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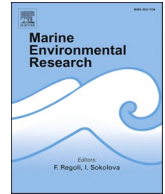
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Assessing the contribution of mangrove carbon and of other basal sources to intertidal flats adjacent to one of the largest West African mangrove forests

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ABSTRACT

Mangrove forests are productive habitats and major potential exporters of organic matter and nutrients to adjacent habitats. Here we examine the extent to which mangrove carbon is transferred to adjacent intertidal food webs in the second largest mangrove-covered area in Africa, in Guinea-Bissau. Applying stable isotope analysis and mixing models, we made comparisons at two spatial scales: (1) a large scale, comparing intertidal flats with (mangrove sites) and without (control sites) adjacent mangrove forests regarding the carbon isotopic signature of macrozoobenthos and sediment organic matter (SOM), and the relative importance of potential primary food sources in sustaining macrozoobenthos, and (2) a fine scale, performing stable carbon isotope measurements along 200 m transects from the coastline out to open intertidal flats, to trace mangrove carbon in macrozoobenthos and in the SOM. We found no evidence that mangrove carbon sustains intertidal food webs, despite SOM being significantly more depleted in ^{13}C in mangrove sites. Mangrove leaves had the lowest relative contribution to the diet of macrozoobenthos, while macroalgae, benthic microalgae and POM showed variable but overall relevant contributions. Yet, at a smaller scale, mangrove carbon was detectable in SOM and in most macrozoobenthos, being strongest within 50 m of the mangrove edge and quickly fading with increasing distance. Our results suggest that there is only a marginal input of mangrove carbon into the food webs of unvegetated intertidal flats. Still, this leaves open the possibility of mangrove forests acting as sources of dissolved inorganic carbon and processed nitrogen, which can be assimilated by the algae and subsequently fuel adjacent food webs.

1. Introduction

Mangrove forests are dominant elements in many tropical and sub-tropical coastal and estuarine ecosystems and are among the most productive ecosystems in the world (Donato et al., 2011), providing a wide variety of services benefiting both the human well-being and nearby ecological systems. They serve as nursery and habitat for fish and invertebrates and as roosting habitat to shorebirds during high-tides (Zwarts 1988), provide coastal protection, promote land formation and sediment fixation and stabilization, perform carbon (CO_2) sequestration, storage and recycling, and nutrient exchange with adjacent

waters (Alongi 2014; Lee et al., 2014). Comprising 20% of the world's mangrove forests (Giri et al., 2011), Africa is the continent with the second largest extent of mangroves. Despite their long-term importance for national and local communities, short-term pressures invite continuous degradation due to human exploitation, particularly in West Africa (Feka and Ajonina 2011). Guinea-Bissau is the exception; in fact, recent studies report an increase of 47% in the mangrove area between 1990 and 2015 (Temudo and Cabral 2017). Guinea-Bissau is currently among the 15 countries with the largest extent of mangrove forest in the world, and the second in Africa (Giri et al., 2011).

Due to their high productivity (Jennerjahn and Ittekkot 2002;

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Donato et al., 2011), mangroves are regarded as major potential exporters of nutrients and organic matter for coastal and marine primary and secondary production (Jennerjahn and Ittekkot 2002; Dittmar et al., 2006). Intertidal flats adjacent to mangrove forests constitute a transitional habitat that supports a large variety of intertidal predators (e.g. shorebirds and fish) and their macrozoobenthic prey (Beninger 2018). These areas may benefit from adjacent mangrove productivity through two processes: (1) mangroves can provide direct input of unprocessed biomass, which may then be directly used by macroinvertebrate consumers as a carbon source (e.g. Claudino et al., 2015; Letourneur et al., 2018; Marley et al., 2019; Medina-Contreras et al., 2020); or (2) mangrove forests capture, produce and process organic material, undertaking nutrient recycling via the mineralization of mangrove-derived organic matter, which may then indirectly resupply the adjacent intertidal flats and waters with inorganic dissolved nutrients like nitrogen and phosphorus (David et al., 2018; Taillardat et al. 2018, 2019). While the latter hypothesis has only been receiving increasing attention very recently, the former has been extensively tested in various mangrove stands of different configurations, leading to contradictory results. In fact, while some studies have found mangrove carbon to be important in sustaining various groups of benthic macroinvertebrates (e.g. Le et al., 2017; Marley et al., 2019; Medina-Contreras et al., 2020), several others have found no such evidence (e.g. Bouillon et al., 2002; Guest and Connolly 2005; Heithaus et al., 2011; Viana et al., 2015; Sepúlveda-Lozada et al., 2015).

Alternative carbon sources such as suspended particulate organic matter (POM, including phytoplankton), microphytobenthos (benthic microalgae), macroalgae and seagrass are among the most often reported as sustaining mangrove-bordered intertidal food webs in several tropical and subtropical areas of the world (e.g. Bouillon et al., 2004b; Claudino et al., 2015; Kristensen et al., 2008; Lee, 2008). However, there are still important knowledge gaps, notably in West Africa, where, to our best knowledge, only two studies investigated the relative importance of intertidal primary food sources to macroinvertebrate consumers and fish (Faye et al., 2011; Catry et al., 2016). Catry et al. (2016) suggested that there is little contribution of mangrove carbon to sustain shorebird food webs in the Biosphere Reserve of the Bijagós archipelago, Guinea-Bissau, despite the ubiquity of mangrove forests in the area (Campredon and Catry 2018). However, this study was focused on broad comparisons between shorebird intertidal food webs at different non-breeding areas of the East Atlantic Flyway, and thus did not specifically address the role of mangrove forests.

The movement of organic carbon among ecosystem compartments has been shown to vary according to geomorphic and tidal settings (Hyndes et al., 2014; Saavedra-Hortua et al., 2020), and with the type of consumers (Bouillon and Connolly 2009). Therefore, to better assess the extent to which mangrove carbon is transferred to adjacent intertidal flats, supplying communities there, the sampling design must take into account the local heterogeneities, either among different mudflats or among the sources and consumers.

Stable isotope analysis (SIA) has been extensively used to study the energy flow through intertidal food webs bordered by mangrove forests (e.g. Abrantes and Sheaves 2009; Sepúlveda-Lozada et al., 2015; Soares et al., 2018), as well as to estimate the importance of primary food sources in the diet of macrozoobenthos (e.g. Bouillon et al., 2002; Tue et al., 2012; Le et al., 2017; Letourneur et al., 2018). Carbon isotope ratios of $^{13}\text{C}/^{12}\text{C}$ differ among sources of different origins while nitrogen isotope ratios of $^{15}\text{N}/^{14}\text{N}$ can provide information concerning the trophic position of consumers (Fry 2006). The use of carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in Bayesian mixing models have been widely employed to estimate the contribution of different sources in the diet of consumers (Parnell et al. 2010, 2013). Mangroves are C_3 plants (Robertson and Alongi 1992), typically presenting very low $\delta^{13}\text{C}$ values (around -28‰ ; Fry, 2006), which are clearly distinguishable from other intertidal basal energy sources. This trait allows to reliably infer on the relative importance of mangrove carbon in adjacent food webs in

comparison to other sources.

