



Trophic connectivity and basal food sources sustaining tropical aquatic consumers along a mangrove to ocean gradient



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ABSTRACT

Variations in the relative importance of autotrophic sources to aquatic consumers along environmental gradients and the trophic role of mangrove-derived detritus to marine coastal food webs are still poorly investigated in tropical systems. In this study, we employed stable isotope analyses to investigate the relative importance of basal food sources to macroconsumers (decapod crustaceans and fishes) in a tropical estuary along an environmental gradient extending from the mangroves to the ocean. Additionally, we evaluated the 'outwelling hypothesis', which hypothesizes that mangrove-derived detritus exported to the adjacent marine area is a food source for marine macroconsumers at open and reef-protected sandy beaches. Primary producers and macroconsumers (62 and 214 samples, respectively) were collected at five locations across the main longitudinal axis of the Mamanguape estuary, a tropical Southwestern Atlantic estuary. There were marked shifts in carbon and nitrogen isotope values for both food sources and consumers along the estuarine-marine gradient, and the mixing model results revealed similar patterns of assimilation of basal food sources by decapod crustaceans and fishes. In the inner section of the estuary, consumers tended to assimilate nutrients derived mainly from mangrove and macroalgae, whereas nearer the mouth of the estuary and in the adjacent marine area they assimilated nutrients derived mainly from macroalgae, seagrass and organic matter in the sediment (SOM). These findings support the hypothesis that the relative importance of basal food sources to macroconsumers in this tropical estuarine system reflects the dominant autochthonous primary production at each location. In contrast, our results did not support the outwelling hypothesis that mangrove-originated detritus, in the form of senescent mangrove leaves, makes a significant contribution as a primary source of carbon to high-order consumers inhabiting adjacent ocean sandy beaches.

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1. Introduction

Although estuarine systems occupy a relatively small portion of the marine environment, they provide abundant food and refuge against predators in shallow waters, which is crucial for the development of many fish and macrocrustacean species (Kennish, 1986). However, trophic interactions that sustain this high level of secondary production are challenging to uncover due to the difficulty in quantify trophic relationships between consumers and primary producers (e.g., mangroves, saltmarshes, seagrasses,

macroalgae, phytoplankton) and other basal food sources (e.g., detritus) (Day et al., 2012). High production of organic matter by estuarine vegetation (e.g., mangroves), in association with the absence of direct grazing, contributes to the accumulation of high amounts of detritus, which is usually considered to be the main food source at the base of estuarine food-webs (McLusky, 1989). Most detritus is digested by bacteria and other microorganisms (microbial loop), and many detritivorous metazoans depend on enzymes or biomass produced by microorganisms to derive nutrition from detritus (Nybakken and Bertness, 2005). However, the relative importance of autotrophic sources and detritus as nutritional sources sustaining estuarine consumers are still poorly investigated in many estuaries, especially in tropical and subtropical latitudes.

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Mangroves are found in intertidal areas of estuarine systems in tropical and subtropical regions ($\sim 30^\circ\text{N}$ to $\sim 30^\circ\text{S}$) and account for 0.7% of all tropical forests of the world (Giri et al., 2011). These coastal forests are formed mainly by halophytic woody plants that are adapted to the environmental fluctuations (e.g., salinity, oxygen, water level) typically found in estuaries (Hogarth, 2007). An important ecological function attributed to mangroves is the export of leaf litter carried by currents to adjacent coastal waters, where they can be a potential source of organic matter and nutrients for commercially important fisheries (Day et al., 2012). The formation and exportation of mangrove-derived carbon to adjacent habitats is well studied (Lee, 1995; Bouillon et al., 2007, 2008a; Twilley and Rivera-Monroy, 2009) and ranges from 1.86 to 401 $\text{gC/m}^2/\text{year}$ (Twilley et al., 1992). Much less evidence is available to support the 'outwelling' hypothesis first proposed by Odum and Heald (1975), which suggests that a large fraction of the organic matter produced by mangrove trees is exported to the adjacent marine habitat, where it is assimilated by organisms at the base of a detrital food chain sustaining coastal fisheries. Currently, there is no consensus on the ecological role organic matter produced by mangroves plays in relation to consumers. Most studies agree that the amount of mangrove-derived carbon incorporated by consumers in adjacent habitats is restricted (e.g., Lee, 1995; Loneragan et al., 1997); however, a few studies have shown more extensive incorporation in some locations for specific consumers such as prawns and bivalves (e.g., Chong et al., 2001; Savage et al., 2012). This ambiguity is reinforced by results obtained using stable isotopes, which do not reveal a direct trophic link between mangroves and marine consumers (Schwamborn et al., 1999; Bouillon et al., 2008b), as was suggested early on by gut content analysis, fishery statistics and organic matter mass balance (Day et al., 2012).

The relative importance of autotrophic carbon sources for estuarine consumers can vary along salinity gradients in estuarine systems. For instance, previous studies have shown that fish and macrocrustaceans in some estuaries tend to rely mainly on autochthonous rather than allochthonous food sources originating in freshwater systems (e.g., Deegan and Garritt, 1997; Garcia et al., 2007). Other studies have suggested that estuarine food webs are spatially structured and supported by local basal food sources and detritus from multiple origins, including particulate organic matter in the sediment, C_4 plants such as seagrasses, and, to a lesser extent, seston, and can be seasonally important (e.g., macroalgae blooms) for consumers (e.g., Claudino et al., 2013). However, differences in hydrogeomorphologic characteristics among estuaries and differences in the availability of autotrophic food sources (Hoeinghaus et al., 2011) preclude general conclusions on food assimilation patterns by estuarine consumers along environmental gradients and highlight the need for further studies.

Stable isotope analysis (SIA) has been successfully employed to investigate trophic relationships (Claudino et al., 2013; Abrantes et al., 2013) and trophic connectivity between freshwater-estuary and ocean habitats (Granek et al., 2009; Savage et al., 2012). SIA is usually employed to infer the relative contributions of food sources to consumers (e.g., using carbon isotope ratios of $^{13}\text{C}/^{12}\text{C}$) and to determine a consumer's trophic position in the food chain (e.g., based on nitrogen isotope ratios of $^{15}\text{N}/^{14}\text{N}$) (Fry, 2006). Despite its low taxonomic resolution and inability to distinguish between food sources with similar isotopic composition, SIA can overcome some of the methodological limitations associated with stomach content analysis (Jepsen and Winemiller, 2002) because it provides a time-integrated estimate of the real food assimilated in consumers' tissues (Peterson and Fry, 1987).

In the present study, SIA was employed to investigate the relative importance of basal food sources to estuarine consumers along an environmental gradient (extending from the mangroves to the

ocean) in a tropical Southwestern Atlantic estuary. In addition, we estimated assimilation of mangrove-derived detritus exported to the adjacent marine area by consumers at open and protected sandy beaches. Our hypotheses are as follows: (1) the relative importance of autotrophic sources to consumers will reflect the dominant autochthonous primary production at each location and (2) mangrove-derived detritus exported from inside the estuary to the outside marine area is a secondary source of primary carbon for macroconsumers at open and reef-protected sandy beaches.

