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Tree-climbing behaviour of *Cerithidea decollata*, a western Indian Ocean mangrove gastropod (Mollusca: Potamididae)

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The behaviour of *Cerithidea decollata*, a common western Indian Ocean mangrove tree climbing gastropod, was studied in Mida Creek, Kenya. At the study site, this snail mainly lived in *Avicennia marina* dominated areas, i.e. in the mangrove belt between high water spring tide and high water neap tide levels. Not a single individual was found on the less common mangrove tree *Lumnitzera racemosa*, living just above the *A. marina* level (together with terrestrial grass), and was very rarely recorded on the common *Rhizophora mucronata*, bordering the seaward side of the *A. marina* belt. No significant gradient of *C. decollata* density was found within the whole 150–200 m wide belt. The majority of *C. decollata* rested on tree trunks during high tide, creeping on the mud flat below the tree for part of low tide, and returning on the trunks well before being reached by the water. This migratory pattern was more evident at spring than at neap tide, at day than at night time and it was strongly influenced by the shore level of the mangrove zone in which animals resided. While *C. decollata* from lower shore levels neatly massively migrated twice a day, individuals from upper levels showed a more continuous and irregular activity, sometimes crawling on the mud even at high water of spring tide, when they experience just a few centimetres of water for no more than one to two hours.

INTRODUCTION

In the intertidal habitat, several molluscs are known to perform periodical vertical migrations. These migrations can have either a dominant long-term periodicity, in those sites where the seasonal wave impact variation dominates the tidal excursion (Ohgaki, 1989; Takada, 1996; Warner, 2001), or a prevailing short-term periodicity, on coasts and sites dominated by tidal excursion (Vannini & Chelazzi, 1978; Levings & Garrity, 1983; Warren, 1985).

Among the several species of gastropods more or less strictly associated with mangroves, the species belonging to the genus *Cerithidea* (Mollusca: Potamididae) are known to feed on mud surfaces and to climb mangrove trees, usually resting on the trunk, at various heights, for periods of time which may depend on various degrees on the daylight cycle or more often on the tidal condition (high or low tide) and tidal phase (spring or neap tide) (Macnae, 1963, Brown, 1971; Berry, 1972; Day, 1974; Cockcroft & Forbes, 1981a).

Other littorinids are known to exhibit vertical tidal migrations (on *Spartina* grass, Warren, 1985) but mangrove littorinids are said to be permanently confined on trunks or leaves (Reid, 1985).

Information on *Cerithidea* snails are scanty (Berry, 1972; Cockcroft & Forbes, 1981b) and contradictory as shown by Cockcroft & Forbes (1981a). *Cerithidea decollata* (L.) is said to rest at low tide (Cawston, 1922), to migrate on the trunk at low tide (Day, 1974), to be active both at high and low tide (Macnae, 1963), and to rest on trees at spring tide, foraging on the mud surface mostly at neap tide (Brown, 1971). Cockcroft & Forbes (1981a) studied *C. decollata* in South Africa and found that these gastropods, like most of their congenerics, congregate around *Avicennia marina* trunks, i.e. on the mangrove species typical of the upper zones of the mangrove belt, hardly reached, if ever, by the water during neap tide, resting more or less continually on the trunk at spring tide, and foraging on the mud surface at neap tide, apparently both at day and night time. *Cerithidea anticipata*, an endemic Australian species, is said to be less active and to climb higher at neap than at spring tide (McGuiness, 1994).

These reports are somehow conflictual with what was occasionally observed by us, i.e. that *C. decollata* was regularly migrating both a spring and at neap tide, resting during high water periods.

We were thus interested in studying the distribution and the zonation pattern of *C. decollata* in a mangrove site, in Kenya, where we knew that this species was very common, as well as in describing their general migratory pattern and in understanding how this could be influenced by diurnal, tidal and monthly lunar cycles.

MATERIALS AND METHODS

The Site

Mida Creek is a roughly circular mangrove swamp 20 km south of Malindi (Kenya), bordered by a nearly continuous belt of mangroves, dominated by *Avicennia marina*, on the upper shore level, and by *Rhizophora mucronata* together with *Ceriops tagal*, on the lower level. Along the north-western margin of the creek, which has been selected for this study, the whole belt is about 300 m wide, and the area dominated by *A. marina* is nearly half of it.

The tidal range on the surrounding Kenyan coast is about 4.2 m while within the creek the range hardly exceeds 2 m.

The vertical level difference of the whole mangrove belt is about 130 cm which gives an average gentle slope of about 0.4–0.5%.