Here we investigate the role of mangrove forests in fuelling the intertidal food web of the Bijagós archipelago by providing direct carbon inputs to the adjacent intertidal ecosystem. We do this at a large spatial scale, in different areas of the archipelago where we compared mangrove-bordered intertidal flats (hereafter mangrove sites) with intertidal flats without bordering mangroves (control sites) with respect to (1) the $\delta^{13}\text{C}$ values of sediment organic matter (SOM) and of macrozoobenthos, and (2) the relative importance of primary food sources in sustaining macrozoobenthos (using C and N stable isotope mixing models). Then, at a finer scale, we trace the presence of mangrove carbon along a distance gradient coastline-waterline in macrozoobenthos of different trophic guilds and of SOM, within these mangrove and control intertidal flats. Assuming a small importance of mangrove carbon to intertidal food webs in this area (Catry et al., 2016), we predict that at a large scale, the carbon contribution from mangroves to SOM and to macrozoobenthos will be similar in mangrove and control areas. If proven true, at a finer scale we would then expect the mangrove carbon movement to be spatially restricted, with $\delta^{13}\text{C}$ values of macrozoobenthos and SOM in mangrove sites being lower near the mangrove border but significantly higher with increasing distance to the coast. In control sites no similar trends should occur.

2. Materials and methods

2.1. Study area

This study was conducted in the Bijagós archipelago, a group of 88 islands and islets off the coast of Guinea-Bissau, West Africa, classified as a Biosphere Reserve and a Ramsar site due to its rich biodiversity (Campredon and Catry 2018). This area is characterized by strong tidal currents (Cuq et al., 2001), with semi-diurnal tides that have the highest tidal ranges of the West African coast (with spring tides occasionally ranging from 0.5 to 4.5 m; Campredon and Catry 2018). The archipelago is predominantly influenced by marine waters and freshwater input into the intertidal areas only occurs through seasonal rains, from May to November. It covers a total area of ca. 10,470 km², of which 1,200 km² are intertidal mudflats and sandbanks (Cuq et al., 2001; Pennobler, 1999) and 461 km² are covered by mangrove forests (Cardoso 2017). Besides the fringing mangrove forests, the intertidal flats are generally unvegetated, despite many areas being covered by extensive filamentous macroalgae mats. There is very little seagrass in the Bijagós, and none in the intertidal flats selected for this study.

Sampling took place in two of the main islands, in intertidal flats with and without adjacent mangrove forests: Formosa, which is the main island of the Community Marine Protected Area of Urok, with a total mangrove forest cover of ca. 40.1 km² (8.7% of the Bijagós' mangroves); and Bubaque, in which the main human settlement of the Bijagós archipelago is located, with mangrove forest covering 21.9 km² (4.8% of the Bijagós' mangroves).

2.2. Sample collection, processing and analysis

Samples were collected during the dry season, between January and April 2018, and in late November 2019. Sampling in November was conducted in the last days of the month, and thus the samples collected were mainly influenced by environmental characteristics typical of the dry season. Samples were collected in two intertidal areas bordered by mangrove (Anrumai and Bijante), located in the islands of Formosa and Bubaque, respectively, and the control site (Bruce), located in the south of Bubaque (Fig. 1).

To trace the presence of mangrove carbon at a large scale, we compared mangrove and control sites by combining all samples of SOM and of each macrozoobenthos taxa collected in each sampling site. Also at a large scale, we assessed the contribution of basal carbon sources to the diet of macrozoobenthos in both mangrove and control sites by

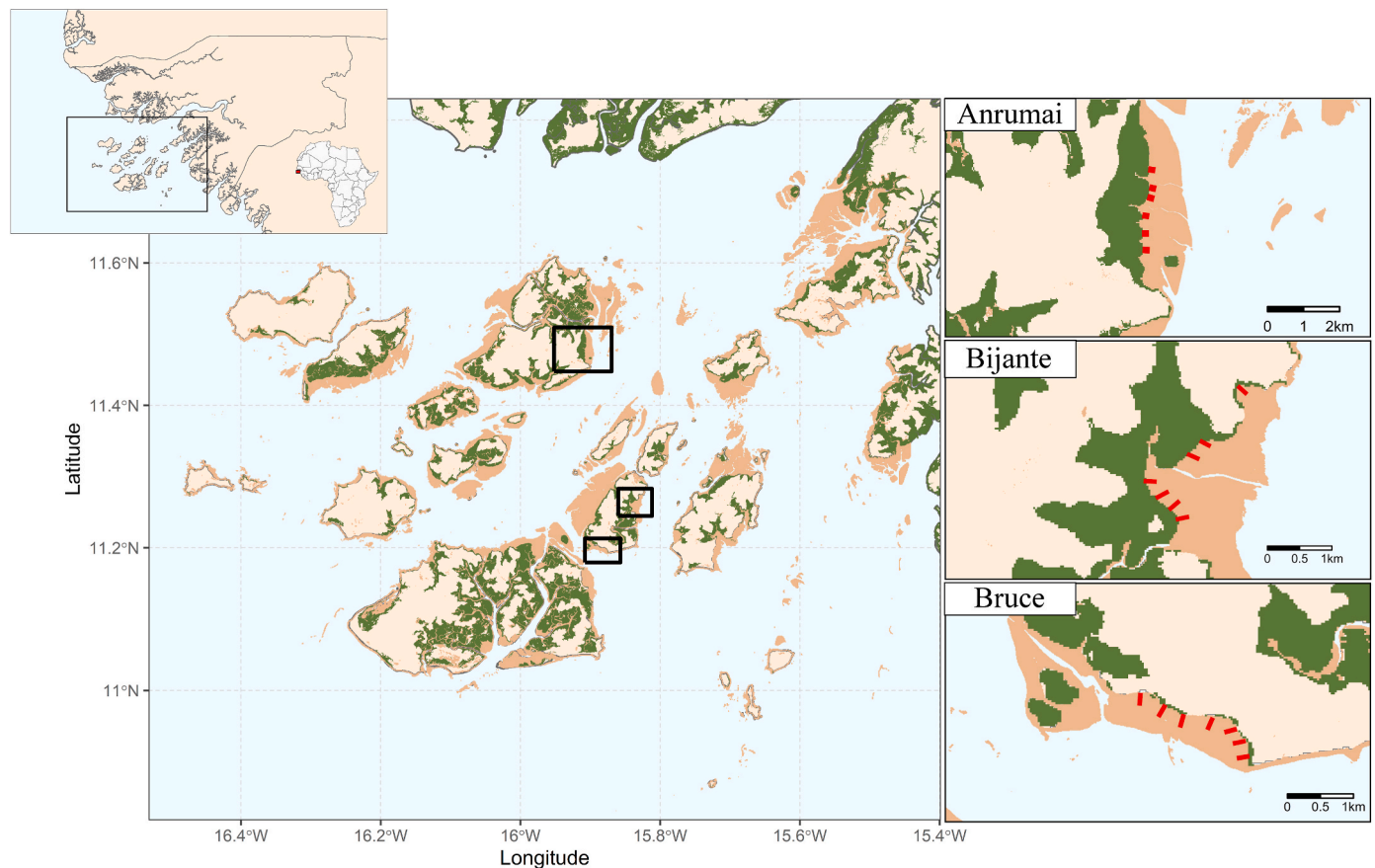


Fig. 1. Study area, in the Bijagós archipelago Biosphere Reserve, off Guinea-Bissau, West Africa. Green (online version) or black (print version) represent the mangrove cover, brown (online version) or dark grey (print version) areas are the intertidal flats, and beige (online version) or light grey (print version) areas are land. Black squares mark the three study sites selected, in the intertidal areas of Anrumai and Bijante (representing intertidal flats bordered by mangrove forests) and Bruce (control area, without adjacent bordering mangrove forests). Red (online version) or white (print version) lines are the transects on which we sampled macrozoobenthos and sediment.