2. Material and methods

2.1. Study area

The Mamanguape River estuary is a Protected Environmental Reserve with an area of 16,400 ha located in the State of Paraíba in northeast Brazil ($06^\circ 46'\text{S}$, $34^\circ 56'\text{W}$) (Fig. 1). This estuary harbors a great variety of habitats including sandy coastal beaches bordered by field dunes, coastal reefs with dense mats of macroalgae, seagrass beds (*Halodule wrightii*), restinga forests, tableland forests and a well-preserved mangrove area with approximately 6000 ha (Silvestre, 2011; Xavier et al., 2012). An important feature in this coastal system is an 8.5 m long barrier reef perpendicular to the shoreline, which creates a protected region at the mouth of the estuary (Nascimento, 2012). The regional climate is characterized by dry and wet periods that occur from October to April and May to September, respectively (Barletta et al., 2009). The tidal cycle is characterized by a mesotidal regime with a 2.7 m amplitude and an average high tide of 2.18 m and 1.04 m at the spring and neap tides, respectively. To the south and north, tidal waves are coincident with inflow and outflow conditions in the estuary (Davies, 1964).

2.2. Field collections and sample processing

Primary producers and macro-consumers (fish and macrocrustaceans) were collected during the wet period in April 2012 at five locations across a longitudinal axis of the estuary. Habitats sampled included mangroves at the northern end of the estuary, mudflat areas in the southern portions of the estuary, and marine sandy beaches adjacent to the estuary (Fig. 1). Two sampling locations (M1, M2) were established in the mangrove wetland (both within creeks or *camboas*), another one was in a tidal mudflat (TF) and the final two were located at coastal sandy beaches (one protected and another not protected by the coastal reef) (SB1, SB2) outside the estuary (Fig. 1B). All primary producers (mangrove, macroalgae, seagrass), consumers (fishes and decapod macrocrustaceans), and basal food sources such as particulate organic matter in suspension (POM) or in the sediment (SOM), were collected in triplicate whenever possible using sampling gear appropriate for each group (Garcia et al., 2007; Claudino et al., 2013). Macroalgae and seagrass beds could not be sampled in April 2012 at the TF and M2 sites. Hence, an additional field survey was carried in these sampling sites in August 2012 to collect representative species (*Gracilaria mammillaris* and *H. wrightii*, respectively) of these primary food sources.

Fishes and decapod macrocrustaceans were collected using beach seine hauls (13 mm mesh size in the wings and 5 mm in the center of the net) and by local fishermen in the mangrove areas using a passive sampling fishing method locally known as *tomada*. This method consists of setting up multifilament fishing nets at the edge of the mangrove wetland at the peak of the high tide and removing the nets during the following low tide (Bezerra et al., 2012). Infaunal organisms were collected using PVC tube (10 cm in diameter, area of 0.0078 m^2). All samples were stored in plastic bags and preserved on ice until transported to the laboratory,

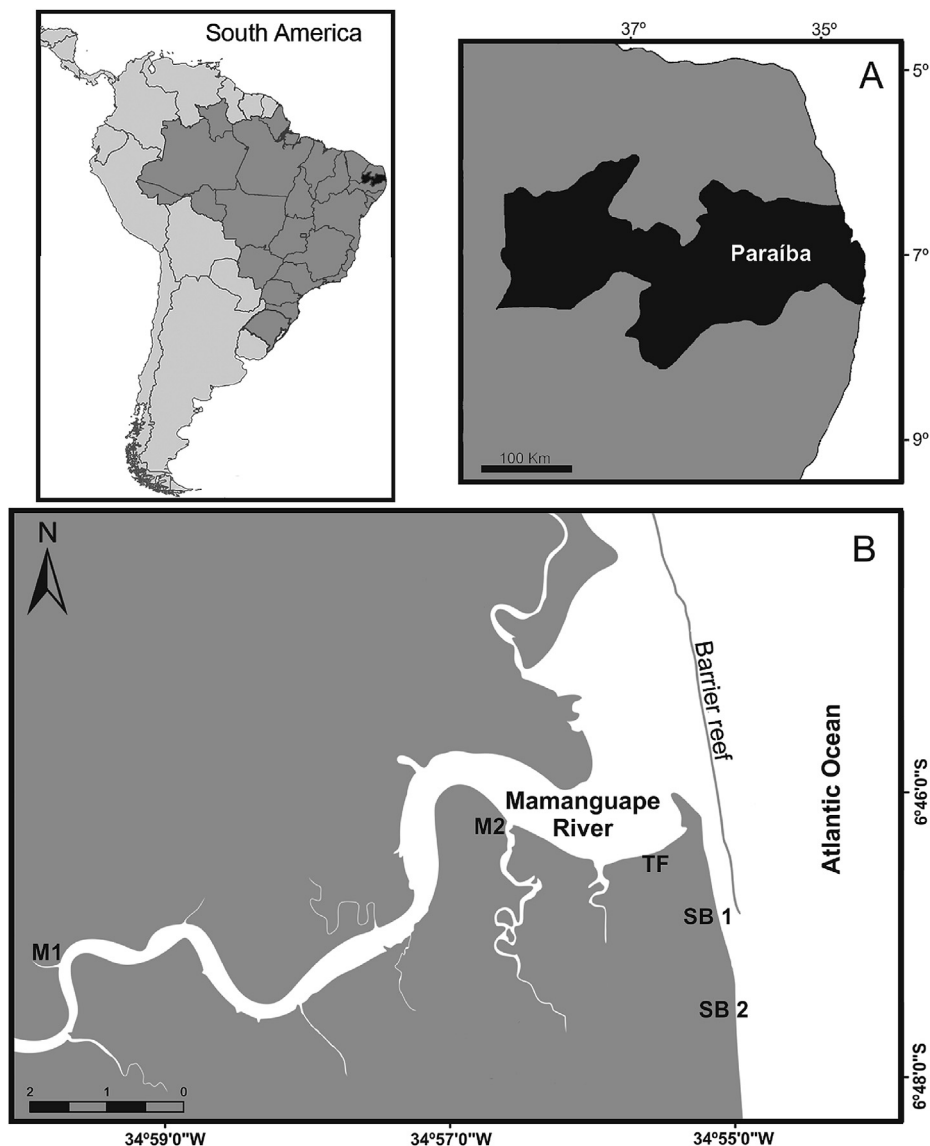


Fig. 1. State of Paraiba in northeast Brazil (A) and the Mamanguape River and its estuarine zone (B) with the locations of the sampled habitats: mangroves (M1 and M2), tidal flat (TF) and sandy beaches (SB1 and SB2).

where they were stored in a freezer until processing. Each sample was cleaned in distilled water, placed in sterile Petri dishes and dried in an oven at 60 °C for 48 h. Dried samples were ground to a fine powder with a mortar and pestle and stored in clean 2 ml plastic tubes. Subsamples were weighed (1–3 mg for animal tissues, 25–30 mg for SOM, and approximately 3 mg for other basal sources), pressed into ultra-pure tin capsules (Elemental Microanalysis), and sent to the Analytical Chemistry Laboratory of the Institute of Ecology, University of Georgia, for analysis of carbon and nitrogen isotope values. Results are expressed in delta notation (parts per thousand deviation from a standard material): $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. The standard material for carbon was Pee Dee Belemnite (PDB) limestone, and the nitrogen standard was atmospheric nitrogen. Standard deviations for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ replicate analyses of internal standards were 0.12‰ and 0.09‰, respectively.

