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José Paula and Michael H. Schleyer
(Guest Editors)

Population structure, density and food sources of *Terebralia palustris* (Potamididae: Gastropoda) in a low intertidal *Avicennia marina* mangrove stand (Inhaca Island, Mozambique)

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ABSTRACT

Population structure and distribution of *Terebralia palustris* were compared with the environmental parameters within microhabitats in a monospecific stand of *Avicennia marina* in southern Mozambique. Stable carbon and nitrogen isotope analyses of *T. palustris* and potential food sources (leaves, pneumatophore epiphytes, and surface sediments) were examined to establish the feeding preferences of *T. palustris*. Stable isotope signatures of individuals of different size classes and from different microhabitats were compared with local food sources. Samples of surface sediments 2.5–10 m apart showed some variation ($-21.2\permil$ to $-23.0\permil$) in δ^{13}C, probably due to different contributions from seagrasses, microalgae and mangrove leaves, while δ^{15}N values varied between $8.7\permil$ and $15.8\permil$, indicating that there is a very high variability within a small-scale microcosm. Stable isotope signatures differed significantly between the *T. palustris* size classes and between individuals of the same size class, collected in different microhabitats. Results also suggested that smaller individuals feed on sediment, selecting mainly benthic microalgae, while larger individuals feed on sediment, epiphytes and mangrove leaves. Correlations were found between environmental parameters and gastropod population structure and distribution vs. the feeding preferences of individuals of different size classes and in different microhabitats. While organic content and the abundance of leaves were parameters that correlated best with the total density of gastropods ($>85\%$), the abundance of pneumatophores and leaves, as well as grain size, correlated better with the gastropod size distribution ($>65\%$). Young individuals (height < 3 cm) occur predominantly in microhabitats characterized by a low density of leaf litter and pneumatophores, reduced organic matter and larger grain size, these being characteristic of lower intertidal open areas that favour benthic microalgal growth. With increasing shell height, *T. palustris* individuals start occupying microhabitats nearer the mangrove trees characterized by large densities of pneumatophores and litter, as well as sediments of smaller grain size, leading to higher organic matter availability in the sediment.

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1. Introduction

Mangrove systems represent complex and highly dynamic environments in which faunal assemblages typically occupy distinct horizontal or vertical zones, and manifest complex temporal patterns in their activities (Robertson and Alongi, 1992; Hogarth, 2007). Although biological, chemical and physical properties are expected to be reflected in strong correlations between benthic fauna and sedimentary properties, most studies have shown these relationships to be relatively weak (e.g., Chapman and Tolhurst, 2007). The crucial role of marine invertebrates in the food web, nutrient cycling and overall energy flux in Indo-Pacific mangrove ecosystems has become a standard paradigm in

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ecological research on these tidal forests (Bouillon et al., 2008). Recently, evidence is emerging that many invertebrates have a small home-range and derive most of their diet from locally available food sources (Guest et al., 2006). Small-scale changes in their stable isotope signatures (derived from the carbon and nitrogen sources of their diet) may be a useful tool to track and explain invertebrate microdistribution patterns (Guest and Connolly, 2004; Guest et al., 2004).

During the last decade, one of the most common and abundant mangrove gastropods, *Terebralia palustris* (Linnaeus), has been the subject of several ecological studies due to the significant quantities of leaf litter that it consumes and processes, and it has become a recognized link in nutrient cycling in mangrove forests (Slim et al., 1997; Fratini et al., 2004). It is found in substrata that range from mud to sand, and extends from the upper *Avicennia marina* belt down to the lower fringe stands (Rambabu et al., 1987; Fratini et al., 2004). *Terebralia palustris* is known to be omnivorous, feeding on detritus, leaf litter, mangrove propagules, carrion, sediment particles, benthic diatoms and bacteria (Nishihira, 1983; Rambabu et al., 1987; Dahdouh-Guebas et al., 1998; Fratini et al., 2000).

A spatial separation between young and older individuals was first observed by Soemodihardjo and Kastoro (1977). Due to anatomical differences in the structure of the radula, only large (shell height > 5 cm) *Terebralia palustris* actively feed on fallen mangrove leaves, propagules and fruits, while small individuals (shell height < 5 cm) are usually detritivorous or deposit feeders (Nishihira, 1983; Houbrik, 1991; Slim et al., 1997; Dahdouh-Guebas et al., 1998; Fratini et al., 2004; Pape et al., 2008). This different feeding strategy has been used to explain the spatial segregation between juveniles (more common in tidal channels and pools) and adults (common in the forest) reported by various authors for Jakarta (Soemodihardjo and Kastoro, 1977), Western Australia (Wells, 1980) and Gazi Bay, Kenya (Slim et al., 1997; Pape et al., 2008). In contrast, some other studies have shown no spatial separation between juveniles and adults (e.g., Fratini et al., 2004 for Gazi Bay, Kenya). Only Pape et al. (2008) have attempted to elucidate the population structure or distribution of *T. palustris* relative to environmental variables and stable isotopic composition. Their study was undertaken along two transects from the landward mudflat zone to the seaward seagrass zone (passing through the mangrove forest), with sampling intervals of 8 m.

The present study aimed to elucidate *Terebralia palustris* microdistribution, as well as its feeding strategies, at spatial scales of 1.25–2.50 m. Its spatial distribution and population structure were compared with important abiotic and biotic parameters, such as organic matter content, sediment granulometry, leaf litter and pneumatophore abundance. Together with the environmental parameters, foot muscle and potential food sources of *T. palustris* were subjected to stable isotope analysis (carbon and nitrogen) to better elucidate the relationship between gastropod feeding strategy and distribution. The variability in stable isotope signatures of the sediments and different size classes of *T. palustris* were also documented in each microhabitat.

2. Materials and methods

2.1. Study site

Inhaca is a small island (42 km^2) situated 32 km off Maputo in southern Mozambique, East Africa (26°S 33°E). The east coast is exposed to the Indian Ocean, whereas the western and southern coasts face Maputo bay. The island is positioned in a transitional region of tropical to warm subtropical conditions and constitutes a barrier between Maputo Bay and the Indian Ocean. The climate of Inhaca island is characterized by hot and wet (September–March) and warm and dry (April–September) seasons (Bandeira, 1995).

In August 2006, this study was conducted in the low intertidal *Avicennia marina* belt in the Saco mangrove during a spring low tide. The Saco bay is located at the southern end of Inhaca Island, occupies an area of 204 ha, and is bordered by mangroves. While *Ceriops tagal*, *Bruguiera gymnorrhiza* and *Rhizophora mucronata* are found along the channels and in the most densely forest areas, *A. marina* covers the upper and lower limits of the mangrove (Kalk, 1995; De Boer, 2000). The subtidal zone is characterized by patches of seagrasses (Kalk, 1995). At the seaward edge, the *A. marina* trees are large, often more than 5 m high, and their pneumatophores can extend to several meters around the trunk (Kalk, 1995). In this lower *A. marina* belt, three areas were randomly selected and, in each of these, four pneumatophore zones were studied (Fig. 1).

Lower – lower half of the pneumatophore zone (over half a pneumatophore zone away from the *Avicennia marina* canopy).

Mid – central pneumatophore zone.

Upper – upper half of the pneumatophore zone (the latter two zones comprising equal divisions of under half a pneumatophore zone from the *Avicennia marina* canopy).

Canopy – under the *Avicennia marina* canopy.

Each of the pneumatophore zones (excluding the Canopy) comprised a belt that was between 5 and 10 m long and an average of 5 m wide (see Fig. 1 for clarification). An Inter-pneumatophore zone was similarly delineated between pneumatophore zones corresponding to the area adjacent to the Upper and Canopy regions of the pneumatophore zones (see Fig. 1).

2.2. Population structure

Four quadrats of 0.25 m^2 were randomly allocated in each of the pneumatophore and inter-pneumatophore zones. All *Terebralia palustris* specimens inside the quadrats were collected (including those with more than 50% of the body inside the quadrat) and stored in a cool box. In the laboratory, they were counted, weighed (wet weight) and their height (shell height – SH – maximum linear dimension of the shell from the apex to the anterior edge of the lip) was measured.

2.3. Environmental data

While some biogeochemistry parameters are known to be relatively constant throughout the year, or oscillate seasonally or with important events (e.g., heavy rains or winds), some fluctuate significantly during a single tidal cycle (e.g., temperature, salinity) (e.g., Chapman and Tolhurst, 2007). Only parameters more or less consistent within a tidal cycle were thus measured in this study, providing a realistic explanation of the observed population structure and distribution patterns.

2.3.1. Pneumatophore and leaf density
The number of pneumatophores (protruding >0.5 cm above the sediment) and leaves were counted in each quadrat.

2.3.2. Granulometry
Two sediment cores (3 cm ∅ and 2 cm depth) were extracted per quadrat. Each core was stored in a plastic vial and stored in a cool box during transport to the laboratory. There the sediment samples were oven-dried at 105 °C to constant weight. The different sediment particle sizes were separated on a mechanical shaker using a series of sieves ranging from 2 mm upwards and graded following the Wentworth scale. The residues in each sieve were weighed and assigned to a textural group according to Folk (1954). The median grain size of each sample and the textural group
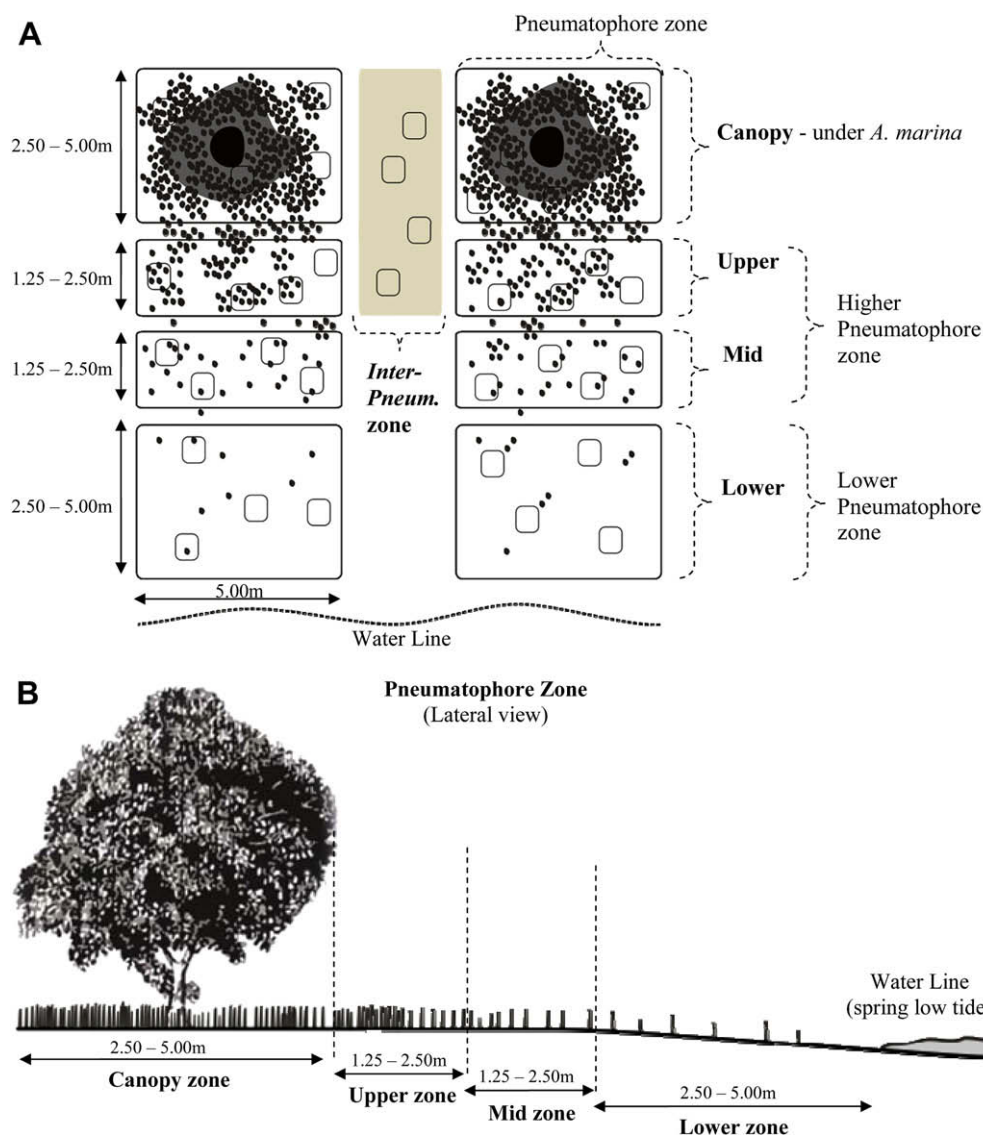
Fig. 1. Zonation in the lower *Avicennia marina* belt in the Saco, Inhaca Island, southern Mozambique, during low tide. (A) Top view of two pneumatophore zones, where Canopy, Upper, Mid *and* Lower sampling zones are shown as rectangular areas 1.25–5.00 m long and 5 m wide. An Inter-pneumatophore zone (grey zone) is also shown. Small black dots designate pneumatophores (●) and small squares sample quadrats of 0.25 m^{-2} (□). (B) Lateral view of a pneumatophore zone.

in each zone (derived from 24 replicates from each of the three study areas) was determined using Gradistat 5 software (Blott and Pye, 2001).

2.3.3. Organic content

Each sediment core was stored in a cool box during transport to the laboratory. There the samples were dried at 105 °C to a constant weight, ignited at 550 °C for three hours and cooled in a desiccator. The loss on ignition (LOI) was measured and the organic content expressed as a percentage of the dry weight (Heiri et al., 2001).

2.4. Stable isotopes

2.4.1. Terebralia palustris

Whenever possible, five (or more) individuals of each size class (SH < 3, 3 < SH < 5 and SH > 5 cm) per zone were washed with distilled water and part of the foot muscle was removed and dried at 60 °C for 72 h. After drying, the samples were frozen until further processing for stable isotope analysis.

2.4.2. Sediment, leaves and pneumatophore epiphytes

Two sediment cores (3 cm ⌀ and 2 cm depth) were collected in each zone. As the isotopic signature of mangrove leaves generally does not change significantly with decomposition (Zieman et al., 1984; Dehairs et al., 2000), at least five mangrove leaves of all the species present (*Avicennia marina*, *Rhizophora mucronata* and *Ceriops tagal*) were randomly picked from different trees in or just around the study area. Pneumatophore epiphytes were gently scraped off with surgical blades. These scrapings were randomly taken from within the range occupied by *Terebralia palustris*. Sediment, leaves and epiphytes were transport to the laboratory in a cool box. Leaves and epiphytes were subsequently washed with distilled water, and dried at 60 °C for 72 h, while the sediment samples were freeze-dried.

2.4.3. Analytical procedures

All samples were ground to a fine powder and subsamples of the sediment and epiphytes were acidified with dilute (5%) HCl before analysis to remove carbonates. $\delta^{13}C$ and $\delta^{15}N$ analyses were performed with a ThermoFinnigan Flash1112 elemental analyzer,

coupled to a ThermoFinnigan delta +XL via a Conflo III interface, with a typical reproducibility of $\pm 0.15\%$ for both δ^{13}C and δ^{15}N. All stable isotope ratios are expressed relative to the conventional standards (VPDB limestone for carbon and atmospheric N_2 for nitrogen) as δ values, defined as:

$$\delta^{13}C = \frac{X_{sample} - X_{standard}}{X_{standard}} \times 10^3 [\%]$$

where $X = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ in the case of δ^{15}N.

2.5. Statistical analyses

Stable isotope signatures of all samples (sediment, leaves and epiphytes) and between *Terebralia palustris* of different size classes and zones were compared using non-parametric tests (Kruskal–Wallis), followed by a Dunn multicomparisons test whenever statistical significances were found. Principal component analysis (PCA) was used to reduce the multidimensional environmental data sets to lower dimensions. The variables used in the PCA were percent organic matter, granulometry, number of leaves and pneumatophores per quadrat. Analysis of similarities (ANOSIM) has been widely used for testing hypotheses on spatial differences and temporal changes in biological assemblages (Clarke and Gorley, 2006). This test was used to separate zones by analysing each of the following data sets separately: (1) population data (*T. palustris* density and average height); and (2) environmental data (% organic matter, granulometry, number of leaves and pneumatophores per quadrat). The link between environmental variables and *T. palustris'* distribution and abundance was analysed using the BEST analysis. This test maximises the rank correlation between the resemblance matrices of the environmental (percent organic matter, abundance of leaves and pneumatophores, and average grain size) and community variables (average shell length and average density), where all permutations of the variables are tried in the BIOENV algorithms (Clarke and Gorley, 2006). Prior to the PCA, ANOSIM and BEST analyses, environmental data were log($x + 1$)-transformed (for PCA and ANOSIM) or log(x)-transformed (for BEST) and normalized, while *T. palustris* population data were square root-transformed. Although ANOSIM compares zones with all variables, for a more detailed analysis of each environmental or population variable, non-parametric tests (Kruskal–Wallis) were used followed by Dunn's test whenever differences were detected using the Kruskal–Wallis test. Kruskal–Wallis and Dunn tests were performed using GraphPad Instat, while PCA, ANOSIM and BEST analyses were performed using Primer 6 software.