combining all samples of each macrozoobenthic taxa in each site. To study the fine scale movement of mangrove carbon, we set up a distance gradient sampling in each intertidal flat, from the coastline/mangrove edge to the waterline (Fig. 1). In each study site, six to seven transects were established, each with four distance sampling bands starting at the coastline/mangrove edge: 0 ± 5 , 10 ± 5 , 50 ± 10 and 200 ± 10 m. Transects were set at least 350 m apart from each other, to ensure sample independence (Fig. 1).

2.2.1. Mangrove and other primary food sources

To describe the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of mangroves and other primary food sources, we collected mangrove leaves at both mangrove sites, and benthic microalgae, macroalgae and sea water for suspended particulate organic matter (POM) analysis in all study sites. Carbon and nitrogen isotope ratios of mangrove leaves are known to vary according to their decomposition stage (Fourqurean and Schrlau 2003). Thus, we collected green leaves (directly from different trees of three genera *Rizophora* sp., *Avicennia* sp. and *Laguncularia* sp.), yellow leaves (from under the mangrove forest trees and at the surface of the mudflat), and brown senescent leaves (buried in the mudflat of mangrove sites). All leaves were rinsed and dried. Green leaves collected from different individuals within each genus were pooled together to form one sample per genus, while yellow and brown leaves were pooled altogether whatever the genus.

Macroalgae were opportunistically collected whenever found on the study mudflats. Samples were washed with sea water and dried. Duplicates were collected and stored in alcohol for posterior identification. Most macroalgae collected in mangrove areas were the yellow-green

algae *Vaucheria* sp., while specimens collected in the control area included the brown algae *Dictyota* sp., green algae *Chaetomorpha* sp. and red algae *Hypnea* sp.

Benthic microalgae undertake vertical migrations, so we used four textile panels 100×100 mm (Whatman, grade 105) laid on the sediment surface for about 2h during low tide to separate them from the sediment. The panels were then rinsed with seawater and decanted to separate the microalgae from the sediment attached to the panels. The remaining water (with the algae) was then filtered through pre-combusted Whatman GF/F filters (retains fine particles down to $0.7 \mu\text{m}$) and dried (Catry et al., 2016).

Water samples for POM analysis were collected during high-tide over the mudflats using plastic bottles at a minimum depth of ca. 50 cm and at a minimum distance to the sediment surface of also ca. 50 cm, thus avoiding the superficial water layer (which contains zooplankton) and resuspended sediment, respectively.

Water samples were pre-filtered through a $200 \mu\text{m}$ mesh size net to eliminate any large zooplankton and detrital particles and then filtered again through pre-combusted Whatman GF/C filters (retains particles down to $1.2 \mu\text{m}$) until enough material was retained (Catry et al., 2016). Filters were subsequently air dried and stored in plastic bags until further processing.

2.2.2. Macrozoobenthos and sediment organic matter

In each distance band we collected macrozoobenthos and sediment to determine $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Macrozoobenthos samples were collected by hand or by sieving the sediment ($0.5\text{--}1.0$ mm mesh-size). Four functional groups were targeted, aiming to include the most common

foraging guilds: bivalves (filter-feeders; Gosling, 2015), sedentary polychaetes (mainly surface deposit-feeders and supplementary filter-feeders; Fauchald and Jumars, 1979), errant polychaetes (carnivores and surface deposit-feeders; (Fauchald and Jumars 1979), and crustaceans (fiddler crabs, which are grazers, surface deposit-feeders and necrophages; Wolfrath, 1992). The taxa used for each group depended on how common and abundant they were, and how widespread: for sedentary polychaetes, individuals from both Paraonidae and Maldanidae families were sampled and pooled together, while for errant polychaetes, only individuals of the species *Marphysa sanguinea* were sampled. Bivalves included the bloody cockle *Senilia senilis* and the knife clam *Tagelus adansonii*, and for crustaceans we sampled fiddler crabs *Afruca tangeri*. Shredders (including crabs and herbivore gastropods), an important macrozoobenthic feeding group in mangrove stands, were not sampled in this study due to their very low occurrence in the intertidal flats of the study area. Whenever necessary to achieve enough biomass for SIA, several individuals of the same taxa were pooled in the same sample. Macrozoobenthos were stored in containers with local estuarine/marine seawater and left alive for ca. 12–24h to clear their guts. Afterwards, specimens were sun dried and stored for further processing. Shells of bivalves and exoskeleton of crustaceans were discarded, and only soft tissues were kept for posterior analysis.

Sediment organic matter (SOM) was collected by taking the upper layer (~1 cm) of sediment into a 40 ml container. Visible detrital particles were removed before drying the samples for storage.

2.2.3. Stable isotope analysis

To prevent samples from degrading in the field, all primary food sources were thoroughly air-dried, while macrozoobenthos and sediment were dried in a sun-oven at temperatures ranging 40 °C to 70 °C. After thoroughly dried, samples were then kept in sealed plastic bags to keep humidity out, and checked periodically for any evidence of degradation. Once in the laboratory in the Faculty of Sciences of the University of Lisbon, all samples were dried again at 50 °C for 24–48h, before analysis. Macrozoobenthos tissues, mangrove leaves and macroalgae were grounded to a homogeneous powder using a mortar and pestle. Lipids were removed from animal tissues by immersing each sample in a 2:1 chloroform:methanol solution, following the protocol described in Lourenço et al., (2017).

SOM samples were tested for the presence of carbonates by adding drops of a solution of 10% HCl to a subsample to check for a reaction (formation of bubbles). If the reaction occurs, more acid is added to the sample, following the protocol described in Lourenço et al. (2017). Because the acidification process can significantly alter $\delta^{15}\text{N}$ values (Claudino et al., 2013), sediment samples selected for acidification were divided in two subsamples: acidified samples, in which $\delta^{13}\text{C}$ values were to be determined, and non-acidified samples, to read $\delta^{15}\text{N}$ values.

