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RESEARCH ARTICLE

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Terebralia palustris (Gastropoda; Potamididae) in a Kenyan mangal: size structure, distribution and impact on the consumption of leaf litter

Abstract Although the role of macroinvertebrates in the nutrient cycling of the Indo-Pacific mangrove ecosystems is now a paradigm of ecological research, most of the research and scientific assumptions deal with decapod crustaceans alone. However, decapods are not the only representatives of mangrove macrobenthos and in certain mangals they are surely outnumbered by gastropods, especially by potamidids of the genus *Terebralia*. This paper aims at bridging the gap in the knowledge of the ecological role of the largest and most abundant potamidid species of the Indo-Pacific mangals, the semiterrestrial *T. palustris*. In particular we studied size structure and distribution in relation to micro-environmental factors and feeding ecology, both in terms of diet composition and grazing rate, of two populations of this gastropod colonising a Kenyan mangrove creek. In contrast to what has been described by various authors concerning other mangals, in our study site juveniles and adults of *T. palustris* were present throughout the whole forest, from the landward belt to the seaward fringe, locally reaching very high densities at various levels. Both life stages showed a preference for patches characterised by soil with high organic content; thus the habitat of juveniles largely overlapped with that of the adults, although they are known to occupy different ecological niches. Indeed, gut-content analysis confirmed that juveniles are detritivorous and adults are mainly leaf-litter consumers. In situ experiments on the grazing activity of the adult snails showed that, in contrast to the litter-consuming crabs, they feed in every light and tidal condition, for an hourly consumption rate of ∼0.65 g per snail. Considering an average density of about 10.5 adults m^{-2}, it is estimated that a total of 10.5 leaves m^{-2} are removed by adult snails in each tidal cycle (i.e. about every 6 h). *T. palustris* is the only leaf consumer capable of searching for food under water during high tide and is responsible for the removal of a great quantity of mangrove litter. The results of the present study strongly suggest that *T. palustris* plays a major role in the food web, mangrove litter degradation and nutrient cycling of the Kenyan mangal.

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Introduction

The crucial role of marine invertebrates in the food web, nutrient cycling and overall energy flux of Indo-Pacific mangrove ecosystems is now a standard paradigm of ecological research on these tidal forests (see Kathiresan and Bingham 2001 for a review). However, most of the studies of the role of mangrove invertebrates in nutrient cycling have dealt with crustaceans, mostly sesarmid crabs and juvenile penaeid shrimps (Twilley et al. 1997; Newell et al. 1995). Crabs abundant on the mangrove floor feed on mangrove litter, while shrimps in shallow waters feed on mangrove detritus. This bias towards decapod crustaceans led to the current assumption that leaf-litter processing and detritus consumption are carried out mostly by these invertebrates (Kathiresan and Bingham 2001).

Although decapods indubitably play a fundamental role in the mangrove food web, other litter-consuming invertebrates, such as the specific mangrove potamidid species of the genus *Terebralia* Swainson, are scarcely taken into account. In particular, the contribution to nutrient cycling of *T. palustris* (Linnaeus 1758), the most widespread of the three species belonging to the genus,

has been probably underestimated. Indeed, this giant potamidid snail, which can reach up to 16 cm in shell length, should be regarded as one of the major constituents of the Indo-Pacific mangal invertebrate fauna, in terms of biomass and of ecological impact.

T. palustris, locally known as mud creeper or mud whelk, is almost ubiquitous in the Indo-Pacific, being common on the substrate of both the landward fringe and the seaward belt, from the forests of East Africa to those of New Caledonia (Plaziat 1984; Houbrick 1991). Its density on the substrate is often elevated, if not impressive, averaging 150 adults m^{-2} and reaching an astonishing 475 juveniles m^{-2} in New Caledonia (Plaziat 1984), but the abiotic constraints that shape its distribution within the mangal are not yet completely understood. In fact, although *T. palustris* is a truly amphibious species, capable of searching for food during both low and high tides (Houbrick 1991; Fratini et al. 2000, 2001), it seems to avoid the driest landward belt and the most exposed patch of the seaward zones, clustering on the typically fine substrata of the most shaded patches and in small tidal pools formed in between the aerial roots (Plaziat 1984; Houbrick 1991; Slim et al. 1997). Juveniles are reported to spatially segregate from adults, mainly colonising the small creeks and large pools on the seaward front of the forests (Plaziat 1984; Houbrick 1991; Slim et al. 1997) and are thought to migrate into the landward belts after reaching the adult stage. Segregation of juveniles from adults was also demonstrated from a trophic point of view, since their maturity is associated with a structural change in the radula, from detritus-eating juveniles to adults capable of grazing plant materials, such as leaf litter, mangrove propagules and fruits (Houbrick 1991; Slim et al. 1997).

Hence, adults of *T. palustris* rely on leaf litter and propagules and overlap and compete, in space and diet, with sesarmid crabs, but the fastest and supposedly more reactive crabs do not always win this race. In fact, in two different Kenyan mangals, Slim et al. (1997), Dahdouh-Guebas et al. (1998) and Fratini et al. (2000, 2001) showed that these mud creepers can be the main responsible in the removal of leaf litter and propagules in belts where a few crabs are present and, moreover, they can still easily reach and consume these resources, clustering on a single fallen leaf, even in patches where the density of litter-consuming crabs is high. Other than the data of Slim et al. (1997), only Nishihira (1983) provided an estimate of *T. palustris* food consumption in Okinawan mangal; thus, in spite of its importance in terms of abundance and biomass, the role of *T. palustris* in the mangrove food web has rarely been investigated.

The present study was aimed at assessing population structure, distribution and feeding habits of *T. palustris* in a Kenyan mangal, in order to estimate adequately the contribution of this snail to mangrove trophic web.

Materials and methods

Study site

This study was performed at Mida Creek (03°21′S, 39°59′E), about 20 km south of Malindi, Kenya (Fig. 1), in March and April 1999. Two sites, Mida and Dabaso, were specifically chosen for the surveys within the large mangrove area. Mida is a mature forest with an approximately 120 m wide landward fringe (sensu Macnae 1968) dominated by *Avicennia marina*, degrading towards land in a bare sandy area dominated by saltworts, and a roughly 100 m wide *Rhizophora* forest (sensu Macnae 1968), largely dominated by *R. mucronata*, with a few *Ceriops tagal* trees.