3. Results

3.1. Environmental factors

Environmental variables were significantly different between zones (Table 1). When analysed with ANOSIM (Table 2), there was a clear separation between all the five zones, defined *a priori* (Global $R = 0.65$). All the pairwise tests between the zones manifested significant differences between them, although some zones were found to overlap (Lower vs. Mid, and Mid vs. Upper). With the help of PCA (Fig. 2), it was possible to reduce all the environmental data sets to two principal components, which explained more than 77% of the cumulative percentage variation (PC1, 50% and PC2, 27%). The Canopy and Upper zone data are found more frequently on the negative side of the PC1 axis, where the number of leaves, pneumatophores and sediment organic matter are higher and the mean grain size is smaller. The Lower and Inter-pneumatophore zones are clearly located at the positive side of the axis, while the Mid zone attained both negative and positive values. In the PC2, negative values are related to an increase in medium grain size and the number of pneumatophores, and a decrease in sediment organic matter. This axis clearly separates the Inter-pneumatophore zone from all the other zones (Fig. 2). Using Gradistat 5, the Lower and Mid zones were classified as "sandy gravel", the Upper and Inter-pneumatophore zones as "muddy sand" and the Canopy zone as "gravelly mud".

3.2. Stable isotope analysis

3.2.1. Primary producers

The mean carbon stable isotope ratio of *Avicennia marina* ($-28.8 \pm 0.5\%$) was significantly lower than the values obtained for *Rhizophora mucronata* ($-27.5 \pm 0.5\%$) and *Ceriops tagal* ($-27.2 \pm 0.3\%$) (Fig. 3). The nitrogen stable isotope ratios manifested the opposite trend with much higher values in *A. marina* ($7.1 \pm 1.2\%$) compared to *R. mucronata* and *C. tagal* (0.9 ± 0.3 and $1.4 \pm 0.5\%$, respectively) (Fig. 3). The carbon stable isotope ratios of epiphytes ($-24.1 \pm 1.1\%$) scraped off the pneumatophores were more enriched than those of the mangrove leaves and their δ^{15}N signatures were rather low ($1.3 \pm 0.3\%$) (Fig. 3).

3.2.2. Sediment

The sediment δ^{13}C signatures ($-22.2 \pm 0.7\%$) were generally enriched compared to mangrove leaf tissue (approximately -28%) (Fig. 5). However, sediment from the different zones manifested some significant differences regarding their δ^{15}N and C/N ratios (Table 3). From the Canopy down to the lower pneumatophore zone, there was a slight increase in the sediment δ^{13}C signatures (going from -22.6 to -21.2%), whereas the C/N ratios remained more or less constant along this transect ($\sim 14 \pm 0.5$, Table 3). In contrast, sediment from the Inter-pneumatophore zone differed from that in the Pneumatophore zone, having δ^{13}C even more depleted than in the Canopy zone and a greater C/N ratio. Although sedimentary δ^{15}N values became enriched from the Canopy towards the Lower zone (from 8.7% to 15.8%), the high variability masked any clear trend. Average δ^{13}C and δ^{15}N values in the Inter-pneumatophore zone were similar to those found in Mid and Upper zones.

Table 1

Average ($\pm$SD) pneumatophore and leaf density, sediment median grain size, percentage of sediment organic matter (LOI), *Terebralia palustris* height, density and total biomass recorded in each of the five study zones. Different letters indicate a significant difference ($p < 0.05$) between the five zones for each variable. (Numbers in parentheses indicate numbers of replicates).

Zone	Local properties				*Terebralia palustris*		
	Pneumatophore density (m^{-2})	Leaf density (m^{-2})	Median grain size (mm)	LOI (% org. mat)	Height (cm)	Density (ind m^{-2})	Biomass (wet weight) (g m^{-2})
Inter-pneumatophore	2.3 ± 5.5^a (12)	23.7 ± 68.5^a (12)	$1.3 \pm 0.2^{a,b}$ (12)	$2.7 \pm 2.5^{a,b}$ (8)	2.3 ± 0.8^a (551)	$182.7 \pm 224.5^{b,c}$ (12)	44.05 ± 58.44^b (12)
Lower	64.7 ± 28.5^b (12)	2.7 ± 3.9^a (12)	1.4 ± 0.4^a (12)	1.6 ± 0.4^a (8)	$2.8 \pm 1.3^{a,b,c}$ (7)	2.3 ± 4.7^a (12)	0.85 ± 1.56^a (12)
Mid	$85.0 \pm 37.3^{b,c}$ (12)	$8.7 \pm 7.2^{a,b}$ (12)	1.4 ± 0.3^a (12)	$3.4 \pm 3.1^{a,b}$ (8)	2.6 ± 0.8^b (582)	193.7 ± 159.3^c (12)	62.42 ± 39.65^b (12)
Upper	$256.3 \pm 77.6^{c,d}$ (12)	$37.3 \pm 27.4^{b,c}$ (12)	$0.9 \pm 0.4^{b,c}$ (12)	$3.1 \pm 1.5^{a,b}$ (8)	3.8 ± 1.1^c (383)	127.7 ± 81.0^c (12)	114.26 ± 46.96^c (12)
Canopy	398.0 ± 142.0^d (12)	140.7 ± 99.4^c (12)	0.8 ± 0.2^c (12)	5.0 ± 1.3^b (8)	4.7 ± 0.6^d (86)	$29.0 \pm 39.9^{a,b}$ (12)	$46.42 \pm 62.36^{a,b}$ (12)

Table 2
Results of ANOSIM global and pair-wise tests using Euclidean distance (for environmental) or Bray–Curtis similarity (for population data), when comparing between study zones: environmental data (% organic matter content; median grain size; number of leaves and pneumatophores per quadrat); and population data (*T. palustris* density and average height). *R*-values > 0.75 were interpreted as well-separated; *R* > 0.5 as overlapping but clearly different, and *R* < 0.25 as not separable.