All samples were weighed (1–3 mg for animal tissues, 25–30 mg for SOM, and ca. 3 mg for other primary food sources), pressed into tin capsules (@Elemental Micro-analysis), and sent to the Stable Isotopes and Instrumental Analysis Facility of the Faculty of Sciences, University of Lisbon, for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ determination. Samples were combusted at 1000 °C in a EuroVector EA Elemental Analyser. Isotopic ratios were determined by continuous-flow isotope-ratio mass spectrometer IsoPrime (MicroMass). Results are presented conventionally as δ values in parts per thousand (‰) relative to the Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}\text{C}$, and atmospheric nitrogen (N_2) for $\delta^{15}\text{N}$. Precision of the isotope ratio analysis, calculated using values from 6 to 9 replicates of laboratory standard material (casein) interspersed among samples in every batch analysis, were 0.11–0.25‰ for $\delta^{13}\text{C}$ and 0.05–0.17‰ for $\delta^{15}\text{N}$ (SD).

2.3. Data analysis

All statistical analyses were performed with R software (R Core Team 2018). To investigate the presence of mangrove carbon in adjacent

intertidal areas at a large scale (i.e. comparison between mangrove sites and the control site), we tested the differences between the mean $\delta^{13}\text{C}$ values of macrozoobenthos and SOM between the three sites with a one-way ANOVA and the post-hoc Tukey HSD for unequal sample sizes, applying the Tukey-Kramer correction. Welch's ANOVA and Games-Howell post-hoc pairwise comparisons were performed when data violated the assumption of homogeneity of variance.

To estimate the relative contributions of primary food sources to macrozoobenthos in each site, dual isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) Bayesian stable mixing models were performed using the SIMMR package (Parnell et al. 2010, 2013). This is based on the assumption that the variability associated with food sources and trophic enrichment is normally distributed (Parnell et al., 2010). Elemental concentrations of N and C (‰) measured for each organic primary food source and consumer were also included to better restrict the models (Phillips et al., 2014). Trophic discrimination factors of $3.4 \pm 1.0\text{‰}$ for $\delta^{15}\text{N}$ and $0.4 \pm 1.3\text{‰}$ for $\delta^{13}\text{C}$ were used, following Post (2002). Samples of mangrove leaves of different decomposition rates (green, yellow and brown leaves) were very similar and therefore were averaged for each intertidal flat, and used in the model as a single mean value representing mangroves. To assess the effects of varying isotope trophic discrimination factors in the estimates of the relative contribution of basal food sources to the diet of macrozoobenthos in the three study sites, we conducted a sensitivity analysis. $\delta^{13}\text{C}$ reference discrimination factor (0.4‰) was varied between -0.6‰ and 1.4‰ while keeping $\delta^{15}\text{N}$ discrimination factor fixed at the reference level, and $\delta^{15}\text{N}$ reference discrimination factor (3.4‰) was varied between 2.4‰ and 4.4‰ while keeping $\delta^{13}\text{C}$ discrimination factor fixed.

The presence of mangrove carbon at a finer scale (up to 200 m) in intertidal areas was investigated by assessing the effect of distance to coastline on $\delta^{13}\text{C}$ values in all three sites and comparing the control site to mangrove sites through analysis of covariance (ANCOVA). The site factor had three levels (Bruce, Anrumai, Bijante) and distance to coastline was used as a continuous variable, with $\log_{10}(x+1)$ transformation. Bruce was used as the reference group in pairwise comparisons.

3. Results

3.1. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of primary food sources and consumers

Primary food sources showed a wider $\delta^{13}\text{C}$ range at mangrove sites (-30.1‰ to -12.6‰) in comparison to the control site (-24.6‰ to -15.5‰), with mangrove leaves appearing as the most depleted in ^{13}C (Anrumai: -27.5‰ \pm 1.4 (mean $\delta^{13}\text{C}$ \pm SD); Bijante: -27.9‰ \pm 1.2) and macroalgae the most enriched (Anrumai: -14.9‰ \pm 2.5; Bijante: -15.2‰). $\delta^{15}\text{N}$ values also presented a wide range in both mangrove sites, with the mean values of POM being the highest (Anrumai: 11.6‰ \pm 1.1 (mean $\delta^{15}\text{N}$ \pm SD); Bijante: 12.6‰ \pm 1.7), and macroalgae the lowest (Anrumai: 3.7‰ \pm 2.5; Bijante: 4.9‰; Fig. 2; Table A.1). In the control site the range of $\delta^{15}\text{N}$ values was narrower (ranging from 5.3‰ to 11.8‰, Table A.1, Fig. 2). The values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of mangrove leaves and microalgae were very similar between sites, while macroalgae had markedly higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in the control site compared with both mangrove sites. The mean $\delta^{13}\text{C}$ of POM showed to be variable between locations (Table A.1, Fig. 2).

The distribution pattern of the five macrozoobenthos taxa in the isospace markedly varied among groups. While the isotopic range of both bivalve species was narrow yet distinct at all sites, errant polychaetes (*M. sanguinea*) had wider ranges that overlapped considerably across most $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of all other macrozoobenthos groups, in all sites (Fig. 2). Fiddler crabs showed the highest mean $\delta^{13}\text{C}$ (Anrumai: -13.1‰ \pm 1.1 (SD); Bijante: -11.8‰ \pm 1.7; Bruce: -12.8‰ \pm 1.2) and lowest mean $\delta^{15}\text{N}$ values (Anrumai: 9.1‰ \pm 0.7; Bijante: 10.0‰ \pm 1.1; Bruce: 9.6‰ \pm 1.7), thus presenting little isotopic overlap with the remaining macroinvertebrate taxa (Fig. 2, Table A.2).