On the other hand, Dabaso is quite different from Mida. It is a less extensive, more muddy area and is characterised by a very narrow *A. marina* belt, about 10 m wide, and a 250 m wide *Rhizophora* forest, largely dominated by *R. mucronata*, and in which *C. tagal* forms a sort of secondary canopy layer.

Size structure and soil analysis

A sea–land transect was defined at each site, and 14 and 13 1 m by 1 m quadrats, in Dabaso and Mida, respectively, were chosen every 20 m along the transect. After being collected, the shell length of the snails present in these quadrats was measured using a calliper (precision 10 μm); they were also divided into two classes, adult and juvenile. Adults were easily distinguishable from the immature specimens by the presence of the thickened lips near the shell operculum (Houbrick 1991). In the quadrats along both transects in the *Rhizophora* forests, snails found eating mangrove leaves were also noted.
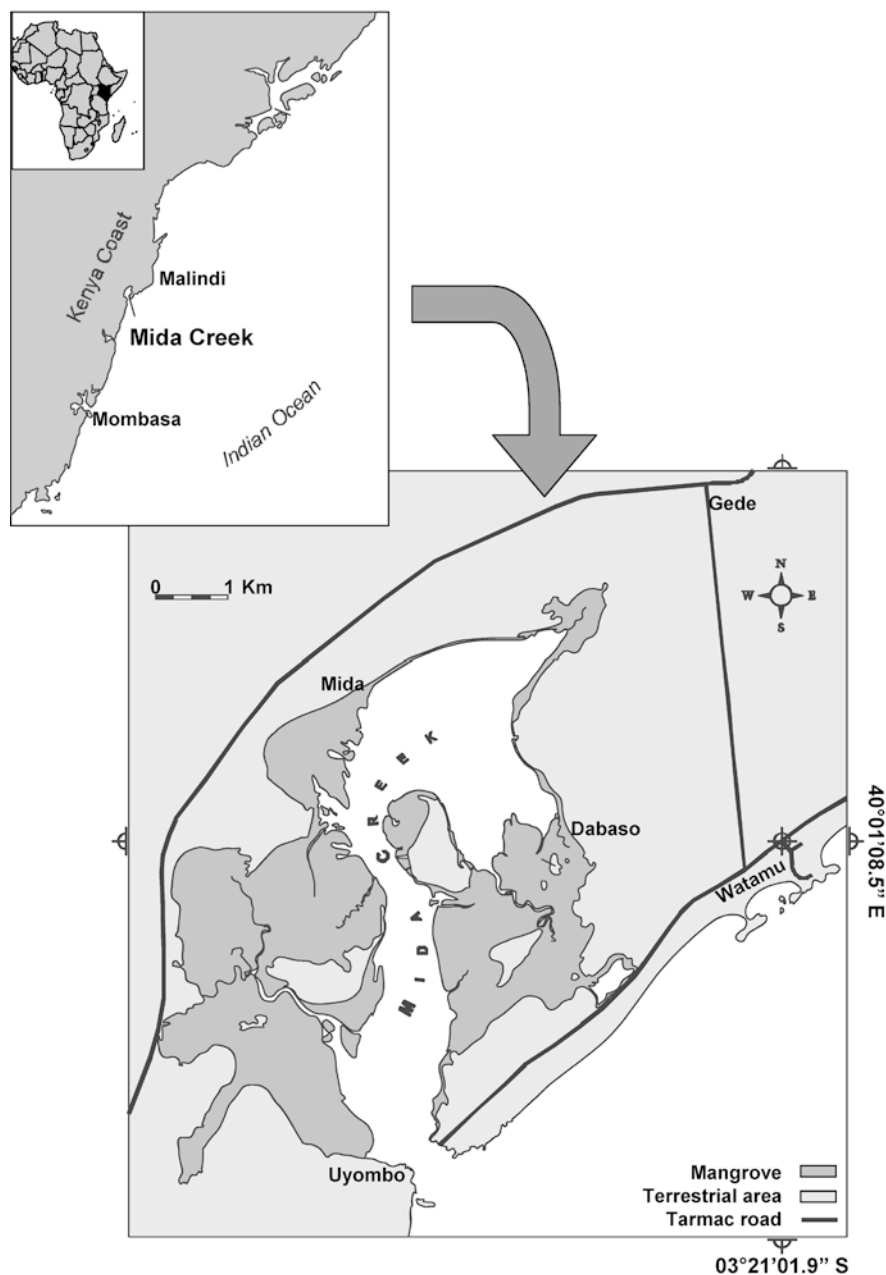
In addition to sampling *T. palustris*, we also measured some environmental factors that are known to affect the presence and the distribution of this mud creeper, as reported by Wells (1980), Rambabu et al. (1987) and Crowe (1997). Organic content, expressed as a percentage of the total dry-soil weight, and grain-size analysis performed on the basis of the median phi parameter, were conducted in laboratory on five cores of soil collected at the four corners and at the centre of 4 m by 4 m quadrats surrounding the snail collection quadrats, using standard techniques. Additionally, soil was scraped from the surface of the same five cores, and salinity and pH were measured by means of a portable conductivity-meter and pH-meter, respectively. The height above chart datum of every plot was assessed and converted into total immersion time (in hours per day) using standard tide tables. The canopy coverage of mangrove trees was determined by taking a picture at the centre of each sampling plot using a 32-mm lens. These photographs were analysed in order to estimate the portion of the sky sheltered by the tree canopy, using image-analysis software (SigmaScan/Image).

Stomach-content analysis

In the *Rhizophora* forest of Dabaso, 102 juveniles and 86 adults were captured in every kind of light and tide conditions and, after breaking their shell, we removed their stomachs and immediately immersed them, individually, in 75% ethanol. At the same time, six surface-soil samples were also taken at the same sites. Sampling was carried out around spring tide, i.e. during the 5 days surrounding the second day from the full/new moon, which is the monthly activity peak of *T. palustris* in Kenya (Slim et al. 1997; Fratini et al. 2000).

For each month, stomach content was examined using the following procedure. The first step consisted of a visual estimate of stomach fullness, scoring it from 0 to 4, i.e. about 0%, 25%, 50%, 75% and 100% of total fullness. The stomach was then opened, its content washed with alcohol into a Petri dish and examined and identified under a binocular microscope. A qualitative analysis was performed calculating the percentage points of each food item (PP,

Fig. 1 Location and schematic map of the Mida Creek area. The distribution of the mangrove forest and the position of the two study sites, Mida and Dabaso, are shown

Gede

0 —— 1 Km

Mida

C R E E K

Dabaso

M I D A

Watamu

Uyombo

Mangrove
Terrestrial area
Tarmac road

40°01'08.5" E

03°21'01.9" S

corresponding to the percentage content of each food category; this was calculated assigning a value from 0 to 100 to each food category and then weighting this value according to the total stomach fullness), as described by Wear and Haddon (1987).

Soil samples were observed under a binocular microscope and the percentage of recognisable leaf-litter residuals was estimated.

Two data sets, the stomach fullness and the PP of leaf litter in the food residues, were analysed by a full-factorial two–way ANOVA designed to test the influence of environmental conditions on the feeding habits of adult snails. Light and tide conditions were both considered fixed and orthogonal factors. The recorded data being score values, a non-parametric test should be used, but tests of this kind are not able to compute a multi-factor data matrix, with an unbalanced number of data in each matrix cell. Using ANOVA in this particular situation, the probability of β errors increases, but its power to reject α-type error is such that ANOVA is still to be preferred to weaker non-parametric tests.

Grazing rate

A total of 130 intact green leaves (i.e. freshly collected among the branches) and 120 senescent leaves (i.e. collected in the same way as the green leaves, but clearly yellow and ready to fall) of *R. mucronata* were placed on the ground at the beginning of each tide–light phase and left in place for the duration of the phase itself. The trials were performed around spring tide at the fringe of the *Rhizophora* forest of Dabaso, where the population of litter-feeding sesarmid crabs was minimal (Fratini et al. 2000).

The leaves had been previously marked with a red numbered tag tied to the petiole (Fig. 2) and the outline of each leaf had been traced on a transparency, allowing the successive use of a scanner and digital image-analysis software (Corel Photo-Paint 8) to estimate its surface area.

During the high-tide trials, leaves were fixed with a piece of iron wire in the muddy ground, so that they could not be transported by
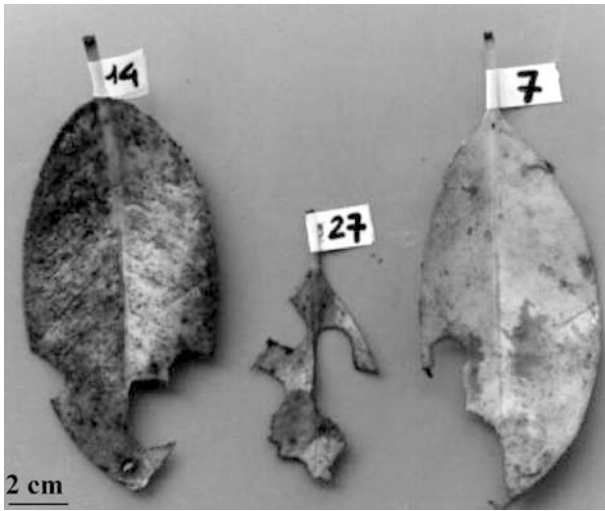
Fig. 2 *Terebralia palustris*. Fresh (nos. 14 and 27) and senescent (no. 7) leaves of *Rhizophora mucronata* grazed by snails

tidal currents. Particular attention was paid not to sever leaves, since snails were attracted by the odour released from broken ones, as demonstrated by Fratini et al. (2001).

At the end of each trial, marked leaves were collected and their outline was traced again on a transparency. The differences between the initial and the collected leaves were used to estimate the amount of leaf (expressed in square centimetres) ingested by *T. palustris* during that phase. For converting this estimation of leaf-litter consumption into grams, the wet weight of 14 fresh and 14 senescent intact leaves of *R. mucronata* was also measured. We were sure that snails had eaten the leaves, because the damage due to the radula was unmistakable: in fact, the mud creepers begin to graze the leaf margin, then they converge towards the inner part of the leaf (Fig. 2). Moreover, they do not generally eat the petiole and the midrib, in accordance with what Nishihira (1983) observed.

A full-factorial three-way ANOVA design, all factors fixed and orthogonal, on log-transformed data, was applied to investigate the influence of light and tide conditions on the percentage of fresh and senescent grazed leaves.

Results

Size structure and soil analysis

T. palustris specimens were absent only at the two most landward plots of the Mida landward fringe (Fig. 3), whereas juveniles and adults were present and abundant throughout the rest of both mangrove transects (Figs. 3 and 4). Shell length (SL) ranged from a minimum of 0.5 cm to a maximum of 13 cm. Both sites were characterised by a bimodal size distribution, but the corresponding maximum frequency peaks were out of phase (Fig. 5). In particular, we collected snails with SL<4cm (Fig. 5). The *G*-test revealed a significant difference between these two size distributions ($G = 640.7$, $df = 10$, $P < 0.001$; *G*-test). The size shift from the immature to the mature stage occurred at a shell length of about 5 cm in Mida and 6 cm in Dabaso (Fig. 5). Moreover, in both localities, the shell length-class marking the transition was completely absent (Fig. 5).
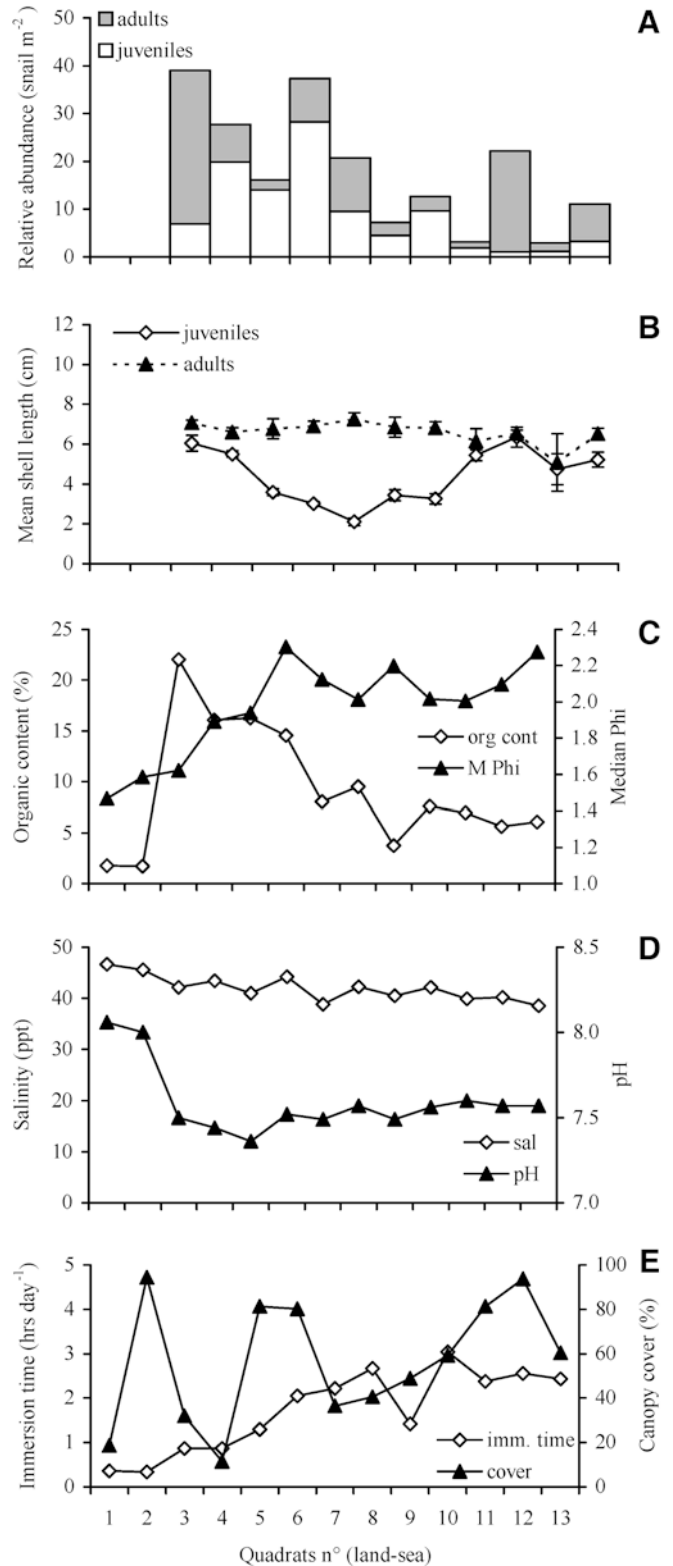

Fig. 3A–E *T. palustris*. Values within the 13 plots sampled at Mida of **A** abundance of adults and juveniles; **B** mean shell length of adults and juveniles; **C** organic content and grain size (expressed as median phi); **D** salinity and pH; **E** immersion time (expressed as hours per day) and canopy cover (%)
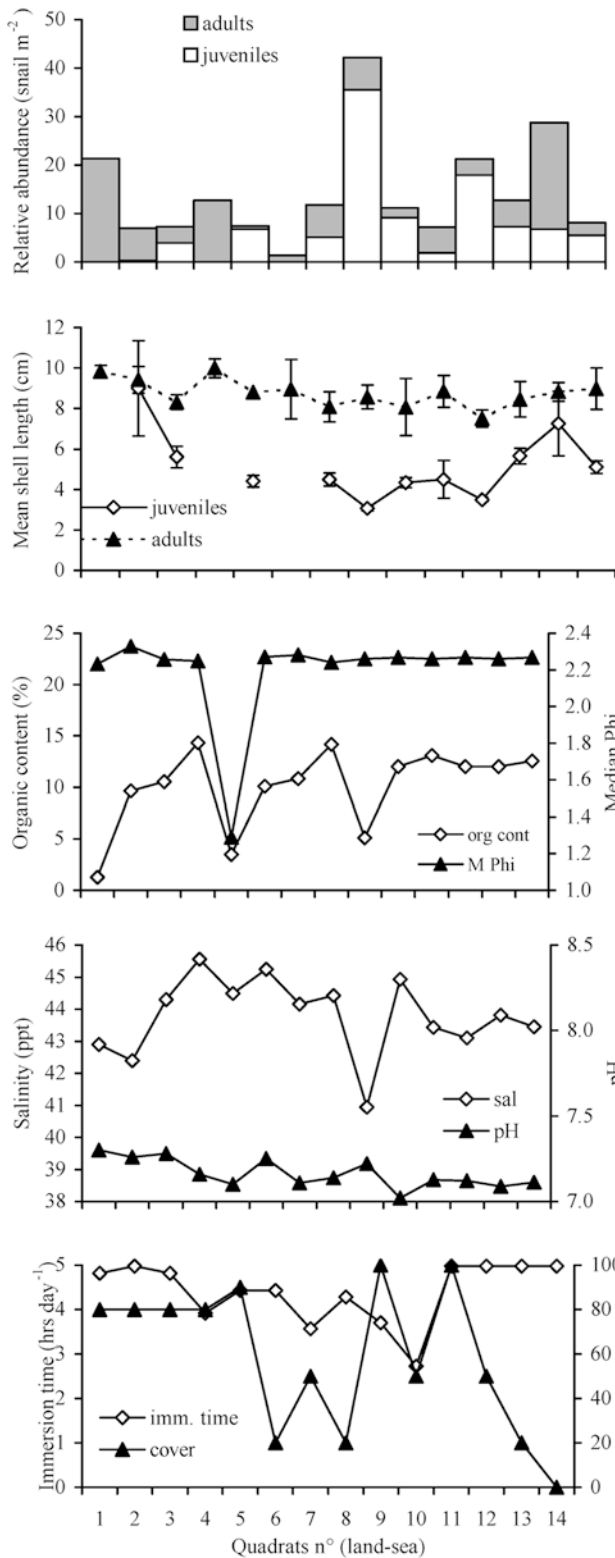
Fig. 4A–E *T. palustris.* Values within the 14 plots sampled at Dabaso of **A** abundance of adults and juveniles; **B** mean shell length of adults and juveniles; **C** organic content and grain size (expressed as median phi); **D** salinity and pH; **E** immersion time (expressed as hours per day) and canopy cover (%)

The average densities of adults and juveniles were greater in Mida (juveniles 210.8 ± 69.8 individuals m^{-2} and adults 25.9 ± 7.8 individuals m^{-2}) than in Dabaso (juveniles 50.1 ± 19.3 individuals m^{-2} and adults 10.9 ± 2.9 individuals m^{-2}), and juveniles were more abundant than adults in both localities.

