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Size-dependent distribution and feeding habits of *Terebralia palustris* in mangrove habitats of Gazi Bay, Kenya

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Abstract

The gastropod *Terebralia palustris* often dominates the surface of muddy to sandy substrates of intertidal mudflats and mangrove forests, where they clearly destabilize the sediment. In the present study, it was investigated whether and to what extent the behaviour of juvenile and adult snails differs among habitats (mudflat vs. mangrove stand) in a *Sonneratia alba* mangal at Gazi Bay, Kenya. For this purpose we: (1) examined their distribution along three land–sea transects; and (2) applied stable isotope analysis to determine the feeding patterns of different-sized snails from the mangrove and mudflat habitats. Additionally, we investigated if these gastropods exert an impact on microphytobenthic (diatom) biomass, and whether this is size-dependent. The latter objective was met by either enclosing or excluding different-sized snails from experimental cages on the intertidal mudflat and the subsequent assessment of a change in pigment concentration of the sediment surface. In agreement with several previous studies conducted in other mangroves and geographical locations, a spatial segregation was demonstrated between juveniles (more common on the mudflat) and adults (more common in the mangrove forest). On the intertidal mudflat juveniles avoided sediment patches characterized by highly saline water in intertidal pools and a high mud content, while adults tended to dwell on substrates covered by a high amount of leaf litter. Stable carbon isotope analysis of the foot tissue of snails sampled from the *S. alba* stand and the mudflat indicated a transition in food source when a shell length of 51 mm is reached. Considering the $\delta^{13}C$ value of juveniles, it seems they might be selecting for microphytobenthos, which might explain their preference for the mudflat. The diet of size classes found in both habitats did not differ significantly, although juveniles inhabiting the mangrove forest were slightly more depleted in ^{13}C compared to those residing on the mudflat. Assuming juveniles feed on benthic microalgae and considering the lower microalgal biomass inside the mangrove forest, this may be a consequence of a higher contribution of other, more ^{13}C depleted organic carbon sources, like phytoplankton, to their diet. Experimental results indicate a negative, but insignificant, impact on benthic diatom biomass by juveniles (due to grazing) and adults (due to physical disturbance). This finding seems to be in agreement with the results of the stable carbon isotope analysis, strongly suggesting the selective feeding of juvenile *T. palustris* on benthic diatoms.

Keywords: Terebralia palustris; stable isotopes; mangroves; cages; microphytobenthos; sediment; meiobenthos; Kenya, Gazi Bay

1. Introduction

Mangroves create unique ecological environments that are characterized by a remarkable biodiversity. The muddy or sandy sediments of these forests are home to a wide variety of marine invertebrates. The important role of these animals in the food web, nutrient cycling and overall energy-flux of mangrove ecosystems has often been the subject of ecological research (for a review, see Kathiresan and Bingham, 2001). Most of the studies have only dealt with decapod crustaceans (Dittmann, 1993; France, 1998; Skov and Hartnoll, 2002), although they are not the sole representatives of mangrove macrofauna and they are greatly outnumbered by gastropods,

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especially by potamidids of the genus *Terebralia* (Kathiresan and Bingham, 2001). Recently, it has become apparent that *Terebralia palustris* (Potamididae: Gastropoda) is crucial in the nutrient cycling process in mangrove forests as this species is responsible for processing a significant amount of leaf litter (Slim et al., 1997; Fratini et al., 2004).

The snail *Terebralia palustris*, also known as mud creeper or mudwhelk, is the largest and most widely distributed member of the family of the Potamididae and should be regarded as one of the major constituents of the Indo-Pacific mangal invertebrate fauna, in terms of biomass and ecological impact (Fratini et al., 2004). *Terebralia palustris* is by far the largest prosobranch in mangrove habitats. In Arnhem Land, Australia, Houbrick (1991) observed *T. palustris* snails, measuring up to 190 mm. In Kenya the largest *T. palustris* shell measured is 130 mm (Fratini et al., 2004). These gastropods often are predominant on the surface of muddy substrates of mangrove forests (Nishihira, 1983). In Gazi Bay, Slim et al. (1997) noted an average density of 33 *T. palustris* m^{-2} in a *Ceriops tagal* vegetation zone.

Terebralia palustris is a truly amphibious species, active both at low and high tides (Fratini et al., 2000, 2001). However, this snail seems to avoid the driest landward and the most exposed seaward zone of the mangrove forest, by clustering on the typically fine substrata of the most shaded patches and in small tidal pools formed in between the aerial roots of mangrove trees (Houbrick, 1991; Slim et al., 1997).

Several authors (Wells, 1980; Houbrick, 1991; Slim et al., 1997) have noted a clear spatial segregation between juveniles and adults. Juvenile *Terebralia palustris* colonise the small creeks and large pools on the seaward front of the forests and are thought to migrate into the landward belts when reaching their adult stage. This migratory behaviour between open mudflats and mangrove forests seems to be related to a change in diet (Houbrick, 1991). However, Fratini et al. (2004) found no separation in habitat selection between juveniles and adults, as they were dwelling together in the mangrove stand and on the intertidal flats in Dabaso (*Rhizophora mucronata*) and Mida (*Avicennia marina*), Kenya.

It is widely recognized that juvenile and adult *Terebralia palustris* differ in their food preferences. Juveniles have been considered as either detrivores (Nishihira, 1983; Houbrick, 1991; Fratini et al., 2004) or deposit-feeders (Slim et al., 1997) while adults graze on plant materials such as leaf litter, mangrove propagules and fruits (Nishihira, 1983; Houbrick, 1991; Slim et al., 1997; Dahdouh-Guebas et al., 1998; Fratini et al., 2004). This has been confirmed by both stomach-content analysis (Fratini et al., 2004) and stable isotope analysis (Slim et al., 1997). The trophic dimorphism between juvenile and adult *T. palustris* has been associated with anatomical differences in the structure of their radula (Houbrick, 1991). The danger of being turned upside down or dragged into a burrow of sesarmid crabs might partly account for the fact that young *T. palustris* do not feed on leaves (Fratini et al., 2000). These crabs have been shown to heavily compete with *T. palustris* as they exhibit wide overlap in food items, zone of feeding and time of feeding (Fratini et al., 2000). This interspecific competition is assumed to be the main reason why adult snails are frequently observed to feed in clusters on a single fallen mangrove leaf, as it is believed that the crabs are only able to steal leaves from clusters that consist of less than eight individuals (Fratini et al., 2000).

