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I: Population dispersion and  
microhabitat selection

by  
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# ASPECTS OF THE BIOLOGY OF NATAL LITTORINIDAE: I. POPULATION DISPERSION AND MICROHABITAT SELECTION

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## ABSTRACT

A detailed study of the dispersion and population structures of three littorinid species (*Littorina africana*, *L. kraussi* and *Nodilittorina natalensis*) was undertaken in the intertidal zone at Chakas Rock on the Natal coast in an attempt to explain their sympatric occurrence.

*L. africana* is numerically the most abundant species and has the most extensive vertical range in the intertidal zone. In the upper midlittoral fringe, the ranges of the three species overlap and they show a marked preference for the same microhabitats, especially crevices. Young *L. africana* are continuously recruited in the lower mid-littoral and these move up the shore as their size increases giving rise to an upshore size gradient. Translocation experiments showed that size gradients are actively re-established by littorinids moved out of their normal habitats. Interspecific competition thus appears to be reduced by subtle differences in niche selection by the three species.

## INTRODUCTION

Species of the family Littorinidae occur worldwide on rocky seashores (Lewis 1964). Studies on their geographical distribution have been conducted throughout the world by Rosewater (1970) and on a more local scale by Barnard (1963). A few studies have been conducted on the intertidal ecology of the Natal coast (Stephenson 1944; Jackson 1976; Lambert 1981) which included littorinids, but apart from the studies on *Littorina knysnaensis* by McQuaid (1981), no detailed specific works have been published on the Littorinidae in South Africa.

The South African coast has been divided into three main biogeographical regions (Stephenson & Stephenson 1972; Kilburn 1982) by examining the dominant faunal elements in each. These are: the cold West Coast, the warm-temperate South Coast and the tropical/subtropical East Coast. If the littorinid zones in each of these subregions are considered, it is evident that the south and west coasts support substantial populations of one species (*L. knysnaensis*), while the east coast supports at least six species (Fig. 1). Several of these can be found sharing the same microhabitats, especially on the Natal coast.

As a result of *L. africana* and *L. knysnaensis* occurring sympatrically throughout much of their range on the east coast, some controversy has arisen with regard to their status. Hughes (1979) suggested that these two forms represent a dimorphic species showing a generic cline correlated with latitude. For the purposes of this study, however, the classification according to Rosewater (1970) and Kilburn (1972) was adopted which considered the two forms to be separate species.

Aspects of the biology of three Natal littorinid species (*L. africana*, *L. kraussi* and *Nodilittorina natalensis*) were investigated at Chakas Rock, on the Natal coast, in an attempt to explain how they are able to maintain apparently viable populations in the same region. This investigation, therefore, gave attention to dispersion of the three species in the intertidal zone, including preferences for specific microhabitats and the maintenance of zonation patterns.

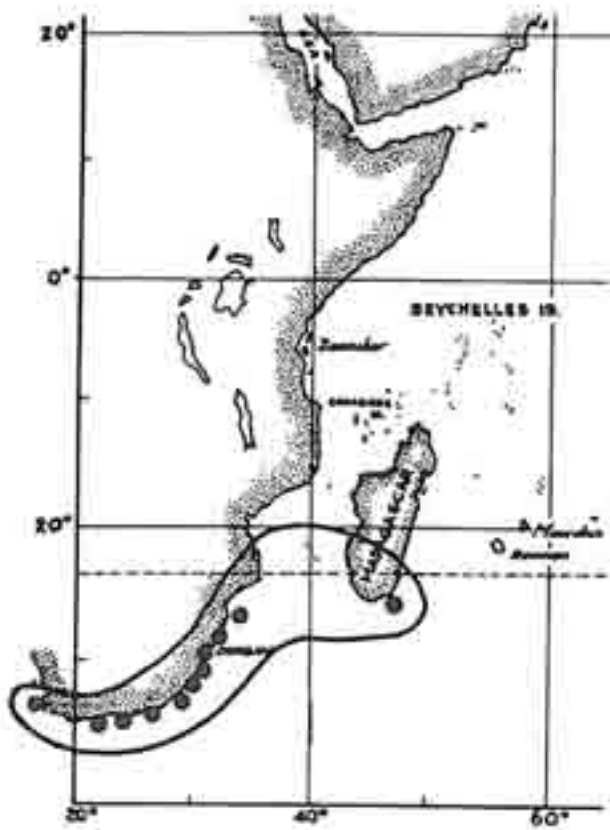
## METHODS

Chakas Rock (19° 31' S, 31° 15' E), situated approximately 45 km north of Durban on the east coast of South Africa, was chosen as the study site. It comprises a large outcrop of Middle Ecca Sandstone (Jackson 1976) which faces approximately 10° north of east to seaward. The rocks

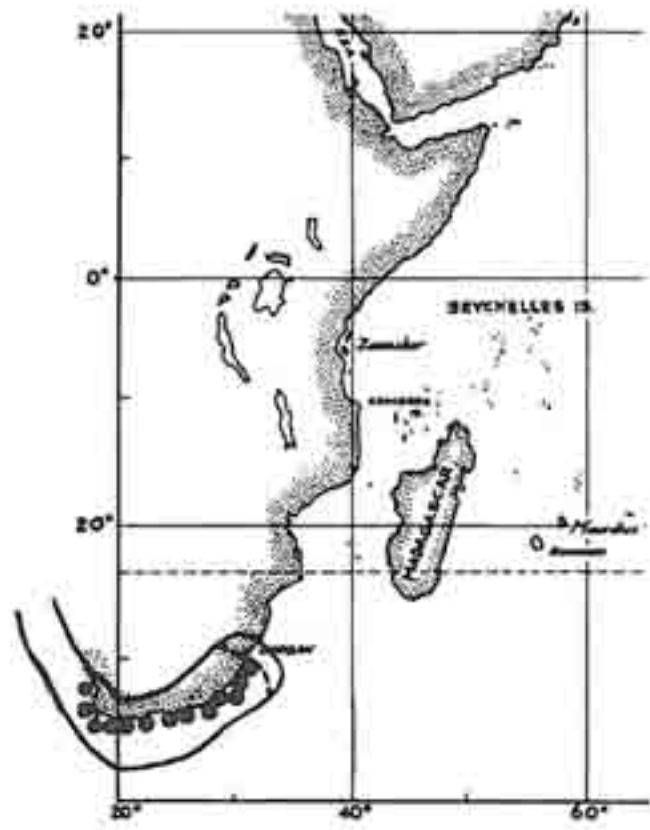
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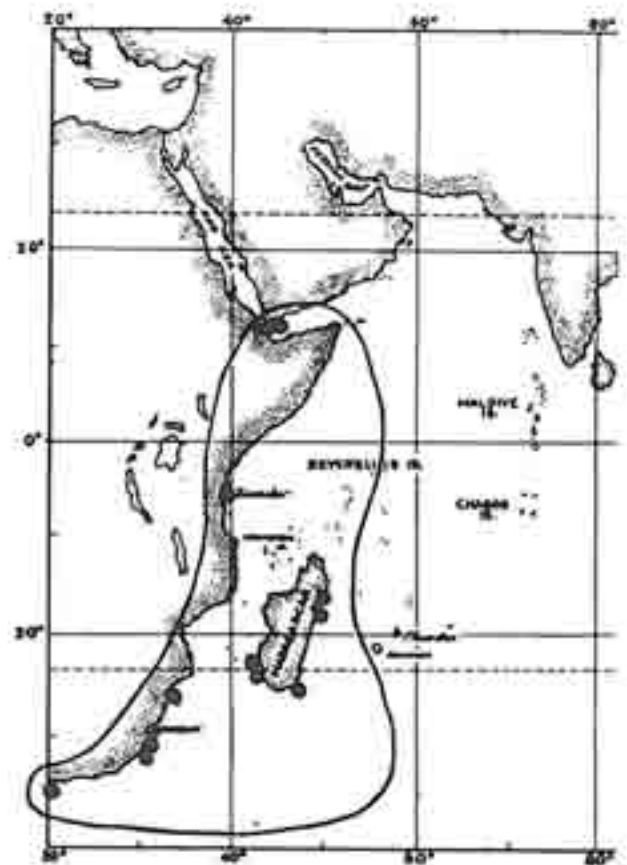
Littorina africana



Littorina knysnaensis



Littorina kraussi



Noxillittorina natalensis

Fig. 1. Distribution maps of the four main littorinid species on the east coast of South Africa. After Rosewater 1970 (modified).

form several platforms and pools and encompass a variety of shore profiles, ranging from near perpendicular to gradual slopes.

Sampling was conducted on a monthly basis from March 1983 until June 1984. Initially sampling was planned to coincide with spring tide, but later this was changed to include all phases of the tidal cycle, thus eliminating any temporal bias.

#### *Population dispersion*

Three transects, extending due east, were surveyed across the shore at Chakas Rock which were selected to represent different profile gradients. The three transects, named Chakas Rock, Cave Rock and Flat Rock, were subdivided into convenient regions which were used throughout the study period. These regions were related to the rock topography and slope such that each transect was divided into five areas. Stratified random quadrats were placed in each of these regions, using a table of random numbers (Campbell 1967) until approximately 20 replicates per region were counted. Total numbers of each species per 0.025 m<sup>2</sup> quadrat were recorded for each replicate. From this the mean number of each species per region, the standard deviation, variance and variance to mean ratios were calculated.

Information was recorded during the sampling, as to whether individuals were living in crevices, rock pools or on vertical surfaces. All others were considered to be on horizontal surfaces. The relative abundance of each type of microhabitat within the three transects was also determined.

#### *Size gradients*

Specimens of *L. africana* were collected monthly from upshore and downshore regions of each transect and measured using a Vernier caliper. Although accurate, this method was found to be very time consuming and a more efficient measuring tool, consisting of a 3 mm thick perspex strip with a series of holes from 2 mm to 18 mm diameter drilled into it, was made. By matching the long axis of the snail with the smallest hole through which it passes, the snails could be rapidly sorted into 2 mm size classes (eg. 4-6 mm).

In order to eliminate any size bias as a result of manual selection, specimens were collected by placing a 0.025 m<sup>2</sup> quadrat on the rock and brushing all the enclosed snails onto a sheet of paper, using a paintbrush. All the snails collected were measured and the data collected were used to determine the size frequency distribution.

#### *Translocation experiments*

Experiments were conducted to determine whether *L. africana*, moved out of their natural habitat (or zone), would move back to their original collection site.

Fifty adult *L. africana* were collected from the upshore region, dried on tissue paper, marked with quick drying non-toxic enamel paint and moved to an established point in the downshore region (downshore experimental sample). Fifty *L. africana*, collected from the downshore region, were marked with a different colour and replaced around a second point on the rocks in the same vicinity (downshore control). A further 50 juvenile *L. africana*, collected from the downshore region were marked and moved to an upshore site (upshore experimental). Finally, a control of 50 snails collected at this site were marked and replaced around a fourth point (upshore control). The two localities were 12 m apart with a difference in elevation of approximately 1.5 m.

The movement of the snails was monitored every low tide over a period of four days. The distance each snail had moved from the central cross was measured using a tape measure, taking into account the topography of the rocks. The direction in which the snails moved was determined by taking a bearing from each point of release with a liquid-filled magnetic

compass. It was also noted whether or not the specimens moved towards crevices or pit holes.

Rosettes were drawn up by summing the number of snails moving in each 30° segment, i.e. those moving from 0-29°, 30-59° and so on. The shoreline was considered to face due east so that the number of snails moving upshore, downshore or longshore could be calculated by referring to the divided rosette (Fig. 2). The mean distance moved each day by *L. africana* was calculated and plotted for control and experimental animals in each zone.

In a separate experiment, *Littorina kraussi* and *Nodilittorina natalensis*, which are found mainly on the upshore regions, were moved downshore to the proximity of the LWN mark in order to determine their subsequent movements. Fifteen specimens of each of the above species were moved downshore, along with 15 large *L. africana*, to serve as a comparison. They were marked with enamel paint and monitored as in the previous experiment. No control animals were used, as *L. kraussi* and *N. natalensis* do not occur naturally in the lowshore region. The same analysis and graphical representations were carried out with the data collected.

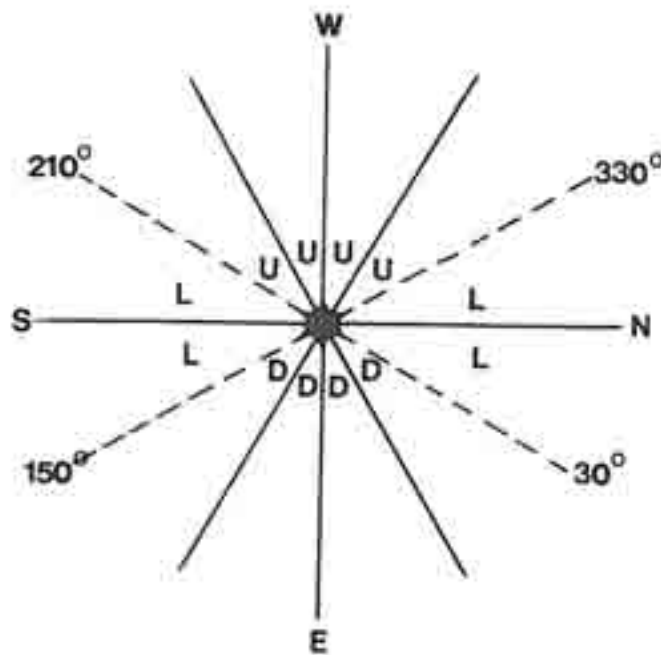


Fig. 2. The division of possible movements measured for littorinids during translocation experiments. This was subdivided further into upshore (U), downshore (D) and longshore (L) movements, according to the above diagram.

## RESULTS

### *Population dispersion*

From the initial sampling, it became apparent that all three species showed a tendency to occur in aggregations, either in crevices and other depressions in the rock, or around rock pools. Hence, the data collected needed to be tested for normality to allow the application of standard statistical methods. The most frequently applied test for randomness in the dispersion of organisms is the variance to mean ratio, or Index of Dispersion (Elliott 1977). This ratio will approximate to unity for a randomly dispersed population in which the data will conform to a Poisson series. Any values which are found to be significantly higher than one, indicate a contagious distribution.

Although random distributions were shown by all three species in some instances, the majority of the samples taken (ie. 87.7% for *L. africana*, 67% for *L. kraussi* and 85.5% for *N. natalensis*) indicated a significantly contagious distribution ( $P < 0.05$  in all three species). The random and regular distributions which did occur were from uniform localities, such as smooth rock faces devoid of crevices and pit holes. The clustering of individuals in all other areas supported the hypothesis that such features attract the snails.

The mean numbers of *L. africana* per quadrat at each level of the three transects, listed in Table 1, display several trends. There were far greater numbers along the Chakas Rock transect than along the other two. Within each transect, the trend was for numbers to be low upshore (levels 1 and 2) increasing to a peak, usually at levels 3 and 4, and then decreasing again. Peak densities could reach over 6000  $m^{-2}$ . The mean density of *L. kraussi* per quadrat was considerably lower than for *L. africana* (Table 1). *L. kraussi* tended to occupy only the upper two levels along all three transects, with numbers decreasing from level 1 downwards. Cave Rock supported the largest population of *L. kraussi* of the three transects, with a peak density of 250  $m^{-2}$ , while Flat Rock had fewer specimens, presumably due to the open unsheltered nature of the transect. Juvenile *L. kraussi* occurred only at the Cave Rock transect.

*Nodilittorina natalensis* occurred in greatest numbers at Chakas Rock, with considerably fewer at Cave and Flat Rocks (Table 1). The spread of the individuals for this species among the levels followed the trends shown by *L. africana* and *L. kraussi* mentioned above: at Chakas and Cave Rocks, highest densities were recorded at level 2, with smaller numbers above and below, while the Flat Rock transect displayed a gradual decrease in numbers from level 1 to 3. Their position on the shore appears to be amongst the *L. africana* and normally lower downshore than *L. kraussi*. The peak density reached by *N. natalensis* was 2000  $m^{-2}$ .

Table 1: Mean number of *L. africana*, *L. kraussi* and *N. natalensis* occurring in each level on three transects (per 0.025  $m^2$  quadrat).

Species	Level	TRANSECT		
		Chakas	Cave	Flat
<i>L. africana</i>	1	4.96	0.20	6.80
	2	39.75	8.32	16.04
	3	51.99	14.40	37.41
	4	44.22	43.39	36.69
	5	39.82	35.87	20.63
<i>L. kraussi</i>	1	0.61	3.50	0.08
	2	0.17	0.83	0.02
	3	0.01	0.07	0.00
	4	0.00	0.00	0.00
	5	0.00	0.00	0.00
<i>N. natalensis</i>	1	2.29	0.43	1.57
	2	3.68	1.33	0.64
	3	0.99	0.24	0.00
	4	0.00	0.00	0.00
	5	0.00	0.00	0.00

The relative proportions of snails occupying the four microhabitat types showed an unequal distribution pattern (Table 2). All three species relied on crevices in the upshore region ( $P < 0.05$ ) even more than would be expected when one considers the low relative proportion of this microhabitat. In the lowshore region, however, *L. africana* was found predominantly on horizontal surfaces, while *N. natalensis* occurred mainly on vertical surfaces. No deviation from this microhabitat distribution pattern was detected between summer and winter months or between spring and neap tide periods. *Littorina pintado pintado* (Wood 1828) and *L. undulata* (Gray 1839), which were rarely found at the study site, occurred amongst *L. kraussi* in the upshore regions.

Table 2: Relative proportion (RP) of *L. africana*, *L. kraussi* and *N. natalensis* occurring in four microhabitats over a six month period. Figures are percentages found on vertical faces (V); horizontal surfaces (H); tide pools (T) and crevices (C). "n" denotes number of individuals counted. RPM denotes the relative proportion of each microhabitat available to littorinids.

SPECIES	n	Microh	RP		RPM
			Upshore	Downshore	
<i>L. africana</i>	30659	C	33.51	18.86	11.30
		T	20.39	4.54	12.00
		V	16.94	33.83	37.30
		H	29.29	42.76	39.30
<i>L. kraussi</i>	531	C	50.66	—	11.10
		T	3.40	—	16.67
		V	32.51	—	37.78
		H	13.42	—	34.44
<i>N. natalensis</i>	1288	C	46.01	6.72	11.30
		T	10.66	32.84	12.00
		V	13.69	46.76	37.30
		H	23.92	12.69	39.30

### Size gradients

Accurate measurements of *L. africana*, showed a definite gradation in the size up the shoreline, with the smallest individuals occupying the lowest position on the shore (Fig. 3). The same size gradient was shown by size frequency histograms (Fig. 4) where it is also evident that much greater numbers occurred in the lower zone than in the upper zone.

If these size frequency histograms are considered on a monthly basis, it is evident that a unimodal distribution of size classes exists (Fig. 4). There are large increases in the 2-4 mm size class in the lower zones of both Chakas and Cave Rocks during March and June, which could indicate waves of recruitment of juveniles from the sea. Corresponding increases in the numbers of the smallest size classes in the upper zone were evident during the same months, especially at Cave Rock (Fig. 4), and this could indicate an upward migration of larger subadult snails from the lowshore.

The size distribution found in *L. africana* was not evident for either *L. kraussi* or *N. natalensis*, as their dispersion was far more localised. The modal size of *L. kraussi* varied

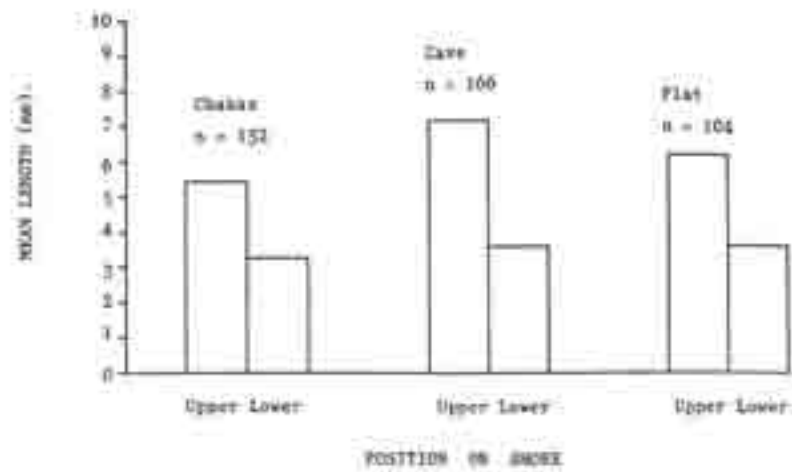


Fig. 3. The relationship between the mean length of *L. africana* and position on the shore at three transects.

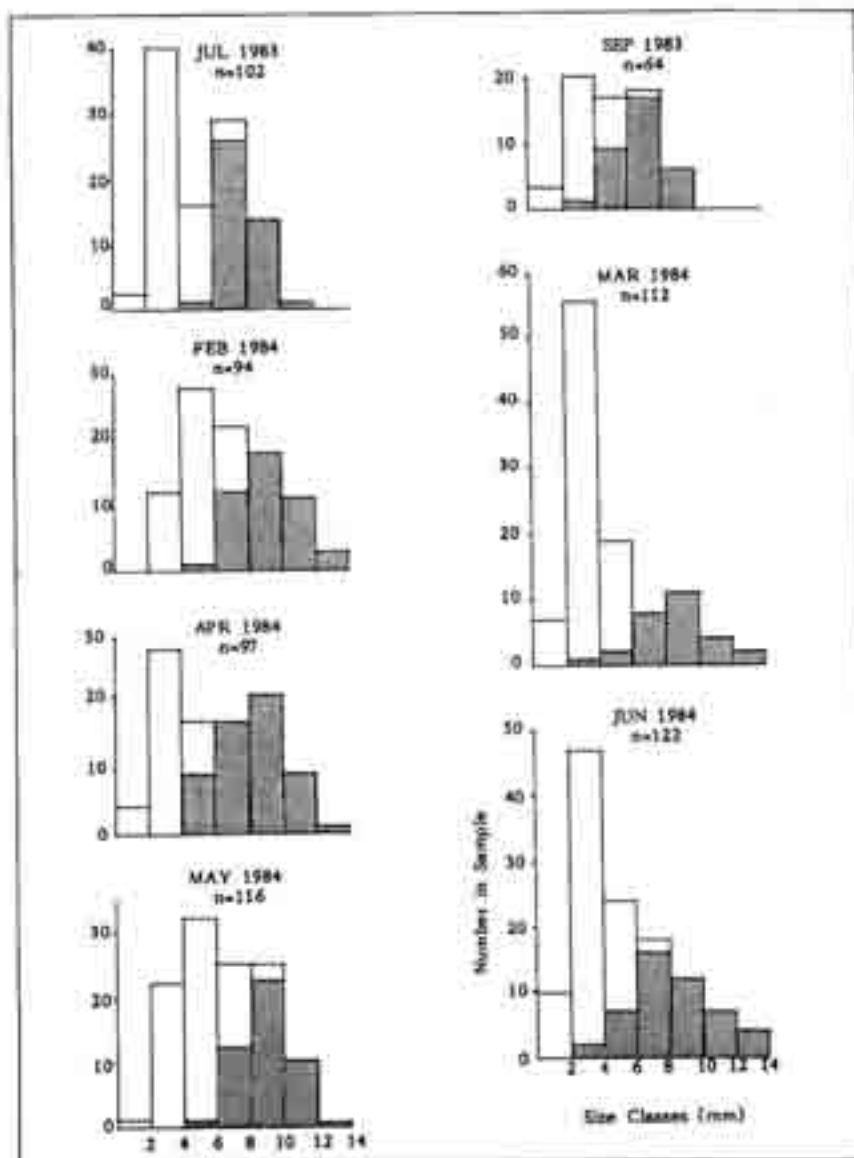


Fig. 4. Size frequency distribution of *L. africana* at Cave Rock; Key: □ Downshore; ■ Upshore. Numbers per 0.025 m<sup>2</sup> quadrat.



between 12 and 16 mm (Fig. 5) over a five month period, while that of *N. natalensis* remained stable at 6-8 mm (Fig. 6).

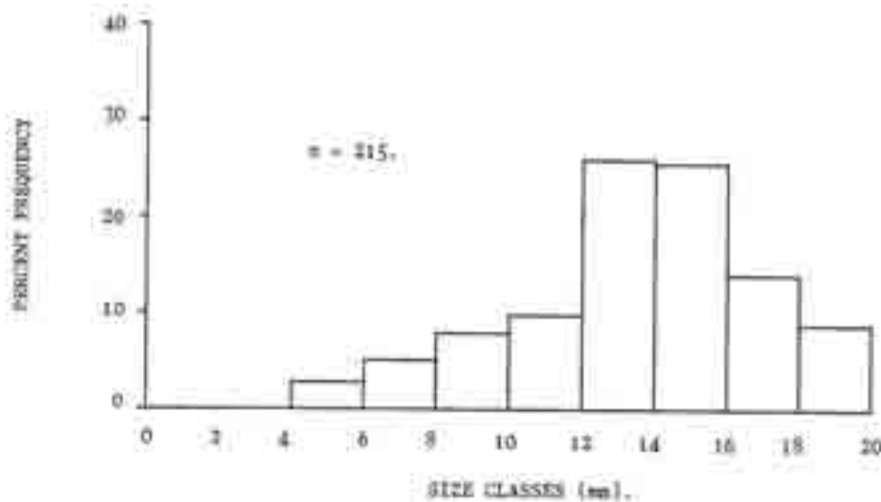


Fig. 5. Size frequency distribution of *N. natalensis*.

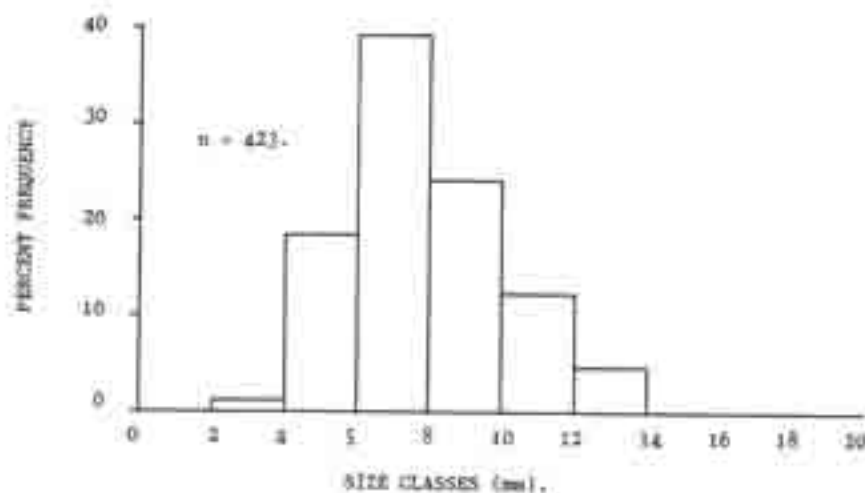


Fig. 6. Size frequency distribution of *L. kraussii*.

### Translocation experiments

*Littorina africana* which were moved out of their normal zones showed a marked tendency to return to their original zone on the shore. Movements after two days and four days are depicted in Figure 7. Dispersion of adults which were moved downshore was clearly in an upshore direction, while juveniles placed upshore showed a downshore trend after four days.

Chi squared tests were used to determine whether the dispersal was random or non-random. Where movement was found to be non-random, a 2x2 contingency table was used to determine the direction of movement. This analysis showed a random dispersal of control animals ( $P > 0.50$ ) except for the lower controls on day 3 and 4, which showed a significant longshore movement ( $P < 0.01$ ) (Fig. 7). The hypothesis being tested here was that snails should move in equal numbers in one of three directions, upshore, downshore or longshore. Non-random directional movement was evident in all the experimental animals ( $P < 0.01$ ),

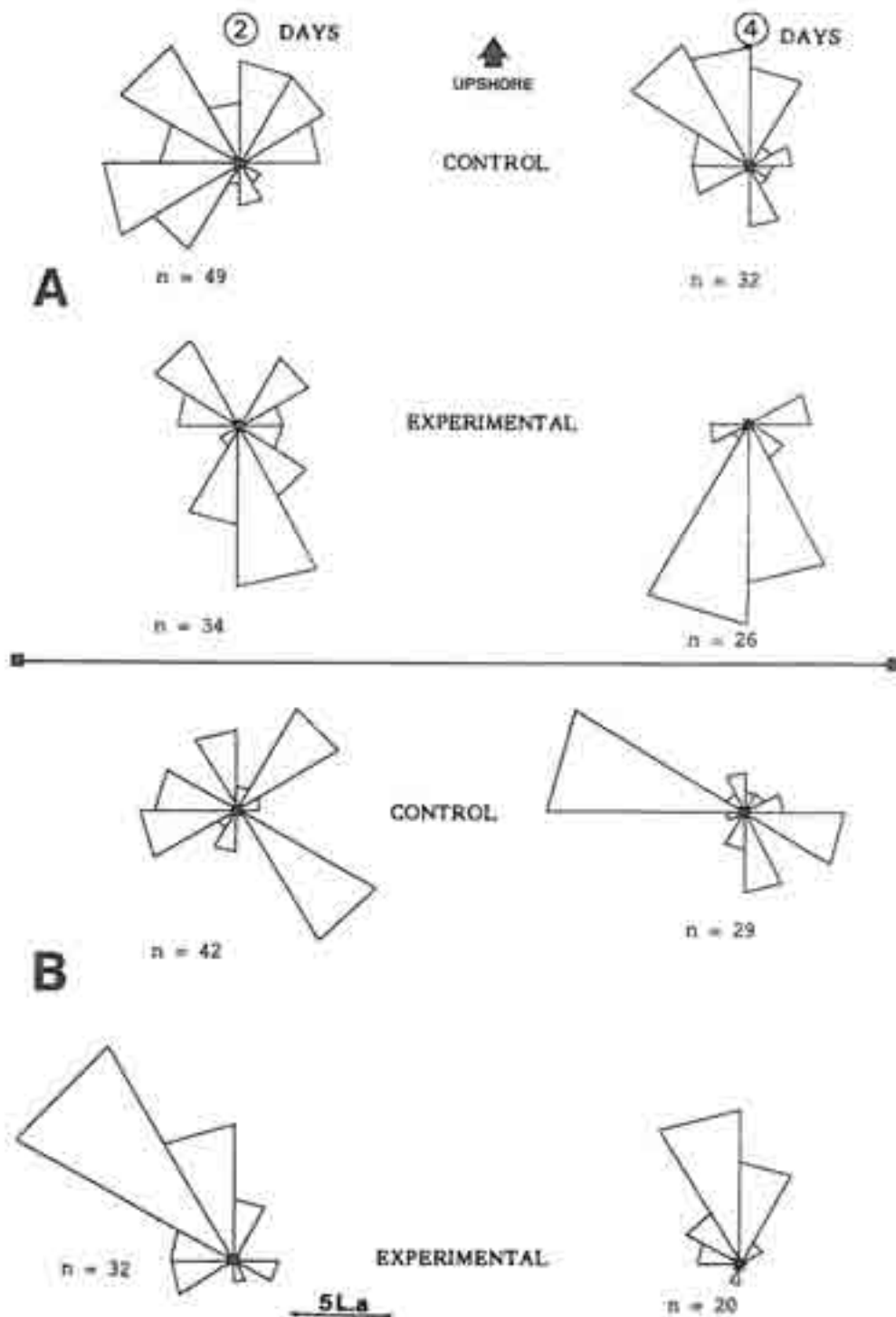


Fig. 7. Direction of dispersal of marked *L. africana* in the upper shore (A) and lower shore (B) regions 2 and 4 days after release. (Method after McQuaid 1981).

the direction being upshore in adults and downshore in juveniles. Movement away from the release point was steady for experimental animals (Fig. 8) and at a much faster rate than the control animals. The distance moved by the experimental animals which had been moved downshore (adults) was much greater than that moved by those moved upshore (juveniles) (Fig. 8). Control animals in both the upper and lower regions were found to cease dispersing after two days, reaching a distance of 0.2 m from the release point (Fig. 8).

In the second experiment involving *Littorina kraussi*, *N. natalensis* and adult *L. africana* which were translocated downshore, a highly significant non-random directional movement

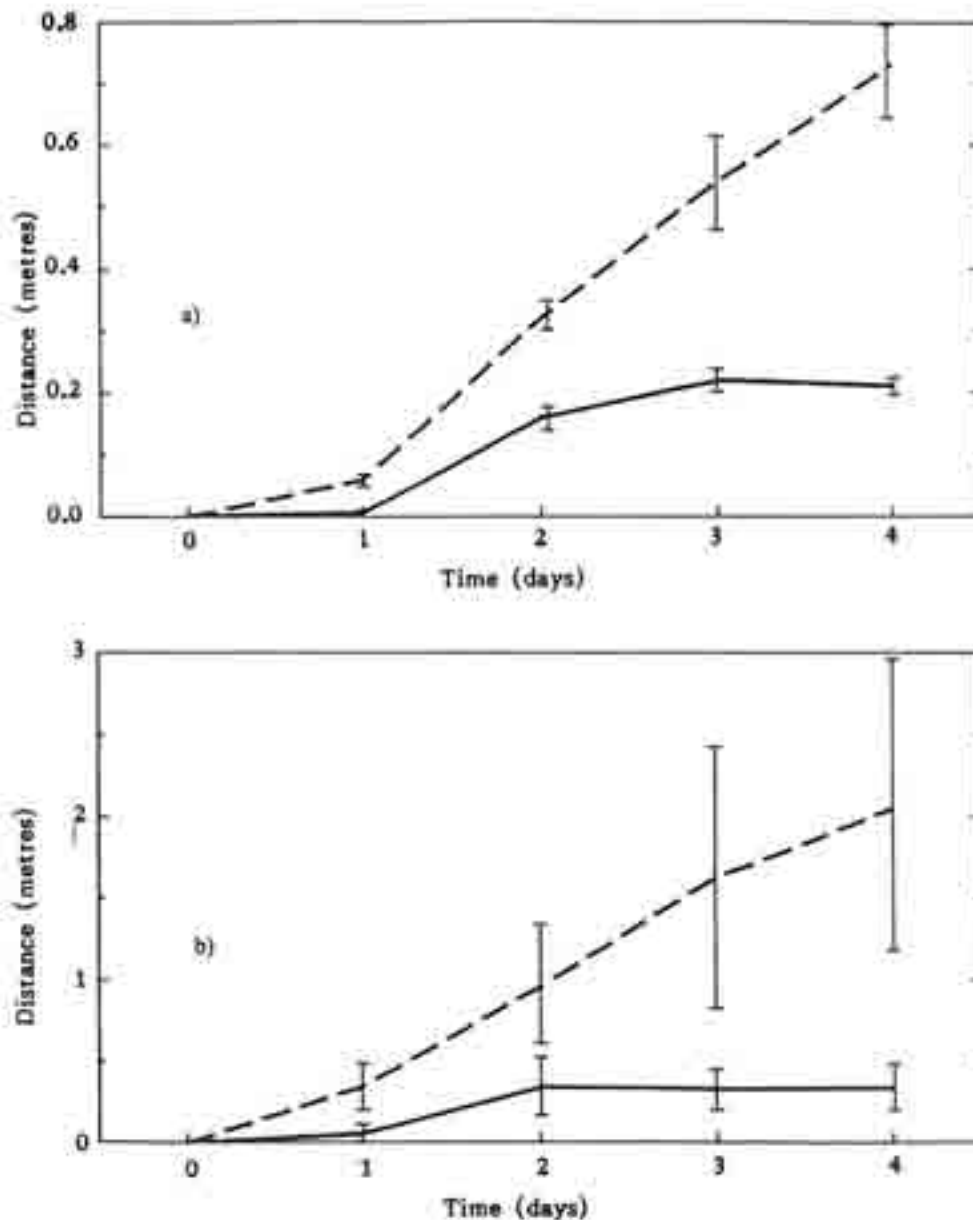


Fig. 8. Mean distance moved ( $\pm$  SE) by *L. africana* from the release point in the:  
 a) upper shore region: — Control; - - - Experimental.  
 b) lower shore region: — Control; - - - Experimental.

upshore ( $P < 0.001$ ) was displayed. The distance moved by the *L. africana* was found to be approximately 3 m in four days (Fig. 9), which is comparable with the original experiment (Fig. 8). *N. natalensis* moved slightly further than this but appeared to be orientated towards crevices, in which they sheltered. *L. kraussi*, however, moved away from the release point exceptionally quickly (Fig. 9), covering a mean distance of 15.63 m in four days. Recoveries of *N. natalensis* and *L. kraussi* after release were not very high, with fewer than 50% of both species being found after four days. This seems to be due to two factors: (1) *N. natalensis* tend to aggregate in available crevices and are thus very difficult to recapture and (2) due to their size, it is probable that *L. kraussi* are washed off the rocks by wave action during their return upshore. It seems unlikely that marking of the snails would have increased predation on this species only.

To determine how actively all three species of littorinids were moving towards crevices during the translocation experiments, note was made of where the snails had settled. Chi squared tests showed that, for *L. africana*, there was significant movement towards crevices by the experimental animals of both zones ( $P < 0.01$ ), but not by the control animals. A similar

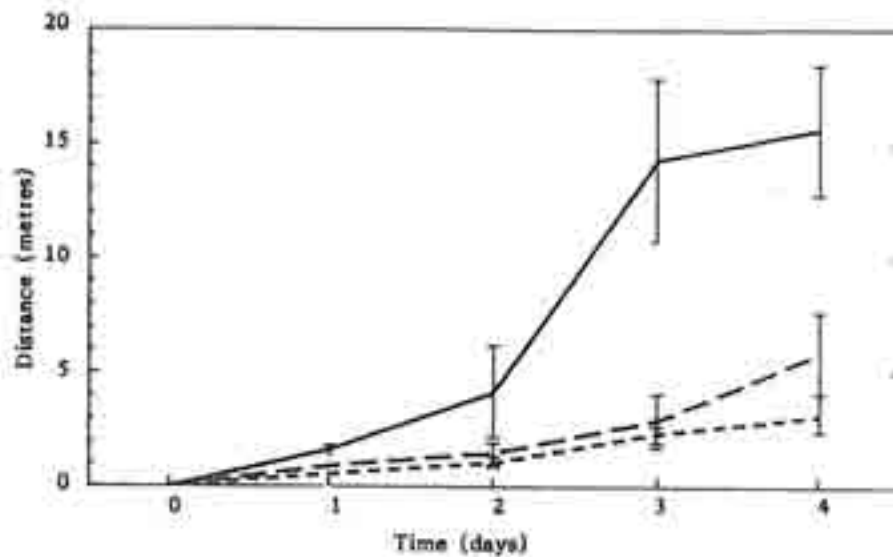


Fig. 9. Mean distance moved ( $\pm$  SE) by three species of littorinid from the release point in the lower shore region:

— *L. kraussi* — — — *N. natalensis* - - - - *L. africana*.

analysis was carried out on the *L. kraussi* and *N. natalensis* individuals which had been moved downshore. This showed that the movement of *N. natalensis* towards crevices was highly significant ( $P < 0.001$ ). The movement of *L. kraussi*, however, was found to be not significant ( $P > 0.50$ ).

## DISCUSSION

The littorinid population at Chakas Rock was found to be characteristic of the subtropical region of the east coast of southern Africa. The most common species occurring here was *L. africana*, while the more tropical species, such as *N. natalensis*, *L. kraussi*, *L. pintado* and *L. undulata*, were not as abundant. The distribution of these species was found to be predominantly contagious, with individuals showing a tendency to aggregate in crevices and pit holes in the rocks.

The local distributions of *L. africana*, *N. natalensis* and *L. kraussi* were found to overlap to a certain extent. *L. kraussi* inhabited the highshore regions, mainly in shaded areas and was seldom found with members of the other two species. *N. natalensis* occurred lower down and formed a definite zone in upper mid-tidal region, confined mainly to erosions and crevices in the rock surface. *L. africana* was found throughout the intertidal region from MLWN upwards. The lowest level occupied by *L. africana* seemed to coincide with the beginning of the *Octomeris angulosa* zone (Potter 1984).

In the highshore region, all three littorinid species were found to occur more abundantly in crevices (Table 2), while in the lowshore region, *N. natalensis* occupied vertical surfaces. This is the same microhabitat usage as reported by Garrity (1984) for ten species of gastropods on the Pacific coast of Panama. *Littorina africana*, however, appears to be an anomaly, actively selecting horizontal surfaces in the lowshore region. This could indicate that crevices are used mainly as protection from desiccation and insolation rather than wave action. Wind is capable of removing gastropods from the intertidal rocks (Courtney 1972) and of increasing the rate of evaporation and desiccation. Thus, by attaching in a depression in the rocks, the snail can avoid the direct line of the wind. The attraction to crevices could also be due to the presence of higher

food levels caught there during the rising or falling tide (Emson & Faller-Fritsch 1976), but this remains to be proven for the species considered here.

Vermeij (1972), in his review on intertidal gastropod size gradients, claims that shell size tends to increase in an upshore direction in species characteristic of the littoral fringe, but often decreases in an upshore direction in species typical of lower intertidal levels. Thus, one would expect littorinids to increase in size in an upshore direction as is found in *L. neritoides* (Lyysaght 1941), *L. planaxis* (North 1954) and *L. scutulata* (North 1954 and Chow 1975). However, there are several exceptions to this rule, as shown by *L. littorea* (Smith & Newell 1955 and Gendron 1977) and *L. knysnaensis* (McQuaid 1981) amongst others.

The size gradients for *L. africana* at Chakas Rock support Vermeij's theories that shell size should increase in an upshore direction (Fig. 3) as was reported by Eyre and Stephenson (1938). There was, however, no discernible decrease in mean shell size in the mid-tidal levels corresponding to the increase in the density as found by Branch and Branch (1981). The situation at Chakas Rock is that juveniles are predominant on the low shore and gradually move upshore as they grow larger, as is described by Smith and Newell (1955) for *L. littorea*. Natural mortalities reduce numbers by some 80% during this upshore movement, such that densities are relatively low. This implies that the juveniles, which are much more susceptible to desiccation and excessive heat loads than the adults, live where they are more likely to be wetted. As the individuals grow larger, they become better able to withstand these environmental stresses and are able to colonise higher levels, although they now tend to rely on crevices for additional protection. However, with reduced numbers of individuals, competition for these favoured sites is not likely to be great.

There has been much discussion of how and why this size gradation occurs. Chow (1975) considers it to be related to environmental factors such as wave action, temperatures and resistance to desiccation. According to North (1954), larger snails occupy higher levels because they are more easily washed off the rocks at low levels than the smaller ones, as a result of having a larger body size relative to the surface area of the foot. Conversely, McQuaid (1981) argues that a reverse gradation occurs in *L. knysnaensis* because the juveniles are unable to withstand the wave action lower down. He also suggests that size gradients are more closely related to food availability; an aspect which was confirmed by this study (Potter 1984, 1988 in press). Vermeij (1972) showed that smaller individuals are more susceptible to extreme physical conditions in the upper shore due to their larger surface area : volume ratio.

Notwithstanding the above, size gradients are actively maintained by littorinids, as is demonstrated by this study's translocation experiments. These showed conclusively, like the work of Gendron (1977) and McQuaid (1981), that littorinids displaced to above or below their preferred habitat will move in the appropriate direction and return to that habitat. *L. kraussi* in the Chakas Rock region tended to move quickly across the wetted rock surfaces to the upper shore when displaced downshore. Gendron (1977) and Levings & Garrity (1983) have shown similar movements for other littorinid species. Once movement stopped, *L. kraussi* individuals usually aligned themselves with the spire away from the sun (Potter 1984), which could indicate solar orientation similar to that found by Newell (1958) and Warburton (1973). Similarly, *N. natalensis* showed a movement upshore in the translocation experiment (Fig. 9), although not quite as marked as *L. kraussi*. This can either be related to the greater degree of movement of *N. natalensis* towards crevices (Table 2), or the availability of crevices of a suitable size. *L. kraussi*, being generally larger than *N. natalensis*, may not find as many crevices that can accommodate it and will thus commonly be found on open rock. The experiments conducted with *L. africana* also showed significant movements of snails back to their normal habitat. The movement of the juveniles back downshore is possibly due to positive geotaxis evoked by the higher temperatures (Evans 1961) and the effects of being wetted with seawater after desiccation. The same reaction was found with *L. irrorata* by Bingham (1972), where desiccation followed by

wetting with seawater elicits a positive geotactic response. The adults displaced downshore could be moving in response to the wave action or to return to a zone of optimal food availability (Bock & Johnson 1967).

Downshore control *L. africana* showed a significant longshore movement (Fig. 7) which is a similar result to that shown by Hamilton (1978) with *L. irrorata*. Several workers (Fraenkel & Gunn 1961; Warburton 1973; Hamilton 1977) have found that many species which are displaced, initially exhibit circuitous movements upon release (klinokinetic response) followed by a straighter path (orthokinesis), regardless of experimental conditions. Translocated *L. africana* specimens supported this theory, moving a short distance initially (Fig. 8). Once a set direction, either upshore or downshore was established, however, movement was more rapid.

Considering the resources available to the littorinids at Chakas Rock, it becomes evident that the animals are effectively separated into slightly different niches which probably results in only minor interaction between the three species at the prevailing densities. *L. kraussi* occurs in the upshore region, *N. natalensis* occurs in the midshore regions, mainly confined to crevices, while *L. africana* occurs throughout. However, *L. africana*, which is recruited at the downshore in high numbers, gradually making its way upshore as it grows, has high mortalities. Thus, the number of adults remaining in the upper shore, overlapping with *L. kraussi* and *N. natalensis* are relatively small.

It is likely that all three species could be limited by food availability and space to a certain degree, although for *L. kraussi* and *N. natalensis*, which are normally well spaced, this competition will not be as marked. Competition for food within the *L. africana* population may be high in the lowshore regions, where there are large numbers of individuals, even though the food supply in this region may be replenished during each high tidal period (Potter 1984, 1988 in press). This apparent overlap in niche infers that for all littorinid species, the competition will be dependent on the population size and recruitment rate of the separate species. Consequently, it appears that inter-specific competition is reduced by subtle differences in niche selection by a variation in dispersion on the shore, microhabitat preferences, rates of feeding and breeding periodicities (Potter 1984). In this way, although the Littorinidae do compete for favoured spaces and food, the intertidal resources required by these species are seldom, if ever, seriously depleted and their co-existence on the shore remains essentially stable.

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