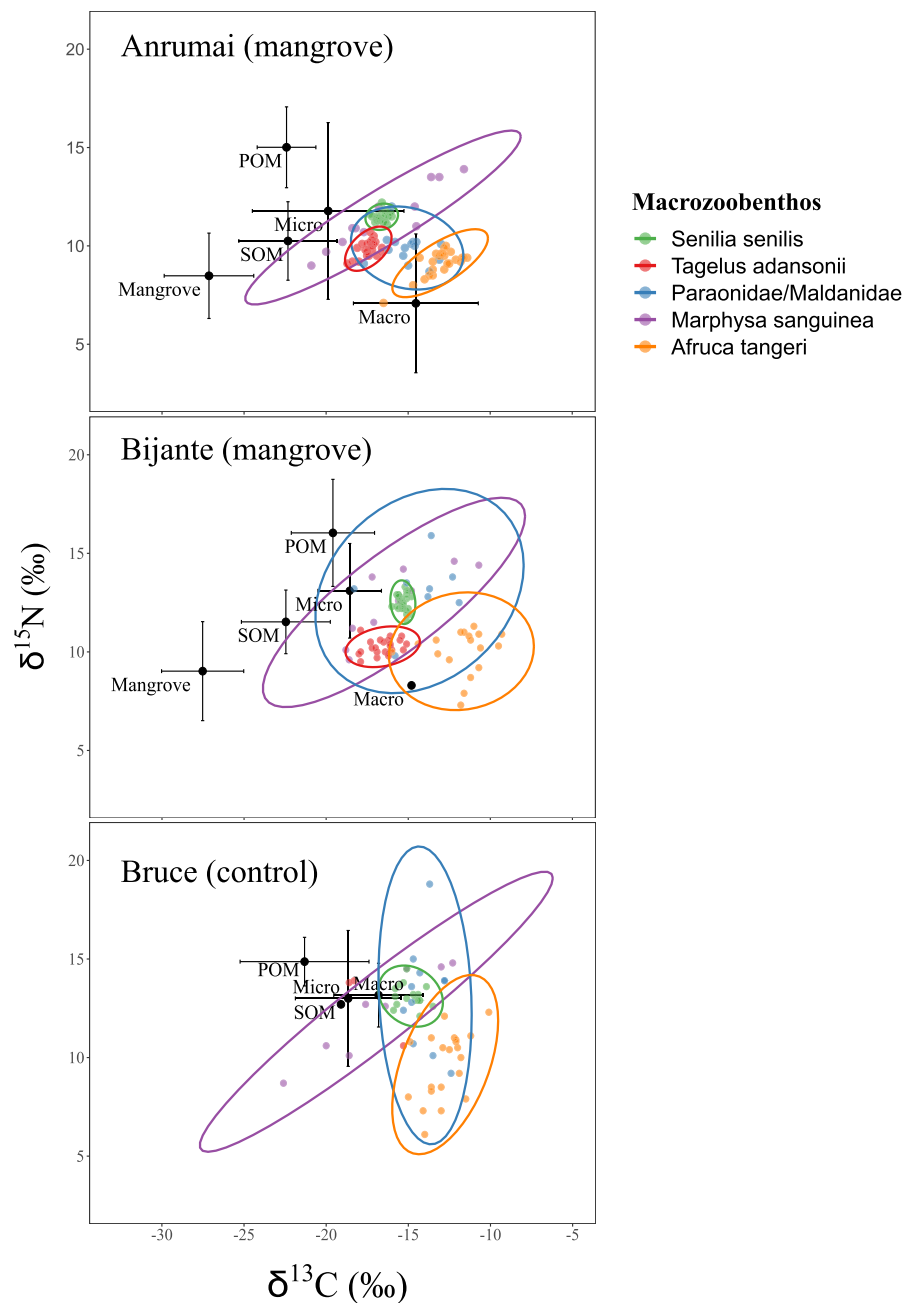


Fig. 2. Mean \pm SD $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of basal food sources and isotopic niches of macrozoobenthic consumers (as depicted by 95% ellipses) sampled at three study sites of the Bijagós archipelago, Guinea-Bissau. Anrumai and Bijante represent intertidal flats with adjacent mangrove forests and Bruce is the control site (no adjacent mangrove forests). Source values were corrected relatively to consumers using a fractionation factor of 0.4‰ for $\delta^{13}\text{C}$, and of 3.4‰ for $\delta^{15}\text{N}$ (see methods). The isotopic niche of *Tagelus adansonii* in Bruce was not included due to few data points. Macro – Macroalgae; Micro – Microalgae; POM – particulate organic matter; SOM – sediment organic matter.

3.2. Large scale comparisons of $\delta^{13}\text{C}$ of macrozoobenthos and SOM

The two bivalve species presented significantly different mean $\delta^{13}\text{C}$ values according to the sites (Fig. 2, Table A.2). $\delta^{13}\text{C}$ values of *S. senilis* in both mangrove sites were lower than in the control site, while for *T. adansonii*, only the two mangrove sites presented differences, and no differences were found between mangrove and control sites. Sedentary polychaetes (Paraonidae/Maldanidae) showed no significant differences in $\delta^{13}\text{C}$ between sites, according to pairwise Tukey HSD (Table A.2). Likewise, errant polychaetes *M. sanguinea* did not show any significant differences among sites, and fiddler crabs *A. tangeri* showed no significant differences between mangrove and control sites (Fig. 2, Table A.2). SOM $\delta^{13}\text{C}$ values, on the other hand, were significantly different between sites because both mangrove site values were lower than the control site (Table A.2, see also Table A.1).

3.3. Large scale comparisons of the contribution of primary food sources to macrozoobenthos

In both mangrove sites, mangrove leaves had the lowest relative contribution to the diet of macrozoobenthos consumers, often approaching zero (Fig. 3). The most important primary food sources for all macrozoobenthic groups were macroalgae, microalgae and POM, but the estimated proportions of each varied greatly between groups and sites. In Anrumai, POM was the most important food source for both bivalves (*S. senilis* and *T. adansonii*) and for errant polychaetes (*M. sanguinea*), while macroalgae were dominant for sedentary polychaetes (Paraonidae/Maldanidae) and fiddler crabs (*A. tangeri*). In Bijante, on the other hand, POM was only the most important for *S. senilis*, with macroalgae (for *T. adansonii* and *A. tangeri*) and microalgae (for sedentary Paraonidae/Maldanidae and errant polychaetes) as the most relevant primary food sources. In the control site, macroalgae