2.3. Data analyses

Spatial patterns in carbon and nitrogen stable isotope values of

basal food sources and macroconsumers (decapod macrocrustaceans and fish) were initially investigated using biplot diagrams (Fry, 2006). Differences in the average isotopic values between locations within each group were evaluated using analysis of variance (ANOVA) and Tukey HSD post hoc test.

We employed the Bayesian stable isotope mixing model in the Stable Isotope Analysis in R (SIAR) package (Parnell et al., 2010) to estimate the relative contributions of basal food sources to decapod macrocrustaceans and fish at each location. SIAR assumes that the variability associated with food sources and trophic enrichment is normally distributed (Parnell et al., 2010). To better restrict our model, we used elemental concentrations (%C and %N) measured for each organic basal source in this study (Phillips et al., 2014). We used fractionation values of nitrogen 2.54 ± 0.11 (Vanderklift and Ponsard, 2003) and carbon 0.47 ± 1.23 (Vander Zanden and Rasmussen, 2001) to distinguish between trophic levels.

Acidification was used to correct $\delta^{13}\text{C}$ values in samples of sediment (SOM) with potentially higher levels of inorganic carbon (e.g., carbonate). We divided our SOM samples into two treatments: one receiving acidification (AC) and the other not receiving

acidification (N-AC). AC subsamples were used for $\delta^{13}\text{C}$ values, and N-AC subsamples were used for $\delta^{15}\text{N}$ values. Samples were acidified with approximately 2 ml of 1 M HCl, and after bubbling had ceased, they were dried at 60 °C for 18 h (Ryba and Burgess, 2002).

3. Results

A total of 276 samples were collected (62 basal food sources and 214 consumers) at the five sampling locations (Tables 1 and 2, Fig. 1). Fishes and macrocrustaceans were collected along all five sampling locations, but a greater number of individuals were found in the estuarine areas (63 and 19 at M1, 40 and 12 at M2 and 32 and 10 at TF, respectively) than in the marine adjacent areas (11 and 5 at SB1, 21 and 6 at SB2, respectively) (Table 2).

The total variation in average carbon isotope value ($\delta^{13}\text{C}$) of the overall community at each location was approximately three-fold higher in the tidal flat (from -26.68 to -1.76) and sandy beach areas (from -30.66 to -0.14 at SB1 and from -29.66 to 1.65 at SB2) compared to mangrove areas (from -28.93 to -20.76 at M1 and from -26.83 to -18.87 at M2) (Fig. 2). The large variation in $\delta^{13}\text{C}$ values at the TF and at both SB locations can be partially explained by higher interspecific differences in average $\delta^{13}\text{C}$ values among consumers, but was mainly due to the occurrence of basal food sources with extremely high carbon isotope values at these areas, especially SOM (-1.76 , -0.14 and 1.65 at TF, SB1 and SB2 locations, respectively) (Figs. 2 and 3). Although much less pronounced, a similar trend was also observed for nitrogen isotope values ($\delta^{15}\text{N}$), with a steady increase in overall variation from the inner estuary

(e.g., from 3.40 to 12.65 at M1) to the marine adjacent areas (e.g., from -1.28 to 14.44 at SB2) (Fig. 2).

Average $\delta^{13}\text{C}$ values of basal food sources showed an abrupt shift in their values along the study region, with lower values at the two mangrove areas (M1: -26.01 and M2: -23.22) and higher values at marine sandy beach areas (SB1: -19.43 ; SB2: -14.29) ($p < 0.001$ one-way ANOVA with Tukey HSD post-hoc test). A similar pattern was observed for both fish and macrocrustaceans, which had statistically significant higher average $\delta^{13}\text{C}$ values at TF (-16.47) and SB1 (-16.35) and SB2 (-15.50) when compared with M1 (-23.45) and M2 (-22.57) ($p < 0.001$ one-way ANOVA with Tukey HSD post-hoc test) (Fig. 3A).

Nitrogen isotope values ($\delta^{15}\text{N}$) of basal food sources showed a gradual increase from the inner estuarine areas (M1: 3.79; M2: 3.34) towards those located in marine adjacent areas (SB1: 5.39, SB2: 5.21; $p < 0.001$ one-way ANOVA with Tukey HSD post-hoc test) (Fig. 3B). The same pattern occur for consumers, with low values at M1 (8.03) and M2 (9.73), and higher values at sandy beaches (SB1: 12.54; SB2: 12.22; $p < 0.001$ one-way ANOVA with Tukey HSD post-hoc test).

In general, macrocrustaceans and fishes were approximately four and two per mil higher than average values of basal food sources, respectively (Fig. 3B).

Overall, isotope mixing models revealed similar patterns of assimilation of basal food sources by fishes and macrocrustaceans across the studied habitats. In the inner section of the estuary (M1 and M2), consumers tended to assimilated nutrients derived mainly from mangrove and macroalgae, whereas

Table 1
Mean values (± 1 SE) of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C:N ratios of basal food sources sampled along the mangrove to ocean gradient in Mamanguape estuary. *Denotes basal food sources collected during an additional field survey (see M&M).