Pair-wise	Environmental data, Global $R = 0.65$ $(p = 0.001)$	Population data, Global $R = 0.26$ $(p = 0.001)$
Lower vs. Mid	$R = 0.176$ $(p = 0.009)$	$R = 0.077$ $(p = 0.002)$
Lower vs. Upper	$R = 0.822$ $(p = 0.001)$	$R = 0.768$ $(p = 0.001)$
Lower vs. Canopy	$R = 0.997$ $(p = 0.001)$	$R = 0.203$ $(p = 0.041)$
Lower vs. Inter-pneumatophore	$R = 0.453$ $(p = 0.002)$	$R = 0.542$ $(p = 0.002)$
Mid vs. Upper	$R = 0.218$ $(p = 0.012)$	$R = 0.007$ $(p = 0.847)$
Mid vs. Canopy	$R = 0.800$ $(p = 0.001)$	$R = 0.017$ $(p = 0.017)$
Mid vs. Inter-pneumatophore	$R = 0.500$ $(p = 0.001)$	$R = 0.041$ $(p = 0.701)$
Upper vs. Canopy	$R = 0.902$ $(p = 0.001)$	$R = 0.131$ $(p = 0.043)$
Upper vs. Inter-pneumatophore	$R = 0.830$ $(p = 0.001)$	$R = 0.022$ $(p = 0.517)$
Canopy vs. Inter-pneumatophore	$R = 0.936$ $(p = 0.001)$	$R = 0.058$ $(p = 0.142)$

3.2.3. Terebralia palustris

Stable isotope signatures in *T. palustris* individuals changed according to individual size, as well as to the zone they inhabited. Irrespective of the sampling zone, the overall picture was that, with increasing animal size, δ^{13}C values tended to decrease but the δ^{15}N values were more irregular (Table 3, Fig. 5). The δ^{13}C signatures of individuals larger than 5 cm was significantly different ($p < 0.001$) from smaller size classes ($-20.1 \pm 0.8\permil$, $-19.9 \pm 0.8\permil$ and $-21.3 \pm 0.9\permil$ for size classes <3, 3–5 and >5 cm, respectively) (Table 4). Small individuals (<3 cm) collected in the Mid zone were significantly ($p < 0.001$) depleted in δ^{13}C when compared to the ones collected in the Upper and Inter-pneumatophore zones, while individuals 3–5 cm in height were significantly ($p < 0.001$) enriched in the Inter-pneumatophore zone relative to those found in the Mid and Upper zones. The δ^{15}N signature of small *T. palustris* was significantly enriched in the Upper zone when compared to the individuals collected in the Mid ($p < 0.05$) and Inter-pneumatophore ($p < 0.001$) zones, while mid-size individuals inhabiting the Inter-pneumatophore zone were significantly enriched relative to those found in the Canopy zone ($p < 0.05$) (Fig. 4).

3.3. Population distribution and structure

A clear pattern was found in *Terebralia palustris* microscale distribution (Fig. 5). In the Lower zone, none or very few individuals were found (Table 1). The smallest animals occurred predominantly in the Inter-pneumatophore and Mid zones, where the highest densities of *T. palustris* were observed. Small to large individuals were collected in the Upper zone, although the latter at much higher densities, while only larger individuals were observed in the Canopy zone. There was a significant increase in size in *T. palustris* from the Mid zone towards the Canopy zone (Table 1). Although the mean biomass (wet weight) mirrored the average density, the former is strongly influenced by the average size, resulting in a very low biomass in the Lower zone and very high in the Upper zone (Table 1).

ANOSIM analysis (Table 2) indicated that the zones were barely separable with regard to both *Terebralia palustris* density and average size (Global $R = 0.26$). However, the pairwise tests indicated that the Lower zone was significantly different from all the other zones ($p < 0.041$), as was the Canopy zone from the Mid ($p < 0.041$) and Upper ($p < 0.041$) zones, but they were barely separable ($R < 0.25$). All the other pairwise comparisons overlapped and were not significantly different from each other (Table 2).
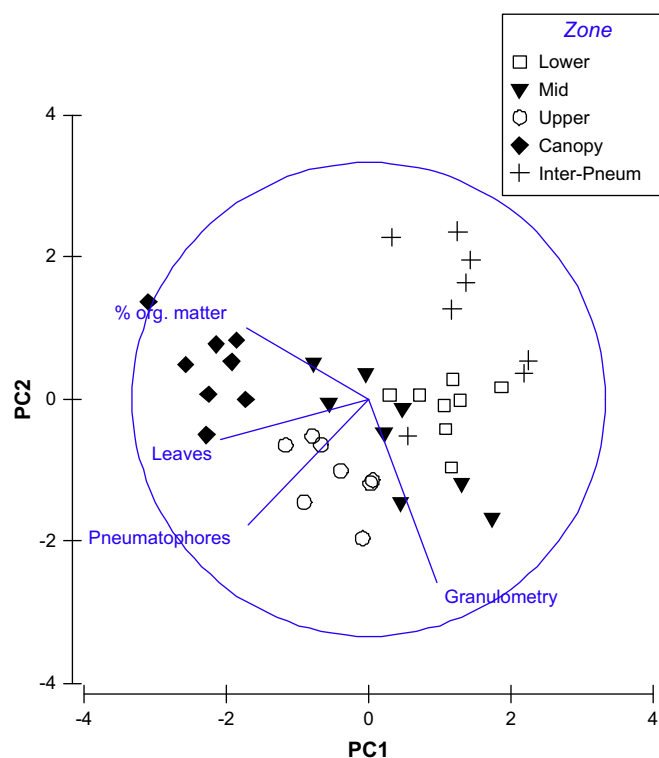

Fig. 2. Two-dimensional scatter plot of the First and Second Canonical axes for all environmental variables measured in each study zone. Variable eigenvectors for PC1 (*x*-axis) and PC2 (*y*-axis) are, respectively, leaves (-0.626; -0.173), pneumatophores (-0.510; -0.528), organic content (-0.516; 0.304), and average grain size (0.285; -0.774) (see text for further explanation).