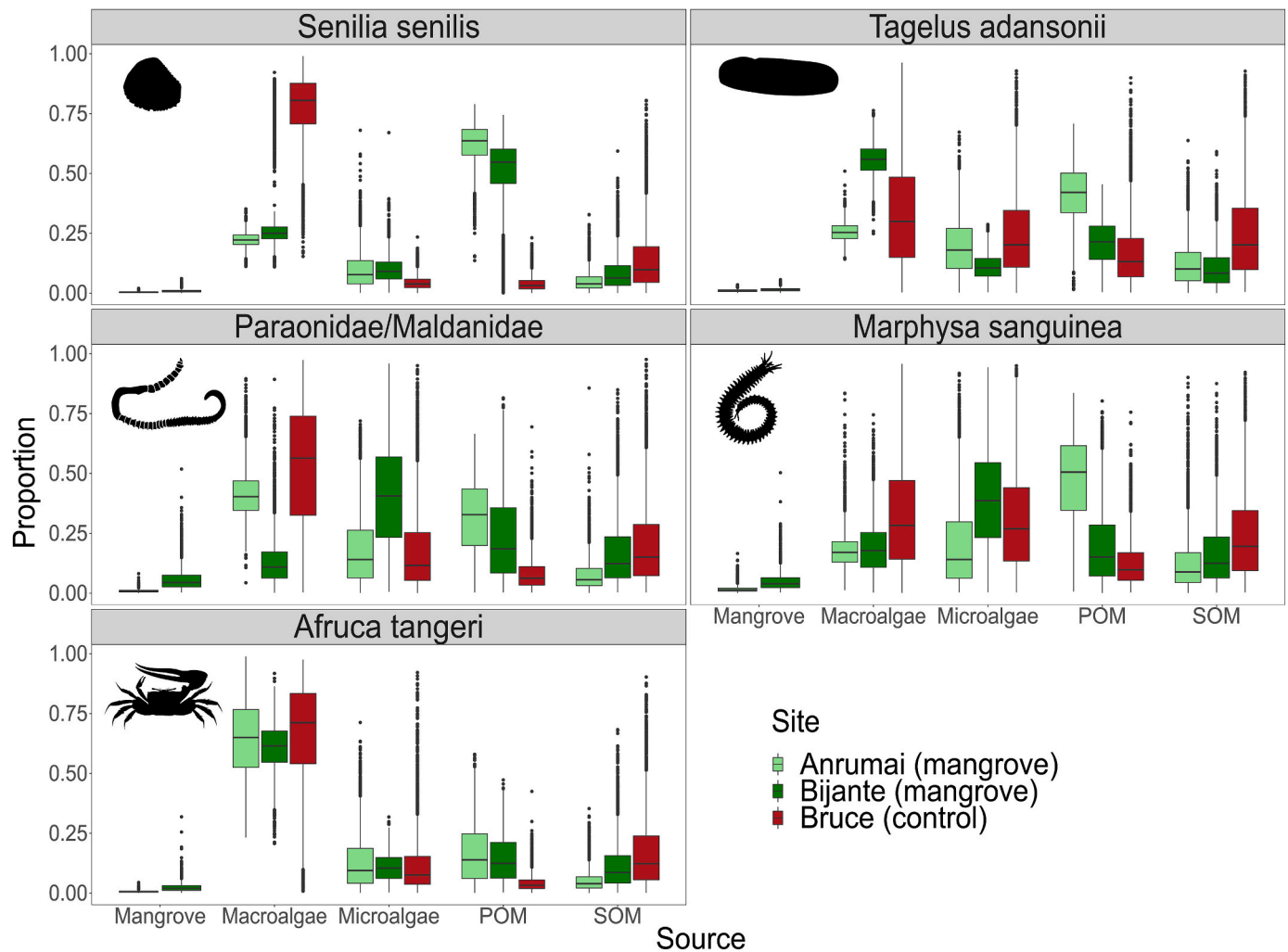


Fig. 3. Relative contribution of primary food sources to the diet of macrozoobenthos consumers in three study sites of the Bijagós archipelago, Guinea-Bissau, as estimated by isotope mixing models. Anrumai and Bijante are bordered by mangrove forests and Bruce is the control (no mangrove) site. Boxplots include the median, 25th and 75th percentiles and outliers.

dominated the estimates as the most important primary food source for all macrozoobenthos groups. Estimated values of the most important food sources for the bivalve *S. senilis* and for the fiddler crab *A. tangeri* were particularly high in the two mangrove sites (*S. senilis*: mean POM contribution of ca. 60% in Anrumai, and 55% in Bijante; *A. tangeri*: mean macroalgae contribution of ca. 64% in Anrumai, and 60% in Bijante), while in the control site this was also the case for *S. senilis*, sedentary polychaetes and *A. tangeri* in relation to the estimated values of the contribution of macroalgae for their diet (77%, 66% and 52%, respectively). *Afruca tangeri* was the only invertebrate group for which the most important food source was concurrent between control site and the two mangrove sites.

Sensitivity analysis showed that mixing model estimates were overall consistent across varying values of trophic discrimination factors of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Fig. A.1).

3.4. Fine scale comparisons of $\delta^{13}\text{C}$ of macrozoobenthos along a coastline-waterline distance gradient

The variation in $\delta^{13}\text{C}$ values of SOM, sedentary polychaetes, fiddler crabs and bivalves along the gradient of distance from the coastline differed among sites (ANCOVA, significant interaction term for SOM: $F_{2,62} = 7.00$, $p = 0.002$; *S. senilis*: $F_{2,57} = 7.00$, $p = 0.002$; *T. adansonii*: $F_{2,41} = 7.69$, $p = 0.002$; Paraonidae/Maldanidae: $F_{2,28} = 8.39$, $p =$

0.001; and *A. tangeri*: $F_{2,57} = 3.60$, $p = 0.03$): mangrove and control sites showed significant differences for SOM, sedentary polychaetes (only significant in one of the mangrove sites) and fiddler crabs, with their $\delta^{13}\text{C}$ values lower near the mangrove and significantly increasing with distance to the mangrove edge in mangrove sites, while remaining stable or significantly decreasing with distance to coastline in the control site (Fig. 4; Table A.4); for both bivalve species, mangrove and control sites were again significantly different, but with no apparent effect of distance to mangrove edge in their $\delta^{13}\text{C}$ values in mangrove sites, whereas in the control site we observed a significant decrease of $\delta^{13}\text{C}$ values along the distance gradient (Fig. 4; Table A.4). Errant polychaetes showed no differences among sites (ANCOVA interaction term: $F_{2,24} = 0.97$, $p = 0.39$), with both mangrove and control sites presenting a positive significant effect of distance to coastline on their $\delta^{13}\text{C}$ values.

4. Discussion

4.1. Mangrove carbon contribution to adjacent intertidal food webs

In this study we used $\delta^{13}\text{C}$ analysis at two spatial scales, combined with dual stable isotope mixing models, to assess the importance of direct input of mangrove carbon to adjacent intertidal species assemblages. The results of all approaches suggest that the contribution of the carbon from mangrove leaves to the sediment carbon pool of adjacent

