Tidal activity rhythms in the mangrove snail *Cerithidea decollata* (Linn.) (Gastropoda: Prosobranchia: Cerithiidae)

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Activity rhythms in *Cerithidea decollata* which migrates between the trees and the substrate in south-east African mangrove swamps were investigated in Durban Bay, South Africa. No light/dark rhythms were found. Activity followed a 14-day tidal rhythm. Maximum activity occurred over neap-tide periods and least over spring-tide periods when snails tended to remain on the trees over both high and low tides. Snails descended to the substrate more frequently in the upper intertidal area where inundation was less frequent and of shorter duration. Descent to the substrate appears to be associated with feeding. Tree-climbing is suggested to be a predator-avoidance mechanism.

S. Afr. J. Zool. 1981, 16: 5 – 9

Aktiwiteitsritmes van *Cerithidea decollata* wat migreer tussen bome en die grondlaag in Suid-Afrikaanse wortelboom-moerasse is in Durban-baai, Suid-Afrika, ondersoek. Geen lig/donker ritmes kon gevind word nie. Aktiwiteit was volgens 'n 14-daagse getyritme. Maksimumaktiwiteit het met ebgety plaasgevind en minimumaktiwiteit met springgety, wanneer slakke in die bome gebly het met beide hoogwater en laagwater. Slakke het meer dikwels na die grondvlak afgekom in die hoër tussengety-gebied, waar oorspoeling minder dikwels en vir korter periodes voorgekom het. Die afkom na grondvlak hou skynbaar verband met voeding, en boomklim vermoedelik met ontwyking van roofdiere.

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A characteristic feature of a number of species of the mangrove snail genus *Cerithidea*, is the tendency to ascend mangrove trees at particular stages of the tide. The Malayan species *C. obtusa* and *C. cingulata* ascend trees on the flood tide and descend on the ebb (Berry 1972). The Southern African species *C. decollata* occurs on the east coast between Swartkops estuary (33°52′S, 25°38′E) and Morrumbene estuary (23°31′S, 35°16′E) in Mozambique (Macnae 1957, Day 1974). It is not restricted to mangrove swamps, having been recorded on open estuarine shores (Cawston 1922), but in mangrove areas it resembles other species of the genus in its tendency to migrate between the substrate and the trees where it gathers on the trunks in distinct, crowded bands. There is however, little agreement on the timing and nature of these movements. Cawston (1922) recorded aggregations at low tide on both trees and substrate; Macnae & Kalk (1962) reported aggregations on trees on Inhaca Island; Day (1974) described the snails as ascending the trees at low tide, while Macnae (1963) considered the snails to be active during both high and low tides. Brown (1971) envisaged a tidally-induced long-term cycle with snails tending to ascend the trees shortly before, and descend after, spring-tide periods.

In order to clarify the existence and nature of tidally associated activity rhythms, observations were made on a *C. decollata* population during both high and low tides over complete tidal cycles.

Materials and Methods

The Study Area

The study area was in Durban Bay (29°51′S, 31°1′E) South Africa. This bay (Fig. 1) is an almost completely enclosed body of water extending inland for 5,6 km. The mangrove area described by Day & Morgans (1956) has been reduced by harbour development and the surviving remnant lies on the south-east shore of the bay. It has a water frontage of approximately 1 km and varies in width from 30 m to 250 m. It is dominated in the seaward and central areas by *Avicennia marina* which attains a height of 8 – 10 m. The canopy begins at 4 – 6 m and is almost continuous. Beneath it is a scattered understorey of *Bruguiera gymnorhiza* 2 – 4 m high, which becomes more common on the landward fringe. Much of the substrate is covered by a thick turf of the green alga *Cladophora* sp. (M.T. Smith *pers. comm.*). At high water of spring tide the entire mangrove forest is inundated, the

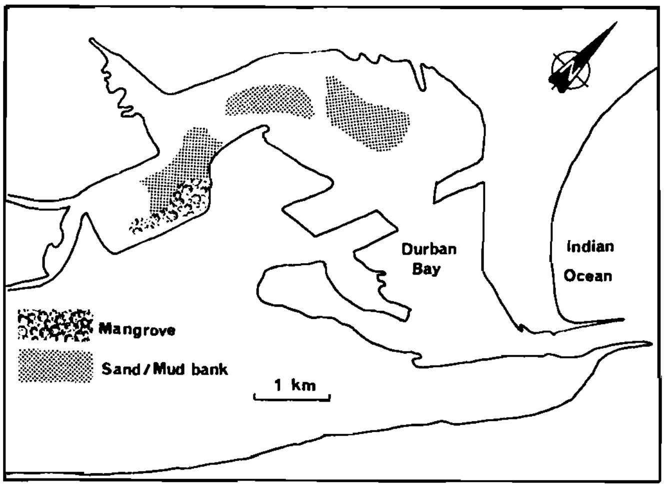

Fig. 1 Location of the study area: Durban Bay mangroves, Natal, South Africa.

landward fringe to a depth of 20 – 30 cm. At high water of neap tide the water laps only the seaward fringe.

Snail migration

Movement between trees and substrate

All observations were made on *C. decollata* on *A. marina*. Snails were marked with acrylic paint without removing them from the trees and included individuals between 3 and 16 mm maximum width; snails smaller than 3 mm width were only occasionally found and always on the substrate. Fifty snails were marked on tree A (Fig. 2) on the seaward fringe and the number of snails on the substrate and on the trees was recorded at each diurnal high and low tide over the following 15 days. Seventy-five snails were marked on tree B and 100 on tree C (Fig. 2). Observations were made at each diurnal low tide over the following 15 days and the number of snails on the substrate and the trees, recorded. In addition, observations were made during nocturnal low-tide periods on alternate nights to test for any light/dark activity rhythms.

Possible effects on snail activity of differing frequencies and periods of tidal inundation in the seaward and landward fringes of the swamp were investigated separately. Three trees at different tidal heights in the landward, central and seaward areas (D, E, F, Fig. 2) were selected and 50 snails marked on each tree. The number of marked snails on the substrate at low tide was recorded daily for a full tidal cycle.

Influence of tidal height on the height of snail aggregations on the trees

Observations were carried out at 2 trees (G and H Fig. 2); one in the seaward fringe and one in the central area. The height of snail aggregations above the substrate was measured at spring tide and again at a high tide every day over one-and-a-half tidal cycles. Isolated snails below the main aggregation were ignored. The recorded heights of the aggregations were then compared with the maximum tidal heights at the trees estimated from tide tables for Durban Bay.

Results

Movement between trees and substrate

Results from tree A (Fig. 3) showed that maximum frequency of movement between trees and substrate occurred over neap-tide periods. Not all snails ascended the trees during neap high tides (days 1 – 3 and 12 – 16 in Fig. 3), but all did so during days 4 – 11 on either side of spring tide. Fig. 3 also shows that the entire marked population remained on the trees during the two-day period around spring tides. Results from trees B and C in the central area (Fig. 4) show that more snails were on the ground during low neap tides than during low spring tides and also that there was no difference in activity between day and night low-tide periods. Counts of marked snails on the ground at night were either very similar to those obtained at low tides 12 h earlier or later or showed the same general trend.

The results obtained from snails marked at trees D, E and F (Figs. 2 and 5) showed that snails nearer the landward fringe spent a greater number of low-tide periods on the substrate than those in the central and seaward areas. There was a tendency, however during the relatively shorter periods of activity in the central and seaward areas for greater proportions of marked snails to be present on the substrate. This was particularly marked in the case of tree E in the central area.

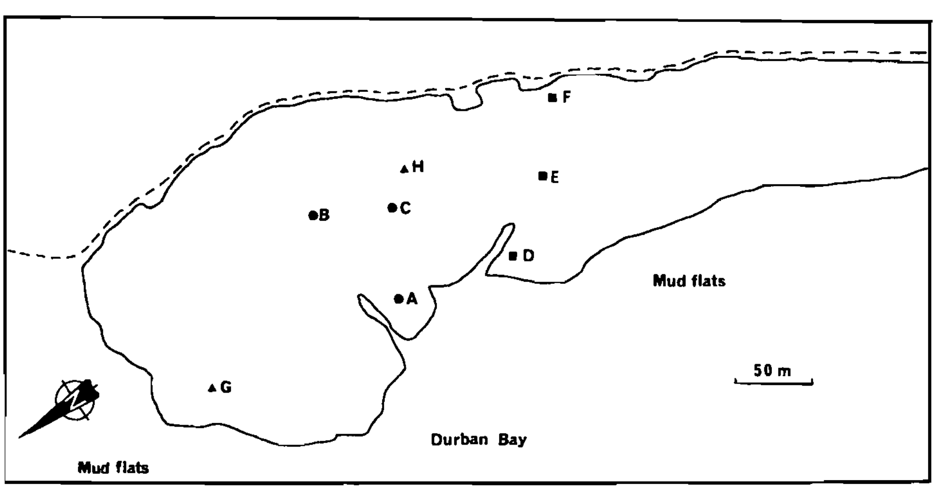

Fig. 2 Northern area of Durban Bay mangroves (continuous line) showing positions of trees referred to in text. Dashed line indicates high-water mark.

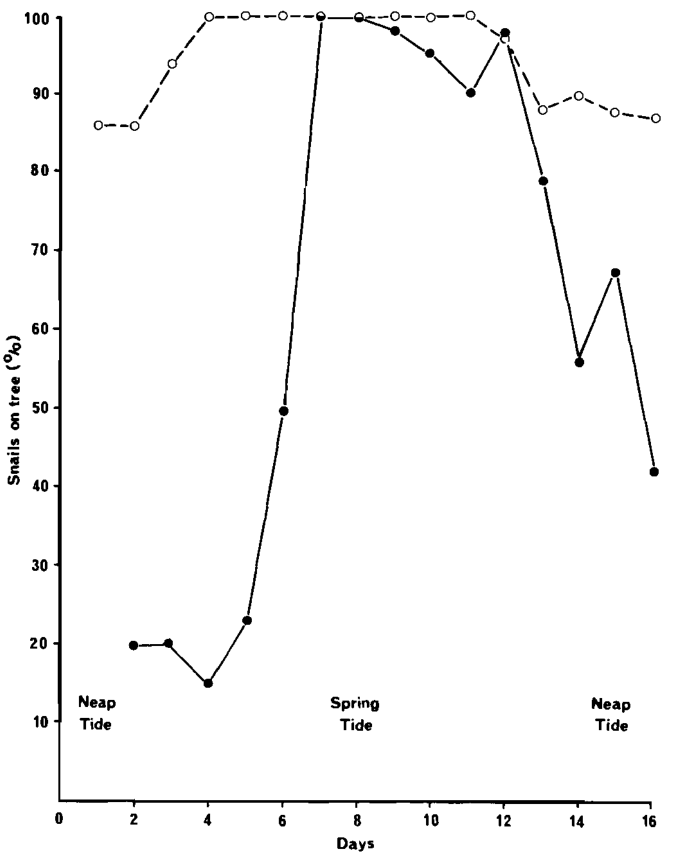

Fig. 3 *Cerithidea decollata*: Percentage of marked snails on trees at alternate high (open circles) and low (closed circles) tides during the day over a full tidal cycle. $n = 50$.

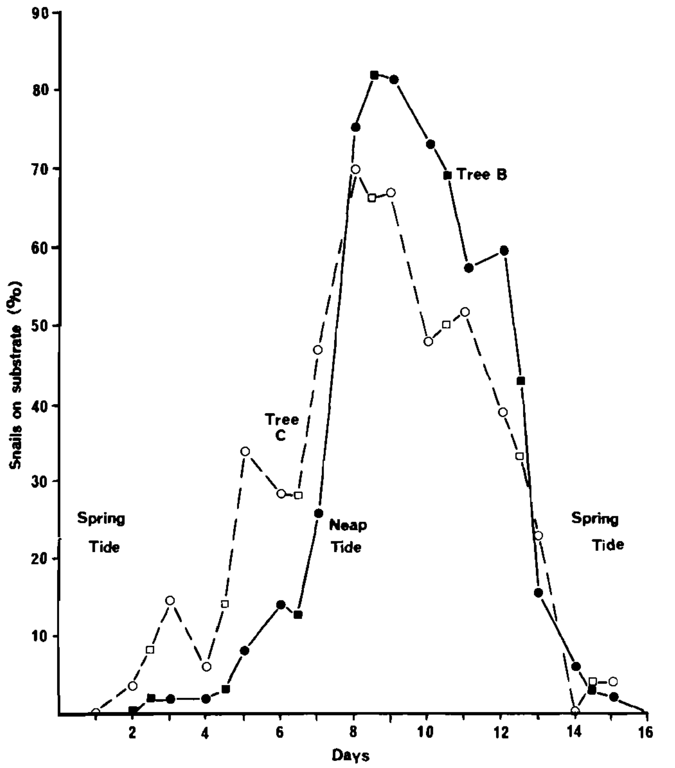

Fig. 4 *Cerithidea decollata*: Percentage of marked snails on the substrate at low tides over a full tidal cycle. Squares (open or closed) refer to counts done at night. $n = 75$ (tree B) and 100 (tree C).

