Marine Biology 92, 425–430 (1986)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Dynamic zonation of *Nerita plicata*, *N. undata* and *N. textilis* (Prosobranchia: Neritacea) populations on a rocky shore in Kenya

R. K. Ruwa [1] **and V. Jaccarini** [2]

[1] Kenya Marine and Fisheries Research Institute; P. O. Box 81651, Mombasa, Kenya
[2] Department of Zoology, University of Nairobi; P.O. Box 30197, Nairobi, Kenya

Abstract

Vertical zonation of *Nerita plicata* Linnaeus, *N. undata* Linnaeus, and *N. textilis* Dillwyn, inhabiting the rocky cliffs of Nyali, Kenya, was studied through several spring-neap tidal cycles from November to December (northeastern monsoon) 1981 and May to July (southeastern monsoon) 1982. For the first time, a monsoon-related cycle of migration in *Nerita plicata* and *N. undata*, superimposed on the shorter term spring-neap cycle is demonstrated. Both species rest predominantly in the upper eulittoral zone and the littoral fringe. *N. plicata* and *N. undata* rest at significantly higher levels during the southeastern monsoon (SEM) than during the northeastern monsoon (NEM) ($P < 0.001$). On and around neap-tide days *N. plicata, N. undata,* and *N. textilis* occupy significantly distinct mean resting positions ($P < 0.001$) in both seasons; *N. undata* being the highest in the SEM, followed by *N. plicata,* with *N. textilis* always in the lowest level. In the NEM, *N. plicata* and *N. undata* sometimes change order. On and around spring-tide days in both seasons, the upper two species, *N. plicata* and *N. undata,* rest close together with no significant difference in their mean resting positions, but with both significantly higher than *N. textilis* ($P < 0.001$). Both the spring-neap and the monsoon migrations of *N. plicata* and *N. undata* are interpreted as either direct or indirect responses to wave action.

Introduction

Although there are some comparative descriptions of the zonations of the common *Nerita* species of the Western Indian Ocean (e.g. Ruwa, 1984), no detailed account of their zonation in relation to the neap-spring tidal cycle and the two contrasting seasons of the northeast (NEM) and the southeast monsoon (SEM) has been published.

According to the behavioural studies on the high-level rocky shore *Nerita* spp. carried out by Maxwell (1970), Hughes (1971), Warburton (1973), Zann (1973), Vannini and Chelazzi (1978), and Ruwa and Brakel (1981), the levels of these snails on the cliffs are mainly influenced by two physical factors, tidal fluctuations and wave action. Wave action, as well as many other environmental factors on the Kenyan coast, is notably influenced by the contrasting wind patterns of the NEM and SEM seasons. During the NEM season, from November to March, the sea surface is calmer than in the SEM season from April to October (Newell, 1957; Norconsult, 1977). The waves outside the fringing reef during the monsoons may reach 1 to 3 m in amplitude, with maximum heights occurring during the SEM (Norconsult, 1977). The tides at the Kenya coast are semi-diurnal. The extreme high-water spring level (EHWS) is 4.1 m, the mean high-water spring level (MHWS) 3.5 m, the mean high-water neap (MHWN) 2.4 m, the mean low-water neap (MLWN) 1.4 m, the mean low-water spring (MLWS) 0.3 m, and the extreme low-water spring (ELWS) –0.1 m (Brakel, 1982; Kenya Ports Authority, 1985).

The three species *Nerita plicata* Linnaeus, *N. undata* Linnaeus, and *N. textilis* Dillwyn, are the most mobile of the *Nerita* species inhabiting the rocky cliffs of Mombasa (Ruwa, 1984). Because of this mobility and the marked difference in physical conditions between the two monsoons, the zonation of these species was studied through several spring-neap tidal cycles under the different regimes of the two monsoons.