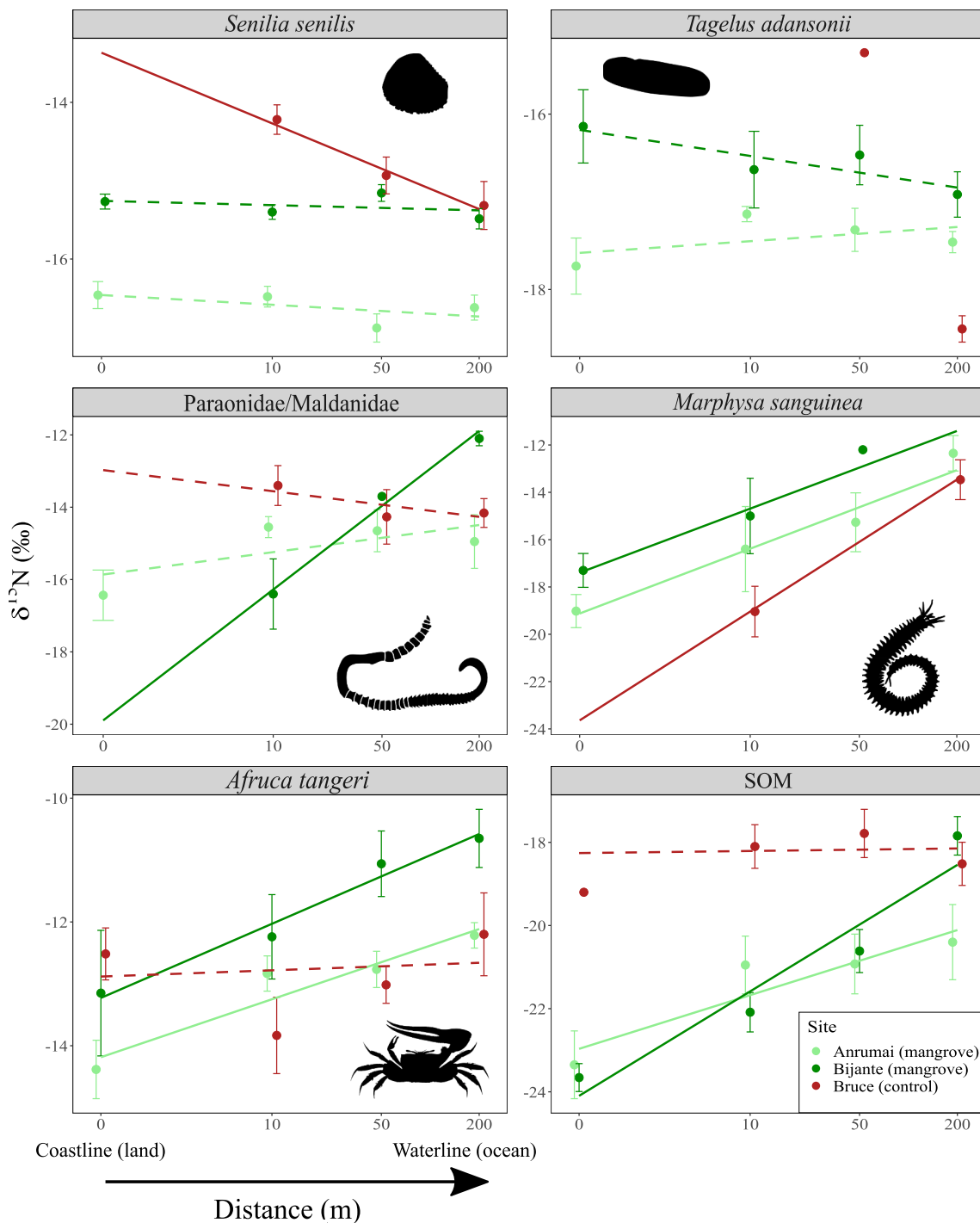


Fig. 4. Variation in $\delta^{13}\text{C}$ values of macrozoobenthos and sediment organic matter (SOM) along a gradient of distances to the coastline (in meters) in three study sites of the Bijagós archipelago. Samples were collected at 0 ± 5 , 10 ± 5 , 50 ± 10 and 200 ± 10 m from the coast. Points represent means \pm SE, solid lines are represented for significant effects and dashed lines for not significant effects of distance on $\delta^{13}\text{C}$ values. Missing points represent distances for which no individuals were found for that specific taxa and site. Distance (x axis) is represented in a logarithmic scale.

mudflats is present but not very strong and quickly fades away with the distance. More importantly, mangrove carbon shows almost no expression in the five macrozoobenthos taxa analysed.

Sediment organic matter had lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in mangrove sites compared to the control site, suggesting that mangrove detritus has a measurable contribution to the sediment organic pool, in particular for the mudflats closer to the mangrove border. At the control site benthic microalgae was most likely the major contributor to SOM, given the

similarities between the stable isotope values of both benthic microalgae and SOM. Nonetheless, we found SOM to be enriched in ^{13}C when compared to mangrove leaves (6‰ higher $\delta^{13}\text{C}$ in Anrumai, and 6.9‰ in Bijante), suggesting mixed contributions of mangrove carbon with more enriched sources to the SOM pool, or changes in the mangrove $\delta^{13}\text{C}$ values in the sediment. Some authors have attributed this increase in $\delta^{13}\text{C}$ of SOM to an increase in microbial and fungal residues caused by the mineralization process of mangrove litter (Ehleringer et al., 2000;

Bouillon et al., 2008; Kristensen 2008). Kennedy et al. (2004) also reported significantly lower $\delta^{13}\text{C}$ in sediment of mangrove stands although still typically $\sim 6\text{--}8\text{‰}$ higher than mangrove $\delta^{13}\text{C}$, but attributed these values to the deposition of more ^{13}C -enriched imported (such as phytoplankton) or locally produced (like benthic microalgae) sources.

The bivalve *S. senilis* was the only macroinvertebrate to present significantly lower $\delta^{13}\text{C}$ values in mangrove sites compared to the control site. However, mean $\delta^{13}\text{C}$ values were not very far from those from *S. senilis* collected at the control site (-16.6‰ and -15.3‰ vs -14.9‰). Moreover, they were higher by $\sim 11\text{--}13\text{‰}$ in relation to mangrove leaves, and mixing models estimated a nearly inexistent mangrove contribution to their diet. This strongly suggests that, rather than because of the influence of mangrove carbon, the observed differences are driven by variations in their diet, comprised of POM in mangrove sites, which is among the sources with the lowest $\delta^{13}\text{C}$, but strongly influenced by the stable isotopic signature of macroalgae detritus in control sites, the source with the highest $\delta^{13}\text{C}$. These results, in addition to mixing models having estimated close to zero contributions of mangrove leaves for all macroinvertebrates, provide evidence to reject the hypothesis of an important mangrove carbon direct contribution to intertidal food webs at a large scale. These conclusions are in line with what was previously suggested by Catry et al. (2016) for this area.

Previous studies have also reached the same conclusions for invertebrate taxa in Shark Bay, Australia (Connolly et al., 2005; Heithaus et al., 2011) and Bay of Bengal, India (Bouillon et al., 2002) except for some herbivore gastropods and sesarmid crabs (Bouillon et al., 2002; Medina-Contreras et al., 2020). However, other studies showed the opposite pattern, reporting that most macrozoobenthos inhabiting mangrove sites were mainly relying on mangrove carbon direct input (Giarrizzo et al., 2011; Medina Contreras et al., 2017; Marley et al., 2019). Yet, this seemed to be spatially restricted and invertebrates inhabiting nearby mudflats without mangroves were relying on other, more locally abundant, food sources (Bouillon et al., 2004a; Claudino et al., 2015). Therefore, the importance of mangrove carbon may be spatially constrained and only detectable at smaller spatial scales, as suggested by Guest et al. (2004b) who argued that carbon movement in mangrove ecosystems occurs at scales of less than 30 m (but see Connolly et al., 2005).

In our study we tested this fine-scale hypothesis and concluded that overall, mangrove carbon signal is stronger within the first 50 m of the mangrove-fringe, but quickly fades across the distance gradient. While we found this pattern in the organic matter trapped in the sediment (SOM) and also in both sedentary and errant polychaetes and fiddler crabs, no apparent relationship was found for bivalves. Unlike the remaining macrozoobenthos, errant polychaetes (*M. sanguinea*) also showed a significant increase in $\delta^{13}\text{C}$ with distance to coast in the control site, implying that an unidentified process other than the effect of mangrove carbon is driving this gradient. Thus, the finer scale approach also supported the previous conclusions, strongly suggesting that mangrove carbon direct input is not sustaining these macrozoobenthos in the Bijagós archipelago. Similar relationship curves have been obtained for an Australian estuary, where an even more restricted movement of mangrove carbon was found (between 5 and 10 m; Guest and Connolly, 2005).

As an alternative to direct carbon input, nutrient recycling through the mineralization of mangrove-derived organic matter of poor nutritional quality may be an important role played by mangrove forests. These nutrients are then assimilated in a second step by suspended algal cells during photosynthesis, inducing their growth and originating a more nutritive organic matter source to the ecosystem (David et al., 2018). This may occur through mangrove porewater export into the suspended matter pool, contributing with high amounts of dissolved organic and inorganic carbon and ammonium, strongly mediated by the tides and seasonal contrasts (Bouillon et al., 2007; Ray et al., 2018; Taillardat et al. 2018, 2019). This has been also suggested for a Mangrove Biosphere Reserve in Vietnam (David et al., 2019).