The upper half of the belt was only colonized by relatively uniformly distributed trees of *A. marina*, usually 4–7 m tall, while the lower half was inhabited by a mixture of *R. mucronata* and *C. tagal*, with a strong dominance of the former one. In the study site, the *A. marina* zone is comprised between the average high water of spring tide (HWST) and the average high water of neap tide (HWNT). A few scattered *Lumnitzera racemosa*, one of the most terrestrial among the East African mangroves, were found above the *A. marina* belt, in areas already invaded by terrestrial plants and grass, corresponding to the level of the extreme HWST.

The whole area is inhabited by various crab species, active at low water: a dense population of *Neosarmatium meinerti* (Sesarmidae), a leaf eater, two species of fiddler crabs, *Uca inversa* and *Uca annulipes* (Ocypodidae) and two predators, *Eurycarcinus natalensis* (Pilumnidae) and especially *Epixanthus dentatus* (Eriphiidae) known for being a predator of *Cerithidea decollata* (Vannini et al., 2001). At high water, the Portunid crabs *Thalamita crenata* and *Scylla serrata* are two powerful predators occasionally foraging in that area. Among gastropods, a high density of *Terebralia palustris* (Potamididae) is present on the mud surface in all the area (Fratini et al., 2004), while two species of *Littoraria* (Littorinidae) live on *A. marina* trunks and leaves, hardly venturing on the soil.

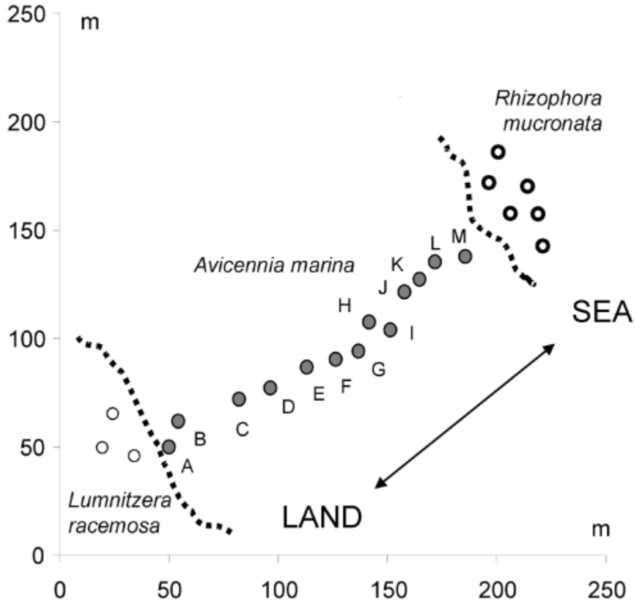

Figure 1. Map of the experimental site. Solid circle, *Avicennia marina* trees where *Cerithidea decollata* were recorded. Empty circles, trees where no (*Lumnitzera racemosa*) or few and isolated individuals (*Rhizophora mucronata*) of *C. decollata* were recorded. Animals on trees A–M were studied in February 2005 while in October 2005 only animals on A–B and J–L areas were studied. The dashed lines correspond to the average HWST (left) and HWNT (right).

A transect was designed by following the sea–land axis and along it 13 trees were marked and measured (Figure 1). During five working sessions (two at night and three at daytime, between ST and NT) the number of *C. decollata* visible on the trunks of the selected trees was recorded