Materials and methods

The investigations were carried out from November to December (NEM) 1981 and from May to July (SEM) 1982 on the rocky cliffs of Nyali, on the mainland north of Mombasa island (Fig. 1). These cliffs, like most of the Kenya coast, are protected from severe wave action by a fringing reef whose seaward edge at Nyali lies about 1.8 km from the shore. The cliffs at this locality face

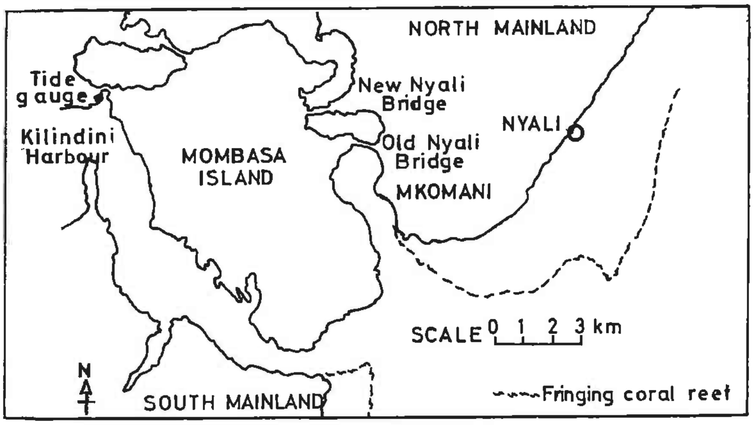

Fig. 1. Map of Kenya coast at Mombasa, indicating position of study site at Nyali

southeast. A full description of this study area, its faunal composition, and calibration of the shore levels above the Kilindini datum level is given by Ruwa and Brakel (1981) and Ruwa (1984). The rocky shore terminology of Lewis (1964) and Hartnoll (1976) is used in the present paper.

To detect the vertical changes in the mean resting positions of the populations of the three *Nerita* species, total daily (with occasional omissions) counts of individuals were made using 25 × 25 cm quadrats at one fixed 3 m-wide sampling site. Counting started from the base of the cliff upwards, to as far as the *Nerita* spp. individuals were encountered during the daytime low tide when they are in their resting positions. On each occasion, records of the number of individuals of each species in each quadrat and the level were noted. Daily mean resting heights above datum and the ranges of distribution were determined for each species. The differences between the mean heights of the resting populations of the different species as well as between these heights and the high-tide level were tested using the Student-Newman-Keuls (SNK) multiple-range test of significance as described by Zar (1974). The high-tide levels were determined from the Kenya Ports Authority tide tables for 1981 and 1982. Regression equations of the mean resting heights of the populations of each species against the high-tide levels from 2.5 to 3.6 m were also calculated for each season.

Results

Figs. 2 and 3 plot the mean resting heights of the three *Nerita* species over several spring-neap cycles for the two monsoons. It is clear from the figures that, firstly, the mean resting positions of the populations change with the spring-neap tidal cycle, reaching a maximum height around spring tides and a minimum around neap tides; and secondly, there is a seasonal difference, with the spring-neap cycles of *N. plicata* and *N. undata* being shifted significantly upwards during the SEM (Fig. 3). The amplitude of the spring-neap cycle of *N. undata* remains approximately the same in both seasons, while that of *N. plicata* is of much greater amplitude in the SEM. The amplitude of the cycle of *N. textilis* does not change with season, and is not shifted upwards; it consistently rests at the lowest level of the three species, the bulk of its population being submerged around spring high-tides, while the populations of *N. plicata* and *N. undata* are almost entirely above water during high tides.

For the period ±2 d around spring-tide days during the SEM (Fig. 3), *Nerita plicata* and *N. undata* occupy mean resting positions which are significantly higher than the mean high-tide level ($P < 0.001$, SNK test) and significantly higher than the mean resting level of *N. textilis* ($P < 0.001$, SNK test). The mean resting levels of *N. plicata* and *N. undata* are not statistically different from each other, and the mean resting level of *N. textilis* is not statistically different from the mean high-tide level.

For the period ±2 d around spring-tide days during the NEM (Fig. 2), the SNK test reveals that *Nerita plicata* and *N. undata* again do not occupy statistically different mean resting levels, but again both occupy significantly higher levels than both *N. textilis* and the mean high-tide level (in all cases, $P < 0.001$). However, unlike in the SEM, *N. textilis* occupies a significantly lower resting level than the high-tide level ($P < 0.001$).

During the period ±2 d around neap-tide days in both the NEM and SEM, all three species occupy significantly different mean resting positions (in all cases, $P < 0.001$, SNK test, except for *Nerita plicata* and *N. undata* in the NEM, which was $P < 0.05$). The order down the cliff is *N. undata, N. plicata, N. textilis* in the SEM (Fig. 3), while *N. undata* and *N. plicata* sometimes change order in the NEM (Fig. 2). All three species occupy significantly higher mean resting positions than the mean high-tide levels around neap tides (in all cases, $P < 0.001$, SNK test).

The upper limit of the eulittoral *Chthamalus* spp. at Nyali is about 4.2 m above datum. Thus, following the biological zonation scheme of Lewis (1964), which takes the upper limit of the barnactes as the upper limit of the eulittoral zone, *Nerita textilis* is clearly an upper eulittoral species throughout the year (Fig. 4). In contrast, *N. plicata* and *N. undata* occupy predominantly the littoral fringe on spring-tide days in the NEM and do so completely in the SEM (Fig. 4 A). On neap-tide days during NEM, *N. plicata* and *N. undata* occur predominantly in the upper eulittoral zone, while in SEM the former are still abundant in the up-

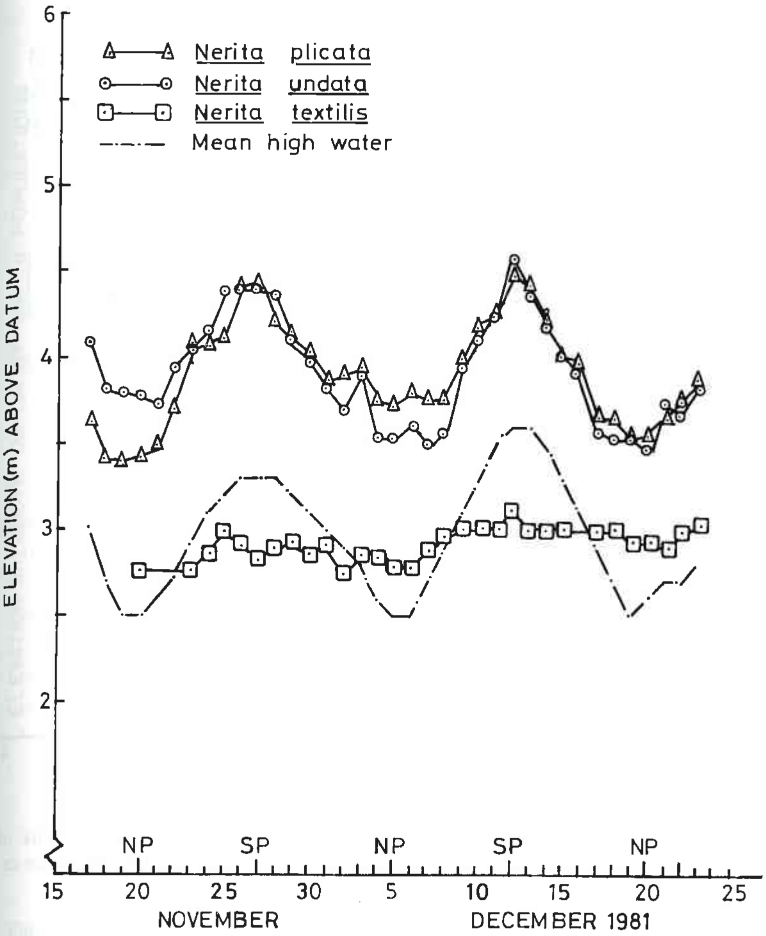

Fig. 2. *Nerita plicata, N. undata,* and *N. textilis.* Mean resting elevations of the populations during northeastern monsoon, over several neap-tide (NP) and spring-tide (SP) cycles

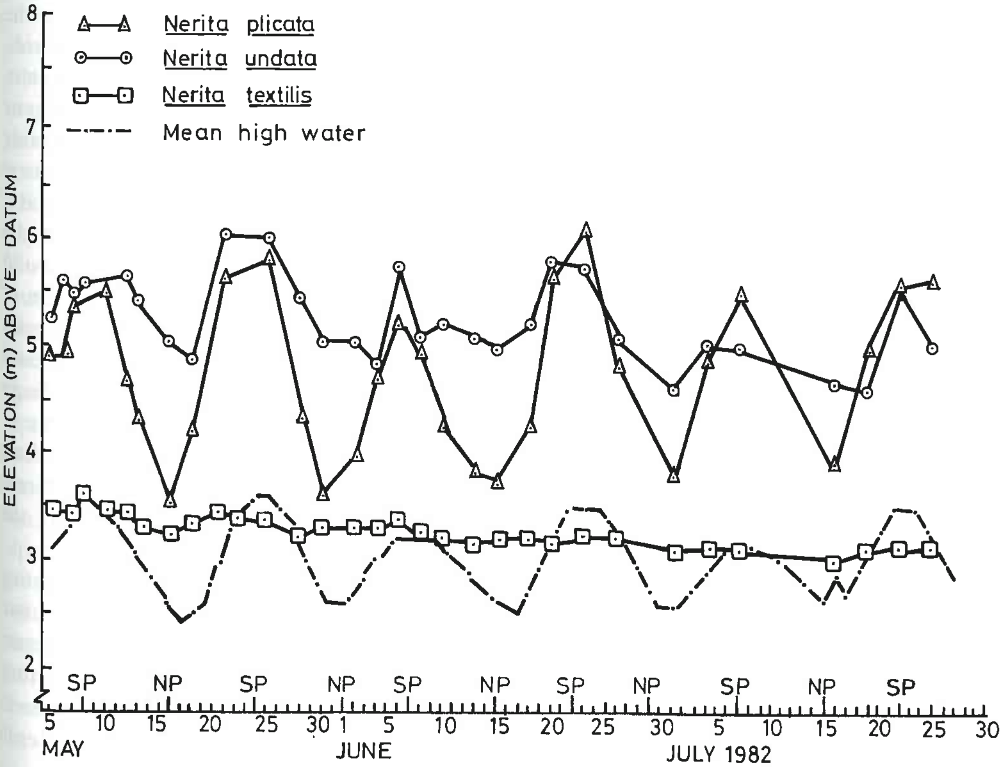

Fig. 3. *Nerita plicata, N. undata,* and *N. textilis.* Mean resting elevations of the populations during southeastern monsoon, over several neap-tide (NP) and spring-tide (SP) cycles

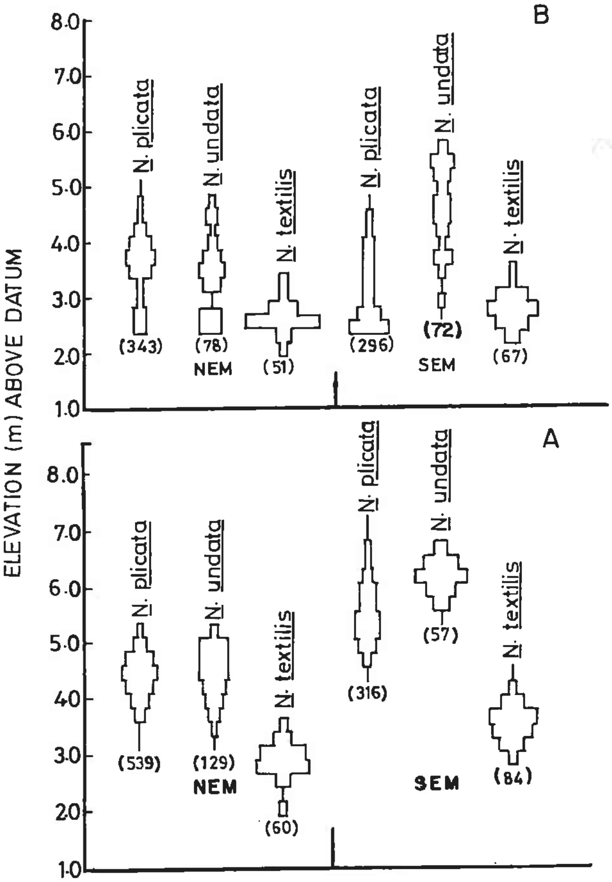

Fig. 4. *Nerita plicata, N. undata,* and *N. textilis.* Histograms showing resting distributions on (A) two spring-tide days, one during northeastern monsoon (12 December 1981) and one during southeastern monsoon (24 May 1982), and on (B) two neap-tide days, one during northeastern monsoon (5 December 1981) and one during southeastern monsoon (16 May 1982). Nos. in parentheses: no. of snails counted

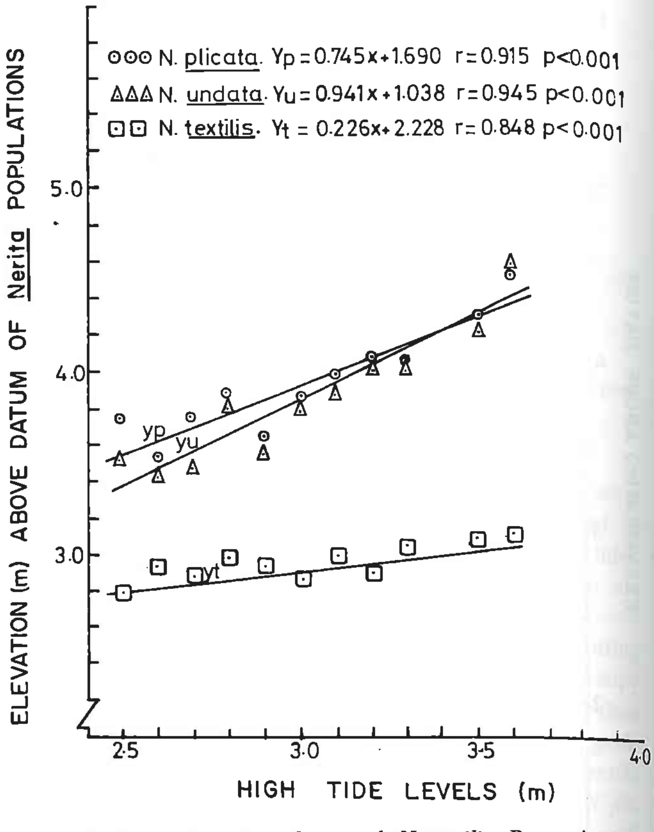

Fig. 5. *Nerita plicata, N. undata,* and *N. textilis.* Regressions of mean resting positions on high-tide levels from ca. MHWN to ca. MHWS during northeastern monsoon

per eulittoral zone but *N. undata* rests higher, predominantly in the littoral fringe (Fig. 4 B).

Figs. 5 and 6 present the regressions of the mean resting positions of the three *Nerita* species on high-tide levels from ca. MHWN to ca. MHWS in the two monsoons. All the correlations were highly significant, except for *N. textilis* in the SEM (Fig. 6). Comparison of the NEM and SEM mean resting positions within each species, revealed that both *N. plicata* and *N. undata* were significantly higher in the SEM (in all cases, $P < 0.001$, SNK test), while *N. textilis* showed no significant difference between seasons.

Discussion

The present study demonstrates quantitatively for the first time that *Nerita undata* exhibits a dynamic neap-spring periodicity in zonation similar to that described for *N. textilis* by Vannini and Chelazzi (1978) and for *N. plicata* by Ruwa and Brakel (1981). It is clear that the vertical migrations of the snails is causally related to the changing elevations of high tides.

This study also shows that for the same tidal heights there are differences between the two monsoons in the mean resting elevations of the two higher-level species, *Nerita plicata* and *N. undata.* These species rest higher in the SEM than in the NEM. This finding in itself suggests that wave action is either directly or indirectly responsible for the differences. The higher elevation in the season which is characterized by more vigorous wave action, is a temporal homologue to the spatial phenomenon of the higher zonation apparent on exposed rocky shores around the world (Lewis, 1964). Comparison of the zonation of these two neritids on exposed and sheltered shores reveals the same phenomenon of an upward shift on exposed shores (our own unpublished results). Clearly, *N. plicata* and *N. undata* are specialized for life in the splash zone or the littoral fringe. In the macrotidal regime of the East African coast, this zone displays vertical movements during the spring-neap cycle, and is elevated during the more vigorous SEM.

A comparison of the cycles of the mean resting elevations of *Nerita plicata* and *N. undata* in the two monsoon seasons suggests that *N. plicata* is more tolerant to wave action than *N. undata,* as evidenced by the much larger amplitude of the spring-neap cycle of *N. plicata* in the SEM (Fig. 3), with the result that around neap tides in

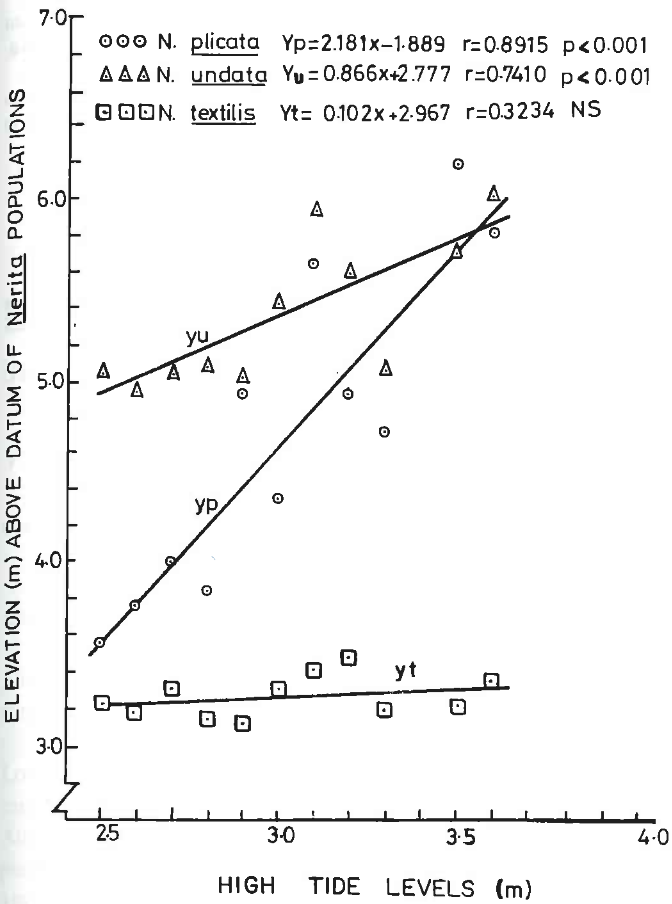

Fig. 6. *Nerita plicata, N. undata,* and *N. textilis.* Regressions of mean resting positions on high-tide levels from ca. MHWN to ca. MHWS during southeastern monsoon

this season *N. plicata* can rest much lower on the shore than *N. undata* (Fig. 4B). *N. plicata* is adapted for this lower resting position by being very robustly built, smaller, thicker-shelled, and more globular than *N. undata,* as well as being a more mobile snail. *N. undata* requires larger crevices in which to lodge than the smaller *N. plicata,* and consequently remains at an appreciably higher level than the latter when both species are at their lowest mean resting positions around neap-tide days. Going upwards from the upper eulittoral into the littoral fringe, the rock surface displays progressively larger holes and crevices. In the calmer NEM season, the two species tend to occupy the same mean elevation throughout the spring-neap cycle going up and down the shore together in phase with the spring-neap cycle of high tides. Around spring tides in both monsoons the two species occupy the same resting positions, since the higher and more vigorous wave action on the cliff face at this time make it advantageous for both species to rest well above high-tide level.

In all discussions of causal factors of animal behaviour one must make a clear distinction between ultimate causes acting through natural selection and proximate causes or stimuli acting as cues for the initiation and maintenance of behaviour. In the present discussion, confining ourselves to the ultimate causes of dynamic zonation, this may constitute an adaptive response of these gastropods to the danger of mechanical dislodgement by waves. Again, tidal wetting and wave action may affect the zonation of their preferred microalgal food and, hence, their own zonation. A third possibility is the effect of cyclical changes in physical environmental conditions such as wetness and temperature at given levels of the shore. Finally, a combination of some or all of the above factors may be involved.

In contrast to the other two species, the lower-level *Nerita textilis* does not change its mean resting elevation significantly with the monsoon seasons. Moreover, its spring-neap migrations are much less pronounced than those of the higher-level *N. plicata* and *N. undata.* Since *N. textilis* is regularly submerged by high tides it is not surprising that it does not show the same degree of response to wave action as that displayed by the two largely littoral-fringe species.

Nerita textilis, a definitely upper eulittoral animal, is clearly better able to resist dislodgement than the other two species. Observations of these snails on the shore confirmed that *N. textilis* are much more difficult to remove from the substratum; this is due to their stronger, larger foot. The lower shell profile of *N. textilis* also makes it better able to resist wave action. In line with this, *N. textilis* is the least mobile of the three species, showing a much less marked response to the neap-spring cycle and responses which are not significantly different between monsoons.

Acknowledgement. We thank the Director of Kenya Marine and Fisheries Research Institute (Mombasa), Mr. S. O. Allela, for his cooperation during this study.

Literature cited

Brakel, W. H.: Tidal patterns on the East African coast and their implications for littoral biota. *In:* UNESCO/ALESCO Symposium on the Coastal and Marine Environment of the Red Sea, Gulf of Aden and Tropical Western Indian Ocean. The Red Sea and Gulf of Aden Environmental Programme, Jeddah, Vol. 2. pp 403–418. Khartoum: ALESCO/UNESCO 1982

Hartnoll, R. G.: The ecology of some rocky shores in tropical East Africa. Estuar. cstl mar. Sci. *4,* 1–21 (1976)

Hughes, R. N.: Notes on the *Nerita* (Archaeogastropoda) populations of Aldabra Atoll, Indian Ocean. Mar. Biol. *9,* 290–299 (1971)

Kenya Ports Authority: Tide tables for East African Ports 1981, 48 pp. Mombasa: Rodwell Press 1981

Kenya Ports Authority: Tide tables for East African Ports 1982, 48 pp. Mombasa: Rodwell Press 1982

Kenya Ports Authority: Tide tables for East African Ports 1985, 48 pp. Mombasa: Rodwell Press 1985

Lewis, J. R.: The ecology of rocky shores, 323 pp. London: English University Press 1964

Maxwell, W. L.: An ecological study of *Nerita plicata* (Gastropoda) on the coast at Shimoni, Kenya. *In:* Final Report of University of Bristol Kenya Coast Expedition, pp 81–120. Bristol, U.K.: Bristol University 1970. (Internal publication)

Newell, B. S.: A preliminary survey of the hydrography of the British East African coastal waters. Fishery Pubis colon. Off. *9,* 1–11 (1957)

Norconsult A. S.: Mombasa water pollution and waste disposal study. Report to the Ministry of Local Government (Kenya), Part VI: Marine Investigations. No. 5, 16 pp. Nairobi: Norconsult A. S. 1977
Ruwa, R. K.: Invertebrate faunal zonation on rocky shores around Mombasa, Kenya. Kenya J. Sci. Technol., Nairobi (Ser. B) *5*, 49–65 (1984)
Ruwa, R. K. and W. H. Brakel: Tidal periodicity and size-related variation in the zonation of the gastropod *Nerita plicata* on an East African rocky shore. Kenya J. Sci. Technol., Nairobi (Ser. B) *2*, 61–67 (1981)
Vannini, M. and G. Chelazzi: Field observations on the rhythmic behaviour of *Nerita textilis* (Gastropoda: Prosobranchia). Mar. Biol. *45*, 113–121 (1978)
Warburton, K.: Solar orientation in the snail *Nerita plicata* (Prosobranchia: Neritacea) on a beach near Watamu, Kenya. Mar. Biol. *23*, 93–100 (1973)
Zann, L. P.: Relationships between intertidal zonation and circa-tidal rhythmicity in littoral gastropods. Mar. Biol. *18*, 243–250 (1973)
Zar, J. H.: Biostatistical analysis, 619 pp. Englewood Cliffs, N.J.: Prentice Hall 1974

Date of final manuscript acceptance: April 25, 1986.
Communicated by J. Mauchline, Oban