			4.35 [1.9 – 7.2]	2.78 [0.8 – 5.6]	<0.01	0.01	1.53 [0 – 3.8]	0.56 [0 – 1.5]	<0.01	0.1
Unidentified Crustacea			14.98 [10.1 – 19.8]	8.34 [4.5 – 13.2]	0.90 [0.4 – 1.7]	7.50	9.92 [5.3 – 15.3]	9.49 [2.9 – 17.9]	2.61 [0.2 – 6.9]	24.76
HEXAPODA			**0.48** **[0 – 1.4]**	**0.08** **[0 – 0.3]**	**<0.01**	**0.01**	**-**	**-**	**-**	**-**
Unidentified Insecta			0.48 [0 – 1.4]	0.10 [0 – 0.3]	<0.01	0.01				
VERTEBRATA			**84.06** **[78.8 – 88.9]**	**46.29** **[37.7 – 54.9]**	**75.10** **[63.5 – 84.4]**	**3252.60**	**71.74** **[64.1 – 79.4]**	**20.17** **[13.8 – 29.1]**	**60.13** **[37.9 – 76.0]**	**1205.15**
Thaliacea	Salpida	Salpidae	0.97 [0 – 2.4]	0.20 [0 – 0.5]	0.09 [0 – 0.3]	0.01	-	-	-	-
Teleostei	Clupeiformes	Clupeidae	1.93 [0.5 – 3.9]	0.70 [0.1 – 1.6]	2.61 [0 – 6.8]	1.82	2.29 [0 – 5.3]	0.89 [0 – 2.5]	7.18 [0 – 19.5]	6.39
		Engraulidae	4.35 [1.9 – 7.2]	1.59 [0.5 – 3.1]	2.46 [0.4 – 5.7]	3.91	3.05 [0.8 – 6.1]	0.45 [0.1 – 1.0]	4.43 [0.6 – 9.9]	1.99
	Gobiiformes	Eleotridae	1.45 [0 – 3.4]	0.30 [0 – 0.7]	0.44 [0 – 1.1]	0.13	0.76 [0 – 2.3]	0.11 [0 – 0.4]	0.90 [0 – 3.4]	0.09
		Gobiidae	23.67 [17.9 – 29.9]	7.55 [5.3 – 10.4]	39.99 [19.7 – 57.6]	301.92	19.08 [12.2 – 26.0]	4.35 [2.4 – 7.3]	33.28 [7.4 – 57.7]	144.76
	Perciformes	Carangidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.16 [0 – 0.6]	0.01	2.29 [0 – 5.3]	2.01 [0 – 5.9]	0.74 [0 – 2.6]	1.48
		Gerreidae	9.66 [5.8 – 14.0]	4.37 [2.0 – 7.8]	2.73 [0.6 – 6.0]	11.93	0.76 [0 – 2.3]	0.11 [0 – 0.4]	0.08 [0 – 0.3]	0.01
		Scianidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.24 [0 – 0.9]	0.02	-	-	-	-

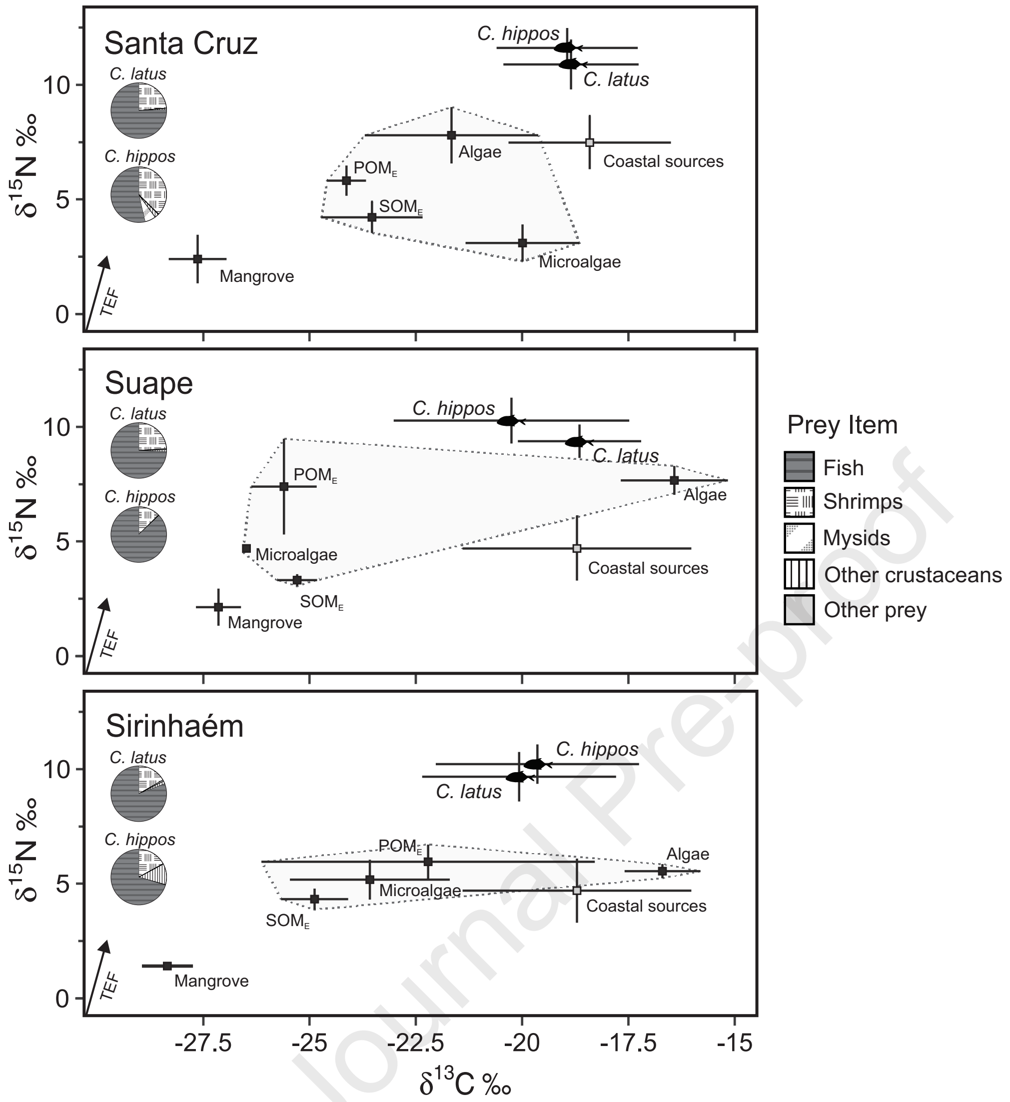
Table 3 Continued.