Terebralia palustris is known to be a surface-dwelling organism and while grazing on the sediment, its heavy shell rearranges the mud surface by leaving an approximately 0.5 cm deep track (Carlén and Olafsson, 2002). Due to its high abundance and surface-dwelling behaviour, *T. palustris* is likely to have an impact on the biotic and abiotic properties of the sediment surface layer. Several authors (for a review, see Olafsson, 2003) have studied the interactions between macroepifauna and infaunal communities in marine soft-bottoms by means of cage exclusion experiments. Several studies (Nichols and Robertson, 1979; Branch and Branch, 1980; Schrijvers et al., 1995, 1997) have indicated a significant increase in microphytobenthic biomass in the absence of macroepifauna. Macrofauna may exert biological disturbance on infaunal communities by physical force, creation of microhabitats, predation or competition for food resources (Sherman and Coull, 1980; Palmer, 1988).

In the current study we investigated whether and to what extent the behaviour of juvenile and adult *Terebralia palustris* depends upon habitat. For this purpose, we compared a *Sonneratia alba* stand and an intertidal mudflat in terms of:

(1) The abundance of juvenile and adult gastropods, by examining their distribution along land–sea transects. Furthermore, snail abundance was studied in relation to relevant environmental conditions (humidity at low tide, leaf litter, etc.)
(2) The diet of juveniles and adults, by sampling several specimens representing different size classes from the mangrove forest and the open mudflat for carbon stable isotope analysis. This way the relative importance of size and habitat selection for the specific food uptake of *Terebralia palustris* was examined.

In addition, we conducted a combined in- and exclusion experiment on the intertidal mudflat to study the short-term (24 h) impact of juvenile and adult *Terebralia palustris* on pigment concentration of the sediment surface as a proxy for microphytobenthic (diatom) biomass.

2. Materials and methods

2.1. Site description

The present study was performed at Gazi Bay (39°30′ E, 4°22′ S), located about 50 km south from Mombasa, Kenya. The bay itself harbours large areas of seagrass beds, which are dominated by *Thalassodendron ciliatum* (Coppejans et al., 1992). The upper region of the bay receives freshwater from the Kidogoweni River, which cuts through the mangroves. Spring tidal range in Gazi Bay is reported to be 3.2 m (Kitheka, 1997). The distribution of *Terebralia palustris* was investigated along transects covering an intertidal mudflat (=degraded *Sonneratia alba* forest), a *S. alba* stand as well as a seagrass field adjacent to the forest (Fig. 1). Both the degraded and the natural *S. alba* site are inundated with each flood tide. The caging experiments were carried out on the intertidal mudflat. The transects and the experiments were run in March 2006.

2.2. Distribution of *T. palustris*

Three adjacent land–sea transects, traversing a degraded *Sonneratia alba* site (also referred to as "mudflat"), a *S. alba* mangrove forest and a seagrass field, were defined (Fig. 1). These transects were approximately 5 m apart. Along each of them, nine quadrats (0.09 m^2) were investigated every 8 m. All present *Terebralia palustris* specimens were collected and their shell length was measured to the nearest mm using a calliper in order to determine their size distribution. Specimens with a shell length greater than 5 cm were regarded as adult, those with a shell length smaller than 5 cm were assumed to be juvenile. Fratini et al. (2004) has shown that the size shift from the immature to the mature stage occurred at about 5 cm. The total number as well as the number of juvenile and adult snails in each quadrat was recorded. Densities were expressed as number of individuals per m^2.

In addition to sampling for *Terebralia palustris*, a number of environmental factors were measured that could explain the distribution and the presence of this species:

(a) Sediment temperature: the temperature of the upper 1–1.5 cm of the sediment was determined using a digital thermometer.
(b) pH: the pH of the water (if humidity > 0%) was recorded by means of a portable multimeter.
(c) Salinity: a refractometer was used to measure the salinity of the water (present in intertidal pools).
(d) Leaf litter: an approximate visual estimate was made of total percentage cover by intact as well as fragmented mangrove leaves and seagrass fragments.
(e) Pneumatophores: a note was made of the percentage cover of pneumatophores.
(f) Humidity: an approximate estimate was made of the percentage of the quadrat area covered by water.
(g) Organic carbon: in each quadrat a 35-mm diameter core was obtained to estimate the organic carbon content of the upper 5 cm of the sediment using a Carbon–Nitrogen analyzer NA 1500 Carlo Erba.
(h) Grain size: samples taken for organic carbon content analysis were also used for the assessment of the granulometric properties of the sediment by means of a Coulter® LS 100 Particle Size Analyzer. Prior to grain size analysis, the gravel fraction (>1 mm) was mechanically separated by sieves.

2.3. Feeding habits of *T. palustris*

2.3.1. Stable isotope analysis

Along each transect snails belonging to different size classes were collected on the open mudflat as well as inside the *Sonneratia alba* mangrove forest for carbon stable isotope analysis. The specimens were kept in a freezer until further processing in order to prevent the snail bodies from decomposing. After the shells were broken, the operculum and shell were removed carefully and a small piece of foot (muscle) tissue was taken. These foot tissue samples (one sample consisting of foot tissue of one snail) were dried at 60 °C for >36 h after which they were ground into a fine powder using a mortar

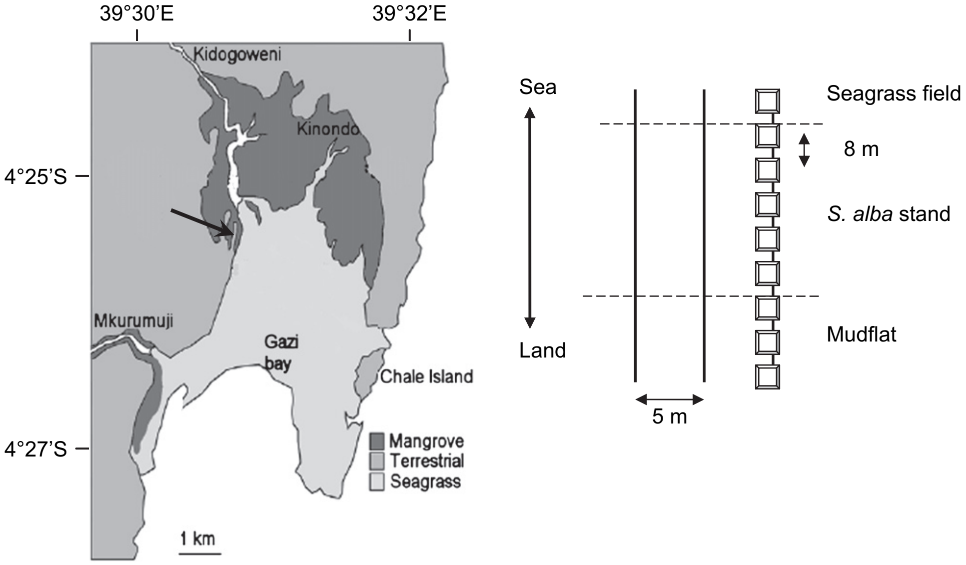

Fig. 1. Left: Map of Gazi Bay, Kenya. The location of the study site is indicated by a black arrow (dark grey area bordering the edge of the bay: *S. alba* forest, medium grey area to the left of the dark grey area: degraded *S. alba* forest). The extent of the seagrass meadows is shown by the lightest shade of grey. Right: Schematic representation of the three sampling transects traversing a mudflat, a *S. alba* stand and part of a seagrass field. The positions of the quadrats (here only shown along one transect) are represented as squares. Not according to scale.