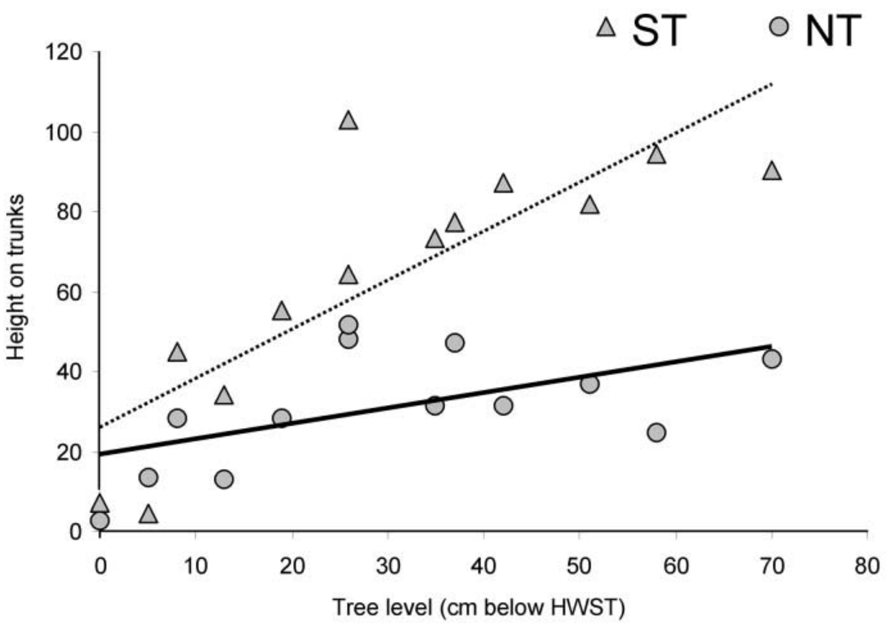

Figure 2. Relationship between average height of *Cerithidea decollata* on 13 *Avicennia marina* trees and tree level below high water of spring tide (HWST), measured both at spring tide (ST: r=0.904, df=11, $P<0.001$) and neap tide (NT: r=0.638, df=11, $P<0.02$).