BEST analysis indicated that 85.5% of the *Terebralia palustris* abundance can be explained by only two environmental variables: sediment organic content and the abundance of leaves, with the former accounting for ~80% of the variation. Granulometry and the density of leaves and pneumatophores account for ~65% of the gastropod size distribution, with the pneumatophore density explaining slightly more than 45% of this distribution.

4. Discussion

4.1. Microhabitat characterization

The environmental variables covered in this study were found to gradually change from Lower and Inter-pneumatophore zones towards the Canopy. The more congested the mangrove root systems (towards the Canopy) the more effective they become as litter traps, increasing the organic content of the soil, and also trap smaller sediment particles, creating a more muddy sediment (Robertson and Alongi, 1992; Hogarth, 2007). This further increases the organic content as finer particles have a larger surface area for the adsorption of organic matter. The Inter-pneumatophore zone had almost no pneumatophores and very sandy sediments. However, the leaf density was also as high as the Mid zone, where pneumatophore density was much higher. This may be due to the fact that the Inter-pneumatophore zones is located between the Upper and Canopy zones, both of these generating considerable leaf litter, and the Inter-pneumatophore zone is a passive corridor that exports mangrove litter (supported by the depleted δ^{13}C values measured in sediment in this zone).

With regard to the stable isotopic analyses, all the mangrove leaves had similar C and N isotopic signatures when compared to
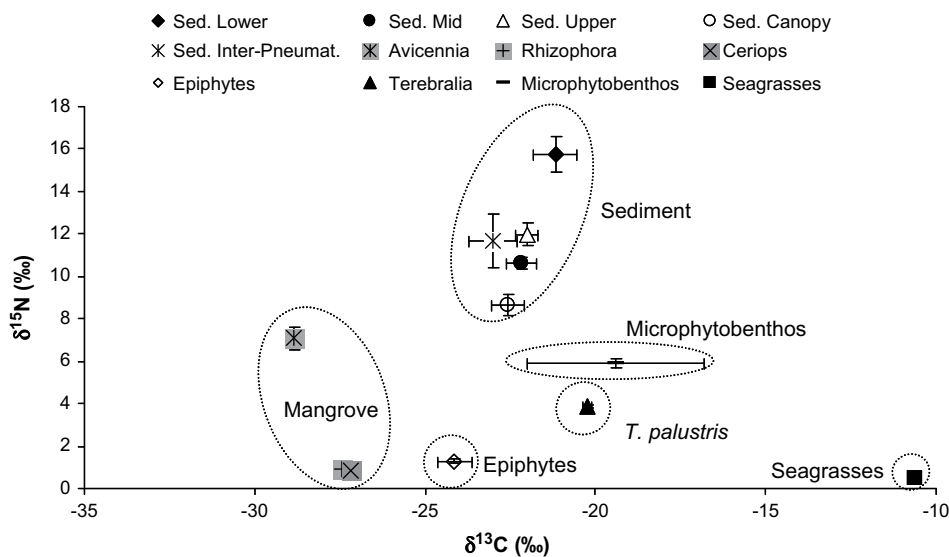
Fig. 3. Plot of average $\delta^{13}C$ and $\delta^{15}N$ values in *Terebralia palustris* foot muscle, sediment and primary producers in the study area. Microphytobenthos data were obtained from previous studies in Saco Bay, Inhaca, Mozambique (Abreu et al., in press). Error bars indicate SE ($n = 5$–60).

previous studies undertaken in the Saco mangrove (e.g., Macia, 2004), except for the $\delta^{15}N$ values obtained for *Avicennia marina* leaves, which were much higher. Results obtained in the surface sediments yielded average $\delta^{13}C$ values that were similar to other studies, although the $\delta^{15}N$ was, on average, much higher (8.7–15.8‰) than that found in previous studies (1.0–4.0‰) (e.g., Bouillon et al., 2002, 2004; Macia, 2004). Previous literature has already recorded high $\delta^{15}N$ signatures for *A. marina* leaves as well as for mangrove surface sediment (for a review see Bouillon et al., 2008). The high values and variability of the $\delta^{15}N$ signatures are likely to be due to a difference in nitrogen processes in the sediments of the different zones. Also, during sampling, runoff water from a nearby village was regularly observed, which could be a source of isotopically enriched nitrogen (Bouillon et al., 2008).

Due to difficulties in sampling, $\delta^{13}C$ data for seagrasses and benthic microalgae were obtained from previous studies (Abreu et al., in press). These data provide a clear distinction between the $\delta^{13}C$ signatures of mangrove tissues (approximately $-28‰$) compared to the other carbon sources available in the area, i.e. epiphytes ($-23.7‰$), benthic microalgae ($-19.4‰$) and seagrass ($-11.9‰$) detritus.

4.2. Population structure microdistribution and feeding preferences

The spatial segregation between juveniles and adults of *Terebralia palustris* reported by various authors for Jakarta (Soemodihardjo and Kastoro, 1977), Western Australia (Wells, 1980) and Gazi Bay, Kenya (Slim et al., 1997; Pape et al., 2008) was also encountered

Table 3
Average ($\pm$SD) $\delta^{13}C$ (‰) and $\delta^{15}N$ (‰) and C/N ratios obtained for sediment samples from different zones. Different letters indicate significant difference – $p < 0.05$ – between the five zones ($n = 6$).