The differences found in the *T. palustris* population structure between the two sites reflected important differences both in values and trends observed in abiotic factors (Figs. 3 and 4). In fact, although dominated by the same tree species, the Mida transect was higher on the chart datum than Dabaso, and its plots were, on average, characterised by significantly fewer hours of inundation per day (Mida 1.73 ± 0.48 h; Dabaso 4.40 ± 0.35 h; $t = 8.58$, $df = 25$, $P < 0.0001$; t-test) and by a coarser, more sandy, soil (median phi$_{Mida}$ $= 1.96 \pm 0.14$; median phi$_{Dabaso} = 2.19 \pm 0.13$; $t = 2.31$, $df = 25$, $P = 0.03$; t-test). Moreover, with only a few exceptions, the environmental parameters did not follow consistent trends moving from landward to seaward plots, as expected in such an intertidal habitat. As a result, only pH and grain size found at each plot were significantly related to the immersion time of the plot itself, i.e. showed a consistent ecotonal trend ($F = 34.0$, $n = 27$, $P < 0.0001$ and $F = 10.6$, $n = 27$, $P = 0.003$, respectively; F-test). On the contrary, the intricate and composite nature of the forest contributed to form a mosaic of microhabitats in which the values of the various abiotic factors were only weakly related to each other (Figs. 3 and 4). In this regard, it is not surprising to find also that juvenile and adult mud whelks are distributed along the transects with no consistent trend, and that they extensively overlapped each other except in the landward belt of Dabaso where only adults were present (Fig. 4). In particular, only soil organic content could be shown to positively affect the numbers of juveniles and adults present in the plots ($F = 7.1$, $n = 27$, $P < 0.01$ and $F = 4.6$, $n = 27$, $P < 0.04$, respectively; F-test; Fig. 6), whereas none of the other recorded parameters was related to snail presence and abundance.

With reference to the shell size of adults, for the two transects we found a positive correlation between both the values of salinity (Fig. 7A) and immersion time (Fig. 7C) and snail shell length, expressed as SL ($F = 16.0$, $n = 25$, $P = 0.0006$ and $F = 24.0$, $n = 25$, $P < 0.0001$, respectively; F-test). On the other hand, values of pH were negatively correlated with the size of adult snail ($F = 30.8$, $n = 25$, $P < 0.0001$; F-test; Fig. 7B).

Stomach-content analysis

Snails longer than 6 cm were found to brush actively on mangrove leaves: the few juveniles found on the leaves were simply crossing on them, as proved by the fact that they did not rest on the leaves. The size distribution of snails found on the leaves was significantly different from that of the individuals found on the mud ($G = 284.46$, $df = 10$, $P < 0.001$; G-test).

Fig. 5 *T. palustris*. Shell length–frequency distributions of juveniles and adults of the Mida and Dabaso mangrove forests
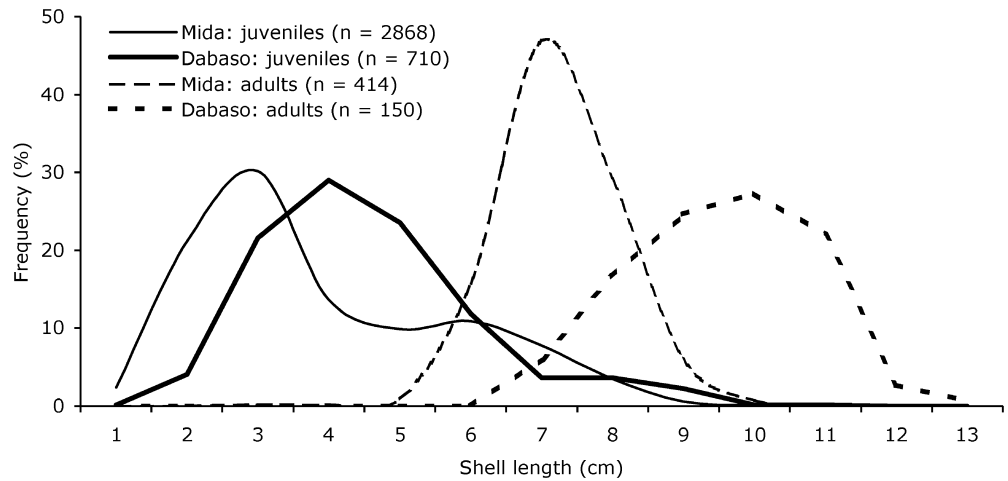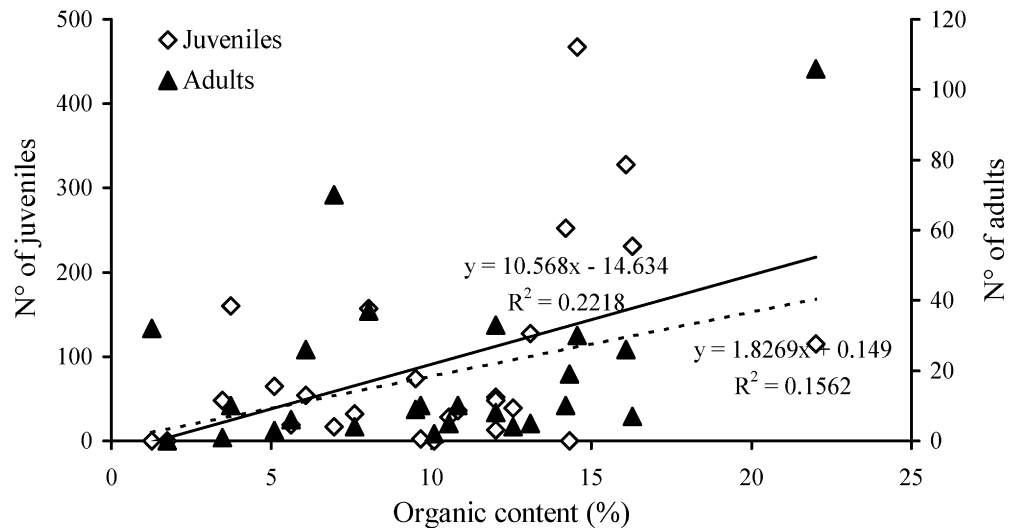

Fig. 6 *T. palustris*. Relationship between the numbers of juveniles and adults and the percentage organic content of the soil. Data for Mida and Dabaso were combined. The regression lines for adults (*dashed line*) and juveniles (*solid line*) are shown

Only a modest percentage of stomachs were found completely empty, both in juveniles (16%) and adults (7%).