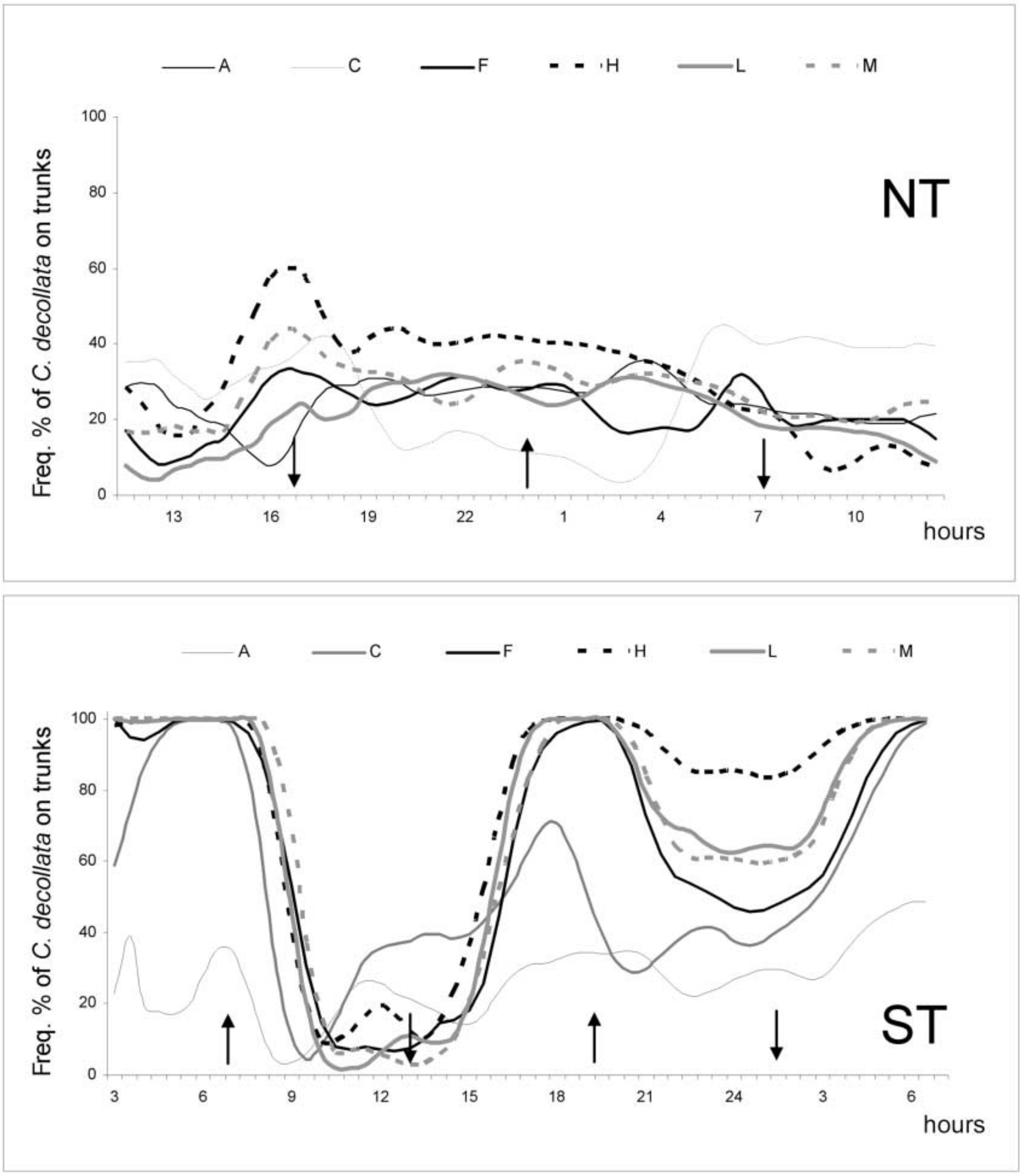

Figure 3. Frequency of *Cerithidea decollata* on trunks at different time (h) and tidal conditions (17–18 February 2005, neap tide; 11–12 February 2005, spring tide). A–M, trees from upper to lower levels (see Figure 1). At NT the water never reached any of the trees while at ST trees F–M were flooded, C hardly reached by the water and A untouched. At each recording session, the relative frequency of *C. decollata* represents the number of recorded animals on the trunk related to the maximum recorded number for that tree (79, 88, 40, 58, 71 and 89 for the trees A–M, respectively). Arrows: up, HW; down, LW.

The transect ran all across the *A. marina* belt, including both the upper scattered zone (bordered by few *Lumnitzera racemosa* trees and terrestrial grass), and the lower thick one (bordered by the dense *R. mucronata* bush).

The following abbreviation will be used: ST, spring tide; NT, neap tide; HW, high water; LW, low water.

The species

Cerithidea decollata, known from Australia, the Red Sea and East Africa, is the only member of this genus in the western Indian Ocean with the exception of *C. obtusa,* known from south-east Asia to Madagascar, and is characterized by the truncated shell apex, about 12.5 mm wide, 30 mm long. All animals on the nine *A. marina* trees chosen at random, along a transect parallel to the sea, were measured with a calibre to estimate the average body size.

Methods

Snails were marked with white fluid corrector (Tippex) and with additional nail varnish on the dried corrector,