Zone	Stable isotopes		C/N ratio
	$\delta^{15}N$	$\delta^{13}C$	
Inter-pneumatophore	11.7 $\pm$ 2.9[a,b]	-23.0 ± 1.6	18.8 $\pm$ 2.0[a]
Lower	15.8 $\pm$ 2.0[a]	-21.2 ± 1.6	13.6 $\pm$ 1.3[b]
Mid	10.6 $\pm$ 0.7[b]	-22.2 ± 1.1	14.5 $\pm$ 1.0[b]
Upper	12.0 $\pm$ 1.2[a,b]	-22.0 ± 0.8	14.5 $\pm$ 0.8[b]
Canopy	8.7 $\pm$ 1.3[b]	-22.6 ± 1.2	13.7 $\pm$ 1.2[b]

in the present study. Small *T. palustris* were more common on lower, open sandflats, while larger individuals tended to reside inside the mangrove forest. Both previous studies (Slim et al., 1997; Pape et al., 2008) suggested that 5 cm was the critical size at which $\delta^{13}C$ decreased, indicating an increase in leaf consumption, most likely caused by an ontogenetic change in diet (Houbrik, 1991). However, it should be stressed that in the Saco, the *T. palustris* population attained a maximum height of 6.25 cm. The clear decrease in $\delta^{13}C$ values in individuals measuring more than 5 cm in height is in agreement with previous research undertaken in *Ceriops tagal* (Slim et al., 1997) and *Sonneratia alba* (Pape et al., 2008) mangrove forests where gastropods reach much larger shell sizes.

Small *Terebralia palustris* were characterized by an average stable carbon isotope value of $-20.1‰$, which was 2.1‰ enriched relative to their suggested main food source (sediment, with a $\delta^{13}C$ average value of $-22.2‰$). Although a general increase of 0–1‰ could partially explain the observed discrepancy (Bouillon et al., 2008), selective assimilation of microbenthic algae could be taking place, as suggested by Pape et al. (2008). Microbenthic algae in the Saco displayed an average $\delta^{13}C$ value of $-19.4‰$ (Abreu et al., in press), a value similar to the one we obtained for smaller *T. palustris*. The high nutritional value of microalgae compared to mangrove tissue may also explain the higher densities of smaller gastropods in the lower intertidal zones, since the microalgal biomass in the upper zones is probably lower due to the lower light intensity under the dense canopy and inhibition caused by soluble tannins released by mangrove leaves (Alongi and Sasekumar, 1992). On the other hand, $\delta^{13}C$ signatures of larger *T. palustris* all fell in a narrow range between -21 and $-22‰$, which is still $\sim6.0‰$ enriched relative to their apparent food source, namely *Avicennia marina* leaves ($\delta^{13}C$ value of $-28.8‰$), which accounted for more than 90% of the total number of leaves found in litter in the study area (personal observation). The large difference in carbon isotope signatures between larger snails and *A. marina* mangrove leaves suggests that other food sources contributed the bulk of their diet. In this study, larger individuals were also observed to actively feed on pneumatophore epiphytes and graze the surface sediments. Both these carbon sources would provide the more enriched values of $\delta^{13}C$ observed. These findings thus suggest that leaves may not be the most important diet of these gastropods and, although they are known to consume a large amount of leaf material (Fratini et al.,

Table 4
Average ($\pm$SD) δ^{13}C (‰) and δ^{15}N (‰) of foot muscle of *T. palustris* for different size classes and zones. Different letters indicate significant difference – $p < 0.05$ – between the zones. Number in parenthesis indicates number of replicates (n.a. – not available).

Size classes (cm)	δ^{13}C stable isotope (‰)				δ^{15}N stable isotope (‰)			
	Inter-pneumatophore	Mid	Upper	Canopy	Inter-pneumatophore	Mid	Upper	Canopy
$x < 3$	-19.4 ± 0.6^a (8)	-20.9 ± 0.4^b (7)	-20.0 ± 0.5^a (8)	n.a.	3.9 ± 0.2^a (8)	3.7 ± 0.2^a (7)	2.9 ± 0.2^b (8)	n.a.
$3 < x < 5$	-18.9 ± 0.7^a (8)	-20.3 ± 0.6^b (9)	-20.5 ± 0.8^b (5)	$-19.9 \pm 0.3^{a,b}$ (4)	4.6 ± 0.4^a (8)	$4.3 \pm 0.3^{a,b}$ (9)	$4.1 \pm 0.2^{a,b}$ (5)	4.0 ± 0.1^b (4)
$x > 5$	-21.2 (1)	-21.1 ± 0.8 (2)	-21.0 ± 1.0 (7)	-22.0 ± 0.8 (4)	4.0 (1)	3.9 ± 0.2 (2)	3.7 ± 0.3 (7)	3.7 ± 0.5 (4)

2004), other food sources merit consideration in global carbon budgets in mangrove habitats. This is especially true of small gastropods that may represent a significant percentage of the *T. palustris* biomass, as in the present study. Despite the potentially large-scale movement of organic matter, the significant differences found between gastropods inhabiting the different zones indicate that they obtain their nutrition variably from the local sediment, leaves and epiphytes. This has been illustrated by Guest et al. (2004) for crabs and other gastropod species inhabiting the perimeter of saltmarshes and mangrove forests. However, it must also be recognized that the δ^{13}C and δ^{15}N in the animals they studied is not only a reflection of their food source at the time of sampling, but also results from the diet consumed during the preceding period (McCutchan et al., 2003).