Species	Codes		n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N
<i>Mangrove 1 (M1)</i>						
<i>Avicennia germinans</i>	AVIGER	Mangrove	3	-24.07 ± 1.04	3.40 ± 0.64	26.81 ± 1.15
<i>Laguncularia racemosa</i>	LAGRAC	Mangrove	3	-28.93 ± 0.27	3.49 ± 0.12	31.78 ± 2.54
POM	POM	Particulate organic matter	3	-26.80 ± 0.04	3.73 ± 3.73	12.51 ± 0.28
SOM	SOM	Organic matter in sediment	3	-24.24 ± 1.01	4.57 ± 4.57	20.82 ± 1.16
<i>Mangrove 2 (M2)</i>						
<i>Gracilaria mammillaris</i> *	GRAMAM	Macroalgae	2	-21.13 ± 0.14	7.76 ± 0.07	14.09 ± 0.40
<i>Laguncularia racemosa</i>	LAGRAC	Mangrove	3	-26.83 ± 0.69	0.00 ± 0.21	82.61 ± 4.03
<i>Rhizophora mangle</i>	RHIMAN	Mangrove	4	-23.96 ± 1.83	4.01 ± 1.66	53.67 ± 18.57
POM	POM	Particulate organic matter	3	-24.84 ± 1.17	3.03 ± 0.30	15.51 ± 1.41
SOM	SOM	Organic matter in sediment	2	-19.35 ± 1.46	1.94 ± 0.93	21.58 ± 6.04
<i>Tidal Flat (TF)</i>						
<i>Rhizophora mangle</i>	RHIMAN	Mangrove	1	-26.67 ± 0.00	1.58 ± 0.00	100.61 ± 0.01
<i>Halodule Wrightii</i> *	HALWRI	Seagrass	3	-13.48 ± 0.32	5.52 ± 0.83	11.29 ± 2.21
POM	POM	Particulate organic matter	3	-22.39 ± 0.04	4.97 ± 0.05	15.60 ± 0.20
SOM	SOM	Organic matter in sediment	2	-1.76 ± 3.13	1.43 ± 1.03	96.06 ± 46.90
<i>Sandy Beach 1 (SB 1)</i>						
<i>Rhizophora mangle</i>	RHIMAN	Mangrove	2	-26.90 ± 0.65	0.52 ± 0.34	117.21 ± 2.91
<i>Acanthophora spicifera</i>	ACASPI	Macroalgae	2	-30.66 ± 0.03	7.85 ± 0.21	12.50 ± 1.19
<i>Bryothamnion seaforthii</i>	BRYSEA	Macroalgae	2	-18.19 ± 1.09	6.81 ± 0.39	16.87 ± 1.72
<i>Criptonemia seminervis</i>	CRISEM	Macroalgae	2	-18.62 ± 0.49	6.22 ± 1.51	22.67 ± 1.86
<i>Gracilaria leirdiae</i>	GRALEI	Macroalgae	2	-19.21 ± 1.16	4.74 ± 1.37	20.50 ± 4.69
<i>Gracilaria mammillaris</i>	GRAMAM	Macroalgae	2	-22.45 ± 3.97	7.01 ± 2.82	17.01 ± 6.54
<i>Hypnea musciformis</i>	HYPMUS	Macroalgae	2	-17.63 ± 1.36	8.63 ± 0.86	16.26 ± 3.16
<i>Sargassum</i> sp	SARSPP	Macroalgae	1	-15.59 ± 0.00	6.05 ± 0.00	18.11 ± 0.00
<i>Halodule Wrightii</i>	HALWRI	Seagrass	1	-17.83 ± 0.00	8.19 ± 0.00	18.06 ± 0.00
POM	POM	Particulate organic matter	3	-26.51 ± 3.41	4.95 ± 0.23	11.17 ± 0.06
SOM	SOM	Organic matter in sediment	2	-0.14 ± 0.05	-1.67 ± 0.11	51.13 ± 10.37
<i>Sandy Beach 2 (SB 2)</i>						
<i>Gracilaria caudata</i>	GRACAU	Macroalgae	2	-17.42 ± 0.29	8.03 ± 0.40	16.39 ± 0.66
<i>Ulva fasciata</i>	ULVFAS	Macroalgae	1	-7.15 ± 0.00	5.97 ± 0.00	36.44 ± 0.00
<i>Ulva lactuca</i>	ULVLAC	Macroalgae	1	-14.50 ± 0.00	7.50 ± 0.00	12.08 ± 0.00
<i>Osmundaria obtusiloba</i>	OSMOBT	Macroalgae	2	-13.72 ± 0.36	7.93 ± 0.14	14.38 ± 3.46
<i>Botryocladia occidentalis</i>	BOTOCC	Macroalgae	1	-14.36 ± 0.00	7.51 ± 0.00	16.10 ± 0.00
<i>Rhizophora mangle</i>	RHIMAN	Mangrove	2	-29.65 ± 2.14	-1.27 ± 1.23	80.66 ± 22.82
POM	POM	Particulate organic matter	4	-19.16 ± 0.61	6.57 ± 0.17	$11.97 \pm .49$
SOM	SOM	Organic matter in sediment	2	1.64 ± 0.16	-0.49 ± 0.28	172.51 ± 9.60

Table 2Mean values (± 1 SD) of total length (TL, mm); mean values (± 1 Se) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of macroconsumers collected along an estuarine–ocean gradient in Mamanguape estuary, NE, Brazil.