Mangrove leaf litter was the main component of the natural diet of adult *T. palustris* (62.5%) and the only other item found in the stomach was mud (37.5%). On the other hand, mud was by far the main item in juveniles' stomachs, rising up to an average of 81%, while leaf litter represented only a residual 19%. Moreover, the percentage of litter debris found in the stomach of juveniles proved not to be significantly different from the litter-debris percentage, about 20%, of the mud collected at the location at which the specimens were captured ($G = 2.97$, $df = 1$, P not significant; G-test).

Two-way ANOVA revealed that adult snails have stomachs significantly more full at the end of the night and at the end of the high tide (Tables 1, 2). The interaction among these two factors was significant too: a subsequent analysis indicated that stomachs collected at the end of diurnal low tides were significantly emptier than those collected at the end of all the other light–tide combinations ($t = -5.16$, $P < 0.0001$; Contrast test).

The PP of mangrove leaves ingested by adult snails perfectly reflected the overall content pattern (Tables 3, 4): their presence was minimal in stomachs collected at the end of the diurnal low tide ($t = -6.77$, $P < 0.0001$; Contrast test).

Grazing rate

Eight of the 250 experimental leaves could not be collected at the end of the trials. Only 55% of the recovered leaves had been brushed and generally more snails were present on a leaf; thus, at the end of the trials in the experimental area, there were feeding clusters on a single leaf close to leaves completely ignored. Since the damage due to the radula is unmistakable (see Materials and methods), it was sure that the mud creepers had grazed the leaves.

Independently of the tide–light phase, more fresh leaves (59%) than senescent ones (28%) were left intact ($G = 21.24$, $df = 1$, $P < 0.001$; G-test), whereas pooling the data for fresh and senescent leaves, it is evident that
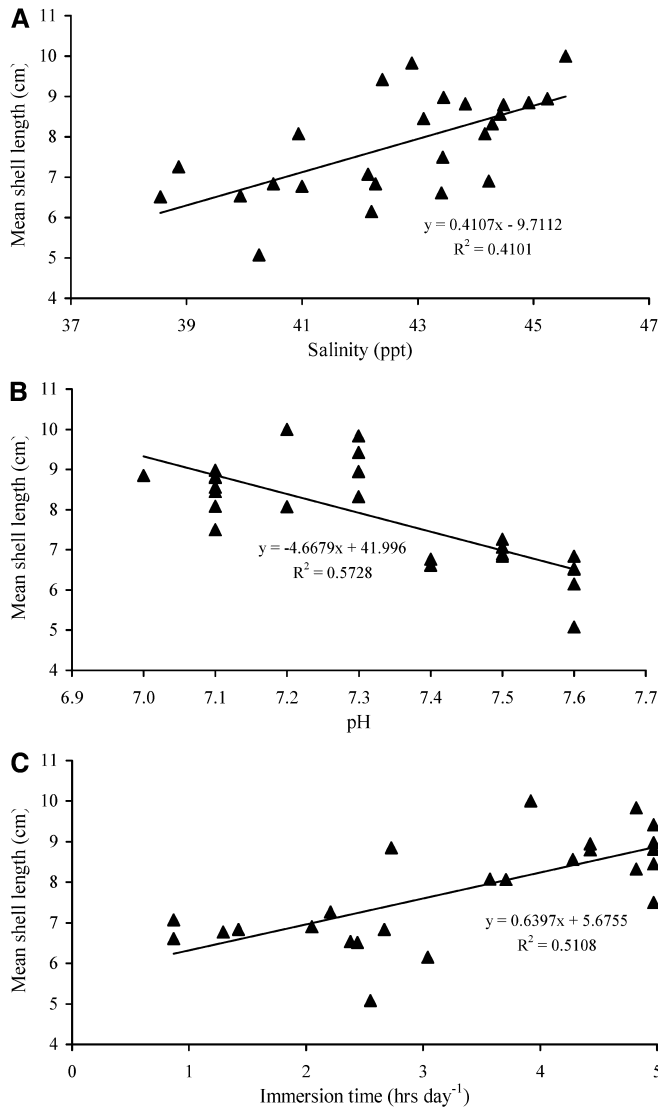
Fig. 7A–C *T. palustris*. Relationship between the average shell length of adults and the values of **A** salinity, **B** pH, and **C** immersion time. Data for Mida and Dabaso were combined. The equations of the regression lines and R^2 values are shown

Plot A: $y = 0.4107x - 9.7112$, $R^2 = 0.4101$
Plot B: $y = -4.6679x + 41.996$, $R^2 = 0.5728$
Plot C: $y = 0.6397x + 5.6755$, $R^2 = 0.5108$

Table 1 *Terebralia palustris*. Adult stomach fullness (expressed as average percentage) in each tide and light condition; n number of analysed stomachs; *SE* standard error of the mean

Stomach fullness (%)	Low tide	High tide	Day	Night
n	48	39	46	41
Average	56.77	76.92	56.52	76.22
SE	4.69	3.94	4.82	3.90

Table 2 *T. palustris*. Influence of tide and light on the total quantity of food ingested; *df* degrees of freedom, *SS* sum of squares, *F* ratio value, *P* level of probability. ANOVA two-factor analysis on non-transformed data

Source	df	SS	F	P
Tide (low/high)	1	8,375.61	10.53	0.002
Light (day/night)	1	7,563.04	9.48	0.003
Tide×light	1	3,106.56	4.54	0.03
Residual	83	60,830.99		

Table 3 *T. palustris*. Average quantity of mangrove leaves (calculated as *PP* percentage point) ingested by adults in each tide and light condition; n number of stomachs analysed

Leaves ingested	Low tide	High tide	Day	Night
n	43	37	40	40
PP	40.12	56.42	35.31	60.00
SE	5.83	5.30	6.09	4.67

Table 4 *T. palustris*. Influence of tide and light on the total quantity of leaves ingested; *df* degrees of freedom, *SS* sum of squares, *F* ratio value, *P* level of probability. ANOVA two-factor analysis on non-transformed data

Source	df	SS	F	P
Tide (low/high)	1	6,322.01	17.42	0.007
Light (day/night)	1	10,899.88	7.84	<0.001
Tide×light	1	22,848.56	29.15	<0.001
Residual	76	62,454.46		

snails encountered and brushed the greatest number of leaves at diurnal low tide ($G = 8.84$, $df = 3$, $P < 0.05$; G-test).

