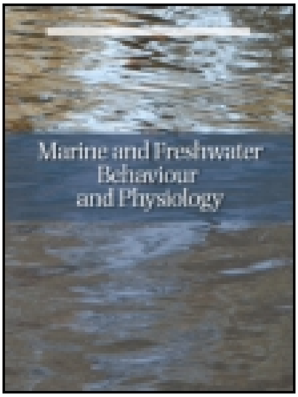

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Activity patterns in Thalamita crenata Portunidae, decapoda): A shaping by the tidal cycles

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ACTIVITY PATTERNS IN *THALAMITA CRENATA* (PORTUNIDAE, DECAPODA): A SHAPING BY THE TIDAL CYCLES

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The activity rhythms of the swimming Portunid *Thalamita crenata* have been studied on the basis of crab sightings in surveys along three transects of a mangrove swamp in Kenya. Activity is well matched to the environmental regime and is prevalent during lhe high tides. However, activity does not occur over the whole of the high tide, but is confined to "temporal windows" corresponding to a water level between 10 and 30 cm. Our findings suggest that activity in *Thalamita crenata* is shaped by the tidal cycles and we propose that variation in hydrostatic pressure as the tide changes is the cue which elicits activity.

KEY WORDS: Tidal rhythms, activity rhythms, intertidal habitat, mangrove swamp.

INTRODUCTION

The activity of the organisms living in the intertidal region is generally governed by sequential tidal cycles (Herrnkind, 1983), resulting in one phase during which they are active and another in which they are inactive. These organisms have been defined as "isophasic" if they keep within the "right" phase by migrating, and "isozonal" if they avoid the "wrong" phase by taking refuge in suitable hiding places (Vannini & Chelazzi, 1985).

Thalamita crenata is a Portunid crab that exhibits isozonal behaviour. As it is a good swimmer, it could be expected to concentrate its activity (foraging, preying and mate-seeking) at high tide, and to seek shelter in crevices and burrows or bury itself in the mud or sand at low tide.

Few studies have been carried out on this and other species of the genus, and those undertaken deal only with their physiology and taxonomy. Consequently there is a lack of information on the ecology and behaviour of *T. crenata*, especially regarding its activity rhythms, feeding habits and reproduction in relation to food availability and tidal cycles. This is curious because it is one of the most common crabs of the Indo-Pacific coasts and perhaps the most widespread predator in mangrove swamps and sheltered muddy beaches.

The present study aims to fill this gap by answering the following questions: 1. How is the activity of *Thalamita crenata* distributed over a tidal day? 2. What ecological factors are behind this distribution? 3. What are the cues which elicit crab activity?

MATERIALS AND METHODS

The study area was in a mangrove swamp in Mida Creek, 20 km south of Malindi, Kenya. It was seaward to the mangrove fringe on an intertidal limestone platform of fossil madrepore and covered by mud of generally organic origin. During low water (LW) the area is exposed except for the rock pools in the depressions or crevices in the platform where *T. crenata* shelters. Animals can also be found half buried in the mud at LW.

Three surveys were carried out along three transects 74 m long, 16.5 m apart (Figure 1) and parallel to the coast. During each survey an approximately 5 m wide strip was observed, giving a total observation area of 1110 m^2. (74 × 5 × 3). The three tracts were surveyed simultaneously and the time, water level and number of moving crabs sighted were recorded. Surveys were made while walking or snorkelling along the tracts, with the use of a flash-light at night.

Four complete surveys (i.e. inspecting all three transects simultaneously) were carried out from 28.10.91 to 22.11.91 during ebb and flow tides, night and day; another 17 surveys where made under the same conditions but along the central tract only.

Records for the LW period, in which the intertidal region was exposed to the air, were obtained from 57 surveys made in an adjacent area of 4624 m^2. (68 × 68) which was inspected daily at every LW from 25.10.91 to 25.11.91.

RESULTS

An analysis of general activity in *T. crenata* shows that it reaches a maximum when the water level is 10–30 cm, both at ebb and flow tide (Figure 2); the same pattern can be seen when nocturnal and diurnal activity is compared (Figure 3).

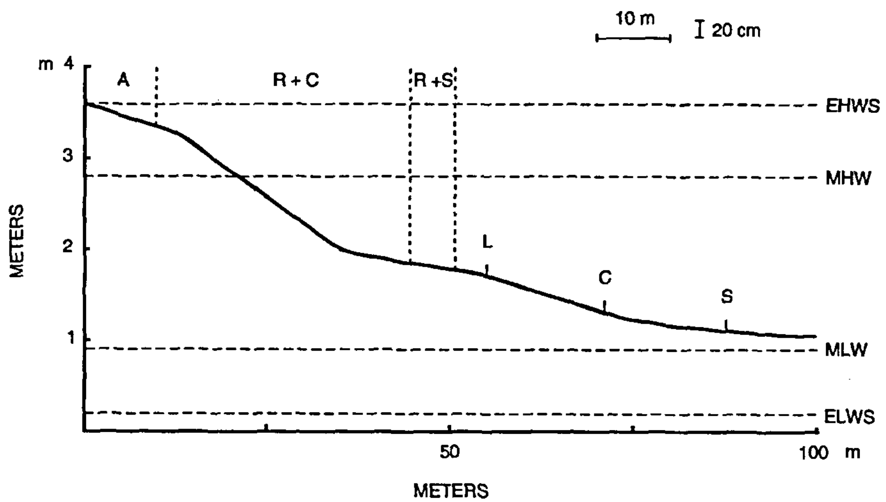

Figure 1 Section of shore along the study area: the three transects (L, landward; C, central; S, seaward) and the pattern of zonation of the main mangrove species (A, *Avicennia marina*; C, *Ceriops tagal;* R, *Rhyzophora mucronata*; S, *Sonneratia alba*) are represented. EHWS, Extreme High Water Spring; MHW, Mean High Water; MLW, Mean Low Water; ELWS, Exterme Low Water Spring.

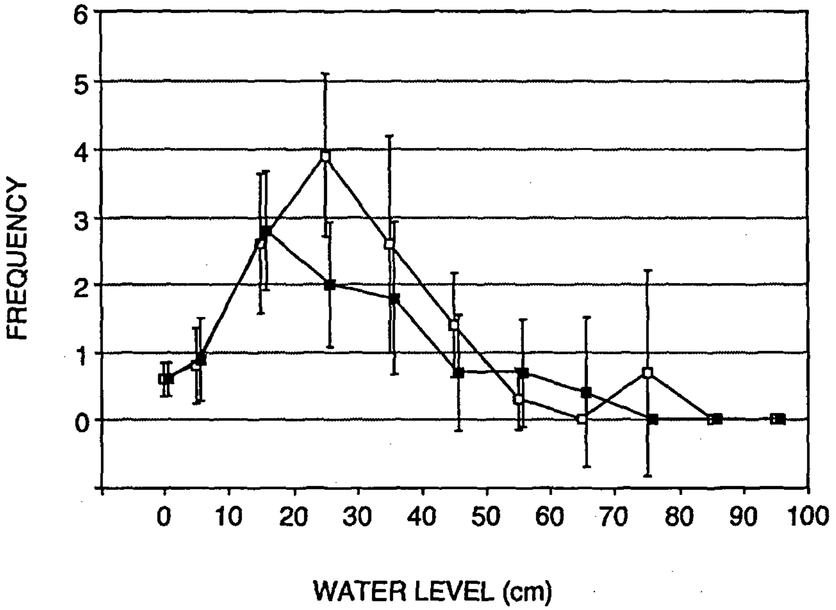

Figure 2 Frequency of specimens (number of crabs/10^3 m^2) during ebb and flow tides. The figure represents the number of moving crabs (± 5% confidence limits) sighted in diurnal and nocturnal surveys carried out during ebb and flow tides. Open squares = ebb tides; filled squares = flow tides.

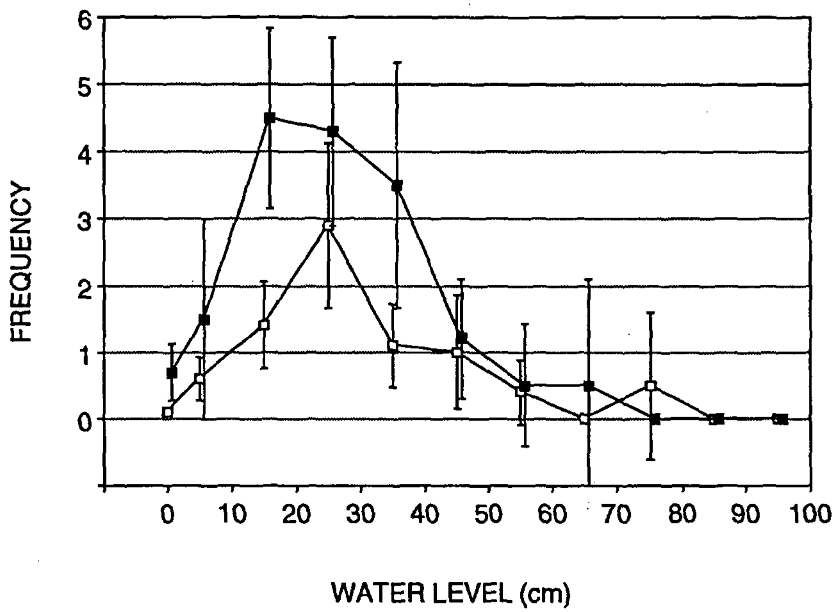

Figure 3 Frequency of specimens (number of crabs/10^3 m^2) during diurnal and nocturnal tides. The figure represent the number of moving crabs (± 5% confidence limits) sighted in diurnal and nocturnal surveys carried out during ebb and flow tides. Filled squares = nocturnal tides; open squares = diurnal tides.

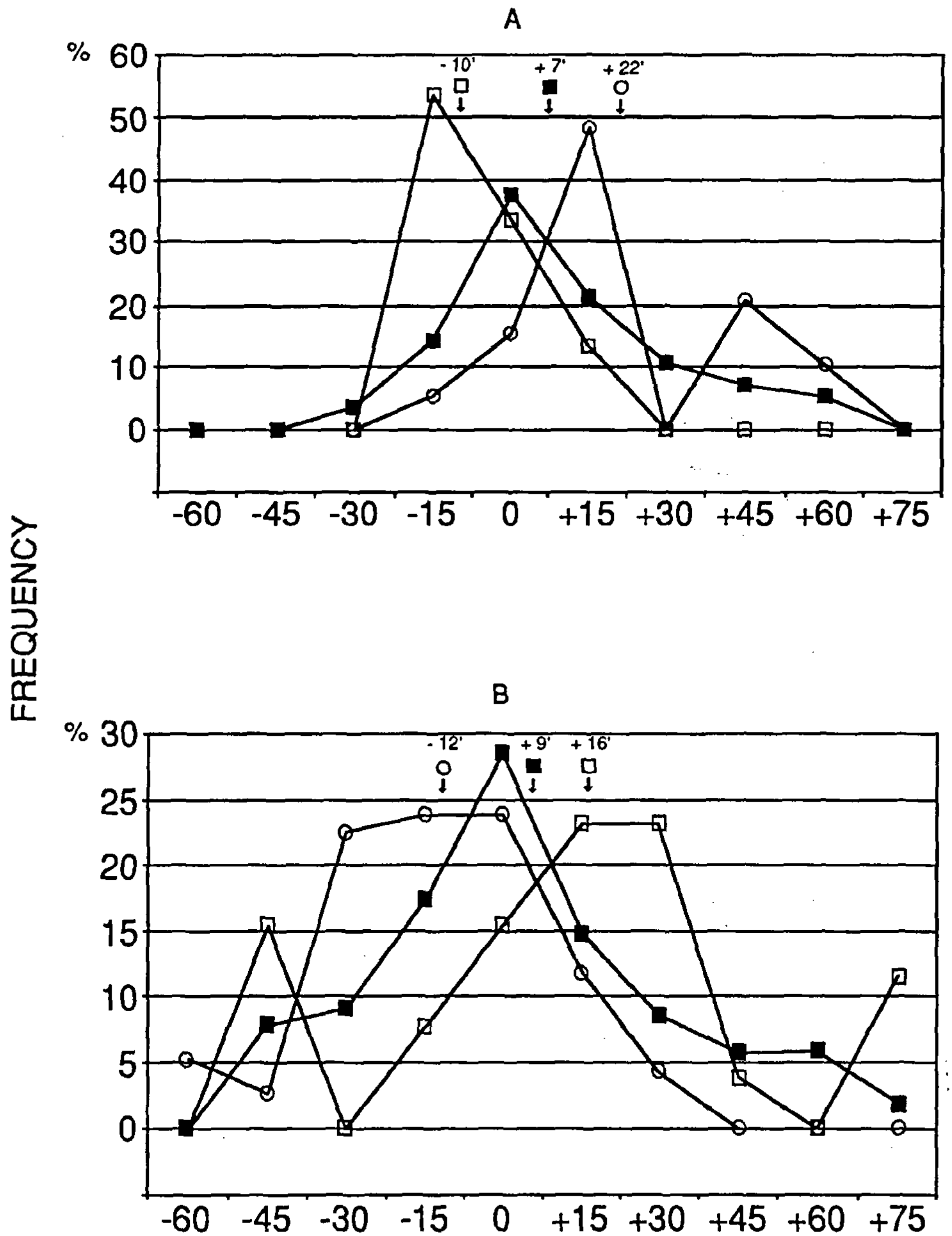

Figure 4 Relative frequency of specimens (number of crabs/10^3 m^2) during flow (A) and ebb (B) tides. The three lines represent the number of moving crabs sighted in diurnal and nocturnal surveys carried out along three different transects during ebb and flow tides: open square = seaward transect; filled square = central transect; open circles = landward transect. X axis = arbitrary time scale, where zero coincides with the water level with the highest frequency of crabs for the central transect. The numbers show the mean delay in crabs' activity in each transect. See text for further explanations.

Table 1 Water: mean delay (minutes) of the water in reaching the same level in two adjacent transects. Animals: mean delay (minutes) in crabs' activity in the seaward and landward transects in comparison with the central one. n: number of tides.

	Water	*SE*	*n*	*Animals*	*SE*	*n*
Flow Tide						
Seaward / Central	– 21'	± 7'	5	– 22'	± 9'	3
Central / Landward	+ 13'	± 1'	7	± 12'	± 3'	3
Ebb Tide						
Seaward / Central	+ 31'	± 4'	3	+ 3'	± 5	2
Central / Landward	– 22'	± 3'	6	– 22'	± 10'	2

Table 2 Mean number of sighted crabs per survey in an area of 10^3 m^2. Each value is the ratio of the number of crabs sighted and the number of surveys for each tract.

	Seaward transect	*Central transect*	*Landward transect*	*Mean*
Day	1.6	3.4	4.8	1.1
Night	4.8	9.7	8.8	2.9
Day + Night	2.9	5.4	6.4	1.7

The relationship between time and crab activity is given in Figure 4, where the mean number of crabs sighted in each strip is plotted against time for flow (Figure 4A) and ebb (Figure 4B) tide. The time is represented as advance or delay in sighting a crab, in comparison with the moment of highest activity in the central transect. The three transects were subject to flooding and exposure at different times. As Figure 4 shows, crab activity did not start simultaneously in the different transects. but at consecutive stages when the water reached the right level. Considering the different advances/delays in sighting each crab, it is possible to calculate a mean advance/delay in each transect. The difference between these values in adjacent transects, gives a mean advance/delay between transects. Comparing these values (Table 1) with the mean delay of the water (in reaching the same level in adjacent transects), we can see that there is good agreement. Comparing the three transects, we find a fall in the number of animals in a seaward direction, probably because the landward transect, near the mangroves, offers more food (Table 2). However, it should also be remembered that the crabs were easier to see in this transect because of the flat, muddy surface.

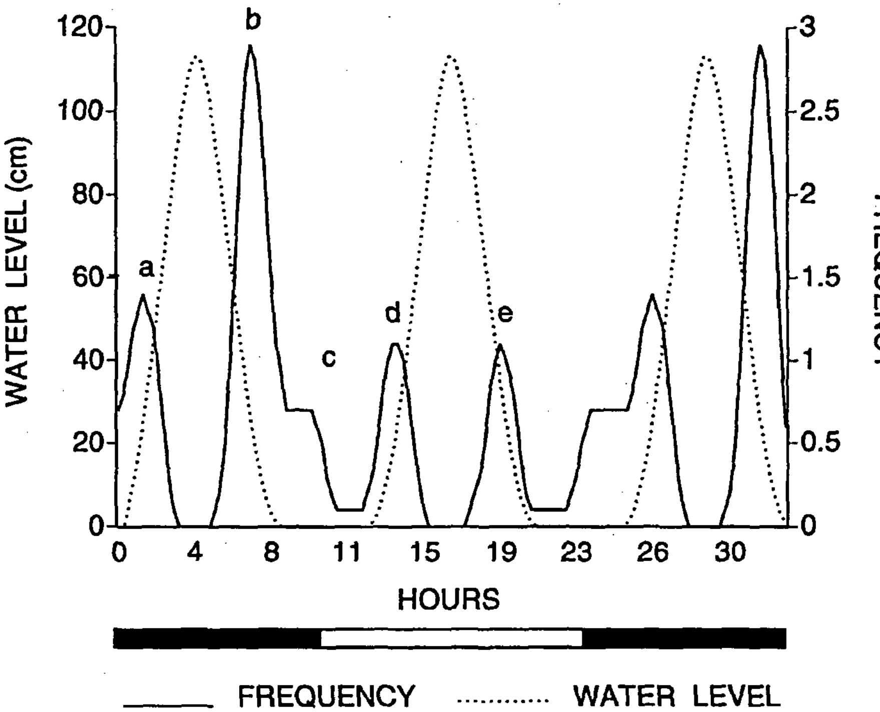

Figure 5 Activity model for *Thalamita crenata* between two nocturnal high tides. Dotted line = water level; solid line = frequency of crabs per 10^3 m^2; black bars = nocturnal hours; white bars = diurnal hours. See text for further explanations.

DISCUSSION AND CONCLUSIONS

These results show that *Thalamita crenata* is not active at either maximum low or maximum high water, but when the water level is 10–30 cm. These findings can be summarized in an activity model for *T. crenata* spanning a tidal day (between two nocturnal high tides) (Figure 5), which shows that *T. crenata* is mainly active at night.

During both night (Figure 5, activity peaks "a" and "b") and day (Figure 5, activity peaks "d" and "e"), *T. crenata* is less active at LW, reaches its maximum activity when the water level is between about 10 and 30 cm and then is inactive when the water is higher than 30 cm. Ecological values and physiological mechanisms can be invoked to explain this behaviour.

Ecological values

The mangrove swamp is characterized by the repeating pattern of tidal cycles during which the intertidal platform is exposed for a long time; thus a powerful swimmer like *T. crenata* would be expected to be especially active when the platform is submerged. Since activity outside its shelter involves higher predation risks during high water (HW), the crabs may move when the water level is too low for swimming predators, such as fishes, squids and other Portunid crabs (*Scylla serrata, Portunus pelagicus*), and hide when the water rises. At LW the most dangerous predators for the population under study are birds, such as the Crab Plover (*Dromas ardeola*), since they ambush the crabs in shallow water.

Thus the "activity windows" of *T. crenata* occur when the water level is too high to allow the birds to prey and too low for marine predators to swim freely.

Physiological mechanisms

As we have seen, activity of *T. crenata* is mostly concentrated in a "window" corresponding to a water level of 10–30 cm and does not last all through HW. This "window" is staggered in the three different transects because they are parallel to the shore and 16.5 m apart, and the water thus ebbs and flows earlier or later in each. The crabs should be synchronized differently on account of the 16.5 m difference (corresponding to about 20 minutes difference in activity peaks in adjacent transects). This suggests the presence of a pressure receptor capable of sensing the hydrostatic pressure and eliciting crab activity at the correct time. This is not the first time that such a mechanism has been proposed for the Crustacea. In *Macropipus holsatus* (Morgan, 1967) *Clibanarius virescens, Calcinus laevimanus* (Gherardi & Vannini, 1989) and *Clibanarius laevimanus* (Gherardi et al., 1991) among the Decapoda and *Synchelidium* (Enright, 1978) in the Amphipoda, the activity periods are probably determined by variations in hydrostatic pressure at different water levels during the tide. At present, two hypotheses can be proposed:

1. *Thalamita* does not possess a biological clock synchronized to the tidal cycles. Variation in hydrostatic pressure "switches" the animal's activity on and off.
2. A biological clock exists which is synchronized to the tidal cycles. Several variables associated with the tide are the entraining agents. Variation in hydrostatic pressure switches the crabs "on and off" during a "temporal window" which is matched to the ecological factors of the environment. Other intertidal Decapods, such as *Carcinus maenas* (Naylor, 1958; Naylor et al., 1971), *Palaemon elegans* and *P. serratus* (Rodriguez & Naylor, 1972) possess this kind of mechanism where tidal variables such as wave action are the entraining agents of a biological clock. Laboratory investigations could explain what mechanisms are involved in the activity rhythms of *T. crenata*.

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