and a pestle. Then sub-samples were taken, weighed (0.4–1.0 mg) into silver cups and treated with diluted (5%) hydrochloric acid until no further CO_2 bubbles were visible to remove carbonates. $\delta^{13}C$ analysis was performed using a mass spectrometer (PDZ Europa Hydra 20/20 Mass Spectrometer, Davis, California, USA) at the isotope analysis facility at the University of California, Davis. All stable isotope ratios were expressed relative to the conventional standard (VPDB limestone) as δ values, defined as:

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

where $X = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$.

2.3.2. Caging experiments

2.3.2.1. Experimental setup. In order to assess the (differential) impact of small and large snails on the sediment, we either enclosed or excluded gastropods of different sizes from experimental cages on the intertidal mudflat. These cages were constructed of a 10-cm high square steel frame (30 cm × 30 cm), in which a steel framework (height: 20 cm) was inserted. To this steel framework a plastic net with a mesh size of 1 mm was attached, covering both the sides and the top. The steel frame was pushed into the sediment, in order to prevent the cages from being washed away by the tide.

On the mudflat a clear difference was observed in the average shell length of *Terebralia palustris* snails between two sites at the same tidal level, approximately 80 m apart. At each site, six plots were identified in which *T. palustris* snails were relatively abundant. By using this experimental setup, we believed differences in organic matter input and output between plots would be minimal. First, all gastropods present in the experimental plots were removed. Then we placed snails in the odd numbered plots. Finally, a cage was placed in each of these plots, so cages with snails and cages without snails alternated. At the site characterized by a larger average shell length, 15 snails were put inside the cages. At the site dominated by smaller *T. palustris* individuals, 30 specimens were placed inside the cages. These numbers were chosen, as they were the maximum densities observed along the land–sea transects for small and big gastropods. The big gastropods (hereafter referred to as "adults") that were put in the cages had a shell length ranging between 41 and 80 mm, while the shell length of the small snails (hereafter referred to as "juveniles") varied between 25 and 47 mm. The experimental cages were set out at low tide for a total duration of 24 h. The experiment was first conducted at the site characterized by a smaller average shell length (hereafter referred to as "site 1"); the day after, the caging experiment was performed at the second location (hereafter referred to as "site 2").

Sediment samples were taken inside the cages at the beginning and at the end of the experiment. Each time the upper 0.5–1 cm was sampled using a small handcorer with a diameter of 12 mm. The sediment cores were analyzed for the concentration of photosynthetic pigments.

2.3.2.2. Pigment sampling and analysis. At each sampling occasion, three sediment cores were taken per cage for pigment concentration analysis. These were pooled together and wrapped in aluminium foil as photosynthetic pigments are highly sensitive to light. Subsequently, the samples were placed in a cooler box and transported to the field laboratory where they were stored in a freezer. The sediment samples were analyzed for the concentration of chlorophyll *a* (chl *a*), fucoxanthin and chl *a* degradation products (chlorophyllide *a*, pheophorbide *a* and pheophytin *a*) using a Gilson HPLC-chain according to a slightly modified method of Jeffrey et al. (1997).

2.4. Statistical procedures

Data on *Terebralia palustris* densities were tested for significant differences between the mudflat and the *Sonneratia alba* stand using a *t*-test or a non-parametric Mann–Whitney-*U* test. Quadrats containing no snails were excluded from all statistical analyses, as they were not located in *T. palustris* habitat (see Section 3.1). Total and juvenile densities were $\log_{10}$ transformed before analysis to comply with the normality assumption of a *t*-test. Numbers of adult gastropods were subjected to a Mann–Whitney-*U* test, as even after transformation the normality assumption was not met. Spearman's rank correlations were computed between adult, juvenile and total densities and the environmental variables. A *t*-test ($\log_{10}$ pH, temperature, $\log_{10}$ leaf litter, $\log_{10}$ organic content, humidity) or a Mann–Whitney-*U* test (salinity, percentage cover of pneumatophores and particle size) was applied to investigate differences in environmental factors between quadrats that contained *T. palustris* and quadrats that did not.

Comparison of the $\delta^{13}C$ values of gastropod size classes found in both habitats was done by means of a parametric *t*-test. In addition, a Spearman's rank correlation coefficient was calculated between shell length and carbon isotope values of the foot tissue of the snails.

Pigment concentration data were subjected to a three-way ANOVA with time (before and after caging), treatment (control cages and cages with *Terebralia palustris*) and site (site 1 and site 2) as factors. A differential impact of juvenile and adult *T. palustris* individuals was defined as a significant time × site × treatment interaction, whereas a significant time × treatment interaction was indicative of a general impact of the gastropods on pigment concentration. In the case of heterogeneous variances, pigment concentrations were square root transformed before analysis. Detailed comparison between groups was done by a Tukey's HSD test. Additionally, square root transformed pigment concentrations were subjected to a non-metric multidimensional scaling ordination (MDS) and an analysis of similarities (ANOSIM) using PRIMER 5.0 to test for possible time, treatment or site effects.

3. Results

3.1. Distribution of *T. palustris*

Terebralia palustris specimens were absent only from the three most seaward plots, located at the edge of the mangrove forest adjacent to the seagrass field and in the seagrass field itself. Clearly, these three quadrats were no longer part of *T. palustris* habitat and consequently they were excluded from further statistical analyses. Juveniles were significantly more abundant on the mudflat ($n = 117.2 \pm 27.8$) than in the *Sonneratia alba* stand ($n = 33.3 \pm 14.0$; *t*-test: $p < 0.05$), while there were significantly more adults inside ($n = 90.0 \pm 15.1$) compared to outside ($n = 14.8 \pm 8.9$) the mangrove forest (MWU: $p < 0.05$). The total number of *T. palustris* did not differ significantly between the mangrove forest ($n = 123.3 \pm 23.2$) and the open mudflat ($n = 132.0 \pm 28.8$; *t*-test: $p > 0.05$).