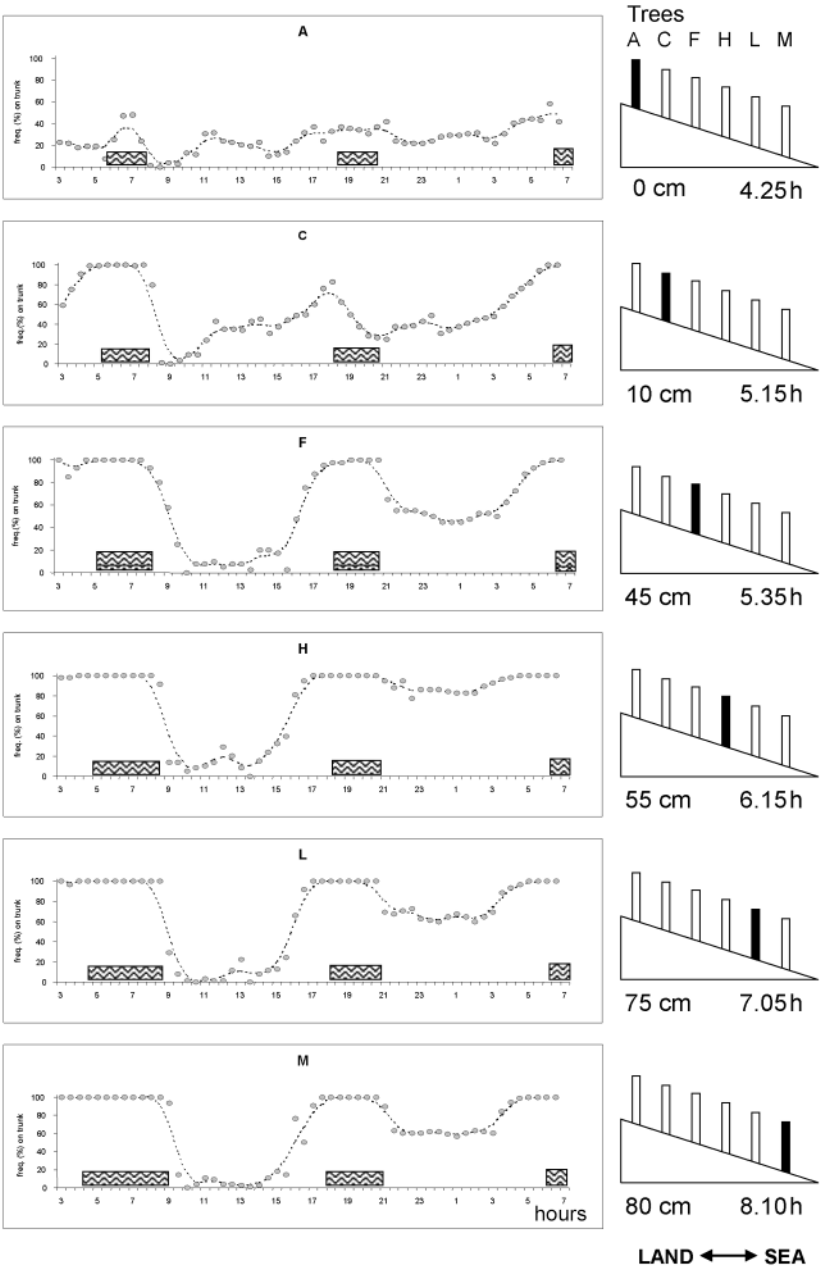

Figure 4. Percentage frequency of *Cerithidea decollata* on the different trunks over all spring tidal day (11/12th February 2005; same data of lower diagram of Figure 3). Stripped bars, submersion periods. On the right diagrams, for each tree, the relative position along the transect, the maximum level reached by the water (value on the left, in cm) and the total time of submersion over 24 h (values on the right).

when resting on the trunks. Other technical details will be presented in the results section.

To estimate the size of snail abundance per tree, all animals were counted on 44 trunks, chosen at random along a linear 150 m transect parallel to the sea; the trees circumference at 1 m above the soil was also measured.

Observations were made during February 2005. Additional data were also gathered in October 2005.

RESULTS

Animal size

By collecting and measuring the width of all the individuals (N=241) of *Cerithidea decollata* present on nine *Avicennia marina* trees, we were able to draw a size–frequency distribution showing a unimodal quasi-normal distribution (average =12.2 mm, SE=0.08 mm) comprised between 9.5 and 16.0 mm, with only two specimens smaller than 10 mm.

Snail density

The number of *C. decollata* living on each tree, recorded during HW, varies greatly. About 77% of the 44 examined trees hosted from 10 to 40 animals (average=24.6, SE=3.26), but larger groups were not rare. On other occasions, more numerous groups, including up to 350 individuals, were found. Large groups of animals often tend to