Total snail leaf grazing was higher during the day than during the night, whereas it was not influenced either by the tide phase or the leaf age (Tables 5, 6).

From the data on the amount of leaf grazed by the snails, we were able to conclude that, in a diurnal low water, about 2,600 cm², corresponding to about 46 entire leaves (leaf surface 56.5 ± 1.01 cm², $n = 250$), were consumed by 50 snails (i.e. the number of snails present on the marked leaves at the end of the diurnal low-tide trial); it is therefore suggested that every snail ate about one leaf for each low tide. Taking the weight of a single leaf to be 4 g (a fresh *R. mucronata* leaf is, on average, 4.03 ± 0.27 g, $n = 14$, and that of a senescent one is 4.58 ± 0.43 g, $n = 14$), this value corresponds to a consumption rate of about 0.65 g per snail per hour, a higher value than that recorded by Nishihira (1983) for *T. palustris* in the Okinawan mangal (about 0.15 g per snail per hour).

Taking into account the fact that the density of adult snail in the *R. mucronata* zone at Dabaso was about 10.5 adults m⁻², 10.5 leaves m⁻² could be consumed by the mud creepers during a single low tide. Since the daily *R. mucronata* production in another Kenyan mangrove was about two leaves m⁻² (Slim et al. 1996), even if the leaf production at our study site was probably higher, since the trees are taller (Dahdouh-Guebas et al. 2002), we may say that mud creepers play a significant role in leaf-litter consumption in mangrove forests.

Table 5 *T. palustris*. Average quantity of senescent and green mangrove leaves grazed by adults in each tide and light condition; *n* number of non-intact leaves

Leaves ingested	Low tide	High tide	Day	Night
Fresh leaves				
n	30	21	25	26
Mean	20.22	15.11	24.49	11.98
SE	3.61	3.63	4.31	2.50
Senescent leaves				
n	43	42	49	36
Mean	18.43	14.49	22.97	7.66
SE	2.74	2.71	2.87	1.36

Table 6 *T. palustris*. Influence of tide and light on the quantity of fresh and senescent leaves grazed. *df* degrees of freedom, *SS* sum of squares, *F* ratio value, *P* level of probability, ANOVA three-factor analysis on log-transformed data

Source	df	SS	F	P
Tide (low/high)	1	0.72	3.35	0.07
Light (day/night)	1	2.74	12.75	<0.001
Leaf type (fresh/senescent)	1	0.15	0.70	0.40
Tide×light	1	0.20	0.93	0.34
Tide×type	1	0.06	0.27	0.61
Light×type	1	0.39	1.81	0.18
Light×tide×type	1	0.14	0.67	0.41
Residual	128	27.54		

Discussion and conclusions

In Mida Creek, *T. palustris* occupies a wide area inside the mangrove forest and farther seaward. In fact, it is present from the landward belt, with the exception of the levels submerged about 3 days per month, to the mud flats that emerge at spring low tide, maintaining high densities in the *Avicennia*- and the *Rhizophora*-dominated forests. The spatial segregation between juveniles (more common in tidal channels and pools) and adults (common in the forest) reported by various authors for Jakarta Bay (Soemodihardjo and Kastoro 1977), New Caledonia (Plaziat 1984), Western Australia (Wells 1980) and Gazi Bay, Kenya (Slim et al. 1997), was not observed in Mida Creek. Individuals belonging to both life stages were not only dwelling together in the experimental plots at all tidal levels, with the sole exception of the uppermost part of Dabaso, where only adults were present, but they were also common under the canopy of mangrove trees and in the open intertidal flats, as well as in the tidal channels and pools (Fratini, personal observation).

T. palustris at the study site can attain a big shell size. In Dabaso we found individuals up to 13 cm long, whereas in Mida the population had a smaller shell length (11 cm). Moreover, in Mida, the snail size–frequency distribution is out of phase relative to that for Dabaso in respect of the peaks of maximum frequency both of adults and juveniles.

In our opinion, the differences in population structure between Mida and Dabaso are linked to the different environmental characteristics along the two transects. Indeed, both the *Avicennia*- and the *Rhizophora*-dominated belts of Mida were higher on the chart datum than that of the *Rhizophora*-dominated Dabaso forest; this determines harsher environmental conditions in Mida, with a smaller degree of flooding per day, a coarser sediment with, on average, a lower content of organic matter, and fewer tall trees providing the mud creepers with less leaf litter than that available in Dabaso. Our data are therefore in agreement with the conclusions reported by Nishihira et al. (2002) for two *T. palustris* populations of Okinawa. These authors found great differences in dimension and structure between two populations colonising neighbouring habitats; a mature forest dominated by *Rhizophora stylosa*, where the molluscs were on average larger, and a recently colonised forest dominated by dwarf trees of *Avicennia marina*, where the population was composed of significantly smaller specimens. Nishihira et al. (2002) explained these size differences in terms of nutrient availability between the two sites, whereas in our case lower availability of water and the generally harsher conditions in Mida can also play a role in determining the differences in the dimensional pattern between the two transects. However, on both transects, the general environmental conditions cannot be considered really limiting for *T. palustris*, since the densities recorded were both higher than the one recorded by Slim et al. (1997) in Gazi Bay, another mangrove forest of the Kenya coast.