Henceforth, the role of mangroves as a source of organic material, which may then indirectly resupply the adjacent unvegetated mudflats and waters with inorganic nutrients, should be analysed to shed more light on the role of this ubiquitous primary producer as a subsidy of these intertidal food webs.

4.2. Alternative basal food sources sustaining intertidal food webs

Mixing models showed that macroalgae, benthic microalgae and POM were the most important basal food sources for benthic macroinvertebrates. Also in the Bijagós archipelago, Catry et al. (2016) detected a strong dominance of SOM contribution for bivalves and errant polychaetes only, having otherwise reported that the food web seemed to be supported by balanced proportions of several basal sources. In the present study, we were able to additionally depict local heterogeneities.

Macroalgae presented the highest $\delta^{13}\text{C}$ values of all sources, consistent with the values compiled in Bouillon et al. (2008), and in the range of those reported for another pristine mangrove-fringed ecosystem in Australia (Heithaus et al., 2011). In the control site, macroalgae $\delta^{15}\text{N}$ values were higher than in mangrove sites, which may be explained by the different macroalgal species composition between the sites (Table A.1). While in both mangrove sites most samples were of *Vaucheria* sp., expected to have lower $\delta^{15}\text{N}$ (e.g. Sullivan and Moncreiff, 1990), in the control site the species pool consisted of *Dyctiota* sp., *Chaetomorpha* sp. and *Hypnea* sp., with higher values consistent with the literature (Sullivan and Moncreiff 1990; Newell et al., 1995; Corbisier et al., 2006). The prominence of macroalgae as an important carbon source for several macrozoobenthos species in all sites are in contrast with the results reported by Catry et al. (2016) and should be interpreted with caution considering a certain degree of uncertainty that derives from the use of mixing models (Parnell et al. 2010, 2013; Phillips et al., 2014). Nevertheless, other studies have also reported its importance sustaining macrozoobenthos in mangrove ecosystems (e.g. Kieckbusch et al., 2004; Claudino et al., 2015; Medina-Contreras et al., 2020), as an important supplier of the suspended organic matter pool in fringing mangrove locations (Saavedra-Hortua et al., 2020) and as part of the sediment in the form of decaying organic matter (Dubois et al., 2012).

The $\delta^{13}\text{C}$ values of POM showed no perceived patterns when comparing mangrove and control sites. This may be due to spatial and temporal variations in the hydrodynamics, even at small scales (Soares et al., 2018), and in the nutrients available for phytoplankton production (Kristensen et al., 2008; Soares et al., 2018), which can significantly change with water height and salinity (Doi et al., 2005; Bouillon et al., 2007). The $\delta^{13}\text{C}$ values of POM in this study were close to those presented by benthic microalgae, suggesting it is partly comprised by resuspended organic carbon from intertidal surface sediments through tidal movements over the mudflats (Bouillon et al., 2007). This source has been estimated to be very important for bivalves and errant polychaetes in mangrove sites, in accordance to studies in other areas (e.g. Doi et al., 2005; Tue et al., 2012).

Benthic microalgae presented similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among sites, and represented the most important source for errant and sedentary polychaetes in one mangrove site, and were among the most important for errant polychaetes in the control site. Although being overall among the most important sources in our study, reaching up to ca. 40% of the diet of these invertebrates, microalgae presented lower importance than what has been reported in mangrove-influenced intertidal ecosystems elsewhere (Abrantes and Sheaves 2009; Viana et al., 2015; Medina-Contreras et al., 2020). Nonetheless, benthic microalgae might also sustain this intertidal ecosystem indirectly through its incorporation in suspended POM, as suggested by the similarities between their stable isotopic values.

Some authors have advocated that the use of food sources by benthic fauna may vary with the form, availability of local vs imported food sources (Bouillon et al., 2004b; Lee 2008; Marcelina et al., 2018), and

with the origin of organic matter in the sediment pool (Bouillon et al., 2003). Our results suggest that in the Bijagós archipelago, like in some other mangrove stands elsewhere (e.g. Abrantes and Sheaves, 2009; Medina-Contreras et al., 2020; Tue et al., 2012), macrozoobenthos in adjacent intertidal flats do not depend on a single dominant carbon source, relying instead on sources with varying availability, form and composition across different locations. This variability in the importance of basal food sources can potentially promote trophic diversity in consumers and lead to a diverse set of trophic pathways and energy flow in this ecosystem (Marcelina et al., 2018), enhancing food web resilience.

5. Conclusions

In this study we found no evidence for a major role of mangrove forests as direct suppliers of carbon to the communities of adjacent intertidal flats. Several studies have provided evidence for a movement of exogenous organic carbon into mangrove ecosystems, while reporting limited to inexistent export of mangrove carbon towards adjacent habitats (Guest et al., 2004; Bouillon et al., 2008; Kruitwagen et al., 2010). Our results support this pattern in the mangroves of the Bijagós archipelago, where intertidal food webs seem to be sustained by a variety of locally produced sources, namely detritus derived from mats of filamentous macroalgae and benthic microalgae, and POM, likely including a mixture of resuspended benthic microalgae and imported phytoplankton through sea currents. These nutritious food sources are more likely to be of use to macrozoobenthos because of their low C/N ratio, as opposed to mangrove leaf litter, typically of little nutritional value (Rao et al., 1994; Lee 1997; Skov and Hartnoll 2002; Bouillon et al., 2003; Kieckbusch et al., 2004; Weiss et al., 2016). Nonetheless, the possible role of mangrove forests as a source of CO₂ and inorganic nutrients originated from the mineralization of mangrove organic matter, and which feed the secondary production, remains open as an alternative hypothesis linking mangrove production and adjacent habitats. Further research to test this hypothesis is essential to increase our understanding of the role of mangrove productivity to intertidal benthic communities.

The reliance of intertidal species assemblages on mangrove carbon has been shown to depend on the ecology of the taxa considered (Kruitwagen et al., 2010; Medina-Contreras et al., 2020). In our study we sampled the most abundant and widespread macroinvertebrates to allow comparisons between sites and across distances to coastline, but this led to the exclusion of herbivores such as leaf-eater sesamid and grapsid crabs, and gastropods, which may play a crucial role in the decomposition of mangrove leaves and in the integration of mangrove carbon into intertidal food webs by shredding and making them available to bacteria and other meiofauna (Lee 1997; Bouillon et al., 2002; Werry and Lee 2005; Kristensen 2008; Bui and Lee 2014). Future research in this area should investigate the potential role of these animals in the integration of mangrove carbon into these food webs.

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Credit author statement

MH: Conceptualization, Methodology, Formal Analysis, Investigation, Writing - Original Draft, Visualization, Project administration. **JPG:** Conceptualization, Methodology, Investigation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition. **TP:** Conceptualization, Writing - Review & Editing, Supervision. **SL:** Investigation. **SP:** Project administration. **TC:** Conceptualization, Methodology, Investigation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2021.105331>.

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