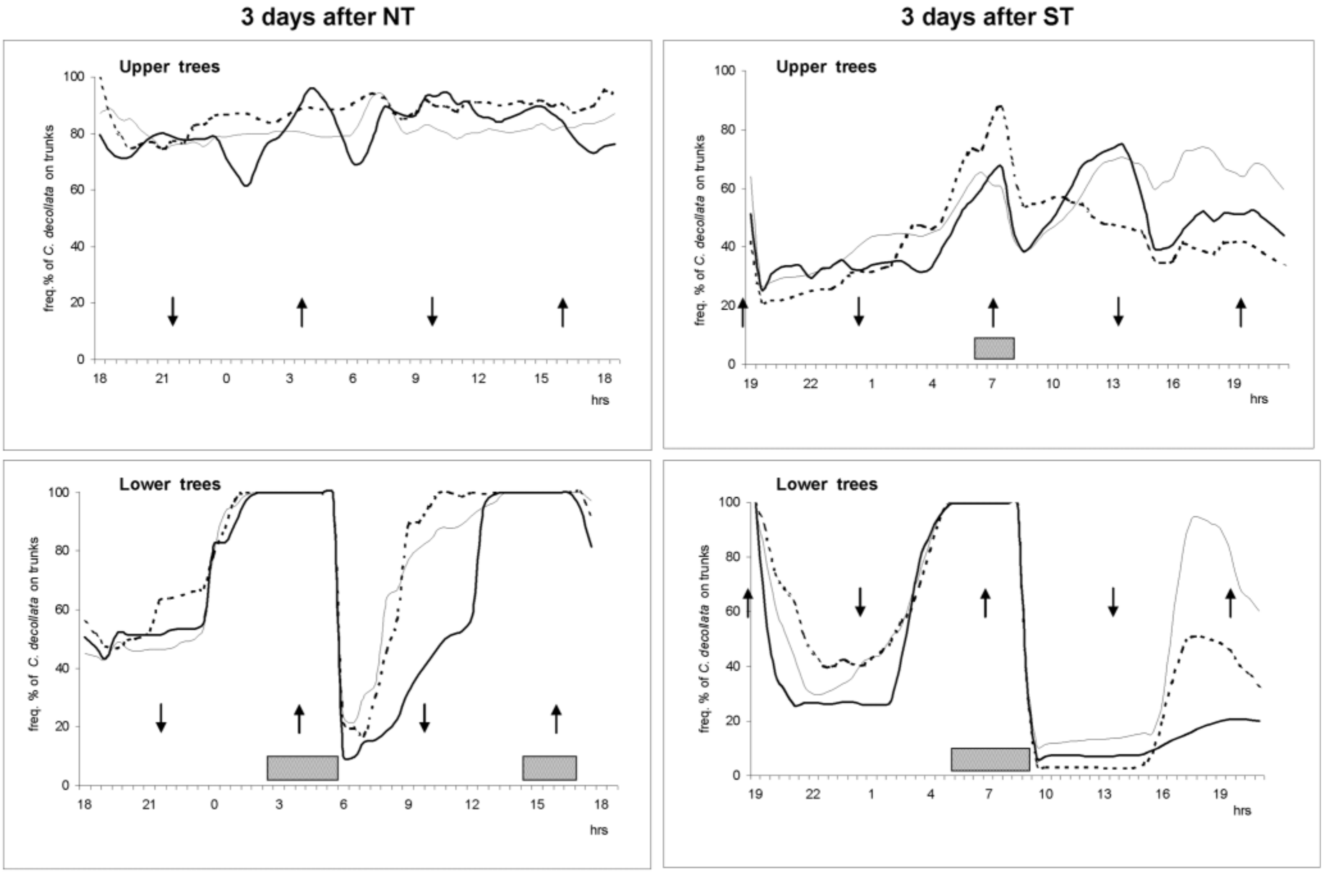

Figure 5. Frequency of *Cerithidea decollata* on trunks at different times (h) and tidal conditions. After ST (20–21 October 2005: right column), the diurnal HW reached three lower trees (each tree between 60 and 180 animals, close to trees L–M of Figure 1) and just lapped the three upper ones (each tree between 80 and 210 animals, close to trees A–B of Figure 1) while nocturnal HW did not reach any of them (left column). After NT (14–15 October 2005, left column) upper trees were never flooded. Arrows: up, HW; down, LW. Dashed boxes, submersion periods.

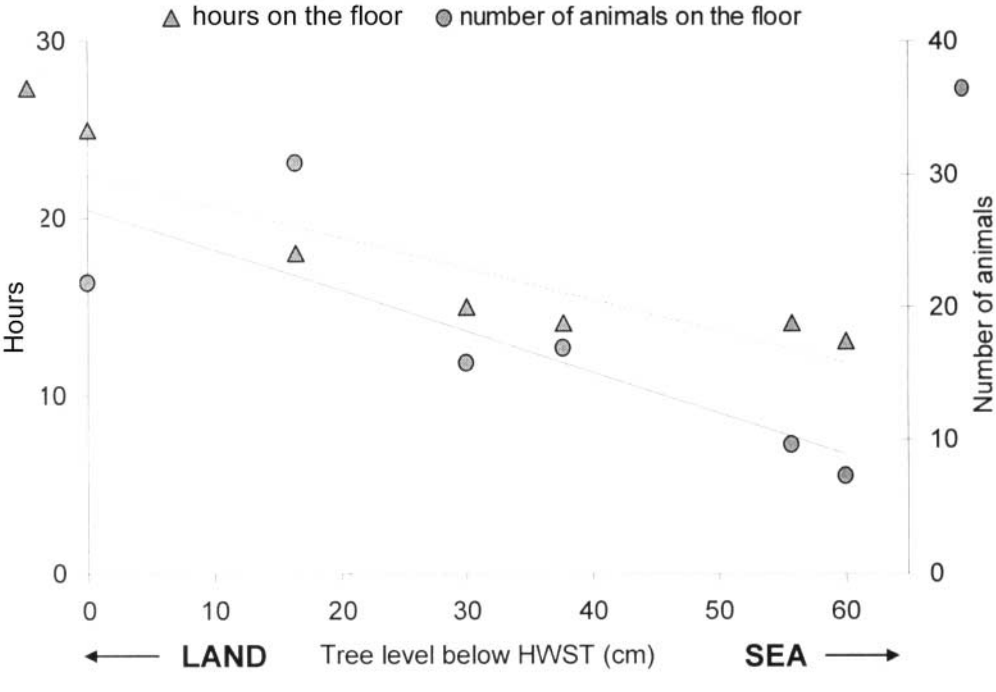

Figure 6. Correlation between tree level and the intensity of diurnal downward migration (same data of Figure 4). Intensity has been measured as the fraction of 24 h during which more than 50% of *Cerithidea decollata* are on the floor (dotted regression line: r=0.896, df=4, $P<0.02$) and as the average frequency of *Cerithidea decollata* on the floor during such a period (continuous regression line: r=0.829, df=4, $P<0.05$).

form real clusters, with most animals closely packed together.

In the study site, trees with any *C. decollata* were never found. The number of *C. decollata* for each tree is significantly related to the tree size ($r=0.510$, $df=42$, $P<0.001$) but the relationship only explains 26% ($R^2=0.260$) of the large variability.

Horizontal zonation

In spite of several inspections conducted both during the recording sessions and in other occasions, along the transect of Figure 1, very few *C. decollata* were ever found on the trunks or among the roots of any *Rhizophora mucronata* (1–2 per tree), and none on *Lumnitzera racemosa*. Hence, this species, at least in the study area, seems strictly confined to the *Avicennia marina* belt.

The density of *C. decollata* on the 13 trees of the transect was independent from the shore level of each tree ($r=0.298$, $df=11$, $P=$n.s.) showing an average of 61.7 animals/tree (SE=5.90).

Vertical zonation

The height on the trees at which individuals of *C. decollata* settled during HW was also investigated (Figure 2), comparing the heights reached at HW around ST (7 February 2005, at 0730) and NT (12 February 2005, at 1200). The trees in the upper *A. marina* zone (trees A and B, Figure 1) were hardly reached by the tide and only at ST. In this area, *C. decollata* was always clustering on the lower part of the trunk or on the surrounding floor. Animals from lower trees behaved markedly differently and, on average, at ST, they settled about 60–70 cm higher than at NT (Figure 2).

Effect of daily and tidal cycle

In order to define the effect of daily and tidal cycles on *C. decollata* migratory pattern, 24 h surveys were performed in February 2005, both at ST and NT, on marked animals. Six trunks scattered along the land–sea transect, chosen among those used for the study of the vertical distribution (see Figure 1), were selected. Surveys were conducted every 30 minutes.

A second series of observations was repeated in October 2005, focusing only on trees of the upper and lower levels.

At high water ST (Figure 3, lower diagram; Figure 4), individuals of *C. decollata* generally remain on the trunk until the water recedes, then most of them spread on the floor, returning on the trunk before the following high tide. At night, the descent is much less pronounced and many snails seem to spend the whole nocturnal low tide on the trunk. This pattern involves most of the animals living on lower trunks (trees F, H, L, M), while animals from upper trunks (A,C) seem to be able to spend a greater part of their time on the floor both at high and low water (Figure 4).

At NT (Figure 3, upper diagram) the above pattern is more obscure and even animals from the lower shore level seem to be able to abandon their trunk both at day and night time, at HW as well as at LW.

Between ST and NT (Figure 5), an intermediate pattern is visible: a less pronounced migration on upper trees, a marked one on lower trees, more intense migration after ST than after NT, and with an analogous discrepancy between diurnal and nocturnal activity.

At ST, the variability in the migratory pattern existing at different shore levels was studied by measuring for each tree the intensity of diurnal migrations in terms of: (A) the maximum ratio between animals on the floor and total number of snails, and (B) the length of time at which more than 50% of the snails were crawling on the floor instead of the trunk (Figure 6). In both cases, two relationships were evident: (A) more animals living on upper levels tend to forage on the floor, and (B) for a longer period than animals living on lower levels.

It is thus evident that, in the study area, animals living on the extremes of the *Avicennia* belt are subject to very different ecological conditions, which define different behavioural responses. Animals from upper levels are able to remain on the floor for most of the time, nearly indifferent to the incoming tide that reaches their area only for about one hour and only 2–3 HWs every ST, while animals from lower levels need to climb back on trees well before each tide, being able to spread on the floor mostly at daytime and mostly at ST, and quickly ascending the tree where they will rest for several hours, waiting the next low tide or the next day.

DISCUSSION

Several intertidal molluscs (Gastropoda, Vannini & Chelazzi, 1978; Polyplacophora, Chelazzi, 1992) and crustaceans (Brachyura Vannini & Gherardi, 1988; Gherardi & Vannini, 1993; Cannicci et al., 1999) are known to undergo through regular vertical migrations in relation to the tidal cycle getting higher on the cliffs or trunks before the high tide. In all cases, the whole migratory pattern shows a regular synodic modulation, with the spring tide migrations constantly appearing more intense (more animals involved and for longer distances) than the neap ones.

The behaviour of *Cerithidea decollata* and its migratory synodic pattern appeared, on the contrary, quite contradictory (see Cockcroft & Forbes, 1981a, and Introduction). The contradictions were probably due to different specific tidal conditions and to the brief recording period of the various authors. In Mida Creek, on the Kenyan coast, we have actually found a difference in the snail migratory pattern depending on: (A) high–low tide cycle, (B) day–night cycle, and (C) spring–neap tidal cycle; in addition, (D) the whole pattern is strongly influenced by the zonation within the wide area that the snails are able to colonize, and which overlaps with the *Avicennia marina* belt, the mangrove species which they tend to aggregate around or cluster on.

