
Estuarine food web structure and relative importance of organic matter sources for fish in a highly connected Northeastern Brazil ecotone

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Abstract :

The lack of knowledge about highly anthropised tropical ecosystems poses a problem for their conservation. Using carbon and nitrogen stable isotopes, we studied the food web structure of the estuarine ecotone of the Santa Cruz Channel (SCC), which constitutes a critical habitat for many socio-economically important species in northeast Brazil. Therefore, we assessed the spatial (estuary/coast) and seasonal (dry/rainy) isotopic variation of basal food sources, invertebrates and fishes. We also used Bayesian mixing models to trace the origin (estuary vs coast) of the organic matter sources supporting SCC fishes food webs according to their feeding habits. We found a wide range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for basal sources, invertebrates, and fish in coastal and estuarine environments, but isotopic compositions showed greater variability in the estuary. This illustrated the heterogeneity of primary producers and sources in estuaries, intensified by SCC morphology, as both accesses to the sea provide strong mixing between riverine and marine inputs. Additionally, we found differences between fish isotope compositions according to their guilds. Coastal basal sources significantly support zoobenthivorous, piscivorous and zooplanktivorous fish estuarine food webs. Conversely, detritivores are supported by enriched sources of organic matter, especially during the dry season, which may be derived from terrestrial inputs. As contaminated land-based inputs can affect food webs and coastal fisheries, developing a management plan that includes all interconnected habitats is necessary.

Highlights

► Coastal basal sources support estuarine fish food webs in the study area. ► Carbon sources supporting fish communities varied according to their trophic guild. ► Estuarine geomorphology may influence food web structure.

Keywords : Trophic guild, Tropical estuary, Bayesian mixing models, Basal sources

1. INTRODUCTION

Coastal biomes contribute substantially to the total economic value of the planet by providing essential ecosystem services (Costanza et al., 2014). For example, the estuarine ecotone constitutes a critical ecosystem for commercially important fish migrating along the succession of coastal and marine habitats (Nagelkerken et al., 2015; Sheaves et al., 2015), carrying out essential ecological functions as feeding, development and nursery grounds for many fish species (Blaber, 2013; Campos et al., 2015; Elliott et al., 2007; Whitfield, 2017). In these complex ecosystems, embodying the transition between coastal and terrestrial environments, food webs can be supported by the large variety of estuarine primary producers or by organic matter derived from adjacent coastal and riverine environments (Choy et al., 2009; Selleslagh et al., 2015). Knowledge of the relative contribution of autotrophic sources to a given food web is fundamental to understanding the relationship between consumers and primary producers (Deines et al., 2015). Moreover, it is essential to have a temporal and spatial understanding of the autotrophic sources that support secondary production to develop effective management policies in dynamic ecotones (Melville and Connolly, 2005). The lack of knowledge regarding the functioning of these ecosystems, some highly anthropised, is expected to be a challenge for their conservation, raising a need for holistic approaches addressing the complexity of their dynamics (Crowe and Frid, 2015).

Stable isotope compositions of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are widely used to depict food web structure, trophic niche of coastal and marine organisms (Faye et al., 2011; Abrantes et al., 2014; Schalk et al., 2017), fishing impacts on the food webs (Funes et al., 2019) and connectivity between areas (Carlier et al., 2015; Claudino et al., 2015). Since $\delta^{13}\text{C}$ values differ significantly among some primary producers (*e.g.*, mangrove trees, marine macroalgae and microphytobenthos), carbon isotope compositions can

provide valuable information on the organic matter origin supporting organisms (Peterson and Fry, 1987). In contrast, $\delta^{15}\text{N}$ values indicate the relative trophic position of the individuals within the food web (Post, 2002). Therefore, Stable Isotope Analyses (SIA) can help reconstruct trophic interactions within a system and determine the feeding ground for a wide range of organisms (Fry, 2006; Herzka, 2005).

SIA contributed to deepening the understanding of coastal and marine ecosystem functioning worldwide (Mancinelli and Vizzini, 2015; Kurle and McWhorter, 2017). However, studies characterising the functioning of tropical coastal ecosystems are scarce (Giarrizzo et al., 2011; Pereira et al., 2020). These areas have been understudied despite being subject to rapid human population growth, poor marine spatial planning and weak mitigation of anthropogenic impacts (Blaber and Barletta, 2016). Thereby, tropical Small-Scale fisheries (SSFs), responsible for the source of income and food of many coastal nations, are likely being threatened by those changes (Lira et al., 2021a; Wenger et al., 2017).

The Northeastern Brazil coast comprises a vast area and a myriad of habitats exploited by several SSFs. However, studies characterising the functioning of tropical coastal ecosystems are scarce. Except for the studies published by Lira et al. (2021b) and (Pereira et al., 2020), those available are monospecific (Gonzalez et al., 2019; Soares et al. 2020, Pelage et al. 2021) or only focus on the relative importance of basal food sources to macroconsumers (Claudino et al., 2015).

Located in the Northeastern region of Brazil, the Santa Cruz Channel (SCC) encompasses the largest estuarine complex of the Pernambuco state. The SCC region constitutes the main fishing hub of the state, providing an essential source of income and food for the surrounding communities (Quinamo, 2006). In addition, the SCC is impacted by various anthropic activities (Pelage et al., 2019; Justino et al., 2021). The SCC is

composed of a mosaic of coastal habitats (mangrove and coral reefs), and its geomorphology provides high connectivity between them (Guimarães et al., 2010; Pelage et al., 2021b). Thereby, SCC exhibits higher biodiversity than the surrounding estuaries (Merigot et al., 2017; Silva-Júnior et al., 2017) due to the intricate migratory patterns of many species moving through the interconnected habitats (Vasconcelos Filho et al., 2003). These peculiarities make the region an appropriate model system of a complex tropical estuarine ecotone with high connectivity.

The study investigates the food web structure of a complex tropical estuarine ecotone constituting a key habitat for commercial species. For this purpose, we propose to 1) assess the spatiotemporal variations of isotope compositions of basal food sources, invertebrates, and fishes and 2) trace the origin of the organic matter sources supporting SCC fishes food webs according to their feeding habit.

2. MATERIALS AND METHODS

2.1. Study area

The Santa Cruz Channel (SCC) is located in the tropical Southwestern Atlantic. The estuarine environment of the SCC is flooded by seawater and connected with the Atlantic Ocean by the Catuama and Orange entrances (Fig. 1). In this estuary, water temperature ranges between 25°C and 31°C and the salinity between 18 and 34 (Macedo et al., 1998). The river discharges are the main source of nutrients, followed by sediment resuspension, mangrove litter, waste input, terrestrial runoff and atmospheric input (Flores Montes et al., 1998).

In the adjacent coastal environment of SCC, discontinuous sandstone ridges, reefs, and sandbanks near the north (Catuama) and south (Orange) inlets form a semi-open elongated lagoon-like coastal environment (Fig. 1). This configuration leads to limited water exchange between the SCC and offshore ecosystems (Medeiros and Kjerfve, 1993).

In this adjacent coastal area, the water temperature varies between 27 and 31°C (Manso et al., 2003), and the mean salinity is 31.2 (Gonzalez et al., 2019). The adjacent coastal area is delimited by a reef barrier parallel to the coast, 4 km from the ocean beach (Kempf, 1970).

The major freshwater inflow comes from the northern part of the SCC system (94% during the dry period and 70% during the wet period) (Medeiros et al., 2001). In general, the water flow is directed towards the two inlets from the middle of the channel. However, in periods of higher freshwater inflow from the rivers and during neap tides, the channel has a residual circulation towards the northern entrance. On the other hand, during periods of lower freshwater input, water masses from the marine environment enter through the northern entrance but not through the southern entrance (Medeiros et al., 2001). The combined flow of the rivers feeding the Santa Cruz Channel varies from 1 m³s⁻¹ in dry periods to 56m³s⁻¹ in wet periods (Medeiros and Kjerfve, 1993). The SCC is part of the Marine Protected Area of Santa Cruz (Northeastern Brazil). The area is highly impacted by industrial effluents, shrimp farming and fishing activity (Gondim et al., 2015; Guimarães et al., 2010; Pelage et al., 2019).

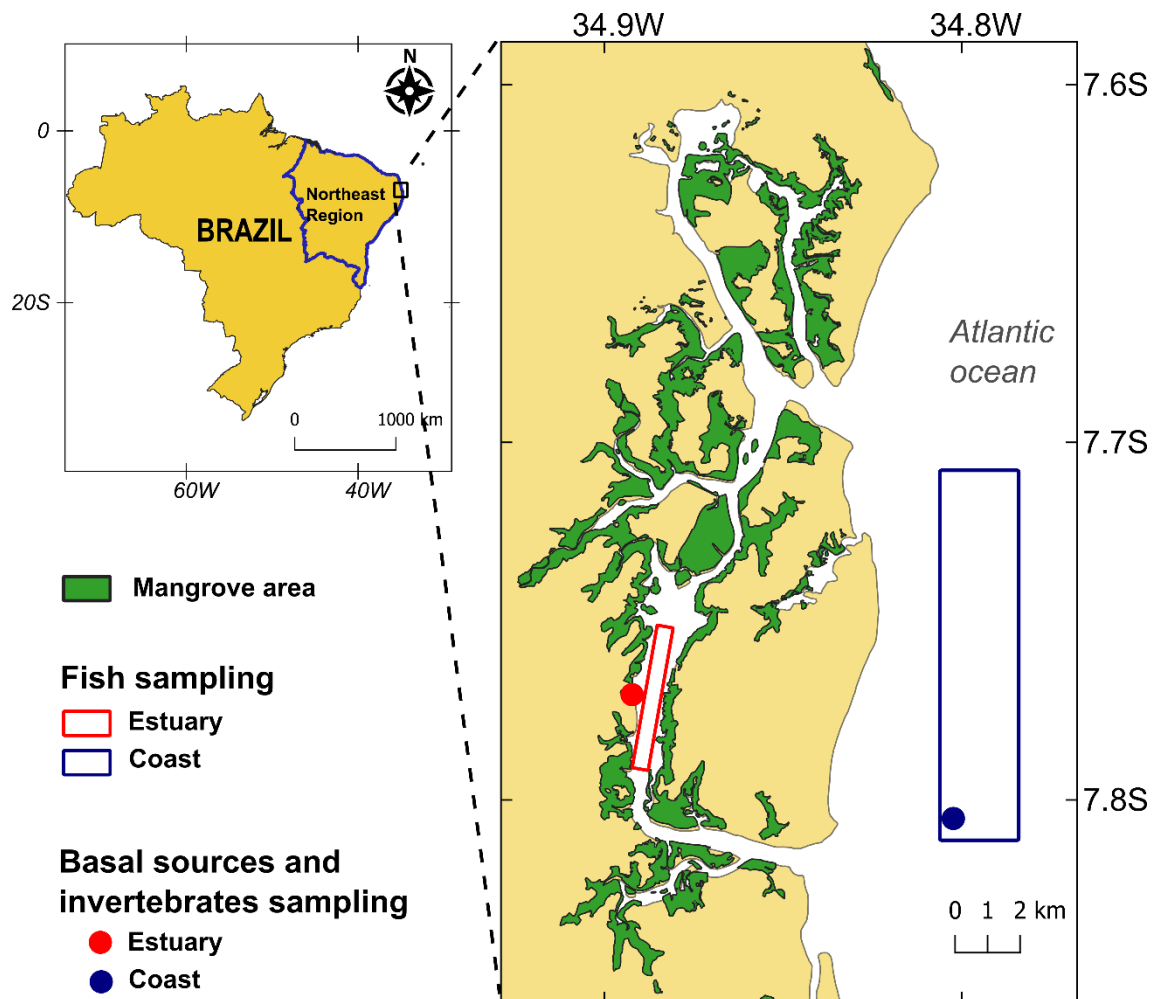


Fig. 1. Study area and location of the sampling sites in the estuary and coast of the Santa Cruz Channel, Pernambuco, Brazil.

2.2. Data collection

Food web components were sampled during the dry (February and March) and rainy (August and September) seasons of 2015 in the SCC estuarine and adjacent coastal environments. They comprised different sources of organic matter and consumers within the food web. The main basal food sources available in the system comprehended particulate organic matter suspended in the water column (POM) and in the sediment (SOM), mangrove leaves, seagrass (*Halodule wrightii*), microphytobenthos (i.e. benthonic microalgae) and macroalgae (*Ulva sp.*). The mangrove, macroalgae and seagrass were manually collected at low tide.

The microphytobenthos was sampled from the sediment surface at low tide and extracted in the laboratory, following the adapted methodology of Riera et al. (1996): sediment samples (2 mm deep) were placed into clear plastic pans and recovered by a nylon screen (63 μm mesh), then a 2 mm thick layer of combusted sand was deposited in the nylon screen. The pans remained under the natural light until the first dense brown mats appeared on the surface (usually between 4 to 6 h). The dense brown mat was removed and filtered on 47 mm pre-combusted GF-3 filters. The POM was obtained by filtering between 0.5 to 1 L of water through a 63 μm mesh to remove zooplankton and detritus, and the remaining suspended matter was collected on 47 mm pre-combusted GF-3 filters. The SOM was collected with a tube core (2 cm diameter), and 2 mm of surface sediment was removed for analysis.

Samples of oyster (*Crassostrea rhizophorae*), zooplankton (copepods), macrocrustaceans (crab and shrimp) and fish species were collected to represent the consumers. Consumer species were selected according to their ecological role and commercial value (Table 1).

The zooplankton was sampled with a plankton net (300 μm mesh) hauled horizontally for 10 minutes at the subsurface. In the estuary, fishes and shrimps were captured with seine (10 mm mesh) and block nets (50 mm mesh) and, in the coast, with gill nets (25, 30 and 40 mm of mesh size) and fixed traps (70 mm mesh). The crabs and oysters were sampled manually. Samples were preserved on ice and transported to the laboratory, where they were processed. Fishes (standard length - cm), oysters and crustaceans (shell width - cm) were measured to the nearest mm.

Table 1. Ecological and economic importance for compartments captured in the Itapissuma/Itamaracá Complex. Functional guild: ES, estuarine species; MM, marine migrants; MS, marine stragglers; Trophic guild: HV, herbivore; DV, detritivore; OV, omnivore; PV, piscivore; ZB, zoobenthivore; ZP, zooplanktivore; IR, relative importance based on the abundance and frequency of species: 1, abundant and frequent; 2, abundant and infrequent; 4, less abundant and infrequent. *Ecological role information obtained by (Ferreira et al., 2019); (Lira et al., 2021b); (Gonzalez et al., 2019). **Economic role information obtained by (ESTATPESCA, 2006; Lira et al., 2010). (-) represents the absence of information about the group. (-) This group does not occur in this environment.

Group/species	Ecological role				Economic role	
	Trophic guild*	Functional guild*	Abundance and frequency*		Use/trade**	Economic importance**
			Estuary	Coast		
<i>Crassostrea rhizophorae</i>	ZP	ES	-	-	Commercial	Yes
Copepoda	-	-	-	-	-	-
<i>Callinectes danae</i>	OV	MS	-	-	Bycatch/Commercial	Yes
<i>Farfantepenaeus subtilis</i>	OV	MM	-	-	Commercial	Yes
<i>Sparisoma axillare</i>	HV	MS	4	4	Bycatch/Commercial	Yes
<i>Gobionellus oceanicus</i>	DV	ES	1	--	Bycatch	No
<i>Gobionellus stomatus</i>	DV	ES	1	--	Bycatch	No
<i>Mugil curema</i>	DV	MM	2	4	Commercial	Yes
<i>Atherinella brasiliensis</i>	OV	ES	4	--	Bycatch	No
<i>Achirus lineatus</i>	ZB	ES	4	--	Bycatch	No
<i>Citharichthys spilopterus</i>	ZB	MM	4	--	Bycatch	No
<i>Diapterus auratus</i>	ZB	MM	2	2	Bycatch/Commercial	Yes
<i>Eucinostomus argenteus</i>	ZB	MM	1	4	Bycatch/Commercial	Yes
<i>Lutjanus analis</i>	ZB	MS	4	4	Commercial	Yes
<i>Micropogonias furnieri</i>	OV	MS	-	-	Commercial	Yes
<i>Opisthonema oglinum</i>	ZP	MS	4	2	Commercial	Yes
<i>Bairdiella ronchus</i>	ZB	MM	4	--	Bycatch/Commercial	Yes
<i>Caranx hippos</i>	PV	MS	4	2	Commercial	Yes
<i>Centropomus parallelus</i>	PV	MM	4	--	Commercial	Yes
<i>Centropomus undecimalis</i>	PV	MM	4	4	Commercial	Yes

2.3. Stable isotope analysis (SIA)

Samples were processed following Garcia et al. (2007) protocol. The dorsal muscle tissue of fish specimens, the oysters' adductor muscles, and the abdomen muscle tissue of shrimps and crabs were extracted. For the zooplankton, several entire organisms of the subclass Copepoda were manually selected and gathered for SIA. All samples were oven-dried at 60 °C for 48 h. Dried samples were ground to a fine powder with a mortar and pestle, then stored in clean Eppendorf tubes. Samples of POM, SOM and zooplankton, were duplicated. One of the samples was acidified to remove all carbonates (Ryba and Burgess, 2002), whereas a raw sample was analysed for the measurement of

$\delta^{15}\text{N}$ values to avoid any bias of acidification on $\delta^{15}\text{N}$ values (Pinnegar and Polunin, 1999).

Carbon and nitrogen isotope compositions were determined considering a CN analyser (Flash 2000, Thermo Scientific) interfaced with an isotope ratio mass spectrometer (Delta V Plus with a Conflo IV interface, Thermo Scientific). The results are expressed in the delta notation as deviations from standards (Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$, N_2 in the air for $\delta^{15}\text{N}$) with $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000$, where X is ^{13}C , or ^{15}N and R is the corresponding ratio, $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$.

Reference materials of known $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were analysed: USGS61, USGS62 and USGS63. The recommended values of the standards were reproduced within the confidence limits. The analytical precision, based on the standard deviation of repeated measurements of an internal laboratory standard (Thermo Acetanilide), was $\pm 0.07\text{‰}$ for $\delta^{15}\text{N}$ and $\pm 0.11\text{‰}$ for $\delta^{13}\text{C}$.

2.4. Data analysis

2.4.1. Spatiotemporal variability

Carbon and nitrogen isotope compositions of basal food sources and consumers were represented on boxplots to investigate seasonal (dry and rainy seasons) and spatial (estuary and coastal environments) variability. Non-parametric Mann-Whitney tests were performed to verify spatiotemporal differences in isotopic compositions. Fish sizes differences between the coast and the estuary were also investigated with Mann-Whitney tests. Moreover, fish were divided into trophic guilds (herbivores, detritivores, zoobenthivores, omnivores, zooplanktivores and piscivores) according to Elliott et al. (2007) (see Ferreira et al (2019) for species guild assignment according to literature). The seasonal differences of the carbon and nitrogen isotope compositions were tested for each guild in each environment. The tests results were shown on the boxplots. Kruskal-Wallis

and Dunn post hoc tests were performed to investigate differences in carbon isotope compositions between guilds for each season and environment.

2.4.2. Organic matter supporting fish food

As fish feeding habits can influence the incorporation of organic matter into food webs, Kruskal-Wallis and Dunn post hoc tests were performed to investigate differences in isotope compositions between guilds for each season and environment. Bayesian stable isotope mixing models were built using the MixSiar package (Stock and Semmens, 2018) to investigate the origin of the organic matter supporting fish food webs. These models were only run in the estuary since estuarine food webs can be supported by the large variety of estuarine primary producers or by organic matter derived from adjacent coastal and riverine environments (Choy et al., 2009; Selleslagh et al., 2015). MixSiar allows the inclusion of a covariate to understand better the variance among both consumer and source tracer values without the need to perform separate models (Stock and Semmens, 2018). We chose to add the factor “season” for both the fish and the basal sources to obtain the contributions of each source during the dry and the rainy season.

Mixing models are highly influenced by selecting a proper trophic enrichment factor (TEF) (Parnell et al., 2010). The TEF consists of isotopic fractionation from source to consumer (Post, 2002) and varies with diet and habitat (Bunn et al., 2013). The input data for the model were the carbon and nitrogen isotopic compositions of fish, the respective means and standard deviations of basal sources for a given season, and the TEF.

A model for second-level consumers (zooplanktivorous, zoobenthivorous, and piscivorous fish) was elaborated after checking that these three guilds did not differ in isotopic compositions (nitrogen and carbon). We applied an appropriate TEF to identify basal sources (primary producers) supporting second-degree consumers inhabiting in

estuaries: $2.0 \pm 0.6\text{‰}$ and $5.6 \pm 1.5\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively (see Kostecki et al., 2012; Selleslagh et al., 2015)

We built another model for detritivorous fish using a TEF of $1.0 \pm 0.6\text{‰}$ and $2.5 \pm 1.5\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively adequate for the isotopic discrimination between primary consumers and primary producers (see Kostecki et al., 2012; Selleslagh et al., 2015). As few herbivorous fish were sampled, no model was run for this guild.

The isotopic compositions of the sources after application of the TEF and the isotope compositions of the consumers were represented on dual plots to verify a geometric prerequisite for the execution of Mixsiar. The mixing models were only run when the consumer isotope compositions were within the mixing polygon bounded by the basal source isotopic compositions representing the trophic limits of the system (Phillips and Gregg, 2003).

Mixing models can also be biased when too many sources allow a single solution. To overcome this problem, sources can be removed (by selecting those most relevant to the system) or combined when ecologically relevant (Phillips et al., 2014). Due to many sources in our models, we combined the POM and SOM into a single source in the estuary and on the coast. Our objective was to determine the origin of organic matter; this simplification, which provides more precise results, should not unduly bias our results.

3. RESULTS

3.1. Spatiotemporal variability

Carbon and nitrogen isotope compositions were determined for five basal sources, four invertebrates, and 16 fish species in the Santa Cruz Channel (Table 2). A total of 200 samples were analysed from the estuarine (fish = 78, invertebrate = 24, basal source = 34) and the coastal environments (fish = 43, invertebrate = 9, basal source = 12) (see Table 2).

A wide range of carbon and nitrogen isotope compositions was measured in both environments (Table 2). In the estuary, the overall $\delta^{13}\text{C}$ of the community ranged from -26.1‰ (*Rhizophora mangle*) to -11.7‰ (*Gobionellus oceanicus*), while the $\delta^{15}\text{N}$ varied from 1.10‰ (*Rhizophora mangle*) to 14.00‰ (*Bairdiella ronchus*) (Table 2). In contrast, the coastal environment had a lower variability in $\delta^{13}\text{C}$, ranging from -20.62‰ (POM) to -13.9‰ (*Mugil curema*), and $\delta^{15}\text{N}$ ranging from 6.1‰ (SOM) to 16.5‰ (*Micropogonias furnieri*).

Table 2. Samples code ,mean (\pm Standard Deviation) values of stable isotope compositions of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) and sample number (n) of basal food sources and consumers from the Santa Cruz Channel, Northeastern Brazil, during dry and rainy seasons.

Group/species	Estuary							Coast					
		Dry			Rainy			Dry			Rainy		
		$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n
Basal sources													
Particulate organic matter	POM	-24.1±0.4	7.2±1.7	3	-23.2±0.3	6.4±0.3	3	-20.5±0.1	8.2±0.1	3	-18.2±2.0	9.0±0.2	3
Sedimentary organic matter	SOM	-24.0±3.0	5.0±0.3	3	-24.1±1.0	3.6±0.1	3	-18.0±0.7	6.1±0.6	3	-16.1±1.2	7.1±0.4	3
Microphytobenthos	m.fit	-20.3±0.2	3.9±0.0	3	-19.6±2.8	2.7±0.4	3						
<i>Rhizophora mangle</i>	r.man	-26.1±0.6	3.9±0.5	6	-28.3±0.9	2.7±1.9	6						
<i>Ulva</i> sp.	ulva	-23.4±0.4	8.9±0.2	3	-23.0±0.4	6.3±0.2	3						
<i>Seagrass</i>		-18.4±0.1	-1.2±0.3	3	-16.5±0.3	1.5±0.5	3						
Invertebrate													
<i>Crassostrea rhizophorae</i>	c.rhi	-23.0±0.2	7.6±0.4	3	-22.5±0.1	8.3±0.2	3						
Pelagic copepods	cop	-24.2±1.0	8.1±0.1	3	-22.2±0.6	9.2±0.4	3	-19.9±0.8	10.7±0.2	3	-19.4±0.7	8.8±1.2	3
<i>Callinectes danae</i>	c.dan	-17.1±1.3	8.5±0.5	3	-16.7±0.6	10.4±0.9	3						
<i>Farfantepenaeus subtilis</i>	f.sub	-16.4±0.6	8.0±0.1	3	-19.5±0.1	10.1±0.1	3						
Fish													
Herbivores													

<i>Sparisoma axillare</i>	s.axi				-21.1±0.1	10.8±0.5		-16.2±0.0	12.4±0.2	3	-16.9±0.7	6.1±0.7	3
Detritivores													
<i>Gobionellus oceanicus</i>	g.oce	-12.2±0.6	5.8±0.2	3	-16.2±0.5	7.1±0.7	3						
<i>Gobionellus stomatus</i>	g.sto	-13.4±0.5	4.5±0.3	3	-14.9±0.8	7.5±0.8	3						
<i>Mugil curema</i>	m.spp				-14.7±0.8	7.7±0.4	3				-14.6±0.9	8.7±1.8	3
Omnivores													
<i>Atherinella brasiliensis</i>	a.bra							-14.9±0.4	15.2±0.2	3	-14.8±0.2	15.1±0.2	3
Zoobenthivores													
<i>Achirus lineatus</i>	a.lin	-18.0±0.9	9.6±0.6	3	-19.2±1.0	8.9±1.2	3						
<i>Bairdiella ronchus</i>	b.ron	-19.7±0.3	12.9±0.3	3	-19.6±1.1	13.8±0.2	3						
<i>Citharichthys spilopterus</i>	c.spi	-17.8±0.5	10.4±0.8	3	-16.7±0.5	10.4±0.4	3						
<i>Diapterus auratus</i>	d.aur	-17.6±1.6	9.7±1.2	3	-19.3±0.9	9.7±2.2	3	-18.1±2.5	11.7±1.3	3	-16.5±1.1	13.1±1.1	3
<i>Eucinostomus argenteus</i>	e.arg	-16.17±1.31	9.48±0.44	3	-17.05±0.34	11.56±0.85	3						
<i>Lutjanus analis</i>	l.ana	-16.6±1.1	10.4±0.6	3	-18.4±1.1	12.7±0.5	3	-14.9±0.8	9.6±0.7	3	-15.5±0.3	10.7±0.7	3
<i>Micropogonias furnieri</i>	m.fur	-19.5±0.1	11.8±0.6	3			3	-15.7±0.3	16.0±0.7	3	-15.3±1.3	14.3±0.5	3
Zooplanktivores													
<i>Opisthonema oglinum</i>	o.ogl	-17.4±2.4	12.0±1.1	3	-18.2±1.9	12.1±0.5	3	-16.4±0.2	10.4±0.3	3	-16.5±0.3	12.2±0.3	3
Piscivores													

<i>Caranx hippos</i>	c.hip	-18.5	11.1	1	-17.7±1.0	11.7±0.4	3	-15.3±0.4	12.6±1.3	3	-16.0±0.2	13.1±1.7	3
<i>Centropomus parallelus</i>	c.par	-22.5±2.1	13.1±0.5	3	-18.1±0.5	10.9±0.5	3						
<i>Centropomus undecimalis</i>	c.und	-19.5±2.8	11.1±1.2	3	-17.5±0.7	11.9±0.8	3				-16.4±1.2	14.4±1.1	3

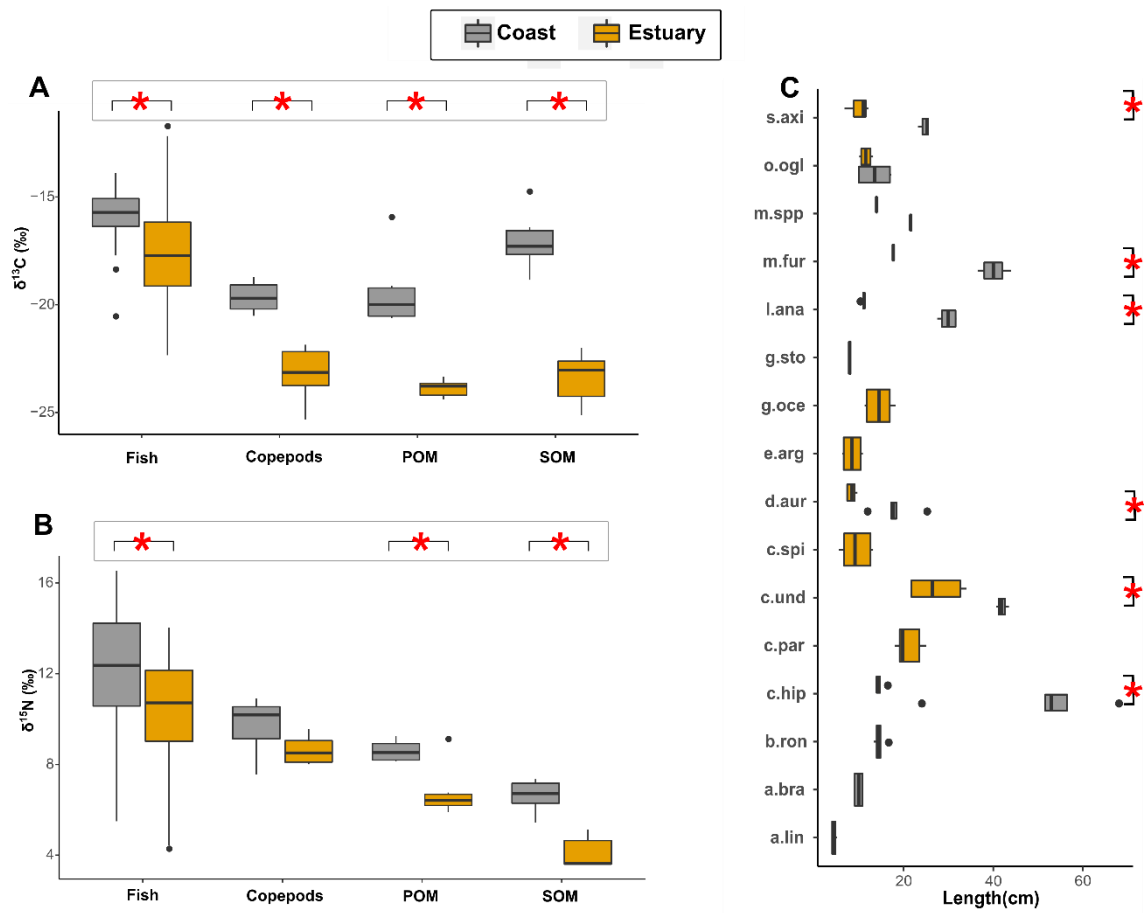


Fig. 2. Spatial variability of A) carbon compositions of fish copepods, POM and SOM, B) carbon compositions of fish copepods, POM and SOM, and C) fish sizes in the estuary and adjacent coastal area of the SCC. Fish species acronyms are defined in Table 2. The red asterisks indicate the significant differences between estuary and coast (Mann-Whitney tests).

Spatial differences in isotopic compositions were observed (Fig. 2). The carbon isotopic compositions of fish, copepods, POM and SOM, were significantly higher on the coast than in the estuary (Fig. 2A). Similarly, the nitrogen isotopic compositions of fish, POM and SOM were significantly higher on the coast (Fig. 2B). Most of the fishes sampled in both environments exhibited a larger size at the coast than in the estuary (Fig. 2C).

No seasonal patterns were observed for basal sources or invertebrates in terms of carbon and nitrogen isotopic compositions (Fig. 3). Conversely, the isotopic compositions of detritivorous fish varied seasonally. During the dry season, detritivores exhibited higher $\delta^{13}\text{C}$ values and lower $\delta^{15}\text{N}$ values. Piscivore fish had lower $\delta^{13}\text{C}$ values during the dry season.

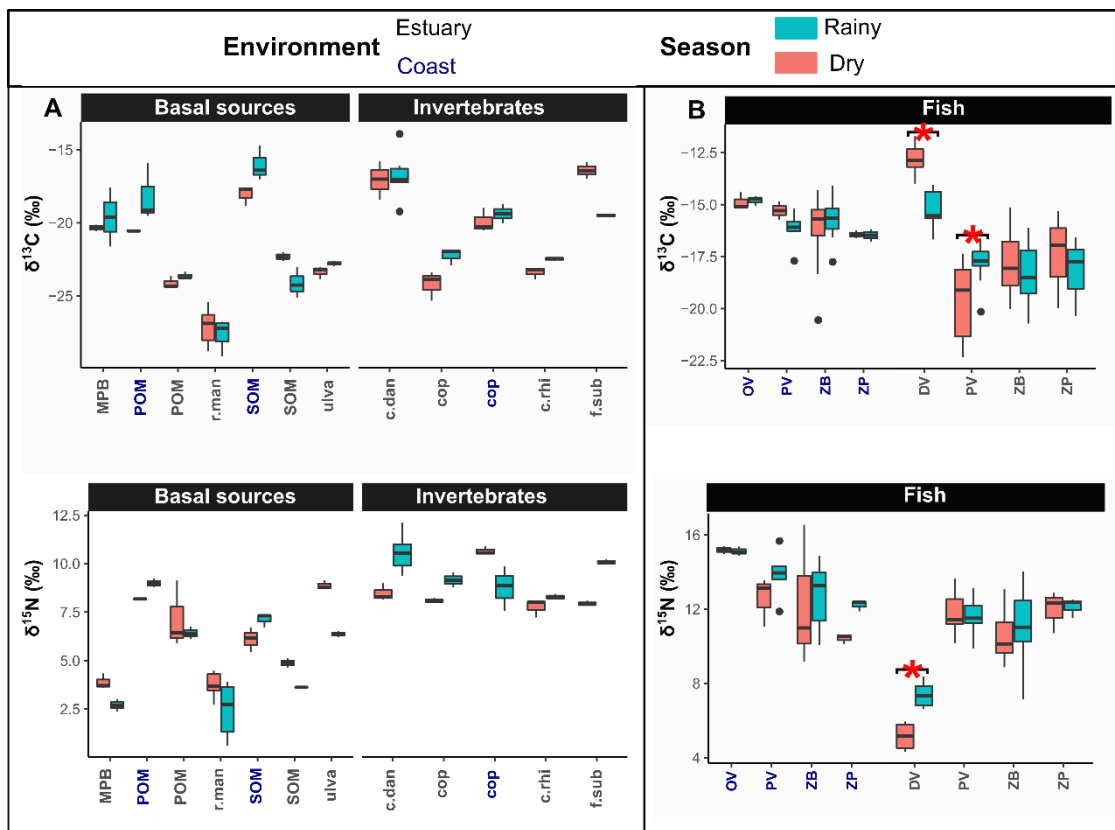


Fig. 3. Seasonal variability of A) carbon and nitrogen compositions of basal sources and invertebrates, B) carbon and nitrogen compositions of fish guilds in the estuary (with black font) and adjacent coastal area

(with blue font) of the SCC. Species acronyms are defined in Table 2. Trophic guild: HV, herbivore; DV, detritivore; OV, omnivore; PV, piscivore; ZB, zoobenthivore; ZP, zooplanktivore. The red asterisks indicate the significant differences between seasons (Mann-Whitney tests).

3.2. Organic matter supporting fish food webs

In the estuary, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values varied significantly according to trophic guilds ($p < 0.05$) (Fig. 4). In both seasons, there were no significant differences between piscivores, herbivores, zooplanktivores and zoobenthivores (Dunn's test, $p > 0.05$ for each season) in terms of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. However, detritivores exhibited higher $\delta^{13}\text{C}$ and lower $\delta^{15}\text{N}$ values than the other guilds (Dunn's test, $p < 0.05$) during both seasons. The differences between detritivores and the other guild were exacerbated during the dry season for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

On the coast, during both the dry and rainy seasons, there was no difference in carbon isotopic compositions between the guilds. However, there were differences in nitrogen isotopic compositions. Detritivores showed lower $\delta^{15}\text{N}$ values than omnivores, while herbivores exhibited significantly lower $\delta^{15}\text{N}$ values than piscivores and omnivores during the rainy season.

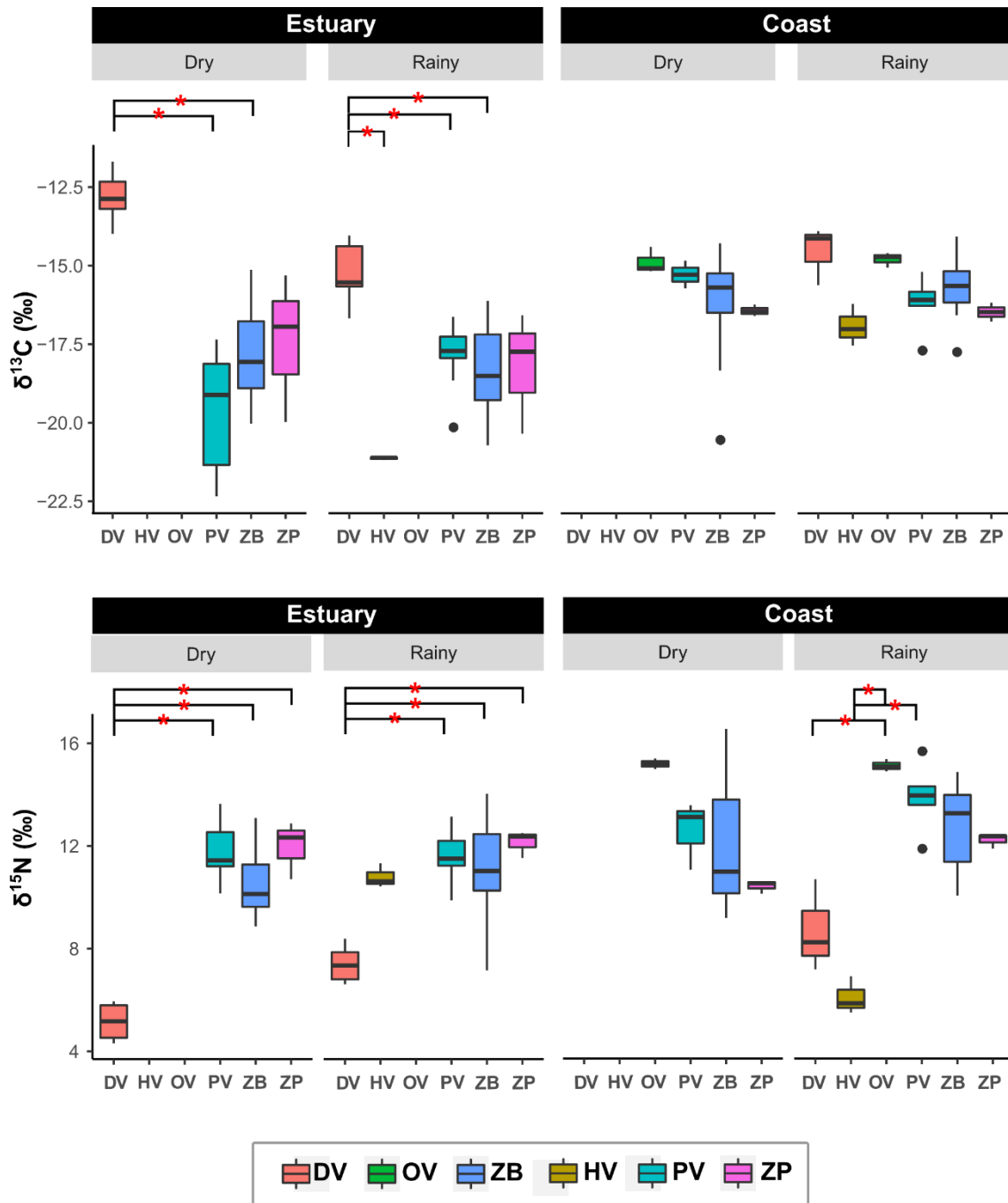


Fig. 4. Differences of carbon and nitrogen compositions between fish guilds in the estuary and adjacent coastal area of the SCC during the dry and rainy seasons. Trophic guild: HV, herbivore; DV, detritivore; OV, omnivore; PV, piscivore; ZB, zoobenthivore; ZP, zooplanktivore. The red asterisks indicate the significant differences between guilds (Dunn's tests).

In both seasons, several estuarine basal sources showed overlapping isotopic compositions (Fig. 5). Indeed, the isotopic compositions of macroalgae were similar to those of estuarine POM+ SOM in both seasons, and seagrasses showed isotopic compositions close to those of microphytobenthos in the rainy season. During both seasons, most of the detritivorous fish isotopes compositions 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 detritivores diet. Thus, the MixSiar model was run only for the zoobenthivorous/piscivorous/Zooplanktivorous (ZB/PV/ZP) fishes whose isotopic compositions were within the polygon.

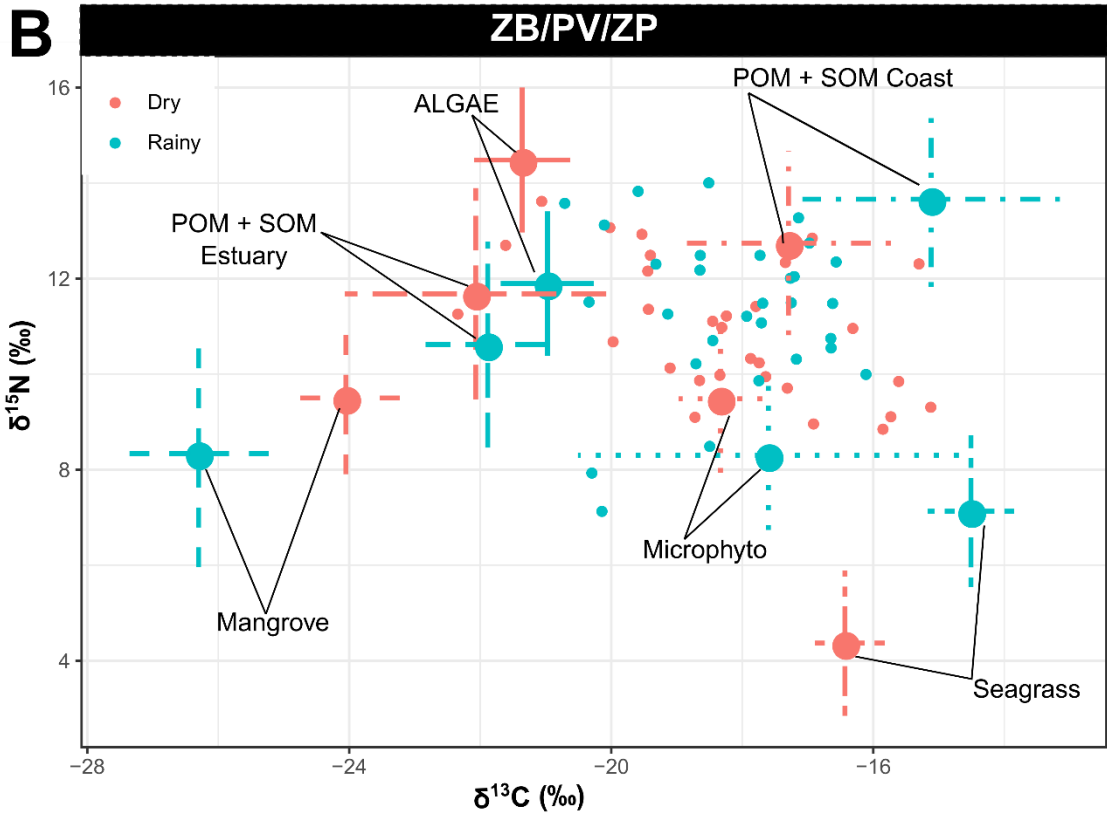
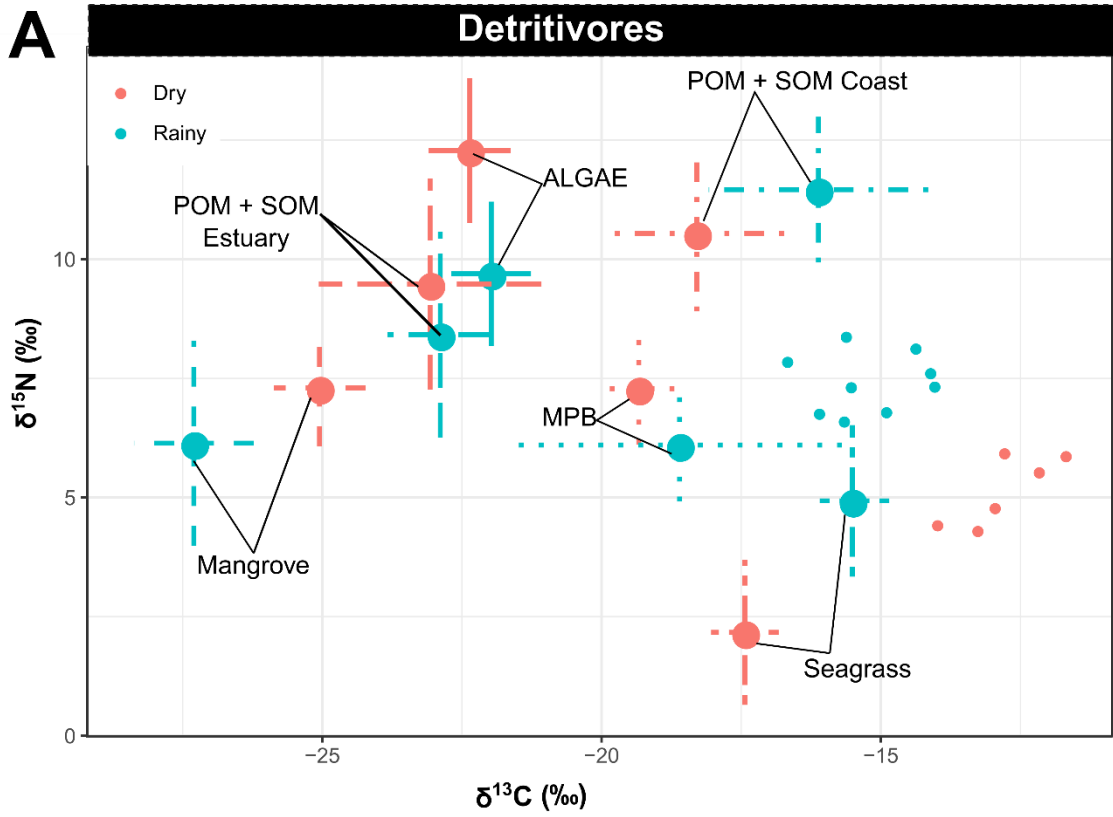


Fig. 5. Dual plots of the sources (represented by the squares and whiskers showing mean values \pm SD of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and the consumers (represented by the points) after applying the trophic enrichment factor to the basal sources A) for the detritivores and B) The Zoobenthivorous / Zooplanktivores and Piscivores. (ZB/PV/ZP). SOM: Sedimentary organic matter; POM: Particulate organic matter; mangrove: mangrove leaves; MPB: microphytobenthos.

In both seasons, the coastal SOM+POM was the source with the largest contribution, accounting for more than 40% of the ZB/PV/ZP fishes diet, while the mangrove contribution was low (6/7%) (Fig. 6). During the dry season, the contribution of the SOM+POM from the coast was slightly higher (46%) than in the rainy season(43%). Moreover, the contribution of the POM+SOM of the estuary was slightly lower during the dry season(9%) than during the rainy season(13%).

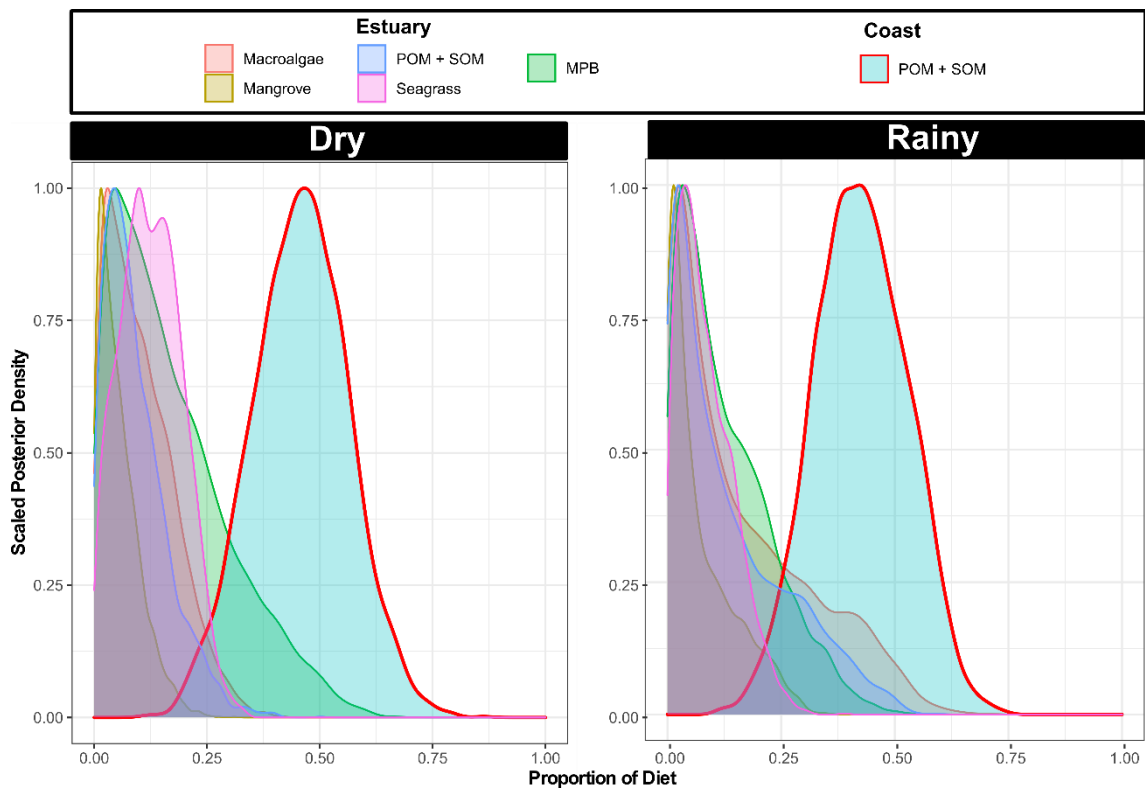


Fig. 6. Density plots representing the seasonal proportion of the basal sources in the diet of ZB/ZP/PV fish at the Santa Cruz Channel. SOM: Sedimentary organic matter; POM: Particulate organic matter; mangrove: mangrove leaves; MPB: microphytobenthos.

4. DISCUSSION

4.1. A spatiotemporal dynamic shaped by SCC morphology

A wide range of isotopic compositions was observed in both estuarine and coastal environments, but $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition showed greater variability in the estuarine part of the SCC. This estuarine heterogeneity was expected and is probably induced by the balance between marine and freshwater inputs (Warry et al., 2016), which results in a wide variety of primary producers and sources of organic matter from terrestrial, estuarine, and marine systems (Selleslagh et al., 2015). The morphology of the SCC intensifies the heterogeneity potential, as the two entrances to the sea provide strong mixing between riverine and marine inputs, resulting in a great diversity of habitats and food resources (Mérigot et al., 2017).

Most of the sampled fish species occurred in both estuarine and coastal environments. These species undertake ontogenetic migrations and depend on the estuary as a feeding ground and/or a nursery for their juveniles (Pelage et al., 2021a). Indeed, SCC morphological characteristics promote a fish assemblage consisting primarily of species that migrate between the estuary and the coastal zone, feeding on different grounds (Ferreira et al., 2019). The fish exhibited higher carbon and nitrogen compositions values and larger body sizes on the coast than in the estuary, suggesting that fish in both environments use different basal sources and prey on other trophic levels.

The lack of seasonal differences in basal sources signatures could also be related to the SCC geomorphology and hydrology. Since the SCC is a large estuary affected by an important discharge of organic matter from different rivers (CPRH, 2003), it does not have the same marked seasonality observed in small tropical estuaries. In such ecotones, freshwater inputs are intermittent, and seasonal nutrient inputs from terrestrial systems are favoured and have a greater effect on the isotopic compositions of organic matter (Abrantes et al., 2015). In this study, the lack of seasonal differences in invertebrate $\delta^{13}\text{C}$ values is consistent with that hypothesis.

However, fishes exhibited seasonal differences. Detritivores showed higher $\delta^{13}\text{C}$ values and lower $\delta^{15}\text{N}$ values of detritivores during the dry season, suggesting a seasonal shift in their diet. As detritivores depend on organic detritus available in the estuary, seasonal changes are expected to have a greater impact on this guild than others (Abrantes et al., 2013; Lin et al., 2007). This result supports the hypothesis that this guild, which is usually dominant in abundance in estuaries, is the most likely to integrate and be affected by seasonal changes, including those caused by humans (Baptista et al., 2015).

4.2. Organic matter sources supporting fish food webs

On the coast, the differences in isotopic composition between fish guilds were exclusively for nitrogen, confirming that the trophic level of detritivores and herbivores is lower than that of second-degree consumers. Conversely, estuarine fish showed differences between guilds in their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values during both seasons, suggesting that different sources of organic matter support fish food webs. Therefore, tracing the origin of organic matter for estuarine fish food webs using Bayesian models was important to illustrate the complexity of trophic pathways in the SCC.

Bayesian models allowed the distinction between coastal and estuarine sources. Despite the need for careful parameterisation, this analysis remains the best method for quantifying the relative contributions of sources to a diet (Parnell et al., 2010). As the selected TEF was measured in the laboratory for second-level consumers living in estuaries (Kostecki et al., 2012), our results should adequately reflect the relative contribution of coastal and estuarine sources. Mixing models lack accuracy in environments where several sources have overlapping isotopic compositions, typically in estuaries (Phillips et al., 2014). Nevertheless, as we aimed to investigate the origin of organic matter supporting food webs, uncertainties in distinguishing the contribution of overlapping estuarine sources are not an issue.

After the TEF was applied, detritus-feeding fish were not found in the polygon that is supposed to delineate the trophic boundaries of the system (Phillips et al., 2014). This hampered the execution of the model and signalled the non-inclusion of a source with high $\delta^{13}\text{C}$ values, essential for supporting detritivore food webs in the SCC. This missing source could be derived from terrestrial primary producers. For instance, terrestrial C4 plants have enriched carbon, and the importance of terrestrial producers for detritus feeders has already been reported in other tropical estuaries (Abrantes et al., 2014, 2013; Prado et al., 2020).

In this highly anthropised ecotone, there is a need to further explore the trophic pathways of detritivores for management purposes. The integration of terrestrial inputs into the food webs of detritus feeders may allow polluted effluents to affect fisheries' resources. In particular, the SCC has suffered from mercury contamination since the mid-60s (Albuquerque et al., 2019). In addition, high microplastic contamination was

observed for detritivorous fish sampled in the SCC (Justino et al., 2021). Within the mosaic of connected habitats forming the SCC, the contribution of terrestrial inputs to fish diets could promote a greater spatial extent of the impact of estuarine anthropogenic activities. For instance, the detritivore *M. curema* contributes to coastal fisheries yields and is an essential source of protein for coastal predators (Pelage et al., 2021a). In this regard, the ingestion of contaminated terrestrial detritus by *M. curema* could affect coastal food webs and fisheries.

This study highlighted the importance of coastal organic matter contribution for zoobenthivorous, piscivorous, and zooplanktivorous fish (Gonzalez et al., 2019; Pelage et al., 2021b). The predominance of coastal sources was already observed for the zoobenthivorous fish *E. argenteus* (Pelage et al., 2021b). Indeed, most of the non-detritivorous species are migratory. Nevertheless, the individuals sampled are likely to feed in the estuary since their juveniles reside there and their adults are not found in the estuary (Centropomidae, Carangidae) or use it as a feeding ground (Gerreidae) (Gonzalez, 2021; Gonzalez et al., 2019; Ramos et al., 2016). Although the high contribution of coastal organic matter may have been enhanced by migration, this pattern is more likely induced by marine intrusion facilitated by the morphology of the SCC. Methods using only stable isotopes cannot separate the effect of fish movements from marine intrusion. However, coastal organic matter can support estuarine food webs, and marine intrusion can even affect resident organisms with limited mobility (Selleslagh et al., 2015). Estuarine sources also contributed significantly, especially during the rainy season, indicating that species inhabiting the SCC estuary use a mixture of organic matter from several environments.

5. CONCLUSION

This study provides a better understanding of food webs in a tropical ecotone where several anthropogenic activities coexist (fisheries, industries, agriculture). It highlighted that habitat connectivity, which offers the possibility to diversify niches and enhance biodiversity, could also facilitate the incorporation of terrestrial and coastal inputs into estuarine fish food webs. Therefore, an efficient management plan of highly connected systems should focus on mitigating anthropogenic impacts in all interconnected habitats.

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Supplementary Material

Variable	Compartment	p-value
$\delta^{13}\text{C}$	Fish	1.457e-06*
	Copepods	0.002165*
	POM	0.002165*
	SOM	0.004329*
$\delta^{15}\text{N}$	Fish	0.0003268*
	Copepods	0.132
	POM	0.04113*
	SOM	0.004329*
Size	Car.hip	0.01587*
	Lut.ana	0.004847*
	Dia.aur	0.004922*
	c.und	0.02381*
	Mug.spp	0.0722
	s.axi	0.01235*
	o.ogl	0.9372
	m.fur	0.04

Compartment	Estuary		Coast	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
MPB	0.1	0.1	-	-
POM	0.4	1	0.1	0.1
SOM	0.2	0.2	0.1	0.2
Ulva	0.4	0.1	-	-
c.dan	0.02381	1	-	-
Cop	0.1	0.1	0.1	0.1
r.man	0.3939	0.1797	-	-
c.rhi	0.1	0.1	-	-
f.sub	0.1	0.1	-	-
DV	0.001463	0.0003996	-	-
OV	-	-	0.5127	0.7
PV	0.03901	0.1	0.1429	0.1429
ZB	0.3347	0.1668	0.8884	0.3704
ZP	0.5127	1	1	0.1

	DV		HV		PV		ZB	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
HV	0.0000*	0.1547						
PV	0.0000*	0.0000*	0.2755	1.0000				
ZB	0.0000*	0.0000*	0.1466	0.9424	0.9838	0.5016		
ZP	0.0402*	0.0000*	0.1409	1.0000	1.0000	1.0000	0.6449	0.4215

DV	HV	OV	PV	ZB
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	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
HV	0.0758	0.5805								
OV	0.8806	0.0109*	0.0374*	0.0010*						
PV	0.4675	0.1700	0.5765	0.0335*	0.3561	0.7267				
ZB	0.5287	0.5376	0.5092	0.1074	0.3059	0.1057	1.0000	1.0000		
ZP	0.0500*	0.6959	1.0000	0.6891	0.0118*	0.0362*	0.6852	0.6054	0.5397	0.9287

Supplementary material 2: Mean and standard deviation of the relative contributions of the organic matter sources in each of the estuaries during the rainy and the dry season.

Season	Basal source	Mean contribution	Standard deviation
Dry	Algae	0.10	0.07
Dry	Mangrove	0.06	0.05
Dry	Microphytobenthos	0.17	0.13
Dry	POM+SOM Coast	0.46	0.11
Dry	POM+SOM Estuary	0.10	0.07
Dry	Seagrass	0.13	0.07
Rainy	Algae	0.16	0.15
Rainy	Mangrove	0.07	0.07
Rainy	Microphytobenthos	0.13	0.10
Rainy	POM+SOM Coast	0.43	0.10
Rainy	POM+SOM Estuary	0.13	0.12
Rainy	Seagrass	0.09	0.06