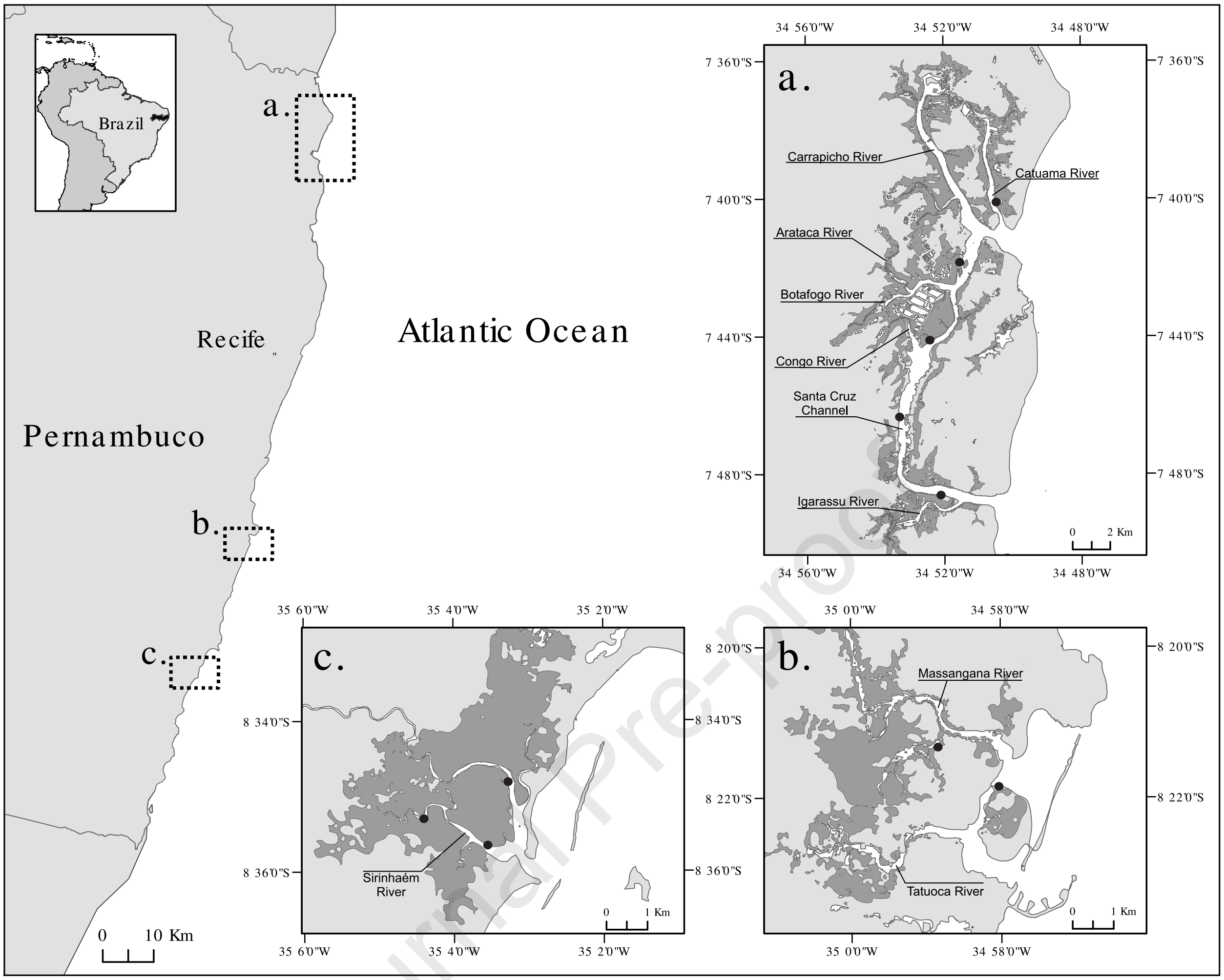
Pleuronectiformes	Cynoglossidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.14 [0 – 0.5]	0.01	-	-	-	-
	Paralichthyidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.04 [0 – 0.2]	0.01	-	-	-	-
Unidentified teleostei		60.39 [53.6 – 67.1]	43.00 [32.2 – 53.6]	27.12 [18.2 – 39.0]	1166.18	54.20 [45.8 – 62.6]	14.96 [9.4 – 23.5]	14.40 [8.4 – 24.0]	215.2
DEBRIS		**29.47** **[23.7 – 35.7]**	**20.46** **[14.9 – 26.2]**	**1.30** **[0.3 – 3.2]**	**-**	**33.59** **[26.0 – 42.0]**	**11.64** **[7.2 – 18.3]**	**1.46** **[0.4 – 3.1]**	**-**
Plastic debris		19.81 [14.5 – 25.6]	13.90 [9.3 – 18.8]	<0.01	-	18.12 [12.2 – 25.2]	6.50 [3.5 – 10.8]	<0.01	-
Unidentified organic matter and sediment debris		14.98 [10.1 – 19.8]	6.56 [3.5 – 10.2]	1.30 [0.3 – 3.2]	-	18.84 [12.2 – 26.0]	5.07 [2.7 – 8.8]	1.45 [0.4 – 3.1]	-