(A) During LW, individuals of *Cerithidea decollata*, in Mida Creek (Kenya), exhibit massive foraging migrations, spreading from the *A. marina* trunk along the mud surface. Within the whole *A. marina* belt, the above migration is more evident among animals living on lower than on upper shore levels.

(B) During diurnal LW, more animals are involved in the foraging migration and for a longer period, than during nocturnal LW. The nocturnal migration may involve less than half of the individuals migrating at day time.

(C) The above pattern is especially evident around ST, while at NT migration appears desynchronized and most animals may permanently dwell on the floor or on the trunk.

Especially on lower shore levels, it appears that *Cerithidea decollata*, during the resting phase (HW), tends to cluster on the trunk, higher at ST than at NT, thus avoiding being submerged and settling, in both cases, just above the high water mark.

(D) The migratory pattern does not involve the whole population in the same manner: animals from upper shore levels, only reached by the HWs of ST, always appear poorly synchronized even when actually reached by the water. Individuals of *C. decollata* living on upper shore trunks seem to behave quite differently in dissimilar tidal phases, being well clustered on the trunks or spreading on the floor or presenting an intermediate reaction. Further investigations could prove if this may depend on the strong variation of temperature and soil humidity due to the rain and to the HWs, which may flood this area twice a day, or may never reach it for a whole week.

Usually, animals from the lower level migrate more massively but for shorter periods.

By analysing the tide table for a year (Admiralty Tide Tables, 2005), it appears that, in the study area, upper trees are flooded only by about 20% of HWs, while lower trees by about 80%, i.e. four times more frequently. Within 24 h, during a February ST (when HWs reached 3.9 and 3.6 m, see Figure 4), upper trees were covered for 4 h 25 min while lower trees were submerged for 8 h 10 min, i.e. 1.8 times longer. Combining those values (4×1.8), it is clear that lower trees are submerged seven times longer than upper ones, in terms of total submersion time.

Furthermore, our results do not apply to younger *C. decollata*, whose lifestyle remains quite obscure. Cockcroft & Forbes (1981b), in South Africa, had also found that very small individuals were rare and were only found on the floor, but the population they found on trunks varied from 3.0 to 16.0 mm width, thus including size-classes well below the smallest we could record (9.5 mm).

In conclusion, this work highlights a quite remarkable pattern: on one side, on upper shore levels, animals reached by the water only by few tides a month are irregularly active, sometimes totally inactive, mostly clustering near the base of *A. marina* and occasionally foraging also under 5–10 cm of water. On the other side, on trees 60–70 cm below and 100–150 m away, we have animals migrating on the mud surface every day as soon as the water retreats, getting back on the trunks well before (1–2 h) the incoming tide, clustering high enough to avoid submersion which affects their trees twice a day nearly every day, for a submersion period about seven times longer than the upper trees.

Avoiding predation is known to play a role in defining mollusc zonation and activity patterns in littorinids (Reid, 1985; Warren, 1985; Behrens Yamada & Boulding, 1996; Duncan & Szelistowski, 1998). Antipredatory strategies may also play a role in *C. decollata* activity pattern. Reducing foraging activity during HW decreases the possibility of facing predators such as fish and *Scylla serrata*, a common Portunid crab actively preying on molluscs, presumably more dangerous than *Epixanthus dentatus*, the Pilumnid crab that *C. decollata* experiences at LW (Vannini et al., 2001). *Epixanthus dentatus* is mostly active at night time and this would also induce *C. decollata* to concentrate its foraging excursion during diurnal LWs. This hypothesis is partly confirmed by the fact that neither of these two predators are present across the upper *A. marina* area, the area where *C. decollata* appears to be active also at night time, occasionally even when submerged. However, the study by McGuiness (1994) did not find evidence of antipredatory behaviour in the tree climbing behaviour of the Australian *C. anticipata* (Northern Territory): this species climbed higher up into trees at neap tide (when tidal predators are not present) than at spring tide (when predators could be present). Preventing snails from climbing trees resulted in snail mortality and McGuiness (1994) therefore suggested that physiological stress (desiccation), rather than predation, could explain the behaviour of the snails. It is likely that a specific eco-physiological study could reveal that physical stress and predation may both play a role, on lower and upper mangrove zones respectively, among *C. decollata* too.

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