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# Journal Pre-proof

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

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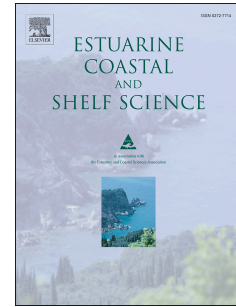
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1 Trophic ecology of the juveniles of two jack species (*Caranx latus* and *C. hippos*) in contrasted tropical  
2 estuaries.

3

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15

16 **Abstract**

17 Jacks are highly prized tropical marine fish. Most of them complete their whole life cycle at sea but some  
18 use estuaries at the juvenile stage before moving back to coastal waters and joining the adult exploited  
19 stocks. Little is known about jacks' trophic ecology in estuaries, although their juveniles' ability to  
20 successfully exploit available resources in these productive environments may strongly affect stock  
21 recruitment success in the species concerned. In this study, stomach content and stable isotope analyses  
22 were combined to investigate diet and food niche overlap of juveniles from two sympatric species of  
23 jacks (*Caranx latus* and *C. hippos*) in three contrasted estuaries (Suape, Sirinhaém and Santa Cruz) spread  
24 along the northeastern Brazilian coast. Overall, although the juveniles of *C. latus* exhibited a more  
25 piscivorous diet than those of *C. hippos*, the two species had very similar isotopic niches, with mean  $\delta^{13}\text{C}$   
26 and  $\delta^{15}\text{N}$  values of  $-19.35 \pm 2.10\text{‰}$  and  $11.03 \pm 1.11\text{‰}$  and of  $-19.10 \pm 1.82\text{‰}$  and  $10.21 \pm 1.21\text{‰}$ , for *C.*  
27 *hippos* and *C. latus* respectively. In all the estuaries sampled, both species mostly ate fish ( $N_i = 20.1 -$   
28  $46.2\%$ ,  $W_i = 60.1 - 75.1\%$ , essentially Gobiidae and Clupeidae) and crustaceans ( $N_i = 26.0 - 65.9\%$ ,  $W_i =$   
29  $23.3 - 38.2\%$ , mainly Penaeidae shrimps). As a result, the overlap between their global estuarine isotopic  
30 niches was  $>68\%$ . However, diet composition for the two species varied among estuaries, indicating that  
31 their juveniles partly adapt their food preferences to local prey availability. Notably, prey preferences  
32 differed significantly between the two species only in the Santa Cruz estuary, where  $\delta^{15}\text{N}$  values were the  
33 highest for both species. Conversely, interspecific differences in  $\delta^{13}\text{C}$  ratios were greater in the Suape and  
34 the Sirinhaém estuaries, likely reflecting a wider diversity in the carbon sources sustaining local food  
35 webs. Thus, combined differences in juvenile diet and food web structure at each location resulted in  
36 much-reduced local isotopic niche overlaps between the two species (from 27% in Suape to 57% in Santa  
37 Cruz). These results have important implications for resource and ecosystem management in northeastern  
38 Brazil and call for systematic cross-site comparisons when evaluating fish ecology and resource  
39 partitioning within estuarine systems.

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

42

## 43 1. Introduction

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

63 Species ecological niches play a central role in defining available resource use and interspecific  
64 interactions at the community level (Van Valen, 1965; Ross, 1986). Among the many facets of the  
65 ecological niche, the trophic niche is perhaps the easiest to evaluate (Ross, 1986). It can be studied using  
66 empirical methods like stomach content analysis (SCA), which provides a snapshot of the items ingested  
67 by the individuals (Hyslop, 1980; Pinnegar and Polunin, 2000), or through the use of natural tags such as  
68 stable isotope analysis (SIA). This later approach, usually combines nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ )  
69 isotopic ratios (Fry, 2006) to provide an integrated image of the food resources assimilated by the  
70 individuals over periods of time ranging from a few weeks to a few months (Herzka, 2005). The method  
71 relies on the assumption that the isotope ratios of an organism reflect, in a predictive way, those of its  
72 food sources (Fry, 2006). In general, the  $\delta^{15}\text{N}$  is used as a proxy for organisms' trophic position in the

73 food chain (Post, 2002; Martínez Del Rio et al., 2009), while the  $\delta^{13}\text{C}$  allows identifying the main organic  
74 matter source(s) supporting their growth (Fry, 2006; Layman, 2007). Combining SIA and SCA enables  
75 better resolution of dietary patterns and accurate identification of the food sources sustaining animal  
76 growth (Silveira et al., 2020). In this study, we applied these complementary methods to describe  
77 variations in diet and compare strategies of estuary resource use in the juveniles of two sympatric species  
78 of jacks along the northeastern coast of Brazil.

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

91         Differences in resource use among juvenile habitats may affect fish early growth and body  
92 condition (e.g. Isnard et al. 2015) and modulate recruitment success in exploited species (Gillanders et al.,  
93 2015). To avoid competition for food and optimize energy acquisition, sympatric species usually tend to  
94 partition resources at multiple scales (Schoener, 1974; Losos, 2000). However, *C. latus* and *C. hippos* not  
95 only have similar body shapes and lengths, but they are also both reported to feed mainly on fish and  
96 crustaceans (Hofling et al., 1998; Smith-Vaniz, 2002; Vasconcelos Filho et al., 2010). Therefore, they  
97 might have similar uses of estuarine resources and their co-occurrence in certain estuaries might result in  
98 an interspecific competition for food, with potentially high consequences in terms of local fisheries  
99 production. To investigate this, we assessed variations in the diets and isotopic niches of their juveniles  
100 among three neighboring Brazilian estuaries with contrasted morphological and biological features, and  
101 where the relative densities for the juveniles of the two species differ markedly (Paiva and Araújo, 2010;

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

104

## 105 **2. Material and Methods**

### 106 *2.1. Study area*

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

118 Although relatively close to each other, the Santa Cruz, Suape and Sirinhaém estuaries exhibit  
119 distinct morphological and biological features and are subject to different freshwater inputs and degrees  
120 of anthropogenic pressures (Table 1). Located in the north of the Pernambuco state, the estuarine complex  
121 of Santa Cruz is the largest estuary of the three, and one of the most important fishery ground of the state  
122 (Medeiros et al., 2001). It consists in a shallow U-shape channel that receives continental inputs from six  
123 rivers (draining three hydrological basins) and is connected to the sea by two large entrances (Silva et al.,  
124 2011). Because the seawater inflow is high, the estuary is under a strong marine influence (Flores Montes  
125 et al., 1998; Figueiredo et al., 2006). Furthermore, the reduced current velocity in the inner part of the  
126 main channel results in a predominance of muddy substrates along the estuary (CPRH, 2003), where  
127 hypersaline conditions prevail during the driest months of the year (Medeiros and Kjerfve, 1993). The  
128 local fauna comprises a large number of marine and estuarine invertebrates and fish that use this estuary  
129 at different stages of their life (Vasconcelos-Filho and Oliveira, 1999). The fish assemblage is diverse,  
130 with numerous species with distinct morphologies, as illustrated by the presence of bottom-associated  
131 species like gobies (Silva-Júnior et al., 2017; Ferreira et al., 2019).

132 The estuaries of Suape and Sirinhaém, both situated in the south of the Pernambuco state, are  
133 smaller (Table 1). Because the annual rainfall in the state increases southwards (CPRH, 2003a), they  
134 receive higher freshwater inputs, especially Sirinhaém (Table 1). The Suape estuary is formed by two  
135 rivers, which flow into a shallow brackish lagoon with limited connection to the sea. It can be classified  
136 as euryhaline and exhibits the lowest primary productivity of the three estuaries studied (Silva et al.,  
137 2019; Table 1). The estuary of Sirinhaém is the smallest estuary studied, but that with the highest  
138 percentage of mangrove cover (Table 1). Located within two marine protected areas (CPRH, 2003a), it  
139 gathers a variety of interconnected lagoons and channels that spread on the shallow flood plain around the  
140 main bed of the Sirinhaém river, which constitutes its sole connection to the sea (CPRH, 2003a). This  
141 particular configuration intensifies the effects of the watershed dynamics, with salinities ranging from  
142 nearly 0 at low tide to up to 30 at high tide (Silva et al., 2009). The fish assemblages of the Sirinhaém and  
143 Suape estuaries are similar, with a common dominance of pelagic species (Bezerra Junior et al., 2011).  
144 Moreover, both estuaries exhibit much lower densities of *C. hippos* than those observed in Santa-Cruz  
145 (Silva-Júnior et al., 2017).

146

## 147 2.2. Fish sampling and diet composition

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



162 silt, and mangrove litter and macroalgae occasionally found on the bottom. Depending on the size and  
 163 geomorphology of the estuary, fish juveniles were collected at 2 to 5 sites per habitat type for each  
 164 sampling date. This allowed covering most of the spatiotemporal variability in juvenile distribution, and  
 165 associated diet variation, between and within estuaries for the two species.

166 Upon collection, all juveniles were identified following specific literature (Figueiredo and  
 167 Menezes, 1980; Smith-Vaniz, 2002), measured (standard length – SL in mm) and stored frozen until  
 168 further analysis. Their stomach contents were assessed under a stereomicroscope until 70 non-empty  
 169 stomachs per species and estuary could be gathered. As densities for the two jack species are rather low in  
 170 estuaries during the wetter months of the year (Vilar et al., 2011; Silva-Júnior et al., 2017; da Silva et al.,  
 171 2018), fish from different years had to be pooled to reach a minimum number of 10 non-empty stomachs  
 172 for both the dry (September to March) and the rainy (April to August) seasons in the area (CPRH, 2003;  
 173 2003a), and a maximum of 30 individuals per year for each estuary. Prey items in all stomachs were  
 174 identified to the lowest taxonomic level possible, depending on their degree of digestion. All identified  
 175 prey items were counted and weighed (g) and well-preserved ones, *i.e.* those only slightly digested, were  
 176 measured (total length, in mm).

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

$$185 \quad Q = N_i \times W_i.$$

186 According to Hureau (1970), prey items should be considered preferential when  $Q \geq 200$ , secondary when  
 187  $20 \leq Q < 200$ , and occasional ( $Q < 20$ ). All dietary indexes were calculated both using major taxonomic  
 188 groups (*e.g.* Teleostei) and applying the lowest possible identification levels, down to family.

189

190 2.3. Stable isotope analyses (SIA)

191 For each species, 10 to 30 juveniles from each estuary were selected for SIA. As the minimum size  
192 for both species in our samples was 35 mm SL, these fish were chosen to measure at least 60 mm in size  
193 (SL) to ensure that the isotopic compositions from their local prey were incorporated within the tissue at  
194 the time of capture (Herzka 2005). Fish were collected in 2015, 2018 and 2019 during both the dry and  
195 the rainy seasons (APAC, 2019), so their isotopic ratios should accurately reflect the temporal (inter and  
196 intra-annual) variabilities in fish diet and food web composition at each estuary. Basal estuarine organic  
197 matter sources, *i.e.* the main benthic algae (*Sargassum* spp., *Ulva* spp., *Gracilaria cervicornis*), the  
198 microphytobenthos, the mangrove trees (rotten leaves from *Rhizophorae mangle*), and the organic matter  
199 present in the surface sediment (SOM) and in the water column (POM), were collected in each estuary in  
200 2015, both during the dry (January to March) and the rainy (July to September) seasons (APAC, 2019).  
201 Mangrove tree leaves and algae were collected manually at low tide. POM was obtained by filtering water  
202 (0.5 – 1 L) on precombusted fiberglass filters (0.75  $\mu\text{m}$ ), whereas SOM was sampled from the 2 mm  
203 surface layer of the sediment. Benthic microphytobenthos was collected from the sediment surface at low  
204 tide and extracted in the laboratory following Riera and Richard (1996). Other potential organic matter  
205 sources for the three estuaries studied, such as marine POM and SOM from the adjacent coastal zone  
206 were also collected, at two locations: one near the entrance of the Santa Cruz estuary and one further  
207 south, near the mouths of the Sirinhaém and Suape estuaries.

208 For fish specimens, white muscle was extracted and rinsed with distilled water while, for organic  
209 matter sources, samples were analyzed whole. Samples were dried in an oven at 60°C for 48 hours and  
210 ground into a fine powder with a mortar and pestle. For all POM and SOM samples, a subsample was  
211 acidified to remove the inorganic carbon prior  $\delta^{13}\text{C}$  analysis, while the remaining material was used  
212 directly for  $\delta^{15}\text{N}$  analyses (Pinnegar and Polunin, 1999). Carbon and nitrogen isotope ratios were  
213 analyzed with a mass spectrometer (Thermo Delta V+) coupled to an element analyzer (Thermo Flash  
214 2000, interface Thermo ConFio IV) at the Pôle de Spectrométrie Océan (PSO - IUEM, Plouzané, France).  
215 Carbon and nitrogen isotopic ratios are reported as  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (in ‰), respectively, derived  
216 from the formula:

$$217 \quad \delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 10^3$$

218 where  $\delta X$  corresponds to  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  and  $R$  to the  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$  ratios of the sample and a known  
219 standard, for carbon or nitrogen, respectively. The standards used for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were the Pee Dee  
220 Belemnite (PDB) limestone and atmospheric nitrogen, respectively. The analytical precisions of the

221 analyses, monitored through the repeated analysis (every six samples) of an internal standard (Thermo –  
222 Acétanilide), was of 0.10‰ and 0.07‰ for carbon and nitrogen isotopes, respectively.

223

### 224 2.3. Data analysis

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

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

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

247 Potential differences in the size (SL in mm) of the juveniles used for SIA and in their isotopic  
248 ratios (both for carbon and for nitrogen, separately) were tested between locations and fish species using  
249 separate ANOVA models. *Post-hoc* Tukey’s tests were applied on variables with significant effects in the

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

264

### 265 3. Results

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

277 Among the 394 fish selected for stomach content analysis, few had empty stomachs (33% for *C.*  
278 *latus* and 6% for *C. hippos*). Relative numbers and size distributions in the 338 remaining ones (207 *C.*  
279 *latus* and 131 *C. hippos*) were similar to those observed in the total catches, with slightly higher mean SL

280 values for *C. latus* than for *C. hippos* in every estuary, and larger juvenile sizes in Suape for both species  
281 (Table 2). Muscle samples from 112 juvenile fish (60 *C. latus* and 52 *C. hippos*) were analyzed in SIA  
282 (Table 2). To allow for muscle signature to reflect the diet in the estuaries, the minimum size of the fish  
283 selected for the SIA was 65 mm (SL). Altogether, the distribution of SIA juvenile sizes was similar for  
284 the two species ( $p = 0.905$ ), however it varied between estuaries ( $p < 0.001$ ), reflecting the differences in  
285 sizes observed in the field. As for SCA, this sub-sample contained a larger number of individuals from  
286 Santa Cruz in order to reflect the higher abundance of juvenile jacks at this estuary.

287

### 288 3.1. Diet composition

289 Overall, diet composition was not significantly different between the two jack species ( $p = 0.089$ )  
290 which both mainly ate fish and crustaceans ( $Q > 1205$ , Table 3). All other prey items were found to be  
291 occasional ( $Q < 20$ ), irrespective of the species (Table 3). However, when considering only the prey items  
292 identified to at least the order level, the two species did show significant differences in diet composition  
293 ( $p = 0.010$ ). Although fish remains in the stomachs were often too digested to be identified, fish prey  
294 belonged to at least nine different families for *C. latus*; six for *C. hippos* (Table 3). Fish (Teleostei) were  
295 the main prey of the juveniles of *C. latus* ( $Q = 3252$ ), whereas *C. hippos* fed on fish ( $Q = 1205$ ) and  
296 crustaceans ( $Q = 2537$ ) in similar proportions (Table 3). Fish dominated the diet of both species in terms  
297 of occurrence and weight, but crustaceans prevailed in number in the diet of *C. hippos* (Table 3). For both  
298 species, most of the fish prey identified were Gobiidae ( $F_i = 19.0$  to  $23.6$ ;  $N_i = 4.3$  to  $7.5$ ;  $W_i = 33.2$  to  
299  $39.9\%$ ), but their consumption was higher in *C. latus* ( $F_i = 23.6$ ;  $N_i = 7.5$ ;  $W_i = 39.9\%$ ). Decapods, in  
300 particular Penaeidae shrimps, were the main crustacean prey found in the stomachs of the juveniles of the  
301 two species (Table 3). However, mysids also contributed significantly to their diet, especially for *C.*  
302 *hippos*, in which they were the most abundant crustacean prey ( $N_i = 36.6\%$ ).

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

310 0.292; Shrimps,  $p = 0.839$ ) and for both jack species (Fish,  $p = 0.184$ ; Shrimps,  $p = 0.515$ )  
 311 (Supplementary Fig. S1).

312 The diet of both species varied according to the estuary, regardless the level of prey identification  
 313 applied ( $p < 0.002$ ). Specifically, differences between estuaries were found only for Suape (Suape – Santa  
 314 Cruz:  $p < 0.015$ ; Suape – Sirinhaém:  $p < 0.027$ ). In this estuary, *C. hippos* presented the most different  
 315 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  
 316 similar between Santa Cruz and Sirinhaém, either when considering all prey items ( $p = 0.060$ ) or only  
 317 those identified to at lowest taxonomic level ( $p = 0.204$ ). Moreover, interspecific differences in diet  
 318 composition were only significant in Santa Cruz, independently of the level of prey identification applied  
 319 ( $p < 0.025$ ). In this estuary, Gobiidae fish prevailed in the diet of *C. latus* and decapod shrimps in that of  
 320 *C. hippos* (Supplementary Table S1). Although the two species had similar overall diets in the two  
 321 remaining estuaries (Suape:  $p > 0.236$ ; Sirinhaém:  $p > 0.113$ ), they presented slight spatial variations in  
 322 their prey preferences. In Suape, the diet of the two species only differed in terms of the type of fish  
 323 consumed, with higher contributions of Clupeidae and Engraulidae for *C. hippos*, and of Gobiidae and  
 324 Gerreidae for *C. latus* (Supplementary Table S2) while, in Sirinhaém, significantly higher proportions of  
 325 crustaceans (Penaeidae shrimps) were found in the diet of *C. hippos* than in that of *C. latus*  
 326 (Supplementary Table S3).

327

### 328 3.2. Stable isotopes analysis

329 The juveniles from the two species had very variable  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values irrespective of their  
 330 estuary of capture, ranging from -24.36 to -15.73‰ and from 8.00 to 13.66‰, respectively (Table 2; Fig.  
 331 3). Due to this variability,  $\delta^{13}\text{C}$  values were not significantly different among estuaries ( $p = 0.088$ ) nor  
 332 between species, with average values of  $-19.10 \pm 1.82\%$  for *C. latus* and  $-19.35 \pm 2.10\%$  for *C. hippos*.  
 333 Differences in  $\delta^{13}\text{C}$  values between the two species were not significant either within each given estuary  
 334 ( $p = 0.147$ ). Conversely, significant differences in  $\delta^{15}\text{N}$  were found according to both the estuary ( $p <$   
 335  $0.001$ ) and the species ( $p < 0.001$ ). Indeed, although  $\delta^{15}\text{N}$  values for both species did not differ  
 336 significantly between Suape and Sirinhaém ( $p = 0.790$ ; Fig. 3), they were consistently higher in Santa  
 337 Cruz ( $p < 0.001$ ). Similarly, although the  $\delta^{15}\text{N}$  values of the two species were similar within each estuary  
 338 ( $p = 0.804$ ; Fig. 4), the juveniles of *C. hippos* exhibited higher  $\delta^{15}\text{N}$  values in overall ( $11.03 \pm 1.10\%$ )  
 339 than those of *C. latus* ( $10.21 \pm 1.21\%$ ) due to differences in spatial distribution among them.

340 The global trophic (isotopic) niches of the two species were similar in size, with areas ( $SEA_C$ ) of  
341 7.3 and 7.0 ‰<sup>2</sup> for *C. latus* and *C. hippos* respectively. They largely overlapped, with 68.4% ( $CI_{95\%}$  54.1  
342 – 82.6%) of their total area in common. However, both the  $SEA_C$  sizes and their overlaps varied  
343 according to the estuary (Fig. 3). Juvenile *C. latus* exhibited slightly wider isotopic niches than *C. hippos*  
344 in both Santa Cruz ( $SEA_C = 5.6‰^2$  for *C. latus* and  $4.5‰^2$  for *C. hippos*) and Sirinhaém ( $SEA_C = 7.9‰^2$   
345 for *C. latus* and  $7.1‰^2$  for *C. hippos*), with high isotopic niche overlaps at both sites (57.5%,  $CI_{95\%}$  40.1 –  
346 73.8%, in Santa Cruz and 54.3%,  $CI_{95\%}$  32.3 – 77.4%, in Sirinhaém). Conversely, in Suape, where the two  
347 species had the most different isotopic niches, niche area was much wider in *C. hippos* ( $SEA_C = 9.5‰^2$ )  
348 than in *C. latus* ( $SEA_C = 2.7‰^2$ ). At this particular site, juvenile niche overlap between the two species  
349 was only of 27.13% ( $CI_{95\%}$  11.5 – 45.0%), but the isotopic niche area ( $SEA_C$ ) of *C. hippos* covered up to  
350 94.6% of that of *C. latus*. In the two remaining estuaries (Santa Cruz and Sirinhaém), the two species  
351 shared between 63 to 87% of their isotopic niche areas.

352  $\delta^{13}C$  and  $\delta^{15}N$  values for the organic matter sources at the base of the food webs ranged from -  
353 29.25 to -14.50‰ and from -1.03 to 10.11‰, respectively, in the estuaries studied (Supplementary Table  
354 S4, Fig. 4). However, the variability in C and N isotopic ratios in the estuarine food webs depended  
355 greatly on the location: for example, the range in  $\delta^{15}N$  values for organic matter source was the widest,  
356 but that in  $\delta^{13}C$  values the lowest, in Santa Cruz (Fig. 4).

357

#### 358 4. Discussion

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



370 Filho et al., 2010; Medeiros et al., 2017), including key species in estuarine food webs (Ferreira, 2018;  
371 Lira et al., 2018). The present study however showed that, although gobies and decapod shrimps are the  
372 main food items ingested by both species, *C. latus* juveniles have a more piscivorous diet than those of *C.*  
373 *hippos*. These benthic prey represent a substantial part of the diet of juvenile jack species in general  
374 (Blaber and Cyrus, 1983; Smith and Parrish, 2002; Figueiredo and Pessanha, 2015; Medeiros et al., 2017)  
375 and are commonly eaten by other estuarine fish (Blaber, 1986; Vasconcelos Filho et al., 2003; Lira et al.,  
376 2017). The juveniles of the two species were also found to largely prey on pelagic fish like engraulids and  
377 clupeids in the three estuaries studied, as already reported from visual census studies in these ecosystems  
378 (Cermak, 2002). This indicates that, at least in estuaries, *C. latus* and *C. hippos* juveniles forage both at  
379 mid-water and directly above the substrate, feeding on a mix of pelagic and benthic prey.

380

#### 381 4.1. Variation in food sources during juvenile life

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

397 Differences in environmental characteristics are also a major source of variation in the diet of fish,  
398 as they influences both the type and the availability of local food resources (Dineen et al., 2007; Jensen et  
399 al., 2008; Evangelista et al., 2014). Given the differences in food web structure and fish assemblages



400 among the three estuaries studied, we expected the juveniles of the two species to display different food  
401 preferences and isotopic ratios among locations (Merigot et al., 2017; Silva-Júnior et al., 2017). However,  
402 although their prey preferences and isotopic niches varied from one estuary to the other, spatial  
403 differences in diet composition were surprisingly small, with only a greater consumption of fish  
404 (particularly of the Clupeidae and Engraulidae families) by *C. hippos* in Suape. As fish from different  
405 years and seasons were pooled in this work and because inter and intra-annual variations in food web  
406 composition and food availability may be significant in estuaries (e.g. Garcia et al. (2012) and Boucek  
407 and Rehage (2013)), seasonal processes might partly bias the results presented here, especially regarding  
408 the average isotopic compositions of jacks at each location. However, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values observed  
409 are within the ranges reported in other tropical estuaries, both for primary producers and for juvenile jacks  
410 (Abrantes et al., 2014; Claudino et al., 2015; Dolbeth et al., 2016). Their high variabilities suggest that the  
411 amplitude in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic compositions of the jacks at each estuary largely reflects those at the  
412 base of local food chains. Thus, in Suape and Sirinhaém, the wide range of  $\delta^{13}\text{C}$  values observed for  
413 organic matter sources is reflected in a greater range of  $\delta^{13}\text{C}$  values for the two jack species. Similarly,  
414 the higher  $\delta^{15}\text{N}$  ratios of the juvenile jacks in Santa Cruz may partly reflect the incorporation of enriched  
415  $^{15}\text{N}$  organic matter from coastal marine sources into the food web in this estuary, which has important  
416 connections with the marine realm (Flores Montes et al., 1998), although we cannot rule out this could  
417 indicate slightly higher trophic levels. Other sources may contribute to the local  $^{15}\text{N}$  enrichments such as  
418 agricultural and domestic wastes (Morris et al., 2015) given the proximity in the region of highly  
419 urbanized areas (CPRH, 2003).

420 Potential biases in diet composition obtained from SCA may arise from the caveats inherent to the  
421 technique. In particular, differences in digestion rates among prey and the difficulty to identify some of  
422 them when partly digested can lead to an over-estimation of the contribution of the food items with low  
423 digestion rates and to greater proportions of unidentified prey in the diet of carnivorous species (Hyslop,  
424 1980). This could partly be the case in our study, as fish and crustaceans (*i.e.* relatively big prey with hard  
425 skeletons) are less easily digested than soft-bodied organisms (Buckland, et al., 2017). Moreover,  
426 sampling for SCA requires to match predators' local feeding strategies across time and space in order to  
427 produce a realistic image of their diets. Although this is yet to be demonstrated, feeding in juvenile jacks  
428 might also take place at times of the day not sampled during our survey. This would explain the high level  
429 of prey digestion in some of the stomachs analyzed and might have contributed to bias our results, by

430 further precluding identification of the prey items with high digestibility. Within estuarine systems, the  
431 types and abundances of the prey available for foraging fish strongly vary according to habitat type  
432 (Svanbäck and Eklöv, 2002; Lecomte and Dodson, 2005; Cardozo et al., 2020), which partly contributes  
433 to diet changes in the predators exhibiting seasonal or size-related shifts in habitat use (Stevens et al.,  
434 2007; Ferreira et al., 2016; 2019). However, juvenile jacks are highly mobile within estuaries, using a  
435 wide diversity of estuarine habitats irrespective of their age (Medeiros et al., 2017). Moreover, the  
436 sampling design in this study attempted to capture most of the spatial and temporal variation in habitat  
437 use by the two species, by capturing juvenile jacks in all their main estuarine habitats (*e.g.* mangrove  
438 creeks, river banks) at each date, over multiple seasons and years. Because our sub-sampling strategy for  
439 SCA accounted for spatiotemporal differences in the abundances of the two species, among and within  
440 locations, the image of the global diet provided here should be rather realistic. Indeed, it reflects their  
441 habitat use but also the inter-annual and inter-seasonal variations in food source availability and food web  
442 structure in the three estuaries sampled, which are also likely to modulate fish diet composition (Boucek  
443 and Rehage, 2013; Garcia et al., 2017; Possamai et al., 2018).

#### 444 4.2. Possibility for trophic competition

445 In estuaries, physico-chemical gradients (*e.g.* in salinity) drive food web structure and determine  
446 habitat suitability for fish (Barletta et al., 2008; da Silva et al., 2018). However, food abundance also  
447 modulates interactions between potential competitors (Sánchez-Hernández et al., 2017; Costa-Pereira et  
448 al., 2019). As a result, co-existing species tend to either share abundant food resources or differ in one or  
449 more dimensions of their environmental niche (Ross, 1986). One major caveat when evaluating resource  
450 partitioning between coexisting species is the measurement of only one dimension of their ecological  
451 niche (Costa-Pereira et al., 2019). With this regard, stable isotope analysis is a valuable complementary  
452 approach to common dietary methods (Silveira et al., 2020), calculating the isotopic niche as a proxy of  
453 the trophic niche (Newsome et al., 2007). However, although the position and the size of the isotopic  
454 niche of a species are primarily driven by variations in its diet, they can be influenced by its biology and  
455 physiology (Gorokhova, 2018; Karlson et al., 2018), and by habitat-driven differences in the isotope  
456 ratios of local food webs (Flaherty and Ben-David, 2010). In this study, SCA and SIA presented opposing  
457 results, especially in the Santa Cruz estuary where the greater difference in diet between the two species  
458 did not result in a reduction in their isotopic niche overlap. Moreover, the variability in  $\delta^{13}\text{C}$  values for  
459 both species at each site largely followed that of the organic matter sources present in the estuary. This

460 suggests that the position and size of the isotopic niches for juvenile jacks in our study area largely reflect  
461 local variation in the isotopic signatures of their prey caused by local differences in food web structure.  
462 This confirms that the isotopic niche approach should be interpreted with caution, and does not  
463 necessarily provide accurate information to evaluate food partitioning between co-existing species  
464 (Flaherty and Ben-David, 2010; Petta et al, 2020; Shipley and Matich, 2020). Because tropical estuaries  
465 often exhibit a wide variety of organic matter sources and consumers, isotopic signals may be mixed  
466 along their food webs (Layman, 2007). Therefore, the isotopic niche approach might prove less valuable  
467 in these complex environments than in lakes or on land, where its application has been successful in  
468 elucidating biological processes at inter and intraspecific scales within food webs (Pettitt-Wade et al.,  
469 2015; Mumby et al., 2018; Sheppard et al., 2018; Costa-Pereira et al., 2019).

470 Resource partitioning has been reported for many fish species, and in diverse types of estuaries,  
471 including tropical ones (Pimentel and Joyeux, 2010; Le Loc'h et al., 2015; Moulton et al., 2017; Stevens  
472 et al., 2020). In the three estuaries studied here, although the two jack species had very similar prey and  
473 isotopic niches in overall, they exhibited slight spatial differences in their diet composition, which  
474 contributed to reduce the actual overlap in their niches at each studied location. This supports the idea that  
475 juvenile jacks adapt their feeding strategies to local food resources' availability in order to reduce trophic  
476 competition among them. This seems to occur in different ways though, depending on local  
477 environmental conditions. Indeed, although prey abundance was never directly assessed in any of the  
478 three estuaries studied, previous work concluded that Santa Cruz is that with the greatest fauna  
479 biodiversity in the area (Silva-Júnior et al., 2017). In particular, it sustains a wide variety of secondary  
480 consumers (Vasconcelos Filho et al., 2010; Ferreira, 2018), many of which are prey for juvenile jacks. In  
481 this rich environment, both *C. latus* and *C. hippos* juveniles occur at higher densities than in other  
482 estuaries (Paiva and Araújo, 2010, Silva-Júnior et al., 2017). They exhibit the most contrasting diets, but  
483 surprisingly also the most similar isotopic niches. Because the high diversity of secondary consumers in  
484 Santa Cruz allows many carnivores to feed upon both pelagic and benthic prey (Vasconcelos Filho et al.,  
485 2003), the local similarity in juvenile jacks' isotopic niches likely reflects the isotopic ratios of their fish  
486 and crustacean prey, as most of these are small predators feeding on both food chains. Thus, it appears  
487 that, when the diversity and availability of food is high like in Santa-Cruz, the juveniles of the two species  
488 avoid trophic competition by exploiting different prey, matching their respective diet preferences.  
489 Nonetheless, they apparently have to adapt these later and partially compete for food in less favorable

490 environments. Indeed, in the Suape and Sirinhaém estuaries, where the diversity of available prey is  
491 limited, the two species focus on the same food resources. The greatest variability in their  $\delta^{13}\text{C}$  ratios at  
492 these sites indicates that they rely on a broader number of food chains though, including those based on  
493 allochthonous sources of organic matter, like freshwater inputs (Abrantes and Sheaves, 2010). This  
494 diversification of carbon sources can be seen as an ecological response to reduce competition between  
495 species (Lecomte and Dodson, 2005). It might allow *C. latus* and *C. hippos* to co-exist in Suape and  
496 Sirinhaém in spite of their similarities in diet. The fact that the abundances of both *C. latus* and *C. hippos*  
497 juveniles are lower in these two estuaries suggests that the higher trophic niche overlap observed at these  
498 sites result in an increased competition for food among them. However, further information on the  
499 temporal fluctuations in prey abundance and the timing of their consumption is needed before one can  
500 conclude about the actual intensity of this phenomenon. First, trophic competition between fish species  
501 with similar global diets can be reduced when these later largely reflect an opportunistic use of seasonal  
502 peaks in the abundances of the most shared prey (Lucena et al., 2000; Boucek and Rehage, 2013). This  
503 might very well be the case here, especially as this kind of opportunistic feeding behavior would explain  
504 the variability in  $\delta^{13}\text{C}$  ratios observed for both species. Differences in feeding rhythms between *C. latus*  
505 and *C. hippos* may also reduce the intensity of the trophic competition among their juveniles at the daily  
506 scale, as already observed for other jack species (Blaber and Cyrus, 1983). Lastly, competition for food is  
507 also often avoided through differences in the periods for juvenile occurrence in the estuaries, as observed  
508 in local snook species with similar diets but distinct spawning periods (Stevens et al., 2020). However,  
509 this does not really apply here as *C. latus* and *C. hippos* in northeastern Brazil both are expected to spawn  
510 from April to June (Heyman and Kjerfve, 2008), and their juveniles are mostly fished in local estuaries  
511 during the late summer (McBride and McKown, 2000; Vilar et al., 2011; da Silva et al., 2018).

512

### 513 **Conclusion**

514 This study contributes to better understanding the drivers of juvenile trophic ecology and its  
515 variation in tropical estuaries. Although the two close species of jacks studied here apparently globally  
516 rely on similar prey during their juvenile estuarine life, our results revealed some plasticity in their  
517 resource use, supporting the idea that resource partitioning processes between sympatric species are  
518 locally dependent (Costa-Pereira et al., 2019). Such plasticity in resource use according to local food web  
519 structure may not only favor the coexistence of a larger number of species but also provide greater

520 stability for estuarine food webs (Kondoh, 2003). In order to evaluate it, cross-sites comparisons should  
521 be systematically undertaken when investigating the trophic ecology of sympatric fish species,  
522 particularly in tropical estuaries that show a high diversity of food sources (Layman, 2007). As spatial  
523 variation in the trophic ecology of predators like *C. latus* and *C. hippos* may not only influence the  
524 growth and survival of their juveniles, but also modulate their respective roles in the functioning of  
525 estuarine food webs, such cross-sites comparisons could be key for evaluating the implications of  
526 different co-existence scenarios, not only on the maintenance of coastal fish stocks but also on the  
527 composition and functioning of estuarine systems. This should be undertaken keeping in mind that both  
528 anthropic pressures and Climate Change may displace the environmental boundaries of estuaries or alter  
529 the composition and productivity of their food webs (Araújo et al. 2016, Chevillot et al. 2019), thereby  
530 affecting the way fish species exploit estuarine resources and modifying their roles in food webs.

531

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- 926

927 **Figure Captions**

928

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

931

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

934

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

939

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

950

951 **Tables**

952

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 (km <sup>2</sup> ) <sup>†</sup>	48.0	23.1	17.0
Water surface area (km <sup>2</sup> ) <sup>†</sup>	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) <sup>†</sup>	0.9 (0.5 - 1.3)	0.3	0.4
Pelagic productivity (mgCm <sup>-3</sup> h <sup>-1</sup> )	14.7	2.0	34.2
Temperature (°C, mean± SD) <sup>‡</sup>	28.5 ± 1.1	27.1 ± 1.1	27.2 ± 2.4
Salinity (mean± SD) <sup>‡</sup>	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		

953 Type, geomorphological classification on the type of estuary according to Pritchard's classification. Human pressure, existent anthropogenic activity with potential  
 954 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  
 955 of marine entrances, number of connections to the sea. Pelagic productivity, mean annual phytoplankton productivity. Temperature, water surface temperature.  
 956 Pluviometry, annual rainfall between 2014 and 2018.

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

960

Estuary	Species	Stomach content analysis <sup>†</sup>		Stable isotopes analysis			
		n	SL (mm)	n	SL (mm)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Santa Cruz	<i>C. latus</i>	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]
	<i>C. hippos</i>	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	<i>C. latus</i>	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]
	<i>C. hippos</i>	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	<i>C. latus</i>	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]
	<i>C. hippos</i>	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]

<sup>†</sup> Fish with non-empty stomachs only.

961

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

Item	Species							
	<i>Caranx latus</i> (n = 207; 102±27 mm)				<i>Caranx hippos</i> (n = 131; 84±25 mm)			
	$F_i$ (%)	$N_i$ (%)	$W_i$ (%)	$Q$	$F_i$ (%)	$N_i$ (%)	$W_i$ (%)	$Q$
<b>ALGAE</b>	<b>12.08</b> [7.7 – 16.9]	<b>4.19</b> [2.4 – 6.6]	<b>0.29</b> [0.1 – 0.7]	<b>0.82</b>	<b>2.90</b> [0.8 – 6.1]	<b>0.86</b> [0.1 – 2.2]	<b>0.18</b> [0 – 0.6]	<b>0.14</b>
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
<b>FORAMINIFERA</b> (Unidentified)	<b>0.48</b> [0 – 1.4]	<b>0.08</b> [0 – 0.3]	<b>&lt;0.01</b>	<b>0.01</b>	-	-	-	-
	0.48 [0 – 1.4]	0.10 [0 – 0.3]	<0.01	0.01				
<b>NEMATODA</b> (Unidentified)	<b>5.31</b> [2.4 – 8.7]	<b>1.11</b> [0.5 – 1.8]	<b>&lt;0.01</b>	<b>0.01</b>	<b>2.90</b> [0.8 – 6.1]	<b>0.48</b> [0.1 – 1.1]	<b>&lt;0.01</b>	<b>0.01</b>
	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
<b>BIVALVIA</b> (Unidentified)	<b>0.48</b> [0 – 1.4]	<b>0.32</b> [0 – 1.0]	<b>&lt;0.01</b>	<b>0.01</b>	<b>0.72</b> [0 – 2.3]	<b>0.10</b> [0 – 0.4]	<b>&lt;0.01</b>	<b>0.01</b>
	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
<b>GASTROPODA</b> (Unidentified)	<b>2.90</b> [1.0 – 5.3]	<b>1.26</b> [0.3 – 2.6]	<b>0.01</b> [0 – 0.1]	<b>0.01</b>	-	-	-	-
	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.

<b>POLYCHAETA (Unidentified)</b>				<b>0.48</b> [0 – 1.4]	<b>0.08</b> [0 – 0.3]	<b>&lt;0.01</b>	<b>0.01</b>	<b>1.45</b> [0 – 3.8]	<b>0.57</b> [0 – 1.7]	<b>0.01</b> [0 – 0.1]	<b>0.01</b>
				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
<b>OLIGOCHAETA (Unidentified)</b>				<b>0.48</b> [0 – 1.4]	<b>0.08</b> [0 – 0.3]	<b>&lt;0.01</b>	<b>0.01</b>	<b>2.17</b> [0 – 17.1]	<b>0.29</b> [0 – 0.7]	<b>&lt;0.01</b>	<b>0.01</b>
				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
<b>CRUSTACEA</b>				<b>49.28</b> [42.5 – 56.0]	<b>26.07</b> [19.7 – 33.3]	<b>23.30</b> [14.2 – 34.6]	<b>705.34</b>	<b>60.87</b> [51.9 – 68.7]	<b>65.97</b> [51.7 – 75.4]	<b>38.22</b> [22.8 – 60.3]	<b>2537.20</b>
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.

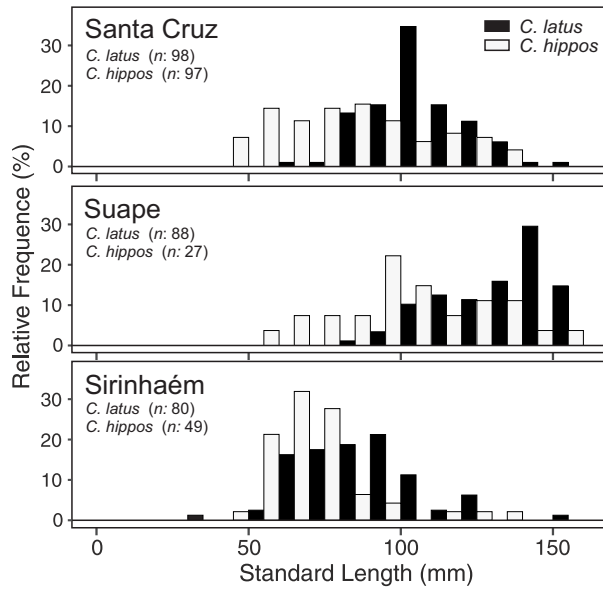
	Mysida (Unidentified)		1.93 [0.5 – 3.9]	0.79 [0.1 – 1.7]	0.01 [0 – 0.1]	0.01	7.63 [3.1 – 12.2]	36.61 [12.7 – 53.9]	4.67 [0.9 – 11.1]	170.96
	Stomatopoda (Unidentified)		-	-	-	-	0.76 [0 – 2.3]	0.11 [0 – 0.4]	0.03 [0 – 0.1]	0.01
	Ostracoda (Unidentified)		4.35 [1.9 – 7.2]	2.78 [0.8 – 5.6]	<0.01	0.01	1.53 [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
<b>HEXAPODA</b>			<b>0.48</b> [0 – 1.4]	<b>0.08</b> [0 – 0.3]	<b>&lt;0.01</b>	<b>0.01</b>	-	-	-	-
	Unidentified Insecta		0.48 [0 – 1.4]	0.10 [0 – 0.3]	<0.01	0.01				
<b>VERTEBRATA</b>			<b>84.06</b> [78.8 – 88.9]	<b>46.29</b> [37.7 – 54.9]	<b>75.10</b> [63.5 – 84.4]	<b>3252.60</b>	<b>71.74</b> [64.1 – 79.4]	<b>20.17</b> [13.8 – 29.1]	<b>60.13</b> [37.9 – 76.0]	<b>1205.15</b>
	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]
			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]
		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]
			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]
		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]
			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]
			Scianidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.24 [0 – 0.9]	0.02	-	-	-

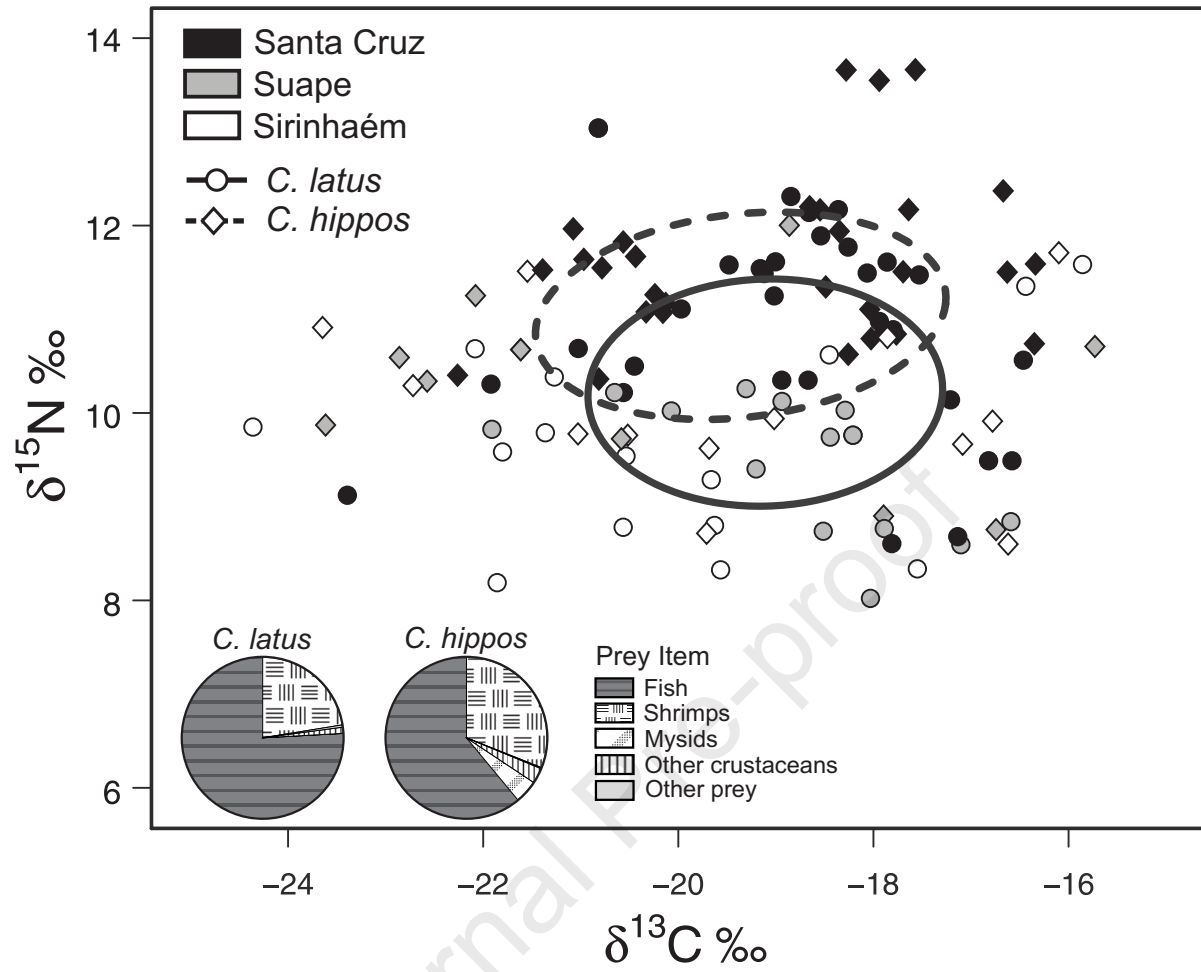
Table 3 Continued.

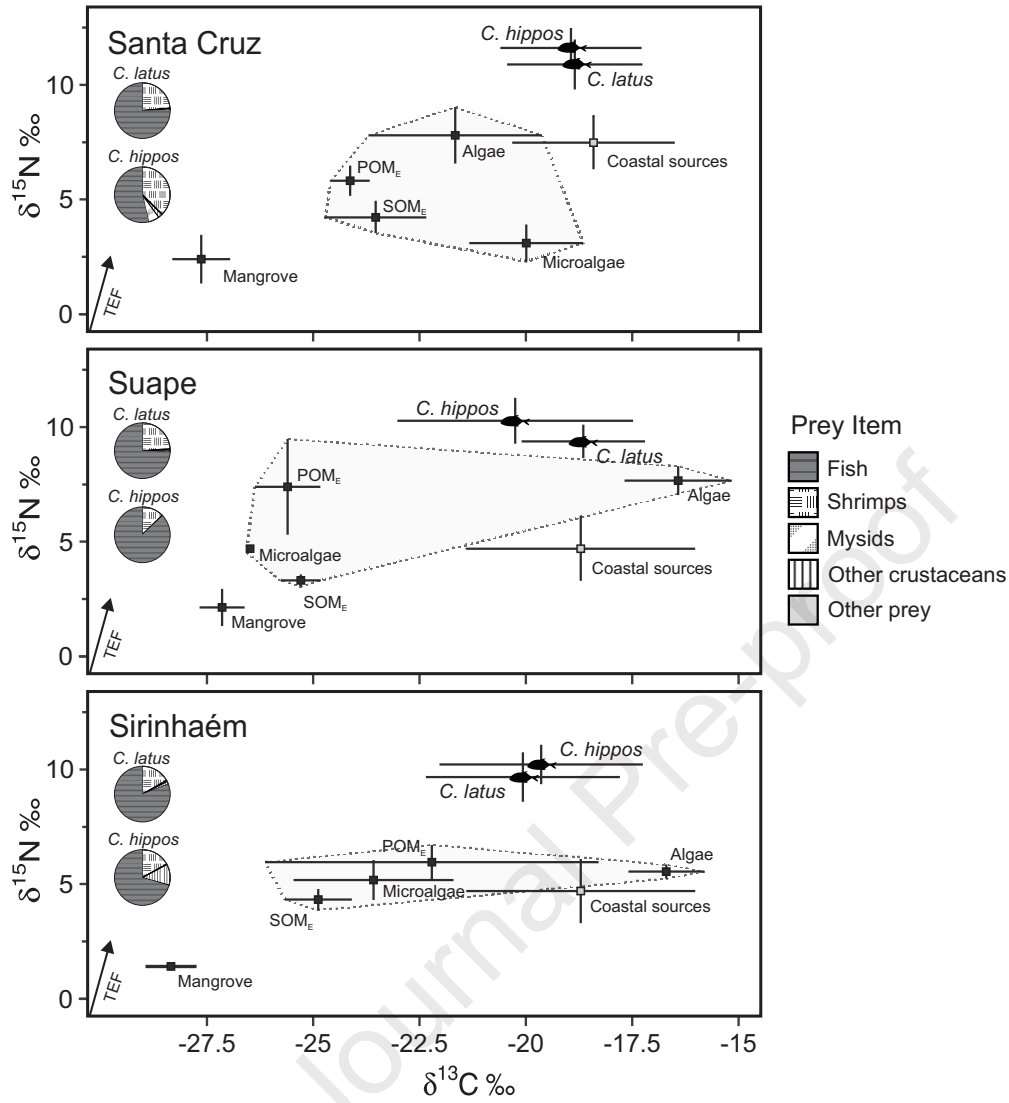


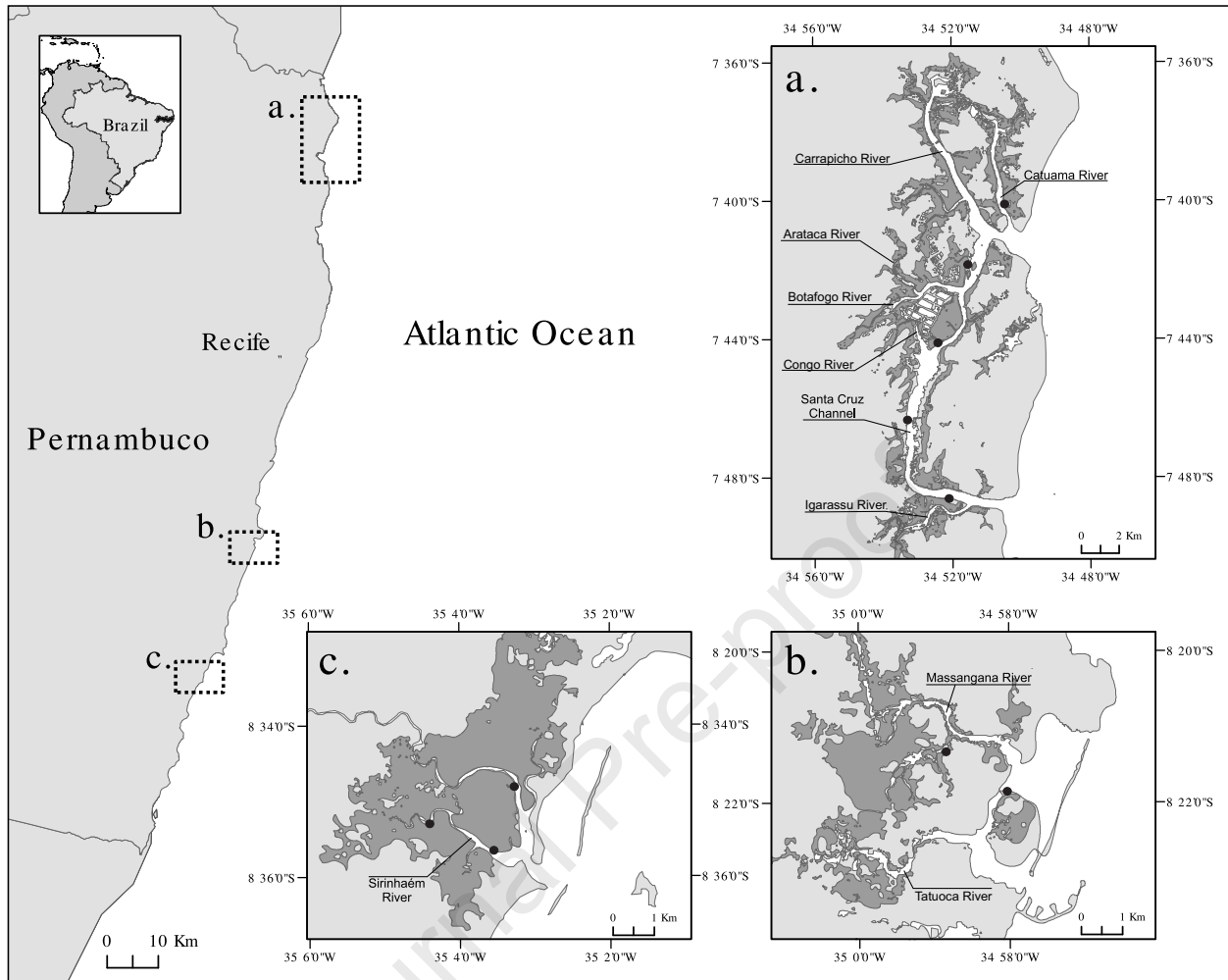
Pleuronectiformes	Cynoglossidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.14 [0 – 0.5]	0.01	-	-	-	-
	Paralichthyidae	0.48 [0 – 1.4]	0.10 [0 – 0.3]	0.04 [0 – 0.2]	0.01	-	-	-	-
Unidentified teleostei		60.39 [53.6 – 67.1]	43.00 [32.2 – 53.6]	27.12 [18.2 – 39.0]	1166.18	54.20 [45.8 – 62.6]	14.96 [9.4 – 23.5]	14.40 [8.4 – 24.0]	215.2
<b>DEBRIS</b>		<b>29.47</b> [23.7 – 35.7]	<b>20.46</b> [14.9 – 26.2]	<b>1.30</b> [0.3 – 3.2]	-	<b>33.59</b> [26.0 – 42.0]	<b>11.64</b> [7.2 – 18.3]	<b>1.46</b> [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.









### 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

Journal Pre-proof

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Sincerely.

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**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:

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