Table 3 Continued.


Santa Cruz
C. latus (n: 98)
C. hippos (n: 97)
C. latus
C. hippos
Suape
C. latus (n: 88)
C. hippos (n: 27)
Sirinhaém
C. latus (n: 80)
C. hippos (n: 49)
Relative Frequence (%)
0
10
20
30
0
50
100
150
Standard Length (mm)


Santa Cruz
Suape
Sirinhaém
C. latus
C. hippos
δ15N ‰
δ13C ‰
14
12
10
8
6
–24
–22
–20
–18
–16
C. latus
C. hippos
Prey Item
Fish
Shrimps
Mysids
Other crustaceans
Other prey


Santa Cruz
Suape
Sirinhaém
C. latus
C. hippos
Algae
Coastal sources
POM$_E$
SOM$_E$
Microalgae
Mangrove
TEF
δ^{15}N ‰
δ^{13}C ‰
0
5
10
-27.5
-25
-22.5
-20
-17.5
-15
Prey Item
Fish
Shrimps
Mysids
Other crustaceans
Other prey


Brazil
a.
b.
c.
Recife
Atlantic Ocean
Pernambuco
0 10 Km
34 56'0"W
34 52'0"W
34 48'0"W
7 36'0"S
7 40'0"S
7 44'0"S
7 48'0"S
Carrapicho River
Catuama River
Arataca River
Botafogo River
Congo River
Santa Cruz Channel
Igarassu River
0 2 Km
35 6'0"W
35 4'0"W
35 2'0"W
8 34'0"S
8 36'0"S
Sirinhaém River
0 1 Km
35 0'0"W
34 58'0"W
8 20'0"S
8 22'0"S
Massangana River
Tatuoca River
0 1 Km

Highlights

- The trophic ecology of two jack species was described for three tropical estuaries
- Both species mostly eat fish and crustaceans during their estuarine juvenile life
- Their overall isotopic niches are very similar and the overlap between them is >68%
- However, spatial changes in diet allow to reduce this latter to 27-57%
- Food partitioning strategies between the two species differ among estuaries

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All co-authors have materially participated in the manuscript preparation (see below for more details) and all approved the present version of the manuscript.

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Audrey M. Darnaude: Data analysis and manuscript preparation.
Paulo José Duarte-Neto: Data analysis and manuscript preparation.
François Le Loc'h: Data analysis and manuscript preparation.
Mayara Constantino de Lima: Sampling and laboratory analyses.
Frédéric Ménard: Data analysis and manuscript preparation.
Valdimere Ferreira: Sampling and laboratory analyses.
Flávia Lucena Frédou: Data analysis and manuscript preparation.
Jean-Marie Munaron: laboratory analyses.
Thierry Frédou: Sampling, data analysis and manuscript preparation.

Sincerely.

Júlio Guazzelli Gonzalez (on behalf of the authors)
Universidade Federal Rural de Pernambuco

Declaration of interests

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

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: