

# Nocturnal feeding migrations of *Nerita plicata*, *N. undata* and *N. textilis* (Prosobranchia: Neritacea) on the rocky shores at Mkomani, Mombasa, Kenya

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## Abstract

The vertical zonation of the three common rocky shore neritids at Mkomani, Mombasa, Kenya, *Nerita plicata* Linnaeus, *N. undata* Linnaeus, and *N. textilis* Dillwyn, as a function of feeding migrations and of size, was studied from 28 February to 24 March 1983. These snails perform feeding migrations at night starting at around mid-ebb tide and return to their resting positions with the flood tide. They remain in their resting positions throughout the day until the next nocturnal ebb tide. The direction of migration is size-related, with the larger snails of each species moving in the opposite vertical direction to the smaller ones, so that the populations as a whole exhibit no statistically significant net vertical displacement. The larger individuals of two of the species, *N. plicata* and *N. undata*, invariably move downwards to their feeding levels, while the smaller individuals move upwards; the larger individuals of *N. textilis* display a different pattern of migration, moving downwards on and around spring-tide days and upwards on and around neap tide days, while the smaller individuals move in the opposite directions. *N. textilis* rest above their feeding level around spring tides, and below that level around neap tides. It is demonstrated how these nocturnal migratory feeding rhythms are integrated into the spring-neap and seasonal cycles of the snails' daytime resting positions. The adaptive significance of these migrations is also discussed.

## Introduction

The extent to which the common rocky shore prosobranchs *Nerita plicata* and *N. undata* move between their resting positions during the day and their feeding levels at night has not been reported previously. Moreover, although the mean resting positions of these two species and of *N. textilis* during the day have been shown to be size-related (Ruwa and Brakel 1981, Ruwa and Jaccarini unpublished results), there

have been no investigations to show whether their feeding migrations are also size-related. The present study investigated the vertical range of movements between the overall mean resting and feeding positions and size-related displacements in each of these three species.

## Materials and methods

To compare the diurnal and nocturnal positions of the populations of the three commonest *Nerita* species, a quantitative study was carried out at Mkomani, Mombasa, Kenya, from 28 February to 24 March 1983. The description of the environment and the topography of the cliff has been given elsewhere (Ruwa and Jaccarini 1986). *N. plicata* Linnaeus, *N. undata* Linnaeus, and *N. textilis* Dillwyn were counted in 25 × 25 cm quadrats covering a 3 m-wide vertical belt of the rocky cliff and platform. Censuses were taken almost daily during both diurnal and nocturnal low tides. Histograms were drawn showing the distribution of each species at each census and the overall mean elevations calculated.

To discover if the diurnal resting positions and the nocturnal feeding migrations showed any relationship to snail size, all individuals in 25 × 25 cm quadrats were collected on a particular spring-tide day and the elevation of each quadrat was recorded. The individuals from each quadrat were measured with vernier callipers to the nearest 0.1 mm. The elevation of each individual was taken to be at the mid-point of the quadrat in which it was located. An adjacent section of shore with similar topography and density of snails was used for the nocturnal measurements. Sampling was performed on the night following the spring-tide day census, and similarly on the night after the neap-tide census. When the tide is at about mid-tide level during the nocturnal ebb tide, the snails start their excursion to their feeding grounds and when they reach this level begin audibly to scrape the substrate. Whilst feeding, the populations seem almost

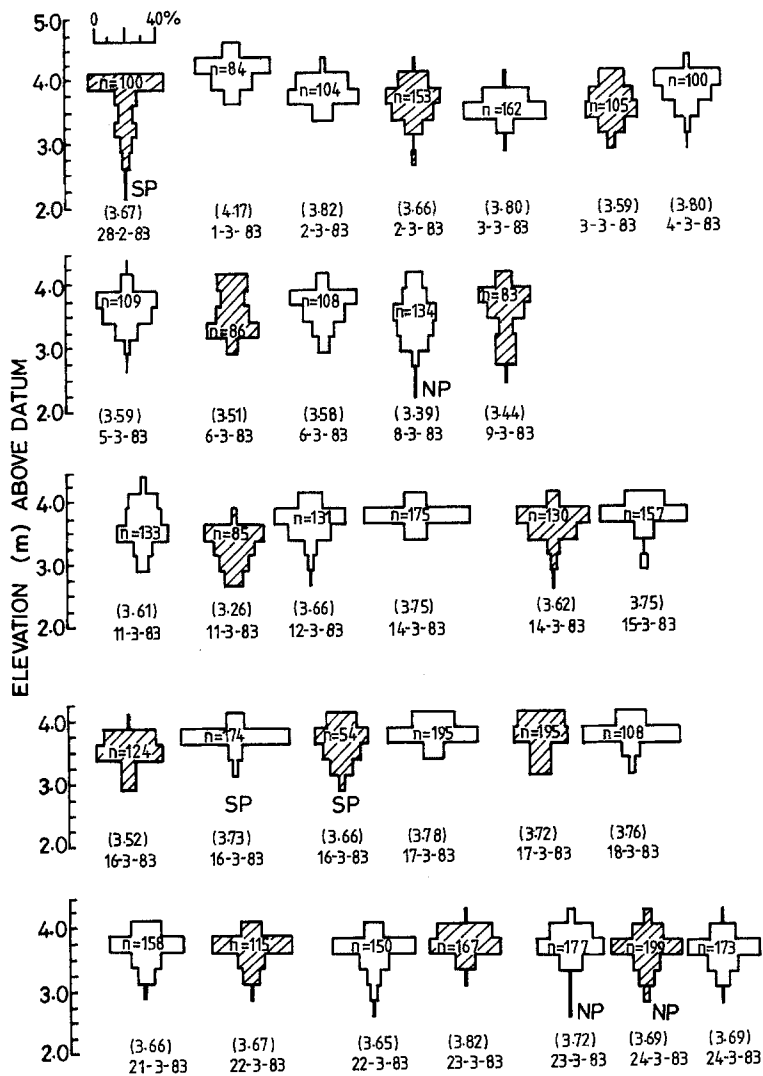


Fig. 1. *Nerita plicata*. Vertical distribution of snails at their day-time resting positions (open histograms) and night-time feeding levels (hatched histograms) in February and March 1983. n: total number of snails counted; mean height above datum, in m, is shown in parentheses. SP: spring-tide day. NP: neap-tide day

motionless. It was at this stage that nocturnal sampling was made by means of an electric torch-light. The regression of snail size against shore elevation was calculated by the method of least-squares for both diurnal and nocturnal determinations for each species.

The Student-Newman-Keuls (SNK) test (Zar 1974) was used to test differences between diurnal and nocturnal mean elevations of the *Nerita* populations around ( $\pm 3$  d) neap and spring tides. The SNK test was also applied to test for differences between diurnal and nocturnal mean elevations of the snails as a function of size (computed for 1 mm size-intervals from the regression equations of snail size vs elevation). The size ranges used for the comparison were 1.7 to 2.4 cm maximum linear dimension of shell in *N. plicata*, and 2.3 to 3.4 cm in both *N. undata* and *N. textilis*. These size ranges comprised the larger individuals in each species, i.e., those undertaking longer migrations. The lower size limits were chosen arbitrarily. The maximum linear dimension of neritids lies in the plane which bisects the aperture antero-posteriorly, the tip of the spire lying well outside this plane.

## Results

Observations of *Nerita plicata*, *N. undata* and *N. textilis* in the field showed that during the nocturnal ebb-tide a certain proportion of the individuals of all three species moved into the upper intertidal to feed. After reaching their feeding levels, the rate of net movement of individuals was barely perceptible. Despite the nocturnal feeding migrations, comparisons within each species revealed no statistical differences (SNK test, in all cases  $P > 0.05$ ) between diurnal and nocturnal vertical distributions (Figs. 1, 2 and 3). Analysis of their vertical distribution as a function of size clarified this unexpected result.

The regression curves of scatter diagrams of diurnal and nocturnal elevation as a function of snail size revealed opposite trends for larger and smaller individuals in each species (Figs. 4 and 5). The correlation coefficients for the two variables, snail size and elevation, were significant at the 5% level in only six out of twelve correlations (see legends to Figs. 4 and 5). However, a trend for smaller snails to move

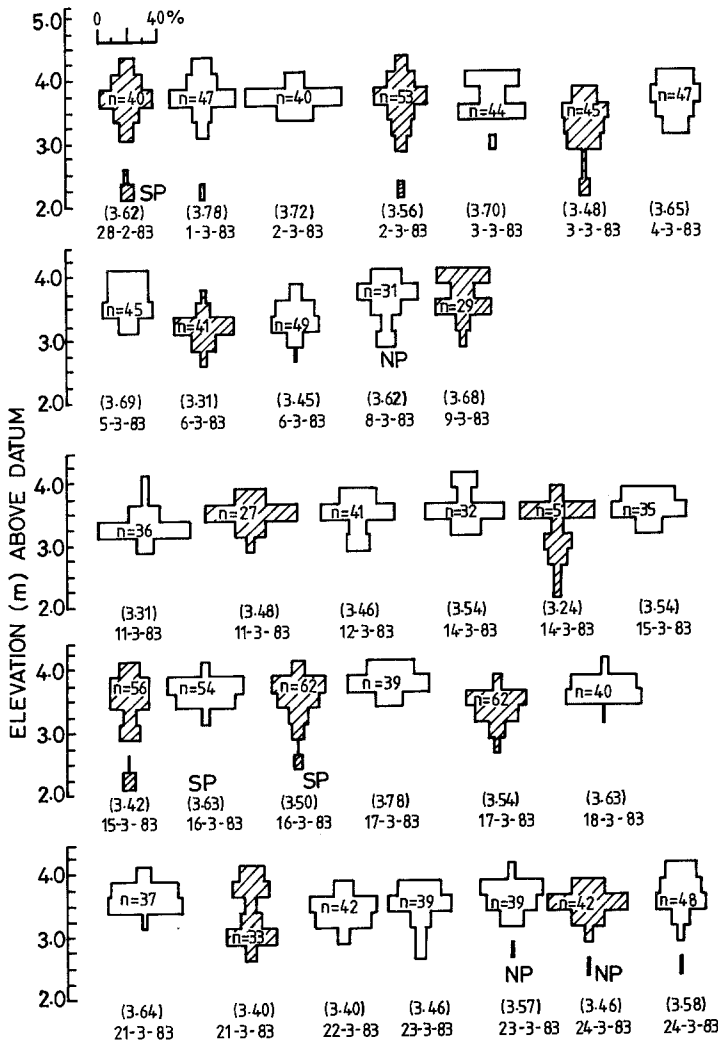


Fig. 2. *Nerita undata*. Vertical distribution of snails at their day-time resting positions (open histograms) and night-time feeding levels (hatched histograms) in February and March 1983. Further details as in Fig. 1

in the opposite direction to larger individuals was discernible from all twelve regression curves.

In both *Nerita plicata* and *N. undata*, the larger individuals moved downwards from their day-time resting positions to their night-time feeding levels, while smaller individuals moved upwards; therefore, the populations as a whole displayed no significant net vertical displacement. This occurred around both spring and neap tides, and presumably throughout the lunar tidal cycle. The SNK test revealed that the larger individuals of each of these two species were at a significantly higher level by day than by night around both spring and neap tides (in all cases,  $P < 0.001$ ).

*Nerita textilis* displayed the same absence of significant difference between the overall mean day resting position and the night-time feeding level, and the larger and smaller individuals again effected mean vertical displacements in opposite directions as indicated by the regression curves of size against diurnal and nocturnal elevation. However, while larger individuals of *N. textilis* moved downwards to feed around spring tides, they moved upwards to feed during neap tides. The SNK test also revealed that larger individuals of *N. textilis* were at a significantly lower elevation during nocturnal feeding than during diurnal resting around

spring tides ( $P < 0.001$ ), but were significantly higher at night than during the day around neap tides ( $P < 0.001$ ).

In all three species, night-time migrations (determined by the vertical difference between mean day and night heights within the different size classes) were more extensive during spring tides than neap tides (Figs. 4 and 5). The greatest differences were exhibited by *Nerita plicata* and *N. undata* during spring tides (SNK test,  $P < 0.001$ ).

In all three species, those individuals which had moved downwards to feed remained at their feeding levels until the incoming tide reached them. They then began to move upwards until they reached their resting position, which they maintained until their next nocturnal excursion. During the daytime, the snails displayed only a few occasional and highly restricted movements within their resting crevices.

## Discussion

### Migratory rhythms

Three principal, superimposed rhythms of vertical migration have been demonstrated for *Nerita plicata*, *N. undata*

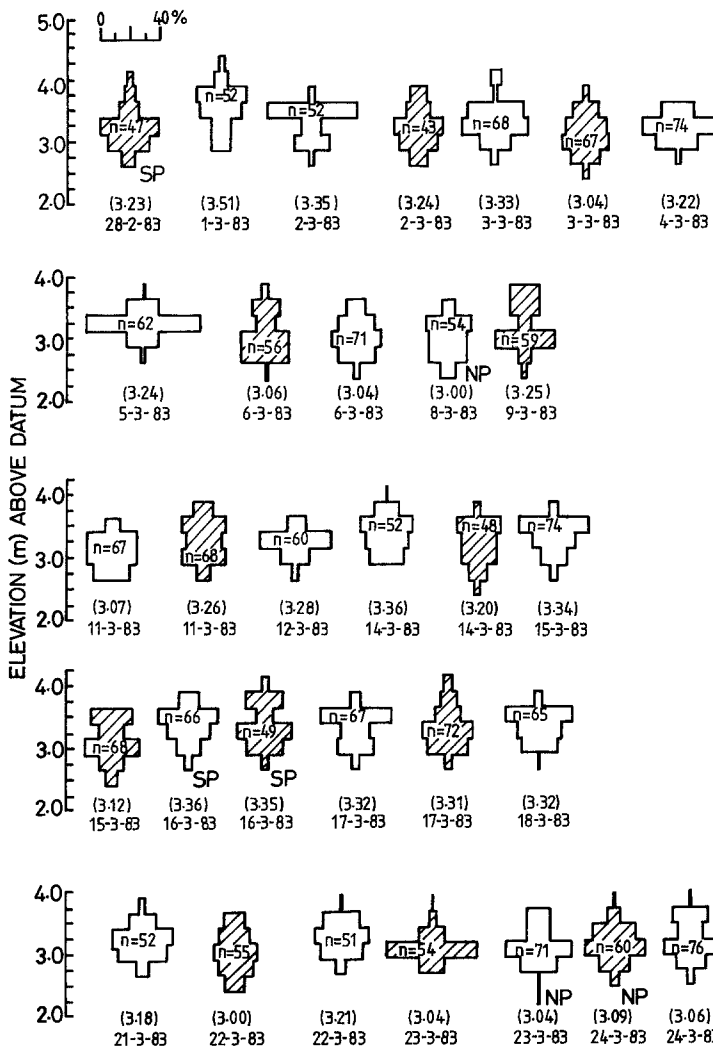


Fig. 3. *Nerita textilis*. Vertical distribution of snails at their day-time resting positions (open histograms) and night-time feeding levels (hatched histograms) in February and March 1983. Further details as in Fig. 1

and *N. textilis*: (1) a diel feeding migration during which the snails move to their feeding levels at the time of the nocturnal ebb tide, returning to their daytime resting positions with the flood tide and remaining there until the next nocturnal ebb tide (Maxwell 1970, Hughes 1971 a, b, Warburton 1973, Vannini and Chelazzi 1978, and present study); (2) a spring-neap cycle in the mean daytime resting positions, with peak elevations around spring tides and a trough around neap tides (Taylor 1971, Vannini and Chelazzi 1978, Ruwa and Brakel 1981, Ruwa and Jaccarini 1986, and present study); (3) a seasonal cycle superimposed on the spring-neap cycle with the snails resting at higher elevations during the southeast monsoon than during the northeast monsoon (Ruwa and Jaccarini 1986).

Considering the diel migration rhythm in more detail, the present study has shown that a certain proportion of the populations of *Nerita plicata* and *N. undata*, i.e., the larger more mobile individuals, migrate downwards during the nocturnal low tide. The mean diurnal and nocturnal positions of the larger snails were significantly different (SNK test,  $P < 0.001$ ). This is in substantial agreement with obser-

vations on neritids in other geographical areas (Maxwell 1970, Hughes 1971 a, Taylor 1971, Warburton 1973, Zann 1973 a, b, Vannini and Chelazzi 1978). The behaviour of *N. textilis* was somewhat different: the larger more mobile individuals of this species moved downwards at night during spring tides, but upwards during neap tides. The diurnal resting position of *N. textilis* fluctuates vertically with the spring-neap tidal cycle (Ruwa and Jaccarini 1986) and, since this position is close to the feeding level of the larger snails, the end result is that during the day the larger snails rest either slightly above or slightly below their nocturnal feeding grounds.

However, for all three species, there was no significant difference between mean resting position and mean feeding level of each population. Within each species, the smaller snails moved in the opposite direction to the larger snails (Figs. 4 and 5). This difference in migratory behaviour between large and small individuals of one and the same species has not been reported previously and is possibly a function of different food requirements by large and small individuals.

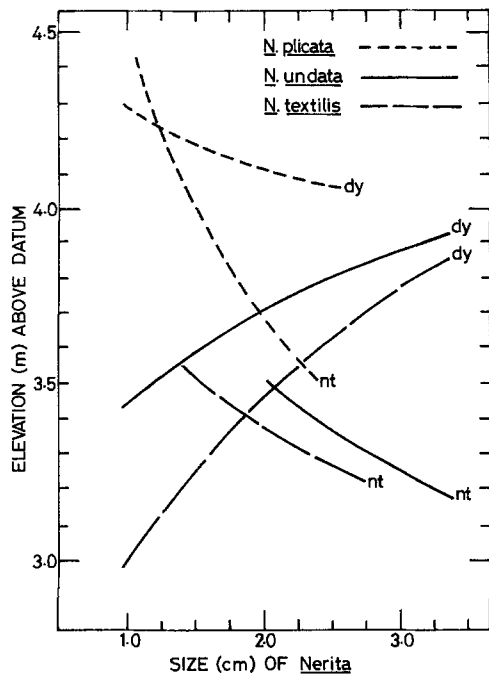


Fig. 4. *Nerita plicata*, *N. undata* and *N. textilis*. Trends of elevation above datum as a function of size during spring-tide day (dy) and during feeding on preceding night (nt).  $P$  values of correlation coefficients are: *N. plicata* at night -  $P < 0.01$ , by day -  $P < 0.05$ ; *N. undata* at night -  $P > 0.05$ , by day -  $P > 0.05$ ; *N. textilis* at night -  $P > 0.05$ , by day -  $P < 0.01$

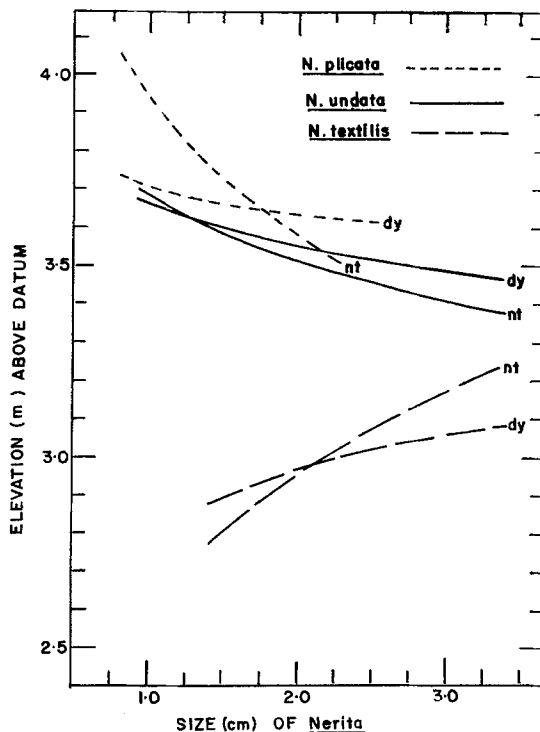


Fig. 5. *Nerita plicata*, *N. undata* and *N. textilis*. Trends of elevation above datum as a function of size during neap-tide day (dy) and during feeding on preceding night (nt).  $P$  values of correlation coefficients are: *N. plicata* at night -  $P < 0.01$ , by day -  $P > 0.05$ ; *N. undata* at night -  $P < 0.05$ , by day -  $P > 0.05$ ; *N. textilis* at night -  $P < 0.05$ , by day -  $P > 0.05$

### Control of migratory rhythms

The nature and timing of the migratory rhythms suggest that they are controlled by tides and tidal height, wave action, and diel endogenous behavioural cycles.

Comparisons between the mean resting levels of snails at exposed and sheltered localities (Ruwa and Jaccarini unpublished results) and between their positions during the rough southeastern and the calm northeastern monsoon regimes (Ruwa and Jaccarini 1986) strongly suggest that *Nerita plicata* and *N. undata* rest well above high-tide levels to avoid wave action. Moreover, their resting elevations display a conspicuous spring-neap periodicity (Ruwa and Jaccarini 1986). The two factors of tidal height and wave energy are synergistic, the height which the waves reach depending partially on tidal height.

The marked spring-neap cycle of their daytime resting elevations arises from the snails' diel activity pattern. The cue for the commencement of downward nocturnal feeding migration must be related to the receding tide, since the onset of migration always takes place around the middle of ebb-tide. On the other hand, since at the Kenyan site such migrations take place only during the night, some other factor must inhibit migration during the day. Surprisingly, this inhibiting factor does not seem to operate in the case of the *Nerita textilis* population of Sar Uanle, southern Somalia, for there, Vannini and Chelazzi (1978), while recording a similarly precise timing of the commencement of feeding migrations  $3.24 \pm 0.13$  h after high tide, observed that these migrations take place not only nocturnally but also diurnally. The cue for the commencement of the upward return migration of the larger *N. plicata* and *N. undata* after feeding is wetting or mechanical disturbance by the incoming tide. Finally, the cue to terminate this return migration is presumably the cessation of stimuli from the sea water. Since the vertical level at which this takes place rises and falls along the shore parallel to the tidal level of the spring-neap cycle, the mean resting level of the snails follows the same pattern. The stimuli to which the smaller snails respond must be at least partly different from those of the larger snails, since the smaller individuals are never covered by the tide.

*Nerita textilis* exhibits the same spring-neap and seasonal cycles in resting levels as the other two neritid species, and, like them, is active only during the nocturnal ebb tide. In other respects, *N. textilis* behaves quite differently; the day-time resting populations are largely covered by spring high tides and largely exposed at neap tide (the other two species rest above high tide during the entire spring-neap cycle). Moreover, the direction of feeding migration in *N. textilis* is opposite to that of *N. plicata* and of *N. undata* around neap tides.

### Function of migratory rhythms

The spring-neap and seasonal cycles of resting levels are of adaptive significance, in that they enable *Nerita plicata* and *N. undata* to rest throughout both the lunar and seasonal

cycles as close to their feeding grounds as avoidance of dislodgement by waves allows. This explanation has already been suggested to explain the spring-neap cycle in resting levels of *N. plicata* by Ruwa and Brakel (1981).

Nocturnal feeding excursions are interpretable as follows. The snails are more liable to be dislodged when the foot is retracted and the operculum closed, i.e., while resting, than when they are actively moving and feeding, when the large expanded foot holds them firmly to the substrate. Conversely, they are more subject to the dangers of desiccation, high temperatures, exposure to solar UV irradiation and predation when the foot is fully expanded than when it is retracted. It is therefore advantageous to shelter at a high level by day, thus avoiding all the above-mentioned dangers, and to undertake feeding migrations, with the better attachment which these involve, at night, when the dangers from exposure of their soft tissues are at a minimum.

The inverse directions displayed by larger and smaller snails during vertical migration are possibly related to differences in the food requirements of different size classes. This aspect requires further investigation.

Vannini and Chelazzi (1978) showed that, at Sar Uanle, *Nerita textilis* migrated around mid ebb-tide not only at night but also during the day, being most active between 12.00 and 24.00 hrs. This is strikingly different from the behaviour of *N. textilis* around Mombasa where, like the other two neritid species, it leaves its daytime resting position only during the nocturnal ebb tide. However, the two environments are not strictly comparable. Sar Uanle is more exposed to wave action, with a narrow platform which is emersed only during very low spring tides and whose edge is less than 0.4 km from the cliff base (Vannini et al. 1977), while the Kenyan coast south of Malindi is protected by a broad erosion platform which is emersed at all spring tides, the reef edge being 0.8 to 1.5 km from the cliff base. This difference is also reflected in the resting levels of *N. textilis*, which extend more than 2 m above mean high water spring level (MHWS) at Sar Uanle (Chelazzi and Vannini 1980), while at Mkomani *N. textilis* barely extend more than 0.8 m above MHWS. Due to the more wave-exposed conditions at Sar Uanle, the snails there would be subjected to less desiccation during the day-time.

Vannini and Chelazzi (1978) also observed that *Nerita textilis* were much more active during the first half of the night (18.00 to 24.00 hrs) than during the second half. Our observations are in agreement with this, not only for *N. textilis* but for *N. plicata* and *N. undata* also. However, we observed that the nocturnal migrations of all three species were greater around spring-tides than around neap-tides (SNK test, in all cases  $P < 0.001$ ), in direct contrast to the behaviour of *N. textilis* at Sar Uanle, which are more active and undertake more extensive migrations around neap tides than around spring tides (Vannini and Chelazzi 1978). A further difference is that the Somali population of *N. textilis* rests above its feeding level throughout the spring-neap cycle, while in Kenya the larger individuals rest above this level

around spring tides and below it around neap tides, so that in Kenya feeding excursions are undertaken in opposite directions at springs and at neaps. Not only the physical environment of the neritids at the Kenyan and Somali sites, but also the biological environment is different. *N. undata*, whose size-range largely overlaps that of *N. textilis*, is very abundant at Mkomani, Kenya, and it possibly preempts suitable resting sites, forcing *N. textilis* to occupy a lower level than that at Sar Uanle, Somalia. *N. undata* is much less common at the Somali site (Chelazzi and Vannini 1980), enabling *N. textilis* to expand its range upwards.

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