Species	Codes	n	TL	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Mangrove (M1)</i>					
Fishes					
<i>Achirus declivis</i>	ACHDEC	1	64.00 \pm 0.00	–25.86 \pm 0.00	9.66 \pm 0.00
<i>Achirus lineatus</i>	ACHLIN	3	35.60 \pm 10.69	–26.70 \pm 0.26	9.74 \pm 0.16
<i>Atherinella brasiliensis</i>	ATHBRA	5	51.80 \pm 11.38	–26.57 \pm 0.82	11.17 \pm 0.43
<i>Bathygobius soporator</i>	BATSOP	1	72.00 \pm 0.00	–26.17 \pm 0.00	10.10 \pm 0.00
<i>Citharichthys arenaceus</i>	CITARE	6	56.50 \pm 13.79	–26.02 \pm 0.35	10.14 \pm 0.17
<i>Colomesus psitacus</i>	COLPSI	1	62.00 \pm 0.00	–20.76 \pm 0.00	12.65 \pm 0.00
<i>Eucinostomus argenteus</i>	EUCARG	2	42.50 \pm 17.67	–25.34 \pm 1.89	10.72 \pm 0.43
<i>Eugerres brasilianus</i>	EUCBRA	6	48.80 \pm 16.66	–26.61 \pm 0.58	10.88 \pm 0.30
<i>Gobionellus oceanicus</i>	GOBOCE	5	110.20 \pm 66.76	–24.61 \pm 1.28	8.01 \pm 1.76
<i>Gobionellus stomatus</i>	GOBSTO	3	99.30 \pm 19.13	–21.91 \pm 0.89	6.01 \pm 0.51
<i>Lycengraulis grossidens</i>	LYCGRO	3	47.00 \pm 3.60	–26.18 \pm 0.61	10.92 \pm .25
<i>Mugil curvidens</i>	MUGCUR	1	113.00 \pm 0.00	–21.95 \pm 0.00	5.96 \pm 0.00
<i>Mugil hospes</i>	MUGHOS	3	109.00 \pm 16.46	–21.20 \pm 0.69	6.16 \pm 0.15
<i>Oligoplites saurus</i>	OLISAU	4	32.50 \pm 9.43	–24.85 \pm 0.30	11.73 \pm 0.18
<i>Rhinosardinia bahiensis</i>	RHIBAH	3	39.00 \pm 6.92	–29.05 \pm 0.60	12.22 \pm 0.20
<i>Sciades herzbergii</i>	SCIHER	6	76.30 \pm 15.30	–23.86 \pm 0.51	10.31 \pm 0.33
<i>Sphoeroides testudineus</i>	SPHTES	8	38.75 \pm 18.49	–24.43 \pm 0.44	9.67 \pm 0.27
<i>Symphurus tessellatus</i>	SYMTES	2	117.00 \pm 4.24	–25.48 \pm 0.34	10.70 \pm 0.20
Macrocrustaceans					
<i>Callinectes danae</i>	CALDAN	9	47.80 \pm 23.37	–24.30 \pm 0.43	8.97 \pm 0.17
<i>Macrobrachium sp1.</i>	MACSP1	1	64.00 \pm 0.00	–25.12 \pm 0.00	9.61 \pm 0.00
<i>Macrobrachium sp2.</i>	MACSP2	2	52.00 \pm 1.41	–23.62 \pm 0.33	10.10 \pm 0.16
<i>Farfantepenaeus sp.</i>	FARSPP	7	53.00 \pm 13.32	–23.45 \pm 0.24	8.03 \pm 0.06
<i>Mangrove (M2)</i>					
Fishes					
<i>Atherinella brasiliensis</i>	ATHBRA	15	69.90 \pm 30.04	–22.51 \pm 0.37	11.60 \pm 0.17
<i>Caranx latus</i>	CARLAT	1	74.00 \pm 0.00	–18.87 \pm 0.00	9.69 \pm 0.00
<i>Citharichthys spilopterus</i>	CITSPI	1	107.00 \pm 0.00	–22.52 \pm 0.00	11.91 \pm 0.00
<i>Hyporhamphus unifasciatus</i>	HYPUNI	3	159.30 \pm 9.81	–22.57 \pm 0.10	10.92 \pm 0.29
<i>Lagocephalus laevigatus</i>	LAGLAE	1	173.00 \pm 0.00	–20.24 \pm 0.00	12.55 \pm 0.00
<i>Lutjanus jocu</i>	LUTJOC	4	113.75 \pm 20.17	–21.93 \pm 0.90	11.54 \pm 0.46
<i>Lycengraulis grossidens</i>	LYCGRO	6	111.80 \pm 10.26	–24.81 \pm 2.12	12.31 \pm 0.61
<i>Sciades herzbergii</i>	SCIHER	6	271.30 \pm 58.11	–23.37 \pm 0.53	8.79 \pm 0.39
<i>Sphoeroides testudineus</i>	SPHTES	3	121.65 \pm 25.65	–23.11 \pm 1.00	9.28 \pm 0.61
Macrocrustaceans					
<i>Callinectes danae</i>	CALDAN	2	69.00 \pm 25.45	–22.57 \pm 0.78	7.11 \pm 1.75
<i>Clibanarius antillensis</i>	CLIANI	4		–25.16 \pm 0.56	7.30 \pm 0.73
<i>Goniopsis cruentata</i>	GONCRU	3	39.00 \pm 1.00	–21.93 \pm 0.36	7.62 \pm 0.54
<i>Ucides cordatus</i>	UCICOR	3	63.00 \pm 3.60	–23.92 \pm 0.30	5.99 \pm 0.61
<i>Tidal flat (TF)</i>					
Fishes					
<i>Atherinella brasiliensis</i>	ATHBRA	6	63.80 \pm 42.40	–18.49 \pm 0.47	11.94 \pm 0.19
<i>Caranx latus</i>	CARLAT	2	76.50 \pm 2.12	–14.41 \pm 0.93	8.16 \pm 0.24
<i>Conodon nobilis</i>	CONNOB	1	94.00 \pm 0.00	–17.26 \pm 0.00	13.03 \pm 0.00
<i>Ctenogobius stigmaticus</i>	CTESTI	1	25.00 \pm 0.00	–12.71 \pm 0.00	7.75 \pm 0.00
<i>Eucinostomus melanopterus</i>	EUCMEL	1	46.00 \pm 0.00	–23.51 \pm 0.00	7.40 \pm 0.00
<i>Hyporhamphus unifasciatus</i>	HYPUNI	4	145.25 \pm 26.39	–18.45 \pm 0.63	11.09 \pm 0.09
<i>Lycengraulis grossidens</i>	LYCGRO	1	118.00 \pm 0.00	–20.34 \pm 0.00	12.85 \pm 0.00
<i>Mugil curema</i>	MUGCUR	1	82.00 \pm 0.00	–12.23 \pm 0.00	4.73 \pm 0.00
<i>Mugil curvidens</i>	MUGCUV	3	77.30 \pm 2.08	–19.82 \pm 1.85	12.25 \pm 0.22
<i>Mugil liza</i>	MUGLIZ	1	30.00 \pm 0.00	–11.73 \pm 0.00	11.27 \pm 0.00
<i>Polydactylus virginicus</i>	POLVIR	1	127.00 \pm 0.00	–16.50 \pm 0.00	12.53 \pm 0.00
<i>Sphoeroides greeleyi</i>	SPHGRE	7	64.00 \pm 16.84	–13.85 \pm 0.36	10.17 \pm 0.68
<i>Sphoeroides testudineus</i>	SPHTES	3	151.00 \pm 20.66	–15.97 \pm 0.80	11.52 \pm 0.20
Macrocrustaceans					
<i>Callinectes danae</i>	CALDAN	5	42.20 \pm 21.70	–12.24 \pm 0.51	8.44 \pm 0.53
<i>Clibanarius antillensis</i>	CLIANI	2	52.50 \pm 17.67	–16.22 \pm 3.14	7.54 \pm 0.06
<i>Ocypode quadrata</i>	OCYQUA	3	35.00 \pm 4.35	–19.89 \pm 0.72	8.17 \pm 0.11
<i>Sandy Beach (SB 1)</i>					
Fishes					
<i>Lycengraulis grossidens</i>	LYCGRO	5	85.20 \pm 21.89	–16.66 \pm 0.38	13.76 \pm 0.10
<i>Menticirrhus littoralis</i>	MENLIT	1	78.00 \pm 0.00	–14.56 \pm 0.00	13.83 \pm 0.00
<i>Polydactylus virginicus</i>	POLVIR	3	83.00 \pm 17.57	–17.19 \pm 1.13	12.41 \pm 0.85
<i>Trachinotus carolinus</i>	TRACAR	2	38.50 \pm 2.12	–16.07 \pm 0.09	11.43 \pm 0.70
Macrocrustaceans					
<i>Callinectes danae</i>	CALDAN	5	42.00 \pm 21.82	–17.28 \pm 1.10	11.30 \pm 0.15
<i>Sandy Beach (SB 2)</i>					
Fishes					
<i>Leptocephalus larvae</i>	LEPLAR	3	49.30 \pm 3.51	–19.11 \pm 0.05	8.01 \pm 0.23
<i>Lycengraulis grossidens</i>	LYCGRO	9	67.55 \pm 24.78	–15.15 \pm 0.30	14.43 \pm 0.30

(continued on next page)

Table 2 (continued)

Species	Codes	n	TL	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Mugil liza</i>	MUGLIZ	1	52.00 ± 0.00	-15.71 ± 0.00	10.82 ± 0.00
<i>Polydactylus virginicus</i>	POLVIR	5	54.60 ± 20.00	-14.97 ± 0.13	13.39 ± 0.88
<i>Selene vomer</i>	SELVOM	1	67.00 ± 0.00	-14.61 ± 0.00	13.99 ± 0.00
<i>Trachinotus carolinus</i>	TRACAR	1	110.00 ± 0.00	-14.70 ± 0.00	12.69 ± 0.00
<i>Trachinotus falcatus</i>	TRAFAL	1	110.00 ± 0.00	-15.11 ± 0.00	12.46 ± 0.00
Macrocrustaceans					
<i>Callinectes danae</i>	CALDAN	6	58.50 ± 13.35	-14.67 ± 0.13	12.01 ± 0.32

at the outer section (TF) and at the adjacent marine area (SB1 and SB2) they assimilated nutrients derived from macroalgae, sea-grass and organic matter in the sediment (SOM). POM contribution to consumers remained similar along the mangrove to ocean gradient and tended to be lower than the other basal food sources (Fig. 4).

The contribution of mangrove-derived nutrients to consumers, in particular, was restricted to the inner section of the estuary (95% Credibility Interval, 0.09 to 0.54 and 0.04 to 0.44 at M1 and M2 for fish and macrocrustaceans, respectively), where mangrove trees were the dominant vegetation along the margins of the estuary. Among the three mangrove species occurring in the estuary, *Laguncularia racemosa* was the only one contributing nutrients to consumers, especially at M1. Despite the fact that a high frequency of senescent mangrove leaves was observed in the outer section of the estuary (TF) and in adjacent marine areas (SB1 and SB2), the isotope mixing models showed that mangroves had no contribution to fishes and a minimal contribution to macrocrustaceans (Fig. 4).

4. Discussion

4.1. Food assimilation across the environmental gradient

Our study revealed marked shifts in carbon and nitrogen isotope values along the mangrove to ocean gradient, which coincides with a concomitant shift in assimilation of carbon- and nitrogen-derived nutrients by both macrocrustaceans and fish. More specifically, there was a notable decreasing trend in the assimilation of mangrove-derived nutrients by fish from the inner section of the estuary towards the adjacent ocean sandy beaches. This pattern contrasted with a tendency for higher assimilation of nutrients derived from macroalgae and seagrass beds by consumers collected at a mudflat near the estuary's mouth and in the adjacent ocean sandy beaches. Overall, these patterns coincided with the spatial shift in dominant vegetation (from mangrove to macroalgae-seagrass beds) along the studied environmental gradient. Mangrove trees (*L. racemosa*, *Rhizophora mangle*, *Avicennia germinans*) are the dominant vegetation covering the intertidal zone near the inner section of the estuary, whereas macroalgae and seagrass beds are conspicuously found at the estuary's mouth and in adjacent marine barrier reef (Silva, 2002; Xavier et al., 2012). Therefore, our findings support our initial hypothesis that the relative importance of autotrophic sources to macroconsumers in this tropical estuarine system varies spatially and seems to reflect the dominant autochthonous primary production at each section of the estuary.

The hypothesis that the consumer's assimilation reflects the dominant autochthonous primary production at each location was further corroborated when we considered the distribution and nutritional value of the mangrove trees found in the studied area. According to our mixing isotope models, *L. racemosa* was the only mangrove tree out of the three species occurring in this estuary that contributed significant amounts of nutrients to consumers. This

species is comparatively dominant in the inner region of the estuary (Iaponira, 2009) and is characterized by a higher nutritional value than *R. mangle* (Lima et al., 2014), which is dominant nearer the southern portion of the estuary. A proxy for the nutritional value is the C:N ratio because lower values indicate higher amounts of nitrogen than carbon and, consequently, a higher nutritional value to consumers (Ashton et al., 1999). In our study, the average C:N ratio value of *L. racemosa* was nearly three times lower than the value found for *R. mangle* (31.78 and 92.70, respectively). Another mangrove tree with a lower C:N ratio (26.81) is *A. germinans*, which occurs in the inner section of the estuary. According to the mixing models, the contribution of this species to consumers was nearly zero. The lower contribution of *A. germinans* to the studied consumers could be explained by its low biomass value compared with *L. racemosa* in this area (Iaponira, 2009). Aside from nutritional values, other factors could be causing inter-specific differences in mangrove-derived nutrients by consumers, such as differences among these mangrove trees in detritus production (e.g., leaf turnover) rate, detritus decomposition rate and feeding deterrent production (Saenger, 2002; Paul and Puglisi, 2004; Day et al., 2012). Future laboratory and field studies would be needed to evaluate the relative role of these mechanisms in explaining the apparently higher assimilation of *L. racemosa*-derived nutrients by consumers in this estuary.

Our stable isotope analysis results reinforce prior evidence that the trophic link between mangrove-derived nutrients and consumers is spatially restricted (Bouillon et al., 2008; Giarrizzo et al., 2011). In our system, mangrove-derived food sources were assimilated only by fish caught in creeks (*camboas*) located inside the mangrove wetlands. Although stable isotope results did not allow a detailed description of these trophic links, we hypothesized that assimilation of mangrove-derived nutrients in this system occurs mainly by benthivorous or zoobenthivorous fish feeding on small invertebrates and detritus e.g., *Bathygobius soporator*, *Gobionellus oceanicus*, *Gobionellus stomatus*, *Lagocephalus laevigatus*, *Mugil curvidens*, *Mugil hospes* and *Sphoeroides testudineus* (Chi-Espínola and Vega-Cendejas, 2013; Soares et al., 2013; Denadaia et al., 2012). These fishes can incorporate mangrove-derived nutrients indirectly via consumption of invertebrates that feed upon mangrove detritus. This assumption is common in the literature and is based on the idea that assimilation of mangrove production by higher trophic level organisms is dependent on and mediated by microbial decomposition of litter fall and consumption by a variety of small detritivores (Odum and Heald, 1972; Hatcher et al., 1989; Yáñez-Arancibia et al., 1993). For instance, prior work using SIA to study the assimilation of mangrove-derived carbon by consumers at mangrove wetlands in North Brazil (Curuçá Bay) showed that vascular plants contribute directly or indirectly via POM to crabs (e.g., *Ucides cordatus*) and zooplanktivorous fish. According to these authors, mangrove-derived carbon would be assimilated by calanoid copepods and transferred to consumers at higher trophic levels through ingestion of these invertebrates by chaetognaths and zooplanktivorous small pelagic fishes (Giarrizzo et al., 2011).

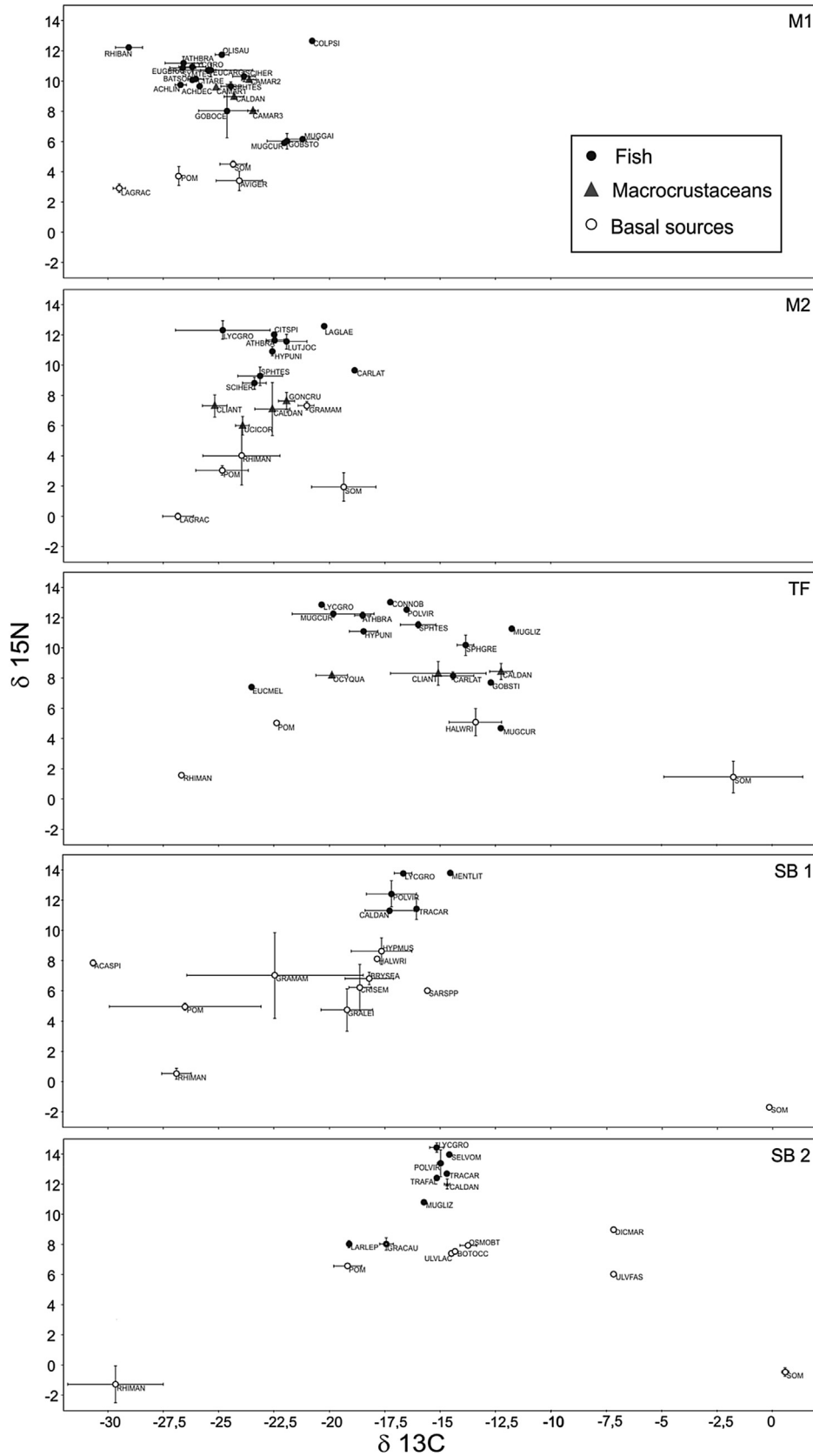


Fig. 2. Biplots of carbon and nitrogen stable isotope values (mean \pm S.E.) for basal food sources (open circles), fish (filled circles) and macrocrustaceans (filled triangles) collected along an estuarine-ocean gradient at the Mamanguape River estuary and its adjacent coast. Codes for food sources and consumers are in Tables 1 and 2, respectively.

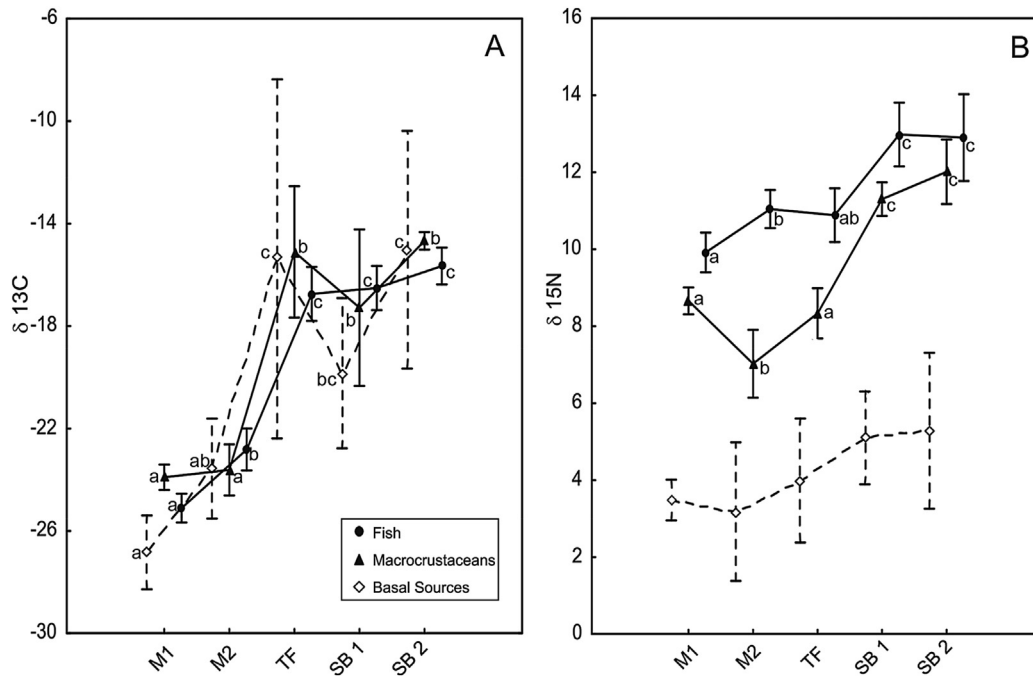


Fig. 3. Carbon (A) and nitrogen (B) stable isotope values (mean \pm S.E.) for basal food sources (dashed lines), fish (filled circles) and macrocrustaceans (filled triangles) collected along an estuarine-ocean gradient at the Mamanguape River estuary and its adjacent coast. Codes for sampled locations are in Fig. 1. Letters indicate statistical differences between locations within each group of consumers.

4.2. Trophic connectivity between estuarine and ocean habitats

Our results did not corroborate the outwelling hypothesis that mangrove-originated detritus, in the form of senescent mangrove leaves, makes a significant contribution as a primary source of carbon to high-order consumers inhabiting adjacent ocean sandy beaches. Despite the fact that senescent mangrove leaves (mainly from *R. mangle*) were commonly found in the central portion of the estuary (tidal flat) and in the surf-zone of both open and reef-protected ocean sandy beaches, our isotope mixing results showed that mangrove detritus was not a significant food source for fishes and macrocrustaceans in these locations. This absence could be explained by the decomposition process of mangrove leaves, which occurs in two steps: a faster loss of soluble compounds followed by a slower decomposition of refractory material as lignin (Lima et al., 2014). This process would explain why mangrove-derived nutrients in our study were assimilated by consumers inside the mangrove wetland, but not by consumers in the adjacent marine area, despite observations of mangrove leaves in adjacent sandy beaches. The mangrove-derived material found in the sandy beaches most likely could not be assimilated by local consumers due its more refractory characteristic (Rodelli et al., 1984) and lower nutritional value (Lima et al., 2014), similar to what has been observed in other coastal systems (Rodelli et al., 1984; Hemminga et al., 1994).

In contrast with the lack of assimilation of mangrove-derived detritus by fish in the studied ocean sandy beaches, assimilation by macrocrustaceans (mainly blue crabs, crabs and shrimp species) ranged from approximately zero to 20%. This pattern suggests that assimilation of mangrove-derived detritus would be more likely to occur by detritivore consumers feeding closer to the base of the food chain rather than by carnivorous fish feeding at intermediate trophic levels at ocean beaches (e.g., *Menticirrhus littoralis*, *Polydactylus virginicus*, *Trachinotus carolinus*, *Trachinotus falcatus*, *Lycengraulis grossidens*, *Selene vomer*) (Rodrigues and Vieira, 2010; Niang et al., 2010). This hypothesis is corroborated by prior stable

isotope studies showing that assimilation of estuarine-derived nutrients usually occurs in recipient consumers feeding at the base of the food chain (e.g., primary consumers). For instance, Savage et al. (2012) found that suspension feeding bivalves (*Dosinia* spp.) inhabiting a shallow sandy shelf system assimilated in their tissues estuarine-derived nutrients from seagrass and fringing vegetation detritus produced by saltmarshes and mangroves in the Whangapoua Estuary (New Zealand). Filter feeding mollusks were not included in our study; therefore, it is possible that the outwelling hypothesis could be occurring at the primary trophic level in this system. Future studies integrating traditional and stable isotope approaches and employing recipient consumers positioned at different trophic levels in the food chain are needed to further evaluate this hypothesis.