Previous studies have demonstrated that the density of these gastropods is strongly correlated to grain size and organic content (e.g., Wells, 1980; Rambabu et al., 1987; Fratini et al., 2004), while others have found no such relationship (Pape et al., 2008). Results of our study indicate that the environmental parameter that best explained *Terebralia* p*alustris* distribution and density (higher than 85%) is the sediment organic matter content, followed by the abundance of leaves. This correlation seems reasonable since a higher availability of food resources usually positively affects the invertebrate biomass inhabiting a particular microhabitat.

The environmental variables that better explained *Terebralia palustris* population size structure distribution (more than 65%) were grain size, and the number of leaves and pneumatophores, with the latter (pneumatophores) accounting for more than 45% of this distribution. The higher the density of pneumatophores, the finer the sediment and the greater the abundance of leaves, leads to a larger animal size in any particular zone. According to our stable isotope analyses, a higher concentration of organic detritus and microalgae would promote higher densities of smaller individuals, while a high density of mangrove leaves would lead to a greater abundance of larger individuals. However, if we focused only on organic matter content and leaf density, we would be unable to explain more than 40% of the *T. palustris* population structure microdistribution.

The absence of juvenile gastropods from muddier sediments in the mangrove forest was observed in earlier studies, and was attributed to the finer sediment and the associated biogeochemical properties, such as high salinity (Pape et al., 2008). It is also known that smaller individuals have a larger surface/volume ratio, decreasing their resistance to desiccation, and may occupy lower zones that provide a longer immersion period, as well as benefiting them with more or less continuous runoff from the upper zones during low tide (personal observation). Although this seems to indicate the existence of an "ontogenic migration" from the Inter-pneumatophore zone to the Mid pneumatophore zone, after which the animals migrate towards the Canopy zone, this was not proven in this study and other reasons may also merit consideration. Differences in recruitment, growth, mortality and predation, as well as intra-specific competition for space or resources, may also be contributors in this regard.
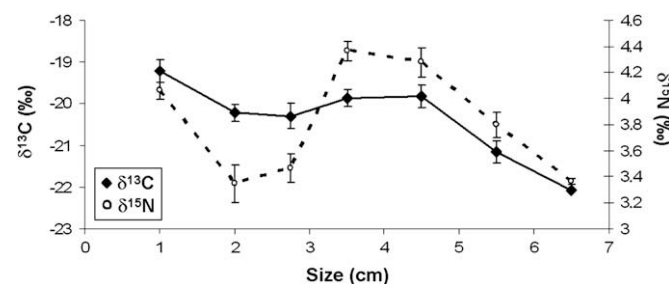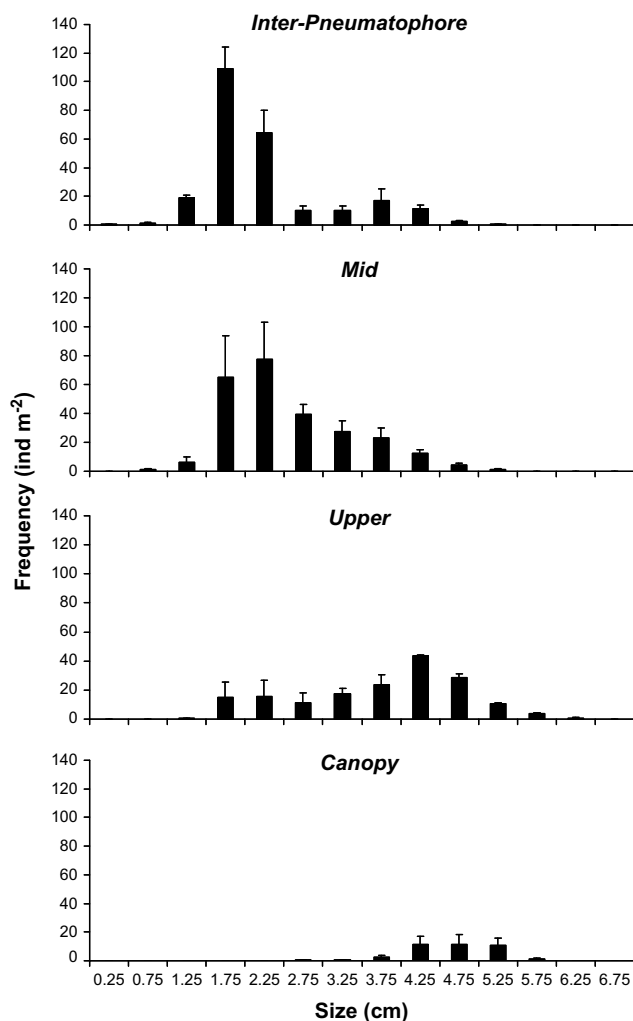

Fig. 5. Size frequency distribution of *T. palustris* (avg $\pm$ SE) in the four (Mid, Upper, CANOPY and Inter-pneumatophore) *Avicennia marina* zones. The Lower zone is not shown due to the very low density of the individuals encountered.

Fig. 4. Changes in δ^{15}N and δ^{13}C (average $\pm$ SE) in *T. palustris* foot muscle with increasing shell height in the study area.

5. Conclusion

Stable isotope signatures suggest that smaller *Terebralia palustris* feed on sediment and benthic microalgae, while larger individuals feed on sediment, epiphytes and mangrove leaves. This further suggests that the population structure and distribution of *T. palustris* are correlated with environmental factors within the different microhabitats. While the organic content seems to better correlate with the density of *T. palustris*, gastropod size distribution correlates best with the number of pneumatophores. Young *T. palustris* (height < 3 cm) occur predominantly in lower intertidal microhabitats characterized by a reduced number of leaves and pneumatophores, reduced organic matter content and large sediment grain sizes. As they grow larger, *T. palustris* are found closer to the mangrove tree microhabitats characterized by a higher density of pneumatophores and litter, as well as smaller sediment grain sizes, providing richer organic matter.

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