For quadrats containing *Terebralia palustris*, a significant difference was seen between the degraded and the natural *Sonneratia alba* site for pH, temperature, salinity, percentage cover of pneumatophores and leaf litter (*t*-test: $p_{\mathrm{pH}} < 0.001$, $p_{\mathrm{temperature}} < 0.05$; MWU: $p_{\mathrm{salinity}} < 0.05$, $p_{\mathrm{pneumatophores}} < 0.001$, $p_{\mathrm{leaf\ litter}} < 0.05$). An overview of the average values for the environmental variables measured in the quadrats is presented in Table 1.

Overall abundances of *Terebralia palustris* were not correlated with any of the environmental characteristics measured in the field. The number of juveniles was inversely correlated with salinity ($r = -0.58$, $p < 0.05$) and the percentage cover of pneumatophores ($r = -0.54$, $p < 0.05$). Adult densities were correlated with pH ($r = -0.61$, $p < 0.05$), salinity ($r = 0.72$, $p < 0.05$), temperature ($r = -0.49$, $p < 0.05$) and percentage cover of pneumatophores ($r = 0.75$, $p < 0.001$). None of the other recorded environmental variables seemed to be correlated with snail abundance.

We also checked for correlations between environmental conditions and snail numbers within each *Terebralia palustris* habitat (i.e. the mudflat and the *Sonneratia alba* stand with the exclusion of the seaward fringe) separately. No significant correlation was found between gastropod numbers inside the *S. alba* mangrove forest and any of the environmental variables. Total density of *T. palustris* residing on the mudflat, was correlated negatively with both salinity (Fig. 2c, $r = -0.71$, $p < 0.05$) and mud content (Fig. 2e, $r = -0.83$, $p < 0.05$). These two environmental factors were both inversely correlated with the number of juvenile gastropods (salinity: Fig. 2b, $r = -0.78$, $p < 0.05$, mud content: Fig. 2d, $r = -0.77$, $p < 0.05$). On the mudflat, salinity and mud content showed a significant correlation ($r = 0.77$, $p < 0.05$). As for adults, a positive correlation between the amount of leaf litter and density was observed on the mudflat (Fig. 2a, $r = 0.78$, $p < 0.05$). The gravel fraction (>1 mm) of the mangrove and mudflat sediment consisted mainly of detritus.

Table 1
Average (±SE) values for environmental variables recorded in quadrats with and without *T. palustris* snails. For the quadrats with snails, a distinction was made between the open mudflat and the *S. alba* forest. The number of quadrats (*n*) investigated in each site is indicated between brackets

	Quadrats with *T. palustris*		Quadrats without *T. palustris*
	Mudflat ($n = 9$)	*S. alba* forest ($n = 9$)	Seaward edge *S. alba* forest + seagrass field ($n = 9$)
pH	6.6 ± 0.2	5.4 ± 0.2	6.0 ± 0.3
Temperature (°C)	31.3 ± 0.1	30.8 ± 0.2	30.4 ± 0.3
Salinity	36.0 ± 0.2	37.7 ± 0.4	37.1 ± 0.2
Humidity (%)	60.1 ± 13.7	47.7 ± 12.6	29.9 ± 10.7
Pneumatophores (%)	0.3 ± 0.2	12.0 ± 1.0	8.3 ± 4.2
Leaf litter (%)	10.1 ± 4.3	1.1 ± 0.5	13.1 ± 4.6
Organic content (%)	3.3 ± 0.7	3.7 ± 1.2	3.6 ± 1.5
Median grain size (μm)	279.1 ± 13.9	267.7 ± 41.9	243.1 ± 8.4
Mud content (%)	14.0 ± 0.8	14.8 ± 2.0	21.9 ± 8.4

When comparing environmental variables between quadrats with snails and quadrats without snails, a significantly higher sediment temperature was observed in patches where *Terebralia palustris* was present (31.0 ± 0.1 °C, $n = 18$ vs 30.4 ± 0.3 °C, $n = 9$; *t*-test: $p < 0.05$).

3.2. Feeding habits of *T. palustris*

3.2.1. Stable isotope analysis

Carbon isotope values ranged between -17.07‰ and -21.82‰. Juvenile *Terebralia palustris* ($n = 13$, $\delta^{13}C$ ranged between -17.07‰ and -19.77‰) showed a greater variability in $\delta^{13}C$ compared to adults ($n = 14$, $\delta^{13}C$ ranged between -20.20‰ and -21.82‰). Juvenile snails found inside the mangrove forest were on the average characterized by a more depleted isotopic value compared to those residing on the mudflat. Adult gastropods inside and outside the *Sonneratia alba* stand had a more similar carbon isotope signature (Fig. 3).

It is believed that *Sonneratia alba* leaves and sediment are primary carbon sources available for *Terebralia palustris.* The sediment consists of an autochtonous (bacteria, microphytobenthos and mangrove leaf litter) and an allochtonous component (imported seagrass detritus and phytoplankton). Information on the stable isotope composition of these food items was obtained by consulting the literature.

Juveniles had an average $\delta^{13}C$ value of -18.29‰, whereas adults were characterized by an isotopic value of -20.82‰. By comparison, the mean carbon isotope signatures were -23.0‰ for surface sediments in a *Sonneratia alba* forest (Bouillon et al., 2004b), -14.3‰ for seagrass tissue, -19.9‰ for microphytobenthos (France, 1998), -27.0‰ for *S. alba* leaves (Rao et al., 1994; Bouillon et al., 2004b), -29.7‰ for bacteria (Bouillon et al., 2004a) and -21‰ for phytoplankton (Mook and Tan, 1991).

The $\delta^{13}C$ values of the foot tissue of the snails decreases with an increasing shell length, inside as well as outside the *Sonneratia alba* mangrove forest (Fig. 3, $r = -0.77$, $p < 0.001$). When the snails reach a size of 51 mm, the $\delta^{13}C$ value suddenly drops with 1.4‰. In the present study it was clear that the shell length differed significantly between the