Influence of tidal height on height of snail aggregations

The height of snail aggregations in both the seaward (tree G) and central area (tree H) followed a pattern similar to that shown by the maximum calculated tidal heights (Fig. 6). Snails tended to collect 0,5 – 0,7 m above maximum

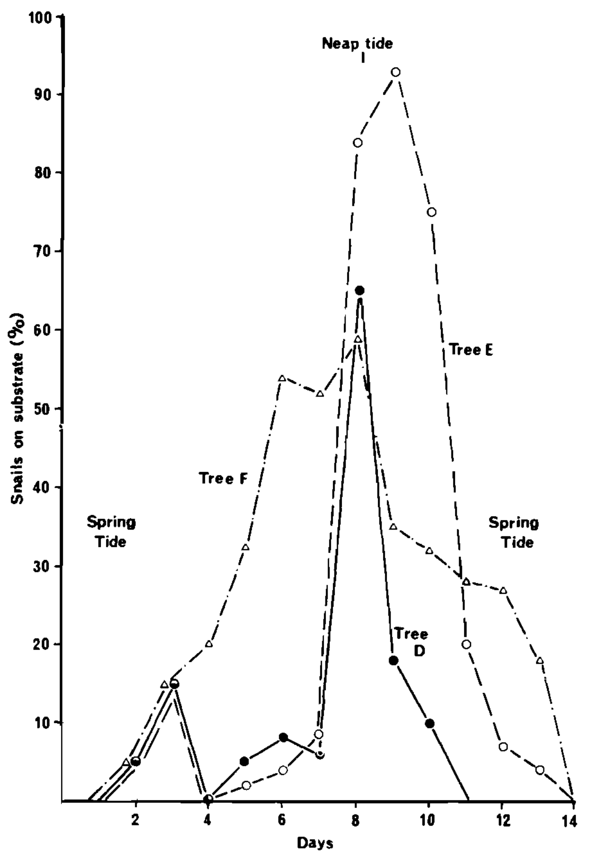

Fig. 5 *Cerithidea decollata*: Percentage of marked snails on the substrate at trees D (seaward fringe), E (middle) and F (landward fringe) at low tide during the day over a full tidal cycle. $n = 50$ in each case.

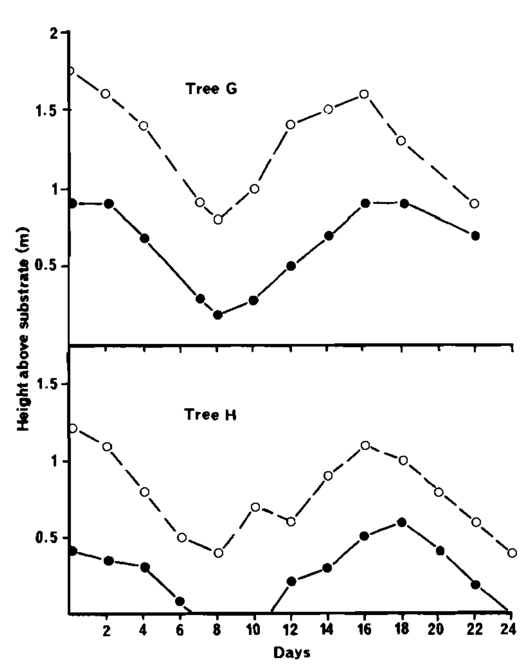

Fig. 6 *Cerithidea decollata*: Height above the substrate of snail aggregations (open circles) in the seaward fringe (tree G) and central area (tree H) compared with the calculated maximum tidal level on the trees (closed circles) over one-and-a-half tidal cycles.

tidal level. There was a significant correlation between aggregation height and tidal height at both trees ($r = 0,87$ and 0,83; $P < 0,01$). Snails began to move up the trees and establish aggregations approximately one hour before the flood tide reached the base of the tree. It was also noted that snails would ascend trees which were not subsequently reached by the high tide.

Discussion

The results demonstrated a clear rhythmic movement of *C. decollata* between the trees and substrate which was related to tidal flooding of the mangrove zone. Snails descended at low-tide periods and ascended the trees before the following high tide. There was no indication of any light/dark activity differences. The overall pattern over the 14-day tidal cycle was for increasing numbers of snails to descend from the trees at low tide during the transition from spring to neap tides and in some cases to remain on the ground, although not submerged, from one low tide to the next. Following neap tides this trend was reversed with increasing numbers of snails remaining on the trees and fewer descending to the substrate. This pattern was modified by the position of the snails in the mangal relative to the range between seaward and landward fringes, hence to the frequency and length of inundation of particular areas. As the frequency of inundadion declined towards the landward fringe of the swamp, there was a tendency for snails to spend a greater proportion of low tides on the substrate during the tidal cycle. The reduced opportunity for descent in the seaward and central areas was to some extent compensated for by the descent of a greater proportion of snails during the more limited period of activity.