Moreover, if it is true that Mida can be considered a harsher environment than Dabaso, it is difficult to explain why the density of juveniles and of adults in the Mida transect are much greater than the corresponding densities recorded in Dabaso. Possible explanations are the currents in the Mida Creek, which can carry larvae mostly towards the Mida forest, and the relative position of the two sites: Mida is close to the entrance of the creek and therefore reached by both neap and spring tides; in contrast, Dabaso is more internal and protected and, for this reason, rarely touched by the internal currents of the creek.

In contrast to what was found by Wells (1980), Crowe (1997) and Crowe and McMahon (1997), the distribution of adult and young *T. palustris* in Mida Creek was not related to the percentage cover of mangrove canopy, but to the organic content of the soil. Although only juveniles directly depend on the soil to feed, and so should be more attracted to patches richer in organic content, the presence of higher densities of adults on the same patches can be explained by the relation of organic content to the amount of leaf litter, which we did not assess, because there was no real accumulation of litter on the bare soil of Mida Creek. Plots with higher organic content are likely to be the ones in which litter production is higher, so snails in both life stages should prefer them, as a richer food source.

Moreover, adults of *T. palustris* exhibited microhabitat preferences according to their size. In fact, larger adults were more common than smaller ones in patches with lower pH and higher salinity levels, as well as within frequently immersed plots (Fig. 7). The fact that larger snails were more numerous in the "best" plots, i.e. the ones flooded more often and the ones with less acidic soil (soil acidity is known to favour shell corrosion), can be explained by inter-specific competition for the richer resources, won, in this case, by the larger specimens.

Size-classes marking the passage from immature to mature snail stages (5 cm at Mida and 6 cm at Dabaso; Fig. 5) were completely absent in our survey; this result is quite difficult to explain, especially since such an observation has never been reported previously. A possible explanation could be that, as *T. palustris* becomes adult, it undergoes a body modification (together with the radula transformation) which leads to a general dimensional increase.

Regarding adults, a diet based on leaves is confirmed both by stomach-content analysis (62.5% of the food residuals are recognisable as leaves) and by the direct observation of individuals grazing the leaves. We have observed adult mud creepers eating different leaf species, such as *Avicennia marina*, *Ceriops tagal* and *R. mucronata*, independently of their age (they also graze the fresh leaves that get detached from branches by the activities of the local population, baboons or birds). *T. palustris* occasionally consumes propagules, propagule calyxes and root bark, as also reported by Plaziat (1984).

Taking into account only the gut-content analysis, there was an apparent discrepancy with what is known of the diet of young individuals: 19% of juveniles' gut content was leaf residuals. This amount, however, corresponds to that found in the mud which is mainly highly decomposed vegetable matter (Odum and Heald 1972), whereas we found about 20% of recognisable leaf debris. This comparison, in addition to what was reported by Nishihira (1983) on the difference in the structure of the radula between the two life stages, allows us to definitely exclude the direct ingestion of leaves by young snails.

Gut-content analysis and field experiments on the grazing rate showed that *T palustris* in Mida Creek fed in all light and tide conditions. Therefore, the present data confirm the results of Soemodihardjo and Kastoro (1977) and Fratini et al. (2000, 2001) about the remarkable amphibious adaptations of this mangrove mollusc which avoids only the hottest and driest hours of the diurnal low tide (Fratini et al. 2000).

Moreover, experiments concerning the in situ grazing rate also showed that mud creepers were able to locate the leaves under water, when the tide was already high. In fact, for the high-tide trials, we placed the leaves immediately before the tidal ebbing and, consequently, those leaves were located and eaten under water. These results lead us to recognise this mollusc as the only leaf-litter consumer active under water at high tide, while the herbivorous crabs are well within their dens, presumably frightened by powerful marine predators (Vannini and Cannicci 1995; Kathiresan and Bingham 2001). High tide is probably not the best period to search for fallen leaves in a mangal, since the leaves that fall float on the surface and do not reach the bottom, whereas the ones that just fell are often caught by the ebbing and flooding currents and washed away. Anyhow, the complex spatial structure of the mangrove forests, with their root systems, often acts as a trap for leaf litter and some leaves are not washed away with the tide and can be easily accessed by *T. palustris* in a situation clearly free from the crabs' competition.

During the day, the snails en masse consume the greatest total amount of leaves independently of the tide phase and leaf age. Moreover, during diurnal low tide, regardless of the amount of leaves eaten, snails graze more leaves than during the other tidal phases. These results show that the total snail feeding activity mainly occurs during low tide (in particular diurnal) even if, during this phase, the amount of leaves ingested by each individual is the smallest.

In Indo-Pacific mangrove forests, intra- and interspecific competition for leaf litter is higher during diurnal low tide, when grapsid crabs (Micheli et al. 1991; Slim et al. 1996, 1997) and *T. palustris* (Fratini et al. 2000) are active. Thus in this crowded period of activity it can be hypothesised that, although there is a greater leaf removal en masse, every single herbivore, regardless of its species, can access a minor amount of food. If this ecological panorama is confirmed for other mangals, the underwater feeding activity at high tide shown by *T. palustris* should be considered one of the most important behavioural adaptations that led to the ecological success of this abundant and ubiquitous potamidid.

The results of the present study strongly suggest that *T. palustris* plays a crucial role in the food web, mangrove-litter degradation, and nutrient cycling of the mangals of Mida Creek. In fact, these mud creepers were present in almost all belts of the forest in quite high densities, and were shown to successfully feed on litter at high and at low tide and were responsible for the removal of a great quantity of mangrove litter (10.5 leaves m^{-2} during a single low tide). They were also shown to be well adapted to harsh environmental conditions, to be the only leaf consumer capable of searching for their food at high tide under water and to compete directly with sesarmid crabs for food (Fratini et al. 2000). Even though sesarmid crabs, with the diversity of ecological niches that they occupy (Giddins et al. 1986; Robertson 1986, 1988; Vannini et al. 1997; Kathiresan and Bingham 2001), are still to be considered the most important macroinvertebrates as far as the Indo-Pacific mangrove food web is concerned, the present data and the evidence that this gastropod can successfully compete with sesarmid crabs for fallen leaves, as suggested by Slim et al. (1997) and experimentally demonstrated by Fratini et al. (2000), show that the contribution of potamidid molluscs to nutrient cycling in mangroves is still notably underestimated.

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