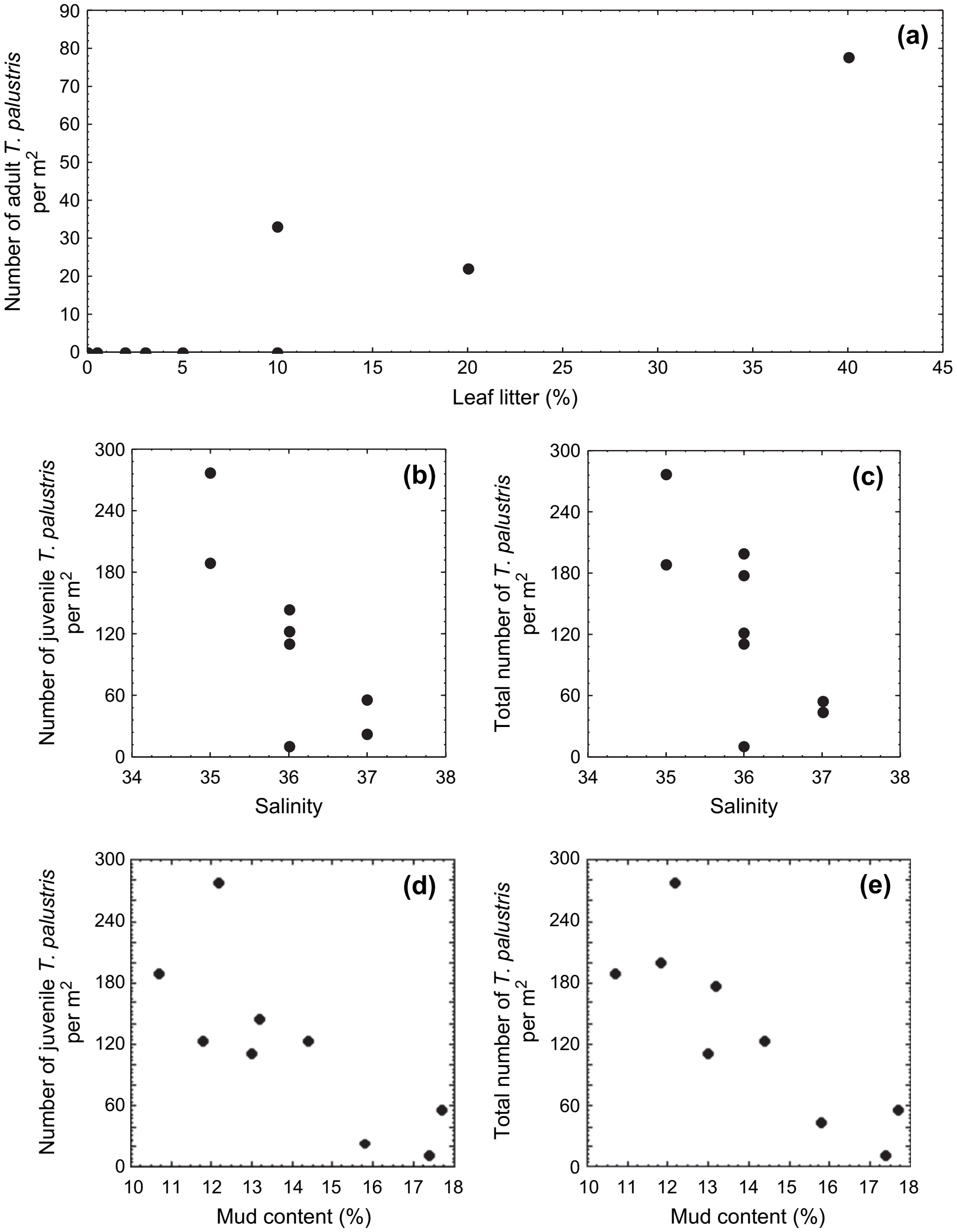

Fig. 2. Relationship between (a) number of adult *T. palustris* and leaf litter (b) number of juvenile *T. palustris* and salinity (c) total number of *T. palustris* and salinity (d) number of juvenile *T. palustris* and mud content and (e) total number of *T. palustris* and mud content, on the intertidal mudflat (analysis of nine quadrats).

mudflat and the mangrove forest (*t*-test: $p < 0.05$). The mudflat was characterized by a significantly smaller average shell length (as most of the gastropods present at this site were juvenile) than the mangrove forest (mainly inhabited by adult snails). Consequently, the observed relationship between the shell length and the $\delta^{13}C$ was considered for the two sites together.

When comparing $\delta^{13}C$ values of gastropods belonging to size classes collected in both sites (i.e. 30–40 mm, 40–50 mm, 50–60 mm), no significant difference was detected between the open mudflat and the *Sonneratia alba* forest (*t*-test: all *p*-values > 0.05).

3.2.2. Caging experiments

The concentration of fucoxanthin, chl *a*, chlorophyllide *a*, pheophytin *a* and pheophorbide *a* did not change significantly due to the grazing activities of the mudwhelks (three-way ANOVA, treatment × time: $p > 0.05$ for all pigments). Moreover, the magnitude of the impact of *Terebralia palustris* on pigment concentration did not differ between juvenile and adult specimens (three-way ANOVA, treatment × time × site: $p > 0.05$ for all pigments). Pheophytin *a* concentration differed significantly between sites (three-way ANOVA, site: $p < 0.001$). A post hoc Tukey HSD test showed significant differences in initial (i.e. before caging) pheophytin *a* concentrations

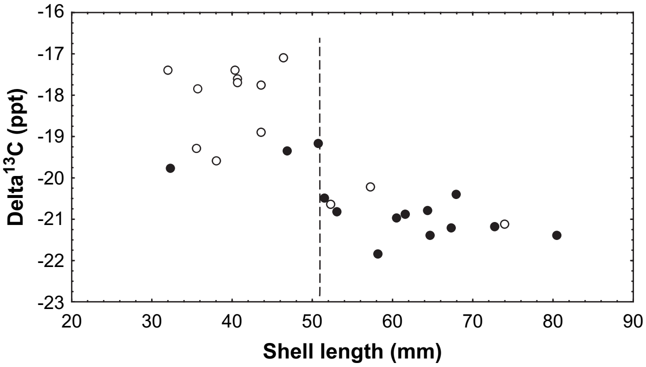

Fig. 3. Change in δ^{13}C of *T. palustris* foot muscle with increasing shell length. Animals were collected on the open mudflat (○) and inside the *S. alba* mangrove forest (●).

between the two experimental locations (Table 2, $p < 0.05$). When subjecting the pigment concentration data to a MDS ordination, a significant site effect became apparent (Fig. 4, ANOSIM, site: $R = 0.25$, $p < 0.05$). As can be seen from Fig. 4, one of the sediment samples, retrieved from an enclosure cage at site 2 before caging, differed substantially from the rest of the sediment surface samples in the composition of photosynthetic pigments. Pheophytin *a* (33.3%) and pheophorbide *a* (21.6%) were responsible for the observed contrast in pigment concentration between the experimental locations. There was no indication of a time or treatment effect.