The export of mangrove-derived detritus and its subsequent incorporation by marine dwelling macroconsumers (e.g., fishes and macrocrustaceans) are not the only mechanism promoting the connectivity between mangrove and marine systems. Due to its high motility, animal migration can substantially affect the interchange of nutrients (especially N and P) and energy between the estuary and the ocean (Deegan, 1993; Oliveira et al., 2014). Detritus exported to the ocean by physical forces (e.g., tides, freshwater discharge) usually have lower nutritional values and have undergone rapid sedimentation before reaching higher trophic levels in the food chain (Nixon, 1980). In contrast, migration of juvenile stages of marine estuarine-dependent fish in and out of estuarine systems can transport high amounts of high-quality organic matter as their own biomass. This higher quality material can be more easily incorporated up the food chain through predation by benthic and pelagic carnivores (Deegan, 1993). For instance, several species of snappers (Lutjanidae) use mangrove wetlands as juvenile habitat and move to coral reefs as adults (Jaxion-Harm et al., 2012; Honda et al., 2013; Kimirei et al., 2013). As pointed out earlier by Xavier et al. (2012), Lutjanidae species could play a role in the connectivity among mangrove, seagrass beds and adjacent coastal reef habitats of Mamanguape estuary. In our study, juveniles (average

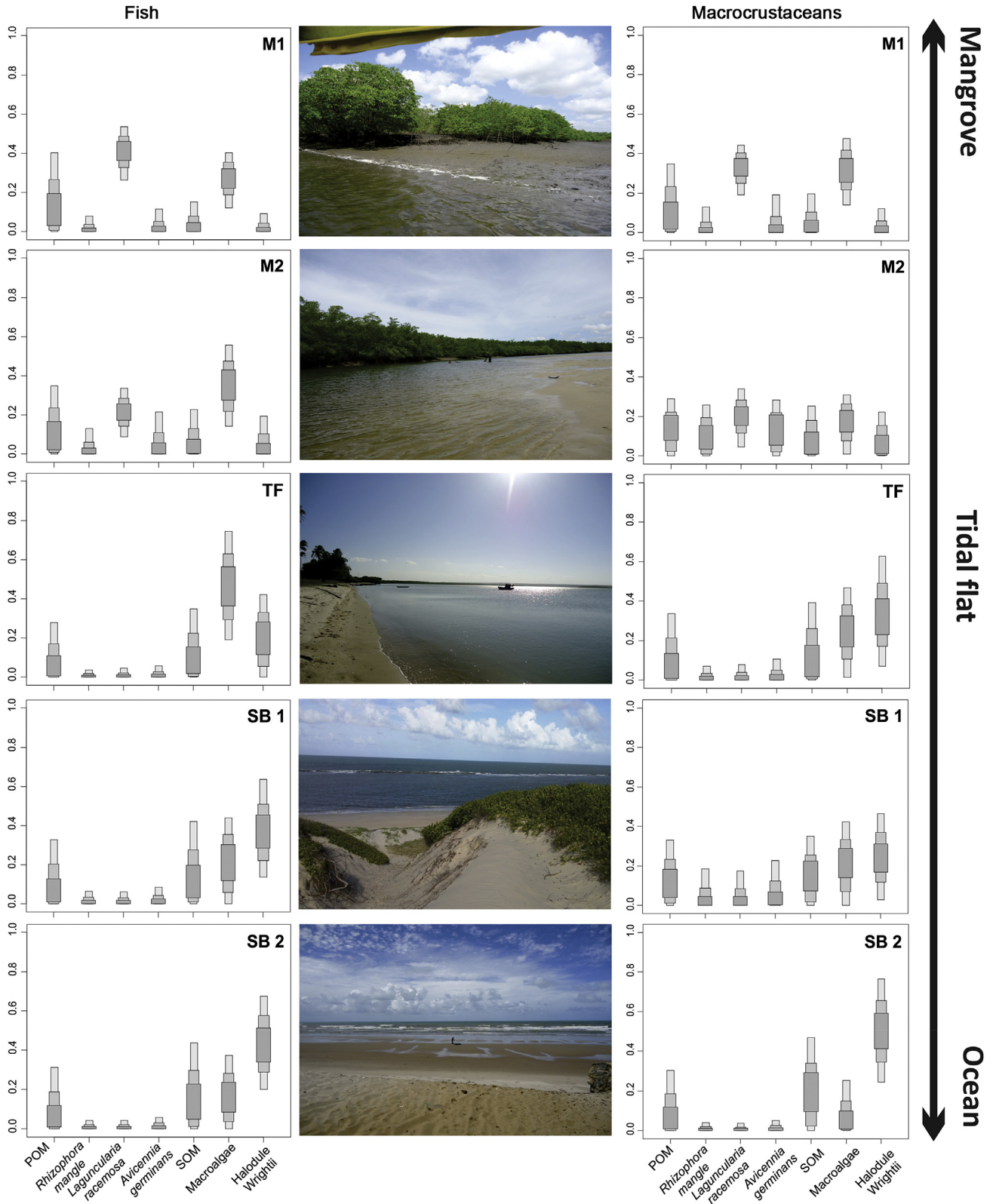


Fig. 4. Results of the stable isotope analysis in R showing estimated contribution (with 95 light grey, 75 grey, and 50% dark grey credibility intervals denoted by light, normal and dark grey bars, respectively) of basal food sources to fish (left) and macrocrustaceans (right) collected along a mangrove to estuarine-ocean gradient at the Mamanguape River. Sampling sites and their respective symbols are: mangroves (M1 and M2), tidal flat (TF) and sandy beaches (protected by reef: SB1 and not protected by the reef: SB2).

TL: 113.75 mm) of dog snapper, *Lutjanus jocu*, were caught inside the studied mangrove sites and their carbon isotope values were similar to mangrove trees. This finding suggests that they

incorporate mangrove-derived nutrients in their muscle tissues, which could be transport to the ocean when they become adults and migrate out of the estuary. Further work is needed to evaluate

the role of this species as a biological vector promoting trophic connectivity in this tropical estuary.

In summary, our findings corroborated the hypothesis that food assimilation by macroconsumers (decapod crustaceans and fish) along a mangrove to ocean gradient varies spatially and reflects the dominant autochthonous primary production at each location. Moreover, our stable isotope evidence did not support the outwelling hypothesis because mangrove-derived detritus transported to adjacent ocean beaches was not assimilated by the studied macroconsumers. Future studies should evaluate the effects of hydrology (e.g., alterations in intensity and duration of dry/wet episodes) and water level changes (e.g., intensification in salinity intrusion) predicted for global warming scenarios on food assimilation and connectivity patterns found in this tropical coastal system. Coupled with these longer-term studies, future work is also need at a shorter-term scale to unravel the role of tides in the lateral transport of mangrove-derived nutrients and their subsequent assimilation by local consumers.

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