Confusion in earlier descriptions of activity of *C. decollata* could easily have arisen if observations were of short duration or restricted to a single area without regard to the importance of the position of snails relative to HWN and HWS levels.

Changes in aggregation heights on the trees were least during the 3 – 4 day period over spring tides (Fig. 6), when movements between trees and substrate were minimal. At other times there was sufficient activity to account for the variation in aggregation heights.

Light/dark activity rhythms are frequently superimposed on tidal rhythms (Chandrashekeran 1965, Barnwell 1966). Zann (1973) considered nocturnal activity in the littoral gastropod *Melanerita atramentosa* to be a mechanism for avoiding desiccation problems during the day. Day/night temperature and humidity fluctuations in the Durban Bay mangroves are less than in local open areas (Cockcroft 1978) so that this problem is reduced and it is possible for *C. decollata* to be active at low tide during both day and night.

While it is clear that tidal activity rhythms exist in *C. decollata* it is also clear that individuals in the population are capable of extensively modifying any basic rhythms as shown by the differing frequencies of tree/substrate migrations at different points between HWN and HWS. It is also shown in the roughly constant heights of tree aggregations above high water mark and hence the varying height above the substrate. As the snails do not show any well-developed homing behaviour (Brown 1971, Cockcroft 1978) and the population mixes readily with individuals moving both seawards and landwards, individual activity patterns must change and the importance of some environmental cue is emphasized.

The problem of environmental cues inducing rhythmic activity in animals has been dealt with extensively in the literature. In the case of littoral animals 'wetting' by the incoming tide (Berry 1963, 1972; Southward & Crisp 1965, Zann 1973), 'acoustic shock' caused by the surf (Chandrashekeran 1965), tidal hydrostatic pressure changes (Moulton 1962, Morgan *et al.* 1964) and the rise and fall of the water level (Underwood 1972a, 1972b) have all been proposed as possible stimuli. *C. decollata* shows a wetting or splash response in that snails on trees respond to splashing by an almost immediate movement further up the tree (Cockcroft 1978). Initiation of ascents and determination of aggregation height cannot, however, be due to this response because both occur without contact with the water. Similarly changes in hydrostatic pressure and water level can be excluded. The environmental cue to which *C. decollata* is responding is thus still obscure. A possibility is a change in humidity gradients at the substrate/air interface associated with a change in water-table height but this would require further investigation.

Descent of *C. decollata* to the substrate appears to be associated with feeding. Earlier reports (Macnae & Kalk 1958) suggested that the snails fed while on the trees although later Brown (1971) considered that *C. decollata* 'apparently feed only on the mud surface'. Observations during this study showed that the snails were inactive with opercula closed, on the trees at high tide; activity being confined to movements within the aggregation (Brown 1971, Cockcroft 1978). All evidence thus suggests that feeding is restricted to the substrate. Unfortunately, gut contents were not analysed in sufficient detail to support this assumption. Desiccation is not considered a significant stimulus for descent, as snails can survive desiccation under laboratory conditions for considerable periods without any significant loss in mass (Forbes *pers. comm.*).

Tree-climbing behaviour thus remains an intriguing aspect of the behaviour of this snail. Berry (1972) suggested that the west Malayan tree-climbing species *C. obtusa* and *C. cingulata* climb trees to avoid the water as they are 'lung-bearing'. *C. decollata* survived under aerated seawater for 14 days (Cockcroft 1978) and the problem of 'drowning' thus appears remote. The Malayan species apparently feed on epiphytic algae on the mangrove trees, but the general pattern of ascent at high tide and descent at low tide suggests a similar strategy to that of *C. decollata*. The tree-climbing habit at high tide and avoidance of water is not restricted to species of *Cerithidea*. In south-east African mangrove swamps movement ahead of the tide or into the trees occurs in unrelated groups such as the mudskipper *Periopthalmus sobrinus* and crabs of the genus *Sesarma*. Avoidance of water during high-tide periods may be a predator-avoidance mechanism. *Littorina irrorata* ascends intertidal plant stems at high tide in an effort to avoid predation by the crab *Callinectes sapidus* (Hamilton 1976).

A possible predator of *C. decollata* is the large portunid crab *Scylla serrata* which is a common inhabitant of mangrove swamps and preys largely on gastropods and smaller crustacea (Hill 1976).

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