Fucoxanthin and chl *a* concentration showed an increasing (although not statistically significant) trend in the absence and a decreasing trend in the presence of *Terebralia palustris* snails. However, at the second experimental location, chl *a* concentration tended to increase inside enclosure cages. All of the degradation products of chl *a* had a higher concentration at the end of the experiment in cages with gastropods enclosed. The amount of pheophorbide *a* either increased (site 1) or remained the same (site 2) in the presence of *T. palustris*. On the other hand, we also noticed an increase in pheophorbide *a* concentration after excluding the gastropods at the second experimental location. An overview of the concentration of photosynthetic pigments in the sediment surface layer is given in Table 2.

Table 2
Average (±SE) concentration of photosynthetic pigments (μg/g DW) encountered in the sediment surface layer in control cages and cages with *T. palustris* at site 1 and site 2 on the intertidal mudflat

	Control cages ($n = 3$)		Cages with *T. palustris* ($n = 3$)	
	Before caging	After caging	Before caging	After caging
Site 1				
Fucoxanthin	0.584 ± 0.049	0.838 ± 0.199	0.874 ± 0.155	0.559 ± 0.096
Chlorophyll *a*	1.438 ± 0.150	2.013 ± 0.297	2.083 ± 0.188	1.637 ± 0.286
Phyllide *a*	0.004 ± 0.0006	0.006 ± 0.0007	0.006 ± 0.002	0.008 ± 0.002
Pheophytin *a*	0.070 ± 0.014	0.089 ± 0.015	0.075 ± 0.013	0.064 ± 0.012
Pheophorbide *a*	0.096 ± 0.030	0.105 ± 0.040	0.078 ± 0.021	0.123 ± 0.027
Site 2				
Fucoxanthin	0.556 ± 0.007	1.015 ± 0.226	1.167 ± 0.435	0.863 ± 0.293
Chlorophyll *a*	1.656 ± 0.145	2.735 ± 0.614	1.651 ± 0.651	2.479 ± 0.837
Phyllide *a*	0.004 ± 0.002	0.008 ± 0.004	0.012 ± 0.005	0.017 ± 0.012
Pheophytin *a*	0.191 ± 0.022	0.239 ± 0.045	0.233 ± 0.075	0.193 ± 0.051
Pheophorbide *a*	0.053 ± 0.001	0.130 ± 0.049	0.201 ± 0.119	0.191 ± 0.096

Grain size analysis of the sediment inside experimental cages pointed out that site 1 has a median particle size of 479.2 μm (medium sand) and a mud content of 8.0%, while site 2 has a median particle size of 247.5 μm (fine sand) and a mud content of 16.8%.

4. Discussion

4.1. Distribution of *T. palustris*

The spatial segregation between juveniles and adults previously reported for a *Ceriops tagal* stand in Gazi Bay (Slim et al., 1997) and a mixed mangrove forest dominated by *Avicennia marina* and *Rhizophora stylosa* in Western Australia (Wells, 1980) was also observed for the *Sonneratia alba* forest at Gazi Bay. Juvenile *Terebralia palustris* were more common on the open mudflat, while adults tended to reside inside the mangrove forest. It has been pointed out that this migratory behaviour between open mudflats and mangrove forests could be related to a change in diet (Houbrick, 1991). Juveniles are assumed to be detrivorous (Nishihira, 1983; Fratini et al., 2004) or deposit-feeders (Slim et al., 1997), while adults have been reported to graze on mangrove leaves, propagules and fruits (Nishihira, 1983; Houbrick, 1991; Slim et al., 1997; Dahdouh-Guebas et al., 1998; Fratini et al., 2004).

All of the correlations between gastropod density and environmental characteristics that turned out to be significant seemed to be a direct consequence of the differential habitat selection of juveniles and adults. Environmental factors differing significantly between the mudflat and the mangrove stand were often correlated with *Terebralia palustris* density.

The observation of a lower salinity on the intertidal mudflat compared to the *Sonneratia alba* stand was unexpected, as one would assume the evapotranspiration rate is higher at this site due a total absence of vegetation, which in turn leads to higher temperatures and wind speed. A possible explanation for the lower salinity on the mudflat could be the seeping through of fresh groundwater.

As the correlations mentioned above were merely the result of a size-related habitat choice, we also considered the distribution of *Terebralia palustris* within each habitat (i.e. the mudflat and the *Sonneratia alba* stand with the exclusion of the seaward fringe) separately. On the intertidal mudflat salinity and mud content were correlated negatively with the total number of gastropods as well as with the number of juveniles. Sediment patches with a higher mud content were also characterized by saltier water in intertidal pools. It is possible that juvenile snails avoid muddier sediment because of the higher salinity as marine molluscs are known to be sensitive to salinity (Fenchel 1975 in Crowe and McMahon, 1997). The opposite, juvenile snails avoiding saline patches due to the higher mud content, may also be true. Rambabu et al. (1987) reported a preference of *T. palustris* for muddy substrates, which is not

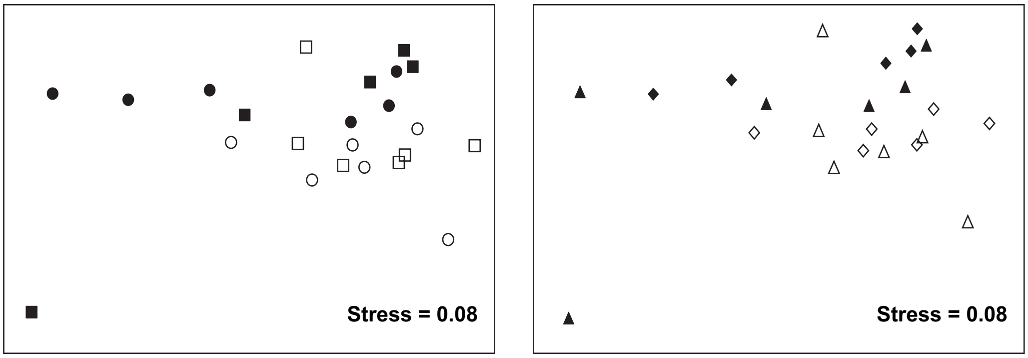

Fig. 4. Non-metric multidimensional scaling ordination of pigment concentrations of the sediment surface inside the experimental cages at the intertidal mudflat. Left: samples taken before (□) and after (○) caging at site 1, and samples taken before (■) and after (●) caging at site 2. Right: samples taken inside cages without (△) and with (◇) *T. palustris* at site 1, and samples taken inside cages without (▲) and with (◆) *T. palustris* at site 2.

necessarily in contrast with our findings. It could be that the muddier sediment patches attract more juveniles and therefore exhibit a faster decline in their fine (<63 μm) fraction. Kanaya et al. (2005) demonstrated a reduction in the silt-clay content due to surface-deposit feeding. An alternative explanation for the negative association between mud content and juvenile densities may be that muddier substrates contain less food sources. On the open mudflat two locations were identified that differed in the number of juvenile gastropods. The site that harboured fewer juveniles exhibited a higher mud content and a slightly lower chl *a* concentration. Chl *a* concentration is widely used as an estimator of the biomass of benthic microalgae, a potential food source for juvenile gastropods. Our findings agree with Cahoon et al. (1999) and Cahoon and Safi (2002) who demonstrated a negative relationship between the proportion of fine sediments and benthic microalgal biomass. Adult gastropods dwelling on the mudflat were found to be more abundant in patches with a higher amount of leaf litter. Adult *T. palustris* are assumed to feed primarily on mangrove leaves (Nishihira, 1983; Houbrick, 1991; Slim et al., 1997; Fratini et al., 2004). When quantifying leaf litter, no distinction was made between intact and fragmented mangrove leaves. May be the few quadrats, investigated on the open mud, which contained adults were also covered by one or more intact leaves. The lower amount of leaf material inside the forest might be attributed to higher grazing pressure or export of leaf material either by the retreating water to the seagrass field or by the onshore wind to the mudflat. Neither grain size, organic content nor humidity appeared to be related to the number of mudwhelks, contrary to what was found in other studies (Wells, 1980; Rambabu et al., 1987; Crowe, 1997; Crowe and McMahon, 1997; Fratini et al., 2004).

When comparing patches that harboured gastropods and those that did not in terms of environmental conditions, a significantly higher sediment temperature was found in the presence of *Terebralia palustris*. This was mostly due to the significantly higher sediment temperature on the mudflat. It is most unlikely that the gastropods avoid the *Sonneratia alba* seaward fringe and the adjacent seagrass meadows because of the lower sediment temperature. It is possible that the absence of the snails from the seaward mangal fringe and the seagrass field is due to predation by *Scylla serrata* (Wells and Lalli, 2003).

At the second experimental location on the intertidal mudflat an unusually high accumulation of large *Terebralia palustris* individuals was observed. Due to the topographical setting, there was a high accretion of mangrove leaves and other organic material (personal observation), which might explain the attraction of adults to this location. The high abundance of adult *T. palustris* on this mudflat location seems to contradict the spatial segregation between juveniles and adults observed along the land–sea transects. However, it is possible that the habitat choice of the growth stages depends on factors which are not necessarily consistent throughout the habitat.

In the present study, a shell length of 5 cm was used to delineate the two age groups. This was done as in Mida, Kenya the size shift from the immature to the mature stage was observed to occur when this shell length was reached. However, the size class marking the transition between the juvenile and the adult stage probably varies throughout the geographic range of this species (Houbrick, 1991). The growth stages of *Terebralia palustris* can easily be distinguished on the basis of shell morphology as maturity is indicated by a thickening of the margins of the aperture, including the outer lip (Houbrick, 1991; Nishihira et al., 2002). Therefore it would have been more accurate to delineate age groups based on the morphology of the shell. However, since stable isotope analysis indicated a shift in diet composition at a shell length of 51 mm, most likely caused by an ontogenetic change in radular anatomy, we conclude that based on this shell size a truthful distinction had been made between juveniles and adults.

4.2. Feeding habits of *T. palustris*

4.2.1. Stable isotope analysis

Carbon stable isotope analysis of the foot tissue of *Terebralia palustris* snails of different size classes indicates a transition in food source when a shell length of 51 mm is attained. This is clearly in agreement with Slim et al. (1997), who reported a sharp decline in the δ^{13}C value of these gastropods in a *Ceriops tagal* stand when a size of about 50 mm was reached. This was believed to be consistent with a shift towards a leaf litter dominated diet. Juveniles are assumed to be either detrivores (Nishihira, 1983; Fratini et al., 2004) or deposit-feeders (Slim et al., 1997), while the diet of adults mainly consists of leaf litter (Nishihira, 1983; Houbrick, 1991; Fratini et al., 2004). The δ^{13}C value of sediment in a *Sonneratia alba* forest is −23.0‰ (Bouillon et al., 2004b), so *T. palustris* individuals smaller than 51 mm, with an average δ^{13}C value of −18.29‰, are still 4.69‰ enriched compared to their food source. As data on the carbon isotope signature of the mudflat sediment were unavailable, the isotopic value of mangrove sediment was used instead. We would expect the δ^{13}C value of the mudflat sediment to be less negative due to a lower amount of ^{13}C depleted mangrove detritus. Since the majority of the juveniles were collected on the mudflat, it would have been more accurate to compare their isotopic value with that of the mudflat sediment. In that case, the difference in stable carbon isotope value would have been smaller. The stable isotope ratios of the food ingested and its consumer are not necessarily consistent because isotope ratios are likely to depend on isotope fractionation during animal metabolism. However, δ^{13}C enrichments are generally about 1–2‰ with each trophic step (Peterson and Fry, 1987), so this can only partly account for the observed discrepancy. Another possible explanation for the large disparity between the isotope values of juvenile gastropods and the sediment which they feed upon could be that a considerable selective assimilation of specific particles is taking place following ingestion of the bulk organic matter. Hemminga et al. (1994) and Slim et al. (1996) have both documented the outwelling of organic particles from the seagrass zone into the adjacent mangrove forests. Because the *S. alba* site was submerged during high tide, organic matter of the surface soil could originate from several sources: litter of *S. alba* trees, seagrass detritus and phytoplankton imported from the aquatic environment, benthic microalgae growing on the surface and bacteria. The isotope signature of juvenile *T. palustris* is closest to that of benthic microalgae (−19.9‰), which implies that juvenile gastropods might be selecting for microphytobenthic particles. Microalgae have a higher nutritional value than mangrove tissue, as shown by a distinctly lower C:N ratio (Hemminga et al., 1994). This would also explain the higher densities on the mudflat, since microalgal biomass in the mangrove sediment is most probably lower due to the low light intensity under the dense canopy and inhibition by soluble tannins (Alongi and Sasekumar, 1992).

Adult *Terebralia palustris* were characterized by an average carbon isotope value of −20.82‰ which is still 6.2‰ enriched relative to their supposed main food source, namely *Sonneratia alba* leaves, with a δ^{13}C value of −27.0‰ (Bouillon et al., 2004b). The large difference in carbon isotope signature between adult snails and *S. alba* mangrove leaves suggests that other food sources contributed to their diet. Due to their high C:N ratios (Rao et al., 1994), mangrove leaves are unlikely to fulfil the nutritional requirements of the gastropods. Therefore one might wonder why adult *T. palustris* graze upon mangrove leaves as was observed by us and many other authors (Nishihira, 1983; Houbrick, 1991; Slim et al., 1997; Fratini et al., 2004). Sesarmid crabs, important consumers of mangrove leaf litter, have been suggested to enhance the nutritional quality of the substrate by first fragmenting leaves during feeding and ingestion followed by faecal production (Skov and Hartnoll, 2002). This kind of feeding behaviour might also be displayed by adult *T. palustris* snails. In support of this hypothesis, the stable carbon isotope ratio of adult snails resembled the carbon signal of the sediment more than that of the leaves of the resident mangrove. Fratini et al. (2004) found both leaf material (62.5%) and mud (37.5%) in the stomachs of adult *T. palustris*. On the other hand, it should be realized that the δ^{13}C value of an animal is not merely a reflection of its food source at the specific moment of sampling but to some extent also of its diet at a younger age, depending on the rates of tissue renewal.

It has been demonstrated that the relative importance of different food items for a certain species can vary by its location and that such difference in diet composition may be related to the relative availability of different potential food sources (Bouillon et al., 2004b; Doi et al., 2005). In the current study, it was found that juvenile snails inhabiting the mangrove forest were (although not statistically significant) slightly depleted in ^{13}C compared to those dwelling on the open mudflat. Since microalgal biomass inside the *Sonneratia alba* stand is lower due to the low light intensity and the presence of soluble tannins (Alongi and Sasekumar, 1992), it is possible that juveniles residing in the mangrove forest are still feeding on the microphytobenthos but that other parts of the organic matter, characterized by a more negative δ^{13}C value, now also contribute to their diet. Moreover, inorganic carbon depleted in ^{13}C is generated by the mineralization of mangrove detritus (Hemminga et al., 1994; France, 1998). Because of the assimilation of this inorganic carbon, benthic microalgae present inside the mangrove forest might have a lower δ^{13}C value than those in areas with less mangrove detritus, such as the mudflat most probably is.

Juveniles exhibited a greater variability in carbon isotope value than adults. A possible explanation for this finding could be that the relative contribution of different carbon sources (i.e. microphytobenthos, seagrass material, phytoplankton, leaf litter, bacteria) to the organic matter of the soil surface, on which these juvenile snails were feeding, showed a greater spatial variation compared to the food items consumed by adult snails.

4.2.2. Caging experiments

4.2.2.1. General remarks. The main drawback of caging experiments is the potential risk of artefacts caused by the structure of the cage. Increased sedimentation, salinity and shading have been reported as possible artefacts (Virnstein, 1977; Hulberg and Oliver, 1980; Schrijvers et al., 1997). In the current study, increased sedimentation was suggested by the occurrence of darker sediment inside cages compared to the surrounding uncaged area. However, this should not have influenced the outcome of the present study dramatically, as the effects caused by the cage construction would have been the same for both treatments and both sites.

4.2.2.2. Pigment analysis. When Schrijvers et al. (1995, 1997) excluded the resident epibenthos, dominated by *Terebralia palustris*, from the mangrove sediment a highly significant increase in chl *a* and fucoxanthin concentration was observed. This augmentation in pigment concentration was also demonstrated after excluding the intertidal gastropod *Bembicium auratum* (Branch and Branch, 1980) and the mud snail *Ilyanassa obsoleta* (Nichols and Robertson, 1979). These changes were in both cases attributed to a reduction in grazing pressure on the microphytobenthic community as effects on the concentration of chlorophyll *a* and fucoxanthin are correlated with changes in the biomass of benthic microalgae such as diatoms (Gerdol and Hughes, 1994).

In the present study, diatom biomass – as shown by chl *a* and fucoxanthin concentration – tended to increase in the absence and to decrease in the presence of juvenile gastropods. This observation and the higher amount of pheophorbide *a* measured inside enclosure cages at site 1, suggests that juvenile *Terebralia palustris* might have been grazing on benthic diatoms. Pheophorbide *a* has been used as a marker for intertidal microphytobenthos grazing (although criticized by Ford and Honeywill, 2002), with pheophorbide *a* concentrations being higher in grazed sediments (Cartaxana et al., 2003). Selective feeding of juvenile gastropods was also implied by the results of the carbon stable isotope analysis (see Section 4.2.1).

Adult gastropods also seemed to have an impact on diatom biomass, although the concentration of chl *a* did not decline inside enclosure cages set out at site 2. However, this might be due to the escape of gastropods from two cages. The decrease in the amount of pheophorbide *a* inside cages with adult snails enclosed, implies adults do not graze on benthic diatoms. Instead, adult *Terebralia palustris* may have impacted the diatoms through the destabilization of the sediment caused by their movement. On intertidal mudflats, benthic diatoms have been reported to develop cohesive mats in order to prevent resuspension (Decho, 2000). Adult *T. palustris* may have prevented the build-up of such biofilms inside enclosure cages due to the frequent and intense disturbance of the sediment surface.

The increase in chl *a* degradation products inside exclusion cages at both experimental sites, might be a direct consequence of the augmentation in algal biomass following exclusion of *Terebralia palustris*. After all, the presence of chl *a* degradation products may be the result of cell senescence or death. At site 2, we observed an increase in the amount of pheophorbide *a* in the absence of *T. palustris*. It is possible that the elevated pheophorbide *a* levels are due to the grazing of meiobenthos on benthic microalgae. According to Buffan-Dubau et al. (1996) meiofauna can produce pheophorbide *a* from microphytobenthos grazing.

The absence of a statistically significant impact on pigment concentration may be attributed to the short time scale applied in this experiment or the possibly high spatial variation in pigment concentration. Not until at least 50 days of caging Schrijvers et al. (1997) noticed a significantly higher microphytobenthic biomass in exclusion cages.

The higher pheophytin *a* concentration together with the presence of finer sediments and the higher organic content at site 2, imply a greater input of phytodetritus relative to site 1. Therefore, the changes in the quantity of chl *a* degradation pigments inside experimental cages at site 2 may not be entirely attributed to the presence or absence of *Terebralia palustris*.

5. Conclusions

The findings of the current research confirm a spatial and trophic segregation between adult and juvenile *Terebralia palustris*, previously observed in other mangroves and geographical locations, for a *Sonneratia alba* mangrove habitat in Gazi Bay, Kenya. Results of the carbon stable isotope analysis and the caging experiments both strongly infer juvenile snails feed selectively on microphytobenthic (diatom) particles. As for adults it was suggested that they, like sesarmid crabs, might be feeding upon sediment nutritionally enhanced by their own faecal deposition after the ingestion of mangrove leaf litter. The diet of the two age groups did not appear to depend upon habitat.

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