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Importance of estuary morphology for ecological connectivity with their adjacent coast: A case study in Brazilian tropical estuaries

Pelage Latifa [1, *], Gonzalez Júlio Guazzelli [1, 2], Leloch François [3], Ferreira Valdimere [1], Munaron Jean-Marie [3], Lucena-Frédou Flávia [1], Frédou Thierry [1]

[1] Universidade Federal Rural de Pernambuco, UFRPE, Departamento de Pesca e Aquicultura, Rua Dom Manuel de Medeiros, s/n, Recife, PE. CEP: 52.171-900, Brazil
[2] MARBEC, Univ. Montpellier, CNRS, IRD, Ifremer, Montpellier, France
[3] IRD, Laboratoire des Sciences de L'Environnement Marin, UMR 6539, CNRS, UBO, IRD, Ifremer, 29280, Plouzané, France

* Corresponding author : Latifa Pelage, email address : latifa.pelage3@gmail.com

Abstract :

Coastal habitats are interlinked by ecological connectivity, defined as the exchange of organic matter or organisms between habitats. The degree of this connectivity will depend in particular on the geometric properties of the landscape. The increasing anthropogenic alterations in estuaries therefore raises the need to understand how their morphological characteristics influence fluxes between habitats. We used stable isotopes to investigate the variability of ecological connectivity between three estuaries and their adjacent coastal areas by tracking the origin of the organic matter (estuarine vs coastal) underlying the diet of the migrant species Eucinostomus argenteus. The chosen estuaries were geomorphologically distinct, exhibiting, in particular, differences in their degree of connection to the sea, corresponding to the morphological features (shape, mouth width) controlling key physico-chemical variables in this habitat (e.g. salinity). The sampling of the basal food sources contributing to the food web was performed in the three estuaries and in their adjacent coasts. The variability in stable isotope ratios between estuaries was examined for both fish and sources of organic matter. In the three estuaries, Bayesian models were applied for each season (dry and rainy) to quantify the relative contribution of sources from estuarine and coastal environments supporting the diet of the silver mojarra. The share of coastal organic matter increased with the degree of sea connection, indicating that the properties of the seascape can regulate the intensity of interactions between ecosystems. Variations in ecological connectivity are likely to affect the functioning of ecosystems as they influence trophic pathways and energy flows between adjacent habitats. Morphological modifications could thus significantly disturb ecosystems by altering the structure of food web, thereby affecting certain ecosystem services such as the availability of living marine resources.

Highlights

►The origin of the organic matter underlying food webs was investigated in three estuaries with distinct morphologies. ► Coastal organic matter contributed more to fish diet when landscape properties enabled a better sea-connection. ► Estuary morphology regulates interactions between estuaries and their adjacent coast.

1. Introduction

The emergence of seascape ecology brought the need to consider coastal habitats as a single continuum rather than as separate biomes (Green et al., 2012; Berkström et al., 2013). This conceptual change aimed at a more integrated management of the coastal zone (Beger et al., 2010). In particular, addressing the connectivity between habitats is essential for fisheries management because coastal habitats provide complementary ecological functions that are critical for marine living resources (Sheaves, 2009). Coastal habitats should therefore not be considered as isolated patches in which different sub-populations occur, since a comprehensive view reflects population dynamics more accurately (Burgess et al., 2014).

Ecosystem interactions can be primarily subdivided into biological, chemical and physical interactions (Ogden, 1997). The connectivity degree between coastal habitats will depend in particular on the geometric properties of the landscape (Olds et al., 2017). More specifically, landscape characteristics affect ecological connectivity which consists of the Interactions between ecosystems through the movement of organisms and the exchange of nutrients and organic matter that are involved in ecological processes within these systems. (Nagelkerken, 2009). Previous work demonstrated that variability in the geometric characteristics of the seascape, such as the distance between habitats, can affect the intensity of flows between habitats (Mumby et al., 2004; Berkström et al., 2013).

Estuaries include a wide range of different transitional water bodies with distinct landscape characteristics (Flemming, 2011). Thereby, the classification of estuaries requires the consideration of physico-chemical variables such as hydrodynamics and bathymetry, as they determine not only the dynamics and structure of the sediments, but also the nature of the primary producers (Elliott & McLusky, 2002; Whitfield & Elliott, 2011). Consequently, the morphology of estuaries and, in particular, the set of geometrical variables controlling the degree of sea water dilution in the estuary (like depth and mouth width), could have an influence on ecological connectivity. This morphological variability, which can be viewed as their degree of connection to the sea, is likely to enhance or prevent flows with adjacent coastal habitats. In addition, estuarine morphologies suffer from increasing anthropic alterations, such as the construction of polders, harbours or dykes which can drastically change the sedimentary dynamics and the composition of estuarine biological communities (Wetzel et al., 2012; Du et al., 2016; Lechêne et al., 2018). It is thus relevant to investigate how estuarine morphological characteristics influence interactions between habitats. The implications of this variability in terms of ecosystem functioning need to be taken into account before deciding to modify seascape features or implement restoration measures through eco-engineering (Elliott et al., 2016).

Understanding ecological connectivity involves studying energy pathways in food webs and their intrinsic trophic relationships in order to assess community structure and functional role of species living in the ecosystems (Pasquaud et al., 2010; França et al., 2011). Hence, estuarine food webs can be described by characterizing trophic relationships, sources of organic matter and energy flows between system components (Pasquaud et al., 2008). In these complex and dynamic ecosystems, food webs can be supported by the production of various local primary producers, as well as the transport of organic matter from adjacent coastal and riverine areas (Choy et al., 2009; Selleslagh et al., 2015). However, identifying the origin of the organic matter at the base of estuarine fish food web can be difficult, in particular because conventional methods like gut content analysis provide only a snapshot of the diet at a given time (Pasquaud et al., 2008 ; Pasquaud et al., 2010; França et al., 2011). Moreover, gut analyses do not enable a comprehensive food web analysis to reliably track the source of the organic matter underlying the diet of high trophic level consumers that do not feed directly on primary producers.

Stable isotope methods produce estimates of trophic position that can both capture complex trophic interactions and track energy flows between habitats (Carvalho et al., 2017; Whitney et al., 2018; Gonzalez et al., 2019). Since a consumer's stable isotope ratios reflect the values of its food sources, trophic position assessment is possible if the differences in isotopic composition between an animal and its prey, i.e. trophic level enrichment, are known (Caut et al., 2009). Indeed stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) have been successfully used to study ecosystem functions and food webs (Le et al., 2018). $\delta^{15}N$ can constitute a proxy for the trophic position of an organism since it increases considerably with the trophic level (Post, 2002; Caut et al., 2009). On the other hand, $\delta^{13}C$ differs substantially between primary producers (Post, 2002; Herzka, 2005), providing an overview of the origin of organic matter (Fry, 2006) .

In estuaries, the origin of organic matter has already been studied with stable isotopes and a high contribution of marine basal sources has been highlighted in some studies (Pasquaud et al., 2008; Selleslagh et al., 2015). Nevertheless, other studies conducted in estuaries have shown that *in situ* primary production can outweigh other food sources and contribute significantly to fish growth (Lobry et al., 2008). Therefore, knowledge on the extent of ecological connectivity between estuaries and their adjacent coastal areas is essential for designing the scale of conservation measures, particularly in the case of migratory species using multiple habitats (Vasconcelos et al., 2010; Reis-Santos et al., 2018).

Migratory species constitute a good proxy to study ecological connectivity between two habitats since their movements represent linkages across the seascape (Selleslagh et al., 2015). In this study, we chose *Eucinostomus argenteus* Baird & Girard (1855) to investigate the intensity of the flows between habitats. The silver mojarra is a member of the Gerreidae family comprising species with complex life strategies that are important for artisanal fisheries in north-eastern Brazil (Pinto et al., 2013). *E. argenteus* is one of the main Gerreidae in the region and can be classified as an estuarine-dependent species, as its juveniles are found in great abundance in the estuarine habitats (Potter et al., 2013) where they reside since their reduced size at this ontogenetic stage (less than 13.5 cm) (Bouchon-Navaro et al., 2006) does not allow them to make large migrations (Franco et al., 2012). In those habitats, they were classified as second-order consumers, feeding opportunistically as well on microcrustaceans (amphipods, copepods, tanaidaceous, ostracods) as on detritus with variations in the proportion and frequency of different items according to their ontogeny and food availability (Chi-Espínola et al., 2018). Although adults of these species are more abundant in adjacent coastal areas (Ramos et al., 2016), they use estuaries as a feeding ground, predating mostly on Bivalvia siphons and polychaetes (Vasconcellos et al., 2018) or as a reproductive ground (Chaves and Bouchereau, 2000). The degree of ecological connectivity between estuaries and adjacent coast would be reflected by the dominant origin of the carbon sources (coastal vs estuarine origin) on which the species diet is based.

The objective of this study is to understand the variability in ecological connectivity between estuarine and coastal habitats. We are thus investigating the flows between three morphologically distinct estuaries and their adjacent coastal areas by tracking the origin of the organic matter (coastal or estuarine) underlying the diet of *E. argenteus*. Our hypothesis is that geomorphological disparities between estuaries influence the origin of the organic matter that supports the *E. argenteus* regime, based on the assumption that flows are enhanced in the estuaries most connected to the sea.

2. Material and Methods

2.1 Study Area

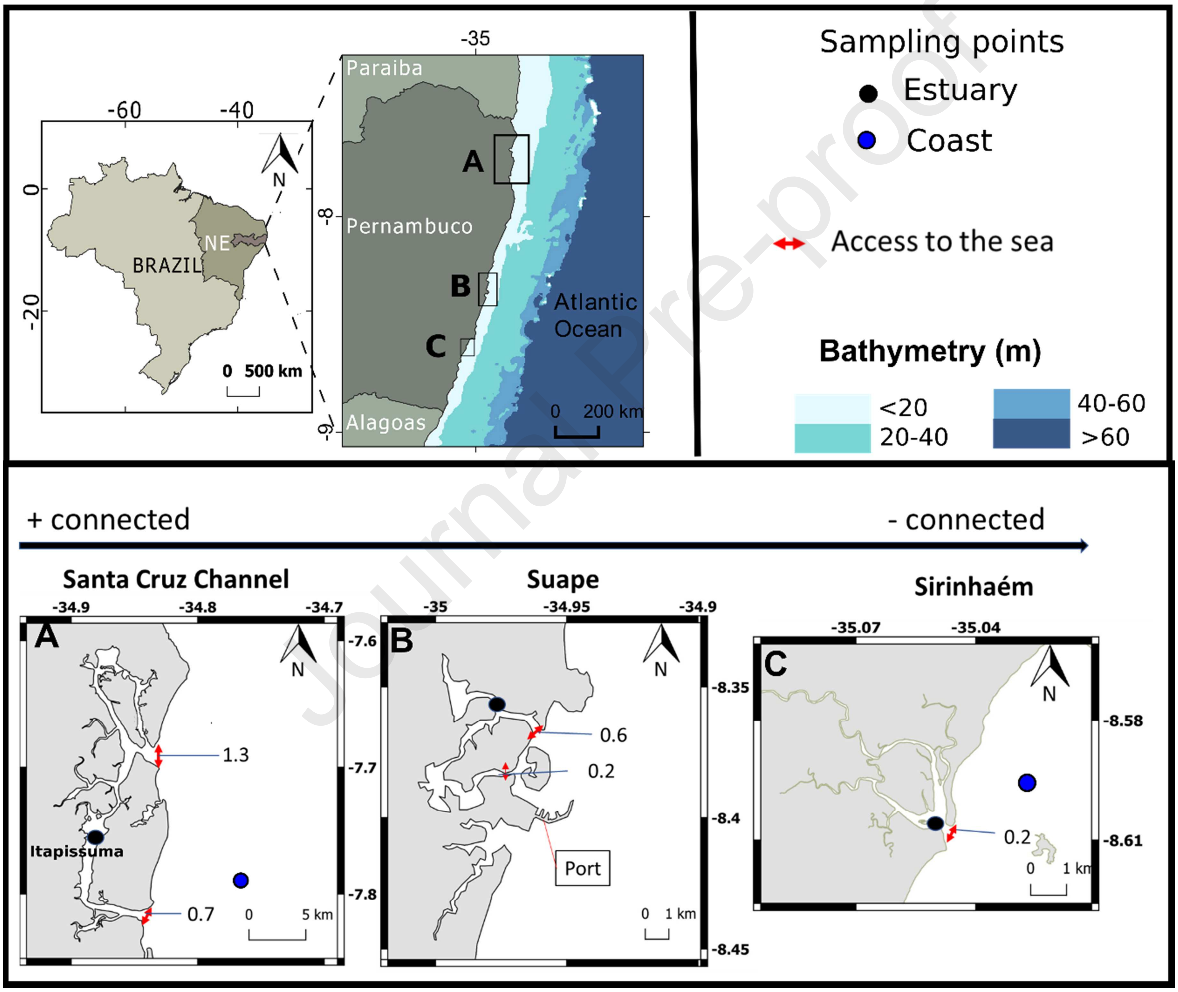

Figure 1: Map of the area under study showing the three estuaries (Santa Cruz Channel, Suape and Sirinhaém) and their adjacent coast where sampling was performed in the state of Pernambuco, Brazil. The widths of the mouths are indicated in kilometers for each estuary to show their geomorphological disparities, providing them with different degrees of connection with the sea.

The area under study encompasses estuarine areas and shallow coastal waters of the continental shelf of the state of Pernambuco, Brazil (Figure 1). This narrow continental shelf (35 km on average),is characterized by shallow and warm waters (typically 26-29°C), soft slope, shelf break between 50 and 60 m, high salinity (>36) and a sedimentary cover composed of carbonatic and terrigenous sediments (Manso et al., 2003;

Assunção et al., 2020). Three estuaries, the Santa Cruz Channel, Suape and Sirinhaem, were chosen because of their diverse morphological characteristics, which differ in particular in the geometric variables controlling the degree of dilution of the sea water in the estuary (such as the depth and width of the mouth) (Table 1, Figure 1). This different degree of connection to the sea is manifested notably by a difference in salinity (Table 1).

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

Characteristics	+ connected	**Estuary**	- connected →
	Santa Cruz	**Suape**	**Sirinhaem**
Type	Ria	Coastal lagoon	Coastal plain
Estuary (km²) †	73.5	29.7	18.7
Vegetated area (km²) †	48.0	23.1	17.0
Watershed area (km²) †	25.5	6.6	1.7
Mean depth (m)	7.5 (North) /3.0 (South)	3.1	2.6
Mouth width (km) †	1.3/0.7	0.6/0.2	0.2
Salinity (mean± SD) ‡	31.2 ± 2.9	17.8± 2.4	9.6 ± 3.7
Pluviometry (mm; mean± SD)	1517 ±122	1869±367	2053±699
Activity	Aquaculture, industrial and domestic waste	Industrial harbour, industrial and agriculture waste	Industrial domestic and agriculture waste
Reference	(Medeiros & Kjerfve, 1993; Guimarães et al., 2010; Medeiros et al., 2001; Silva et al., 2011)	(CPRH, 2001; Borges, 2011; Silva et al., 2011)	(CPRH, 2001; Silva et al., 2011)

† Data obtained with the software ArcGis 10.1 based on satellite images from LANDSAT 7. ‡ Personal data collected during surveys in 2015. Type: geomorphological classification on the type of estuary according to Pritchard's classification. Estuary: estuary's area as the sum of mangrove and watershed areas. Salinity: Salinity at mid-depth of the water column. Pluviometry: Annual mean between 2014-2018 measured in stations near sampling points (APAC, 2020). Activity: existent anthropogenic activity with potential impact on the estuary.

The Santa Cruz Channel is located on the north coast and forms the largest estuarine complex in Pernambuco. It displays a U-shaped surface area of 22 km and has two accesses to the Atlantic Ocean (Silva et al., 2011). These two mouths are 0.7 km and 1.3 km wide, respectively, providing it with a high degree of connection with the open sea, resulting in high salinity (Table 1). In addition, the city of Itapissuma is the main fishing centre of Pernambuco, and also one of the most touristic destinations of the region. (Quinamo, 2006). Aquaculture, artisanal fishing, industry and agriculture are all important anthropogenic activities in the area (Moura and Candeias, 2009).

The Suape estuary, situated in the south coast, is a coastal lagoon with a flattened geomorphological shape (Santos and Costa, 1974). The geomorphological and hydrodynamic conditions were altered by the construction of the port in 1979 (Muniz et al., 2005). The generated landfills blocked the flow of two of the four rivers that previously drained into the Suape estuary. Suape is now formed by two main rivers that flow into a large brackish lagoon and has a restricted connection to the ocean.

Also located in the south littoral of Pernambuco, Sirinhaem is the smallest estuary among the three and presents the narrowest connection to the sea (CPRH 2001). This enclosed lagoon exhibits low salinity and low depth (Table 1). Artisanal fishing, agroindustry and trade are important socio-economic activities in the zone (Valença et al., 2010).

2.2 Sampling

2.2.1 Fish and baseline

E. argenteus was captured in the three estuaries above described, in shallow areas (Figure 1). The specimens were collected in 2015 from March to August and from September to January, which represent the local rainy and dry seasons, respectively (Medeiros et al., 2001) with the help of local fishermen using artisanal fishing gears. All gears characteristics are detailed in the Supplementary Table 1. After identification, all fish were measured to the nearest millimetre (Total length) and weighed to the nearest gram. In addition, a long-lived primary consumer (mangrove oyster *Crassostrea rhizophorae*) was collected to represent the baseline for estimating the trophic position of *E. argenteus*.

2.2.2 Organic matter sources

Organic matter sources were sampled in the estuaries, to provide a background of stable isotope ratios at the base of *E. argenteus* diet. Since mojarras are characterized by their highly protrusible mouth which they use to feed on items they remove from the sediment (Chen et al., 2007), sources associated to the benthic system were selected. Thus, macroalgae (*Sargassum* sp. and *Ulva* sp.), microphytobenthos, rotten mangrove leaves and particulate organic matter in the sediment (SOM) were collected along with seagrass when present in the area.

The SOM was also collected from the adjacent coast (shallow coastal waters) of the Santa Cruz Channel and Sirinhaem to measure the influence of coastal sources. However, as an industrial port is settled in the coast in front of the Suape estuary, the sampling of the coastal SOM could not be realized due to the restricted access to the area. We thus chose to use the coastal SOM isotopic ratios of Sirinhaem as a proxy for Suape considering the vicinity of the two areas.

The rotten mangrove leaves, seagrass and macroalgae were picked up manually during low tide. The SOM was collected from the first 2 mm layer of sediment while microphytobenthos (i.e. benthonic microalgae) was sampled from the sediment surface at low tide and extracted in the laboratory.

2.3 Isotope analysis

For stable isotopic analysis, a fragment of dorsal white muscle from each fish was extracted and cleaned with distilled water to remove any remaining scales or bones. The isotope analysis of the basal sources was performed on the whole collected sample. The material was dried in an oven at 60°C for 48 hours. Then, dried samples were grinded into a homogeneous fine powder with a mortar and pestle. The SOM samples were divided into two subsamples. One was acidified to remove inorganic carbon before the $\delta^{13}C$ analysis and the other was used for $\delta^{15}N$ analysis (Pinnegar and Polunin, 1999). Analysis of the carbon and nitrogen isotope ratios were performed at the Pôle de Spectrométrie Océan (PSO - IUEM, Plouzané, France) with an elemental analyzer (Thermo Flash 2000, interface Thermo ConFio IV) interfaced to a mass spectrometer (Thermo Delta V+).

The isotope ratio for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were calculated from the relation between the sample isotopic value and a known standard:

$\delta^{13}C$ or $\delta^{15}N = [(R\text{sample} / R\text{standard})-1] \times 1000$.

In this equation, *R* represents the ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The R standard is relative to international standards, the Air and V-PDB (Vienna PeeDee Belemnite) for nitrogen and carbon, respectively. The precision of the analysis was monitored through a known standard (Thermo – Acetanilide) every six samples and defined as ± 0.11‰ (standard error) and ±0.07‰ for carbon and nitrogen, respectively.

2.4 Statistical Analyses

All the statistical analyses were performed with the software R version 3.5.2 (R Core Team, 2019). Mann Whitney tests were carried out to determine if there were any differences in $\delta^{13}C$ and $\delta^{15}N$ between the estuarine and coastal SOM. Spearman ranking tests correlation tests were performed to examine the relationship between fish $\delta^{13}C$ or $\delta^{15}N$ and total fish length in each estuary separately and for all estuaries together. Mann Whitney tests were applied to check whether the $\delta^{13}C$ and $\delta^{15}N$ of the fish varied seasonally in each estuary.

The trophic positioning of *Eucinostomus argenteus* was determined using the tRophicPosition package ("tRophicPosition: Bayesian Trophic Position Calculation with Stable Isotopes" (Quezada-Romegialli et al., 2018).The trophic position estimate is influenced by the baseline's representativeness of the target consumer food chain (Post, 2002). In view of the zoobenthivorous diet of the species studied, we proposed an estimate based on a long-lived filter feeder as a reference base (*C. rhizophorae*).

Kruskal-Wallis tests together with Dunn's post hoc tests were used to see if there were differences of $\delta^{13}C$ and $\delta^{15}N$ for the fish and the baseline (*C. rhizophorae*) among the different estuaries.

Moreover, the Standard Elliptical Area (SEA) method was applied to compare the isotopic composition of the fish caught in each estuary. The SEA encompasses about 40% of the data (mean and standard deviation of covariables $\delta^{13}C$ and $\delta^{15}N$) and provides an appropriate method for comparing the isotope niche (variability in isotope ratios) of groups belonging to several communities by eliminating extreme values that would bias the analysis if only the amplitude was considered (Jackson et al., 2011). The SEAc (corrected standard ellipse area) was calculated to overcome the underestimation for small sample sizes (Jackson et al. 2011). The SEAc was estimated for each estuary and season. These analyses were performed with the Stable isotope Bayesian analysis in R (SIBER) package (Jackson et al., 2017).

Bayesian stable isotope mixing models, using the MixSiar package (Stock & Semmens, 2015) were built to estimate the relative contributions of basal sources to *E. argenteus* diet in each estuary. MixSiar allows the inclusion of covariates to better understand the variance among both consumer and source tracer values

(Stock et al., 2018). As estuarine environments are highly dynamic, the factor season was added for both the fish and the sources. The use of separate models for each season would have increased the residual error (Stock et al., 2018). The input data were ratios of carbon and nitrogen from fish along with the respective mean and standard deviations of sources for a given estuary and season. When sources were not significantly different between seasons, the annual average for both the rainy and dry seasons was used. Mixing models are highly influenced by the selection of a proper trophic enrichment factor (TEF) (Parnell et al., 2010). The TEF consists in the isotopic fractionation from source to consumer (Post, 2002). Since this TEF varies with both the diet and the habitat (Bunn, Leigh, and Jardine 2013), we chose a TEF proper to apply between estuarine zoobenthivorous fish (which is a second-degree consumer) and its basal sources of organic matter (primary producers): 2.0 ± 0.6 ‰ and 5.6 ± 1.5 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively (see Kostecki et al., 2012; Selleslagh et al., 2015). As the $\delta^{15}N$ of fish in each estuary were not significantly different between seasons (Supplementary Table 2), the same TEF was applied for both seasons assuming that *E. argenteus* fed at the same trophic levels during the dry and rainy seasons. The signatures of the sources after application of TEF were represented on the same two-dimensional space as the isotope ratios of the consumers in order to verify a geometric prerequisite for the execution of Mixsiar. The mixing models were only run when the consumer isotope ratios were within the mixing polygon bounded by the base source signatures representing the trophic limits of the system (Phillips and Gregg, 2003).

3. Results

3.1 Fish isotopic variability and trophic position

A total of 46 samples of *E. argenteus,* 25 *C. rhizophorae* samples and 112 of basal food sources had their $\delta^{13}C$ and $\delta^{15}N$ isotope values analysed (Supplementary Table 2 and 3). Estuarine fish size ranged from 3.6 cm (in Suape) to 16.6 cm (in Sirinhaem) (Figure 2). The size of the fish was not correlated to their $\delta^{15}N$ nor their $\delta^{13}C$ values when considering all estuaries together (Supplementary Table 4). However, fish size in the Santa Cruz Channel was positively correlated with their $\delta^{15}N$ values and the fish size in Suape were negatively correlated with their $\delta^{13}C$ (Supplementary Table 4, Figure 2).

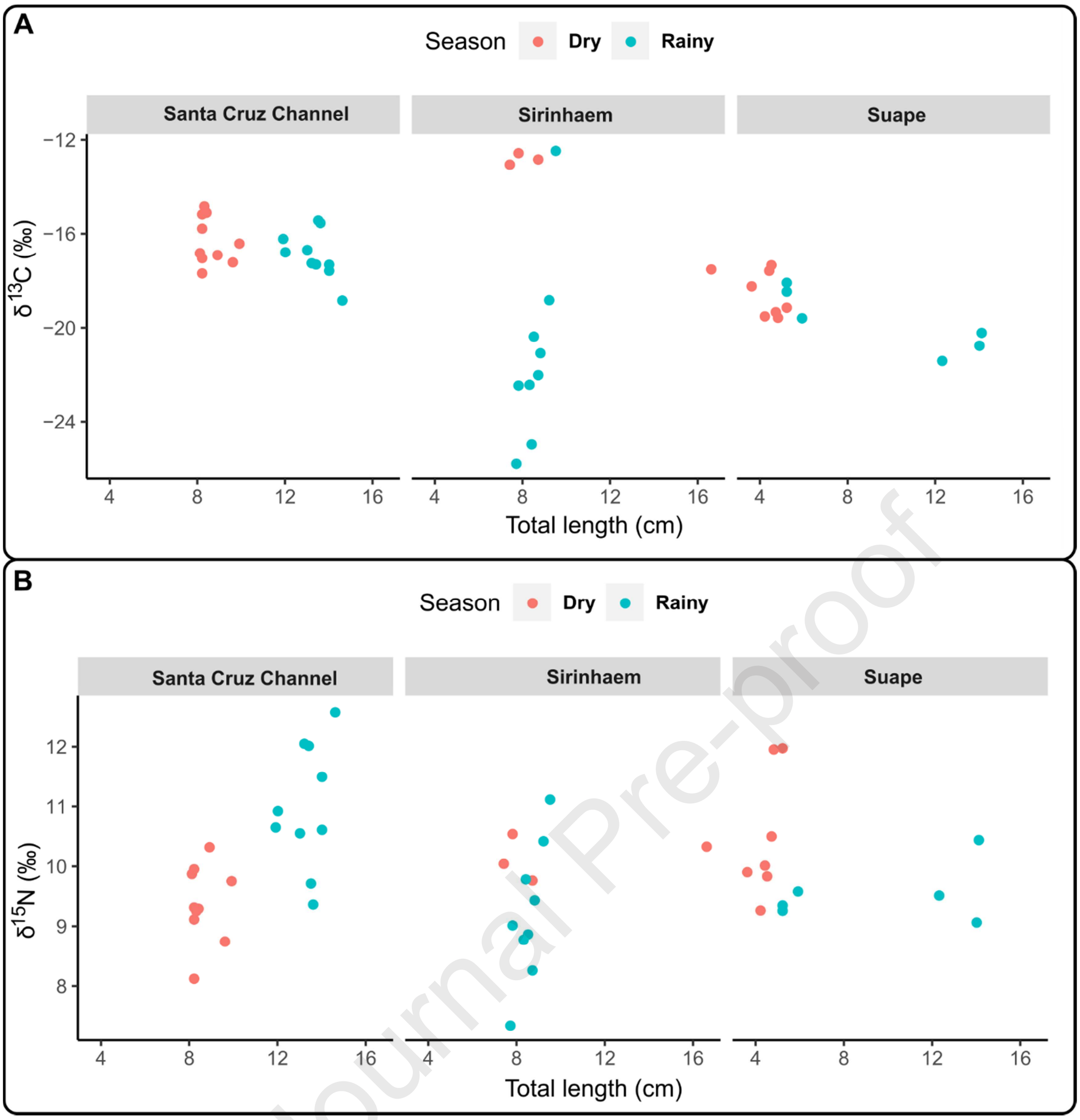

Figure 2: Biplot showing A) the δ^{13}C and B) the δ^{15}N of fish according to their total length in in each estuary (Santa Cruz Channel, Sirinhaem and Suape) during both seasons (dry and rainy).

Seasonal variations in terms of δ^{15}N were only observed for fish captured in the Santa Cruz Channel (Supplementary Table 5). Seasonal differences in δ^{13}C were detected only for Sirinhaem (Supplementary Table 5, Figure 2, 3). In addition, Sirinhaem was the only estuary where the ellipses of both seasons did not overlap. However, the overlap between the rainy and dry ellipses was small for Suape and the Santa Cruz Channel.

Sirinhaem ellipse during the rainy season completely overlaps the Suape ellipse for the rainy season and overlapped an important part of Suape ellipse for the dry season. Sirinhaem fish collected during the rainy season had the most depleted δ^{13}C, followed by the Suape fish in both seasons (Figure 3) while the δ^{13}C of the Santa Cruz Channel fish caught in both seasons exhibited more enriched δ^{13}C values, comparable to those of the coastal SOM. Fish caught in Sirinhaem during the dry season had the highest values of δ^{13}C. The most elevated values of SEAc were observed for Sirinhaem during the rainy season (10.1‰^{2}). All the other estuaries /seasons values exhibited low SEAc (between 1.9 and 3.7‰^{2}).

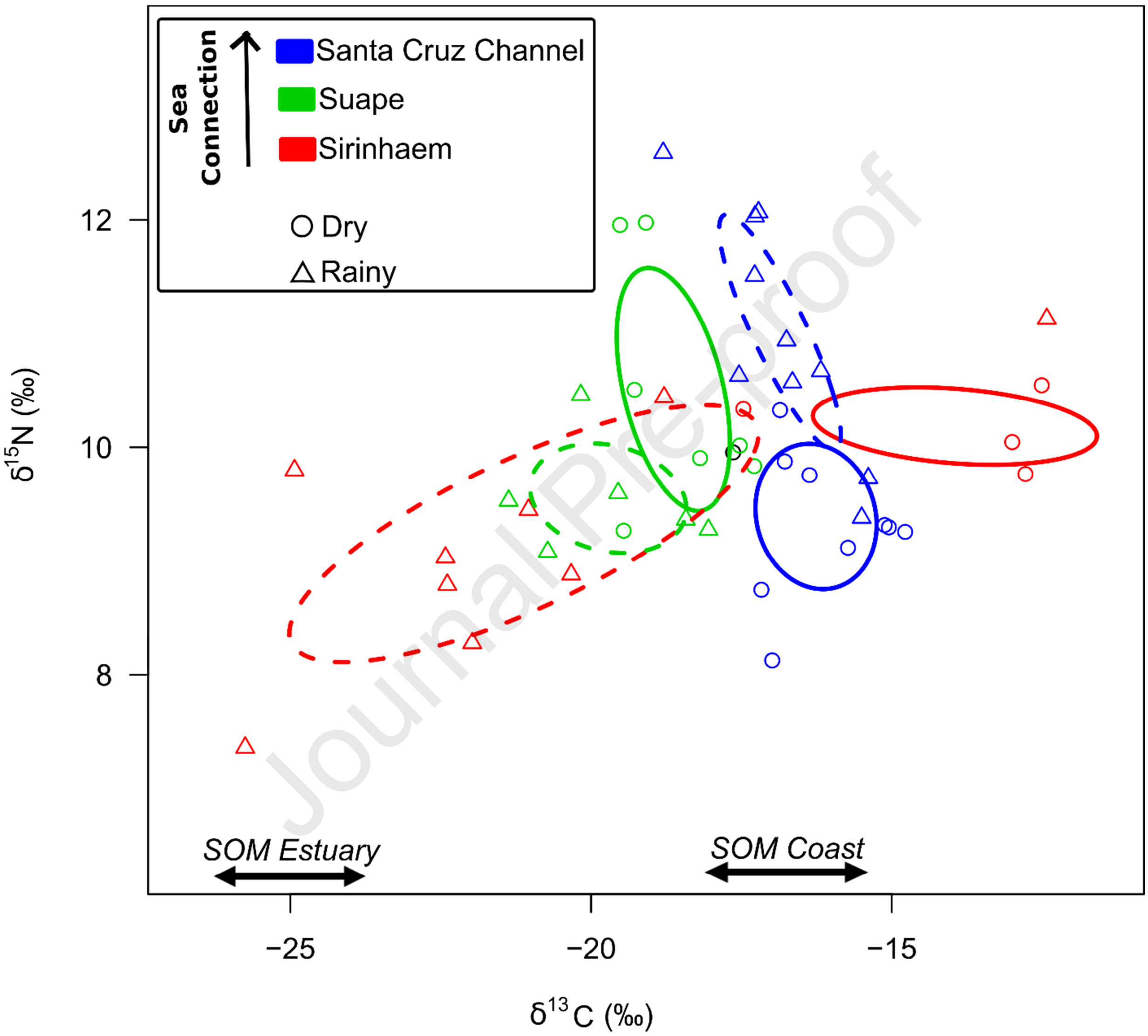

Figure 3: Fish standard ellipses of the three estuaries during both dry (solid line) and rainy (dashed line) seasons. The black points represent the fish sampled in coastal areas which are plotted to highlight the differences in the degree of connection to the sea among the three estuaries (Santa Cruz Channel, Suape and Sirinhaem). The δ13C values of the SOM collected in estuaries (-25 ± 1.2 ‰) and at the coast (-17 ±1.6 ‰) are shown in the graph to give an indication of the δ13C values at the base of each environment.

The δ^{15}N values of the fish among estuaries were not significantly different (Kruskal-Wallis chi-squared = 1.9052, p-value > 0.05) whereas δ^{13}C values varied depending on the estuaries (Kruskal-Wallis chi-squared = 14.458, df = 2, p-value < 0.05) and the Santa Cruz Channel was significantly different from Suape and

Sirinhaem (Dunn's test, p-value < 0.05).Likewise, the *C. rhizophorae* δ^{15}N did not exhibit differences among estuaries (Kruskal-Wallis chi-squared = 5.6029, df = 2, p-value > 0.05) but their δ^{13}C were different (Kruskal-Wallis chi-squared = 15.382, df = 2, p-value > 0.05). The trophic positions of *E. argenteus* were similar among the estuaries: 2.78 ± 0.17 in Sirinhaem, 2.75 ± 0.14 in Suape and 2.66 ± 0.11 in the Santa Cruz Channel.

3.2 Sources contributions to *E. argenteus* diet

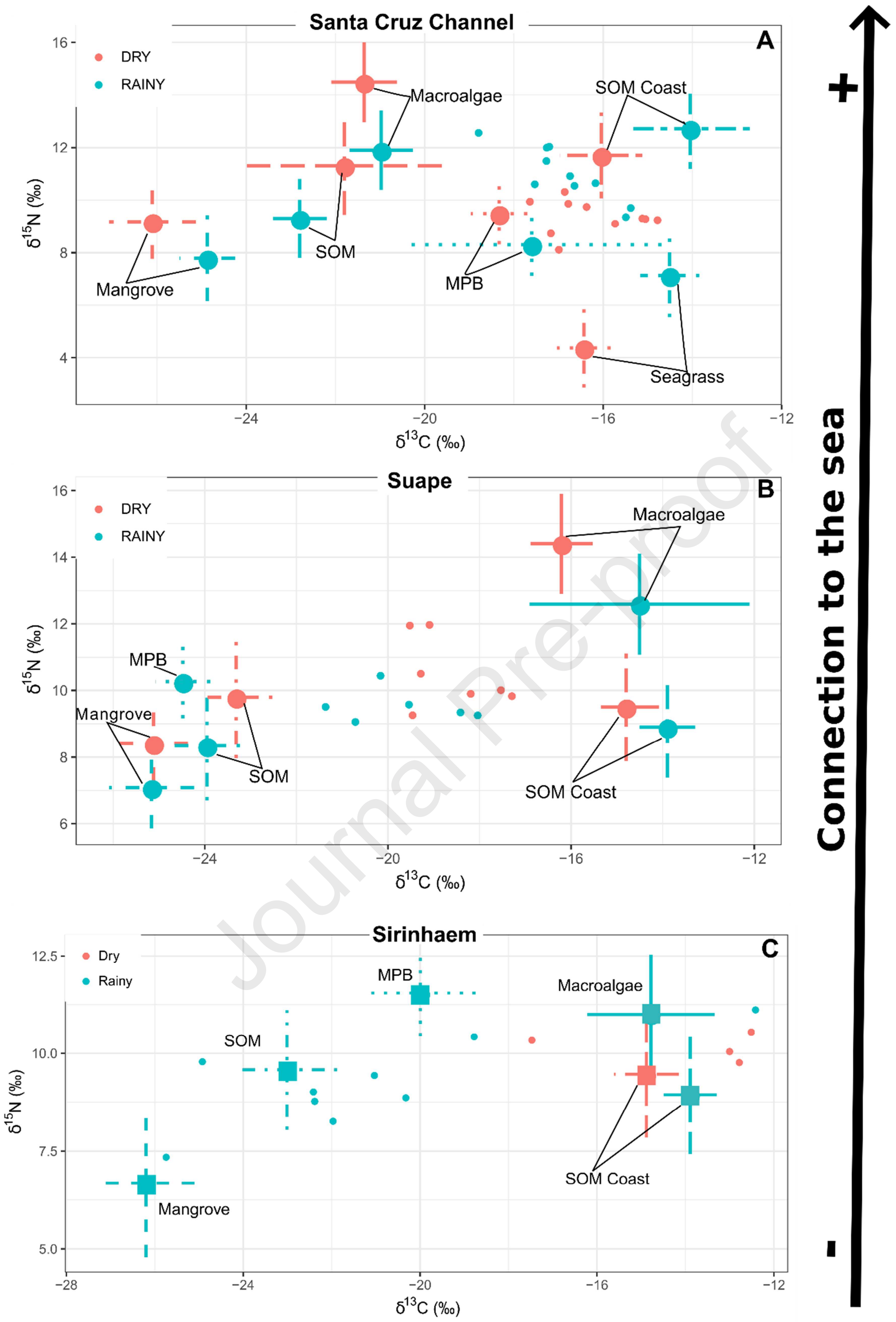

Figure 4: Dual plots of the sources (represented by the squares and whiskers showing mean values ±SD of the δ^{13}C and δ^{15}N) and the consumers (represented by the points) after applying the trophic enrichment factor to the basal sources in the three estuaries (Santa Cruz Channel, Suape and Sirinhaem). SOM: Sedimentary organic matter; mangrove: mangrove leaves; MPB: microphytobenthos.

In all three estuaries, several basal sources exhibited overlapping isotopic signatures (Figure 4). Indeed, the macroalgae ratios were close to those of the SOM in the Santa Cruz Channel while in Suape, depending on the season, both the microphytoplankton and mangrove leaves signatures were similar to the isotopic ratios of the estuarine SOM. Likewise, in Sirinhaem, the macroalgae overlapped the coastal SOM during the dry season. Most of the Sirinhaem fish ratios during the dry season were close to those of the macroalgae and the coastal SOM but were distant from the other sources. During the dry season, most of the Sirinhaem *E. argenteus* points displayed on the dual plot were outside the mixing polygon delimited by the basal sources. This pattern suggests that the selected sources were not appropriate to adequately describe the organic matter that supports the diet of *E. argenteus*. Thus, the MixSiar model was run only for the rainy season in this estuary.

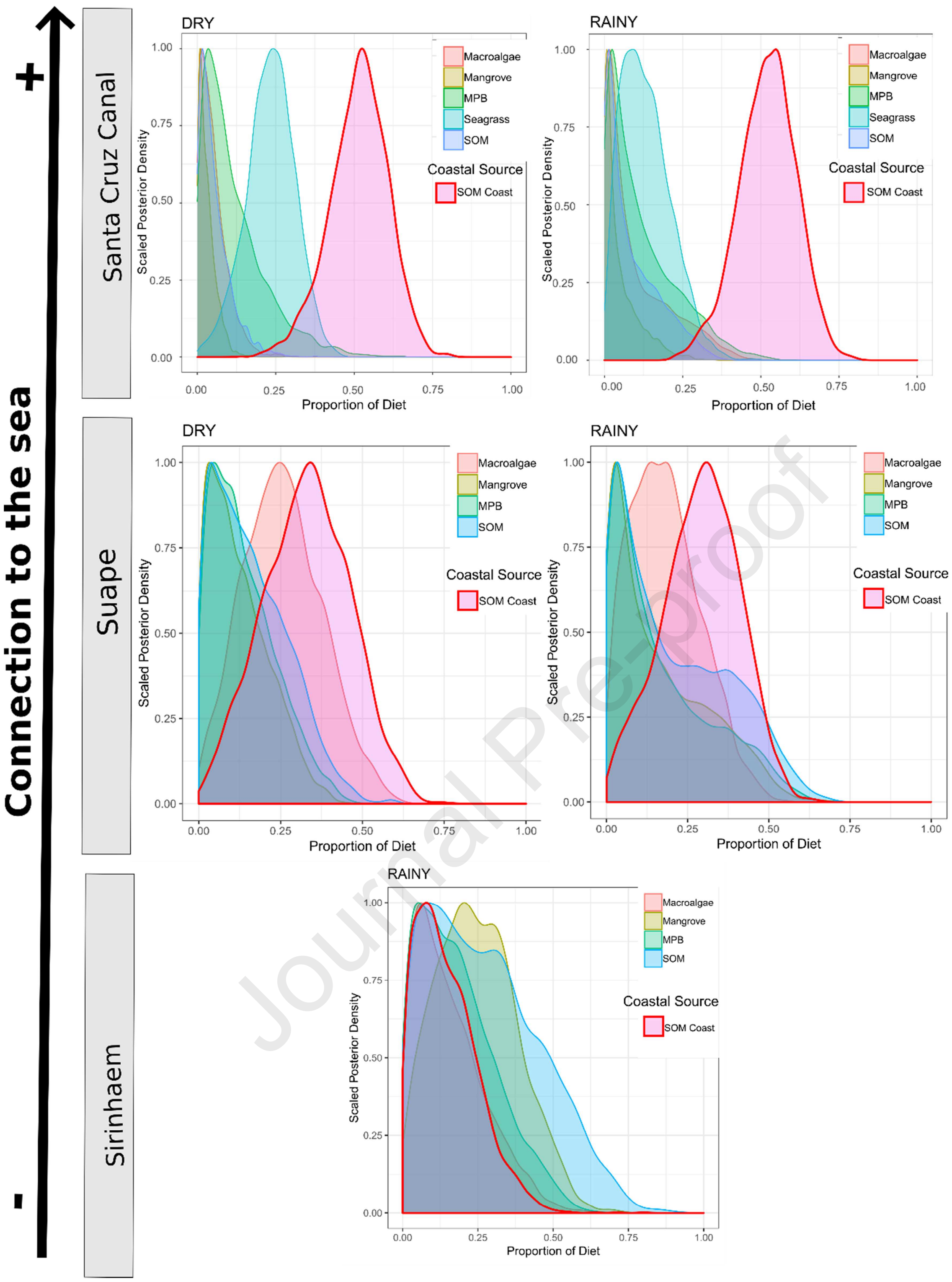

Figure 5: Density plots representing seasonal proportion of the basal sources in the diet of *E. argenteus* at the Santa Cruz Channel, Suape and Sirinhaem. SOM: Sedimentary organic matter; mangrove: mangrove leaves; MPB: microphytobenthos.

Overall, the relative contributions of the basal sources were different between estuaries (Figure 5, Supplementary Table 6). The proportion of coastal source compared to estuarine sources increased with the sea connection (Figure 5, 6 and Supplementary Table 6). The relative contribution of the coastal source is high in Santa Cruz Channel, lower in Suape and minimal in Sirinhaem (Figure 5, 6).

The contribution of the coastal SOM in the Santa Cruz Channel was the largest in both seasons, accounting for slightly more than 50% of the diet of *E. argenteus*. During the dry season, the seagrass had an important contribution during the dry season (23 %) whereas it contributed less during the rainy season (13%). The microphytobenthos contribution was also relevant in both dry and rainy season (around 12 %). The other sources contributions are low (less than 10%).

The coastal SOM had also the highest contribution during both seasons in Suape attaining the value of 32% during the dry season and 29% during the rainy season, but its relative participation was less substantial than in the Santa Cruz Channel. The other sources with relevant contribution in that area were the macroalgae during the dry season (25 %), and the SOM in the rainy season (20 %). The contributions of the other sources were similar, fluctuating between 10 and 20 %.

On the other hand, in Sirinhaem, the Coastal SOM exhibited the lowest contribution during the rainy season. No sources contribution was higher than 30 %. The two sources with relevant contribution were the estuarine SOM (27%) and the mangrove leaves (24%). The rest of the source contributions varied between 10 and 20%. Yet, the amplitude of the curves expressed a high variability among individuals.

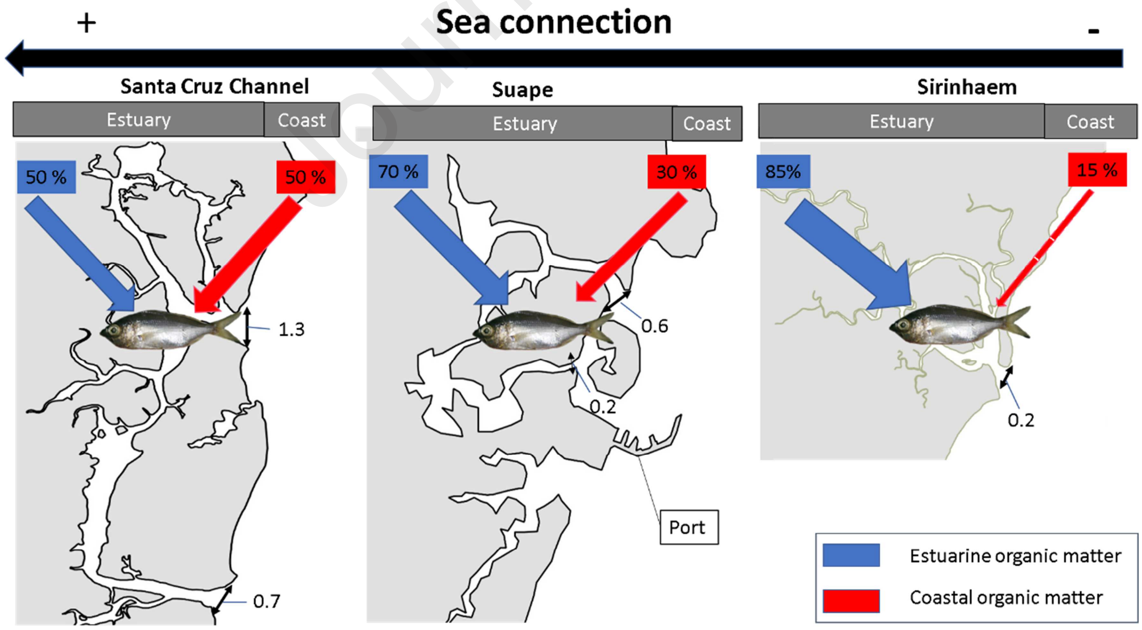

Figure 6: Conceptual model summarizing the relative contribution of estuarine and coastal organic matter supporting the diet of *E. argenteus* in the three estuaries studied. In Sirinhaem, the relative contributions of organic matter correspond only to the rainy season.

4. Discussion

4.1 Landscape properties and ecological connectivity

Our study showed that *E. argenteus* diet varied between the three estuaries studied and that the contribution of coastal resources increased with the connection to the sea. This connection with the sea, embodied by the morphological features (shape, mouth width) controlling key physico-chemical variables in this habitat (depth, salinity), is thus a suitable indicator of the connectivity between estuarine and coastal habitat. Thereby, ecological connectivity was promoted by the high sea connection in the Santa Cruz Channel. The fish of this estuary had high $\delta^{13}C$ values and the coastal SOM was therefore the source that contributed most to the diet.

The coastal SOM was also important in Suape but to a lesser extent since the geomorphological alterations, induced by the construction of the port, resulted in a restricted land-sea connection, isolating the two environments. The landfills caused by the dredging have led to a reduction in the river regime and hence to sedimentation, as well as to a reduction in water exchange and depth (Muniz et al., 2005). In Sirinhaem, estuarine sources were predominant, showing that ecological connectivity is reduced in this enclosed lagoon during the rainy season.

Tracing the origin of basal sources of organic matter was important to illustrate the complexity of trophic pathways between coasts and estuaries. In addition, *E. argenteus* was an appropriate indicator to provide information on the ecological connectivity between these two systems, since the adults (>13 cm) that inhabit preferentially coastal areas, enter the estuaries to feed (Ramos et al., 2016). Thus, no correlation was found between the $\delta^{13}C$ and the sizes of the fish in Sirinhaem or in the Santa Cruz Channel while the larger individuals in Suape presented depleted $\delta^{13}C$ values, characteristics of estuarine sources (Moens et al., 2002). This corroborates the fact that adults of this species use estuaries as a feeding area, as is the case for many species of the Gerreidae family (Ramos et al., 2012).

Though the movements performed by adult fish might exacerbated the connectivity patterns, local variations in marine intrusion are likely to explain the gradient of connectivity seen in the three estuaries. Organisms that have limited mobility can be influenced by this connectivity as estuarine food webs can be supported by coastal organic matter (Selleslagh et al., 2015). Methods using only stable isotopes cannot separate the effect of fish movement from the effect of marine intrusion. A tagging study with artificial loggings would have provided information on the frequency of foraging movements (Olds et al., 2017) and would have helped to distinguish these two components of ecological connectivity. Yet, the influence of ontogenetic migrations on the results seems to be reduced since fish sizes were not correlated to their respective $\delta^{13}C$ and $\delta^{15}N$ values when the three estuaries were grouped. Thus, differences in diet observed among estuaries cannot be attributed to differences in fish size. Furthermore, although fish sizes differed from one estuary to another, trophic positions were similar among estuaries. However, the low trophic position values found in this study (about 2.7) could be due to the tendency of trophic position underestimation with isotopic methods (Hussey et al., 2014) . Indeed, studies in the region of study did find a trophic position a little higher (i.e. 2.95) (Lira et al., 2018)) and diet studies in estuaries classified *E. argenteus* as a second degree consumer (Chi-Espínola et al., 2018; Vasconcellos et al., 2018).

Coastal and estuarine sources have been successfully distinguished using Bayesian mixing models. This analysis, despite the need for careful parameterisation, remain the best method for quantifying the relative contributions of sources in a diet (Parnell et al., 2010). They offered a useful tool for identifying differences in flows between habitats based on landscape properties. Nevertheless, the trophic enrichment factor, which strongly affects source contributions, should be specifically measured in the laboratory (Herzka, 2005). Yet, since the TEF chosen was consistent with those measured in the laboratory for zoobenthivorous fish (Kostecki et al., 2012), our results should appropriately reflect the relative contribution of coastal and estuarine sources.

Another weakness of mixing models is their lack of accuracy in an environment where several sources present overlapping isotope ratios, which usually occurs in estuaries (Phillips et al., 2014). Nonetheless, as our objective was to relate the degree of connection of the sea to the contribution from coastal sources, uncertainties in determining the participation of low contribution overlapping estuarine sources were not an issue. The fact that the coastal SOM was not available in Suape is not likely to bias the model, since Suape and Sirinhaem are part of the same coastal region with homogeneous habitats (Assis et al., 2015). Furthermore, the anthropogenic pressures locally occurring in Suape are not expected to significantly alter the isotope ratios of its coastal area, since Suape is a small estuary.

Contributions of basal sources were also influenced by seasonality. For example, marked seasonal variations in isotope ratios of *E. argenteus* occurred in Sirinhaem, the smallest estuary, due to the fact that in small tropical estuaries, where freshwater inputs are intermittent, seasonal nutrient inputs from terrestrial systems are favoured (Abrantes et al., 2015). Indeed, Sirinhaem location in the south, where rainfall is higher than in the north of the state (CPRH, 2003), allows for a large difference in freshwater supply between seasons. Differences in land use can also affect the seasonal intensity of inputs, but as Sirinhaem is the least anthropized estuary (Pelage et al., 2019) , environmental fluctuations seems to be the main driver of seasonal patterns in this region. Hence, during the dry season, we could not run the model for Sirinhaem because consumers were not within the trophic polygon of sources suggesting the existence of unknown sources probably derived from the sea due to their enriched $\delta^{13}C$ ratios. This implies that the low connection to the sea, inherent in the morphological characteristics of this enclosed lagoon, was not the factor that influenced the ecological connectivity during this season. Therein, high marine intrusion, fostered by high evaporation during the dry season and reduced river flow (Potter et al., 2010), may have caused a diet shift. During the rainy season, freshwater discharges reduce salinity, which is propitious for the development of polychaetes, while during the dry season, evaporation increases salinity, promoting the presence of marine benthic larvae (Chi-Espínola et al., 2018). This shift in marine invertebrates community could thus explain the higher $\delta^{13}C$ values observed in Sirinhaem during the dry season.

Despite the lack of significant differences in $\delta^{13}C$ values between seasons in Suape and in the Santa Cruz Channel, the seasonal shift observed in the models and with the ellipses may also be attributed to a difference in fish size within each estuary. Especially the differences in size between seasons could reflect the reproduction period of *E. argenteus* in the study area, which takes place at the beginning of the dry season and resulted the capture of smaller fish. Ontogenetic shifts were already observed in estuaries and hypersaline lagoons, where smaller specimens fed on zooplankton and larger individuals preyed on polychaetes (Silva et al., 2016; Chi-Espínola et al., 2018).

4.2 Implication for ecosystem functioning

Greater variability in fish isotope ratios was measured at Sirinhaem during the rainy season, translated by a large ellipse area and a high variability in sources contributions. The size range of Sirinhaem fish during that season was narrow so its variability cannot be attributed to ontogenetic shifts. This may be due to resource partitioning to avoid interspecific competition in this closed estuary thanks to the plasticity of *E. argenteus* diet. Diet plasticity is generally associated with the quantification of the extent of the trophic niche, i.e. the set of resources that can be exploited by a population to maintain acceptable growth parameters (Polis, 1984). The ability to occupy wider trophic niches, thus feeding on a wide range of different items, ensures greater adaptability (Pörtner et al., 2010). The opportunistic behaviour of the silver mojarra was already registered (Chi-Espínola et al., 2018) and could promote species adaptation in closed lagoons where coastal foraging opportunities are limited. In tropical estuaries, spatial differences in the diet of *E. argenteus* have already been reported (Guedes et al., 2015). This habit could mitigate the adverse effects caused by natural or anthropic isolation between estuarine and coastal environments. However, more detailed health studies need to be conducted to assess the actual status of the fish population since variation in food web carbon sources, may cause differences in growth and condition (Isnard et al., 2015). Hence, variability in ecological connectivity and thus in diet could lead to variation in growth parameters.

Estuaries are suffering from various anthropic geomorphological modifications (Wetzel et al., 2012Du et al., 2016; Lechêne et al., 2018) which could alter the flows with adjacent coastal areas. Variations in ecological connectivity are likely to affect the functioning of ecosystems as they influence trophic pathways and energy flows between adjacent habitats. Besides, this study shows that ecological connectivity extent evolves with sea connection degree which controls essential environmental variables such as salinity and depth. These variables are key structuring factors for the distribution and abundance of species. Indeed, *E*. *argenteus* is a saltwater species, and in general Gerreidae abundance is usually positively correlated with salinity (Corrêa and Vianna, 2016). In the Santa Cruz Channel, where sea connection is strong, *E. argenteus* was the second most abundant species, while in the other two estuaries, Suape and Sirinhaem, the silver mojarra was not among the ten most abundant species (Merigot et al., 2017).

Indeed, the availability of the prey is controlled by environmental factors (Arula et al., 2012; Martino and Houde, 2010) and a narrow sea connection degree does influence estuarine resources access for saltwater species and coastal resources for estuarine resident. Reduced access to food resources resulting from habitat fragmentation is likely to exacerbate competition patterns (Hasegawa, 2017). In the case of a change in the sea connection such as during the construction of the port, coastal preys were less available for *E. argenteus* juveniles but the diet plasticity of this species may have allowed it to switch to a more estuarine diet, which may have increased competition with estuarine resident species.

In addition, marine migratory species whose juveniles use estuaries as nurseries and whose adults extensively use estuaries as feeding or reproductive grounds (e.g. Mugilidae, Gerreidae) represent an important yield for small-scale estuarine and coastal fisheries in tropical areas (Salas, 2011). Modification in ecological connectivity through alterations in estuarine morphology is susceptible to have adverse effects on these species and could have socioeconomical repercussion since they constitute essential source of proteins for local populations. In addition, they represent key prey for piscivorous fish, therefore a change in their abundance due to habitat degradation would have drastic repercussions on the ecosystem.

5. Conclusion

Differences in the degree of connection to the sea in estuaries influenced the origin of the organic matter supporting the diet of *E. argenteus*, chosen as an indicator of ecological connectivity with adjacent coastal habitats. Consequently, the geomorphological disturbances caused by the increasing human modification of estuaries are likely to seriously affect the functioning of these habitats, by altering the energy flows that support their food networks. The influence of seascape properties on biological processes is complex and assessing their effects on ecosystem services such as fisheries yields is a difficult but necessary task in a context of global change and dwindling resources. Preliminary multidisciplinary studies should be carried out before implementing any changes to the seascape that alter the connectivity between habitats, especially in the case of habitats of significant importance for migratory species. In addition, understanding the extent to which the restoration of geometric properties through eco-engineering allows for ecosystem resilience in terms of connectivity would be of interest.

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SUPPLEMENTARY MATERIAL:

Environment	**Gear**	**net height(m)**	**net length (m)**	**Mesh (mm)**
Estuary	Block net	1.9	80	70
	Beach seine	5.0	180	25
	Seine net	8.0	75	10
Coast	Gill net	1.5	200	50
	Trawler	6.1	10	25
	Bottom trawl	10.0	28	25

Supplementary Table 1: Characteristics of the fishing gears used to capture the fish in the different environment.

Estuary	**DRY**				**RAINY**			
	n	TL (cm)	δ^{13}C (‰)	δ^{15}N (‰)	n	TL (cm)	δ^{13}C (‰)	δ^{15}N (‰)
Santa Cruz Channel	10	8.2-9.6	-16.3±1.0	9.3±0.6	10	11.9-14.6	-16.9±1.0	11.0±1.0
Suape	7	3.6-5.2	-18.6±0.9	10.6±1.1	6	5.2-14.1	-19.8±1.3	9.7±0.5
Sirinhaem	4	7.4-16.6	-14.0±2.4	10.3±0.3	9	7.7-9.5	-21.2±3.9	9.3±1.1
Coast	10	9.4-15.0	-16.9±2.27	11.2±0.8	-			

Supplementary Table 2: Number of samples (n), Total length (TL), Isotopic means (± S.D.) of carbon (δ^{13}C), nitrogen (δ^{15}N) of the fish collected in the estuarine and coastal areas during the dry and the rainy season.

Source	**Environment**	**Area**	**DRY**			**RAINY**		
			n	**δ^{13}C**	**δ^{15}N**	**n**	**δ^{13}C**	**δ^{15}N**
SOM	Estuary	SCC	6	-23.8±1.4	4.5±1.0	6	-24.0±1.0	4.2±0.7
		SUAPE	6	-25.3±0.5	4.2±0.9	6	-26.0±0.4	2.7±0.6
		SIR	6	-25.9±0.7	4.7±0.5	6	-25.0±1.0	4.0±0.3
	Coast	SCC	6	-21.2±1.2	5.5±1.2	6	-20.6±1.1	5.8±1.1
		Sir	6	-16.8±0.4	3.9±0.6	6	15.9±0.1	3.3±0.2
Algae (Ulva sp)	Estuary	SCC	3	-23.4±0.4	8.9±0.2	3	-23.0±0.4	6.3±0.2
Algae Sargassum sp.	Estuary	SUAPE	3	-18.2±0.3	8.9±0.1	3	-16.5±2.3	7.0±0.2
		SIR		-	-	3	-16.8±1.3	5.4±0.4
Microphyto benthos	Estuary	SCC	3	-20.3±0.2	3.9±0.4	2	-19.6±2.8	2.7±0.4
		SUAPE	1	-26.4	4.7	-		
		SIR	4	-24.8±0.7	4.2±0.5	3	-22.0±1.1	5.9±0.2
Seagrass	Estuary	SCC	3	-27.6±0.6	2.4±0.5	3	-28.0±0.3	1.4±0.4

Mangrove	Estuary	SCC	3	-27.8±0.7	3.0±0.9	3	-27.4±0.2	1.8±1.2
		SUAPE	3	-27.1±0.5	1.5±0.5	3	-27.1±0.7	1.5±0.5
		SIR	3	-28.5±0.1	1.8±1.9	3	-28.5±0.5	2.1±0.8
C. rhizophorae	Estuary	SCC	4	-23.2±0.4	7.7±0.4	3	-22.5±0.1	8.2±0.1
		SUAPE	3	-19.3±0.8	7.1±0.3	3	-19.6±1.7	8.0±0.2
		SIR	6	-16.1±0.4	6.8±0.4	6	-20.4±0.2	8.0±0.2

Supplementary Table 3: Number of samples (n) and isotopic means (± S.D.) of carbon (δ13C), nitrogen (δ15N) of basal sources and the oyster *C .rhizophorae* during dry and rainy season in the Santa Cruz Channel (SCC),Suape and Sirinhaem (SIR).

Estuary	**Variable**	**P value**	**Rho**	**S**
ALL	$\delta^{15}N$	NS	-	11975
	$\delta^{13}C$	NS	-	13919
Santa Cruz Channel	$\delta^{15}N$	0.00236	0.6402471	478.47
	$\delta^{13}C$	NS		1795.9
Suape	$\delta^{15}N$	NS	-	428.35
	$\delta^{13}C$	0.009764	-0.6850933	613.37
Sirinhaém	$\delta^{15}N$	NS	-	227.62
	$\delta^{13}C$	NS	-	232.64

Supplementary Table 4: Results of the Spearman ranking tests between the total length off the fish and the the $\delta^{13}C$ / $\delta^{15}N$ of fish in all the estuaries together as well as in each estuary (Santa Cruz Channel, Sirinhaem and Suape). NS: Not Significant (p value >0.005).

Estuary	Variable	p value	W
ALL	$\delta^{15}N$ (‰)	NS	250
Santa Cruz Channel	$\delta^{15}N$ (‰)	0.0007253	8
	$\delta^{13}C$ (‰)	NS	66
Suape	$\delta^{15}N$ (‰)	NS	35
	$\delta^{13}C$ (‰)	NS	33
Sirinhaem	$\delta^{15}N$ (‰)	NS	28
	$\delta^{13}C$ (‰)	0.03357	32

Supplementary Table 5: Results of the Mann-Whitney tests verifying seasonal differences in the $\delta^{13}C$ / $\delta^{15}N$ of fish in each estuary (Santa Cruz Channel, Sirinhaem and Suape) . NS: Not Significant (p value >0.005).

Source	**Estuary**	**Contribution**	
		DRY	**RAINY**
Algae	Santa Cruz Channel	0.051	0.096
	Suape	0.256	0.182
	Sirinhaem	-	0.156
Mangrove	Santa Cruz Channel	0.031	0.050
	Suape	0.123	0.161
	Sirinhaem	-	0.246
Microphytoplancton	Santa Cruz Channel	0.115	0.116
	Suape	0.136	0.165
	Sirinhaem	-	0.181

Seagrass	Santa Cruz Channel	0.233	0.133
SOM	Santa Cruz Channel	0.055	0.084
	Suape	0.157	0.203
	Sirinhaem	-	0.270
SOM Coast	Santa Cruz Channel	0.514	0.521
	Suape	0.329	0.290
	Sirinhaem	-	0.146

Supplementary Table 6: Mean of the relative contributions of the organic matter sources in each of the estuaries during the rainy and the dry season.

Highlights

- The origin of the organic matter underlying food webs was investigated in three estuaries with distinct morphologies
- Coastal organic matter contributed more to fish diet when landscape properties enabled a better sea-connection
- Estuary morphology regulates interactions between estuaries and their adjacent coast

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: