

# Vertical Size Gradients and Migratory Patterns of Two *Nerita* Species in the Northern Gulf of California

by

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*Abstract.* This study addresses patterns of vertical zonation, shell-size variation, and migratory behavior exhibited by two herbivorous intertidal gastropods in the northern Gulf of California, Sonora, Mexico. While actively foraging, *Nerita scabricosta* inhabited a zone from +3.1 m to +4.6 m above mean low water, whereas *Nerita funiculata* ranged from below +1.2 m to +4.6 m. Both species significantly increased in shell size with increasing tidal height. The size of *N. scabricosta* increased faster with tidal height than *N. funiculata*. In addition, *N. funiculata* increased faster with tidal height when inhabiting the zone of overlap with *N. scabricosta* than when in the non-overlap zone. When displaced up or down a tidal gradient, both species actively migrated in the direction of the habitat from which they were taken. This finding suggests that migratory behavior is in part responsible for the maintenance of interspecific zonation patterns.

## INTRODUCTION

Many organisms exhibit striking patterns of vertical zonation in the rocky intertidal (CONNELL, 1961; RICKETTS *et al.*, 1985; NEWELL, 1970; STEPHENSON & STEPHENSON, 1972; LUBCHENCO, 1980; LEVINTON, 1982). Herbivorous gastropods are conspicuous members in many of these communities and often exhibit distinct zonation patterns. These patterns can be maintained by differential rates of growth and survival at various tidal heights, as well as through active migration (PAINE, 1969; VERMEIJ, 1972; BERTNESS, 1977; GENDRON, 1977; UNDERWOOD, 1979; LEVINTON, 1982; MCQUAID, 1982; DOERING & PHILLIPS, 1983; BOVBJERG, 1984).

Interspecific zonation patterns involve differing degrees of overlap between intertidal species, and range from sharp boundaries separating adjacent species to much less distinct gradations (UNDERWOOD, 1979; LEVINTON, 1982). Intraspecific zonation patterns usually involve shell-size variation along tidal gradients. For intertidal mollusks in general, VERMEIJ (1972) hypothesized that high-shore inhabitants tend to increase in shell size with increasing

tidal height whereas lower-shore inhabitants tend to increase in shell size with decreasing tidal height.

Here I report on work conducted in the northern Gulf of California with two herbivorous archeogastropods, *Nerita funiculata* (Menke, 1851) and *Nerita scabricosta* (Lamarck, 1822) (Neritidae). Both species are found on rocky shores throughout the Gulf of California, and their geographic ranges extend to Peru and Equador, respectively (KEEN, 1971; ABBOTT, 1974; BRUSCA, 1980). In the northern Gulf of California, *N. scabricosta* occurs exclusively in the upper intertidal while *N. funiculata* inhabits the mid- and upper intertidal. Both species forage primarily during night low tides and remain inactive during high tides and daytime low tides (personal observations; see also LEVINGS & GARRITY, 1983).

The objectives of this study were to evaluate the zonation patterns exhibited by the two nerites. First, I documented the distribution of both species along a tidal gradient. Second, I determined intraspecific shell-size patterns along this gradient. Following VERMEIJ (1972), I predicted that both nerites would increase in shell size with increasing tidal height, as they are both upper-intertidal species. Third, using transplant experiments, I evaluated the role of migratory behavior in maintaining interspecific zonation patterns. If the two *Nerita* species maintain their distributions

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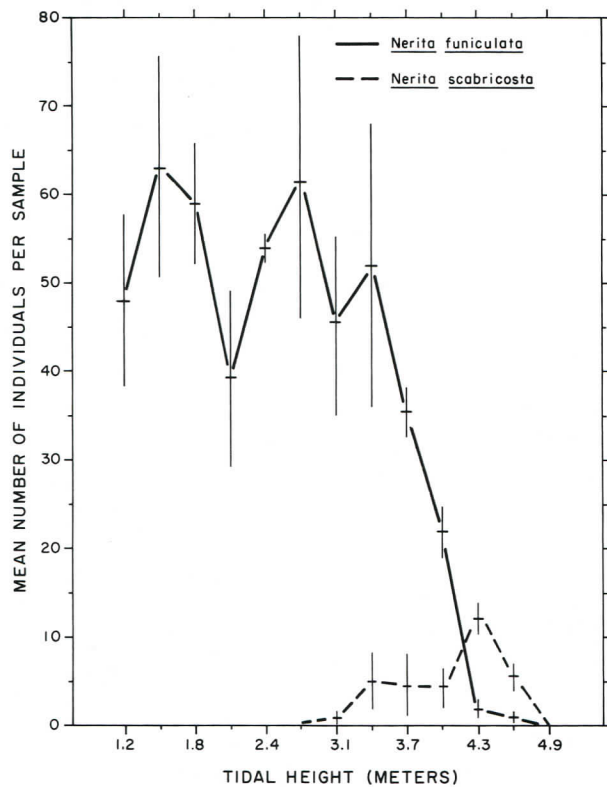


Figure 1

Mean number of *Nerita funiculata* and *N. scabricosta* per sample along a tidal-height gradient at Punta Peñasco, Sonora, Mexico (September 1983). Samples were taken during night low tides when both species were actively foraging. Vertical bars represent  $\pm 1$  SE. Four samples per tidal height.

through behavioral means, I predicted that downwardly displaced *Nerita scabricosta* and upwardly displaced *N. funiculata* should each migrate in the direction of the habitat from which they were taken, while control individuals should move smaller distances and in random directions.

#### MATERIALS AND METHODS

Normal foraging distributions of both species were determined by sampling at 0.3-m intervals along a vertical transect extending from +1.2 m to +4.9 m above mean low water. The transect, sampled in September 1983, was located in a steeply sloping basaltic boulder field at Punta Peñasco, Sonora, Mexico. Sampling procedure consisted of collecting all nerites from within a metal ring enclosing an area of 0.75 m<sup>2</sup>. At each level, four replicate samples were taken at 1-m intervals along a horizontal line.

To evaluate shell-size patterns along this tidal gradient, I measured shell lengths (aperture to apex) with vernier calipers and generated linear regressions of tidal height against shell length for all collected individuals. I performed an analysis of covariance to determine if the two species exhibited significantly different regression-line

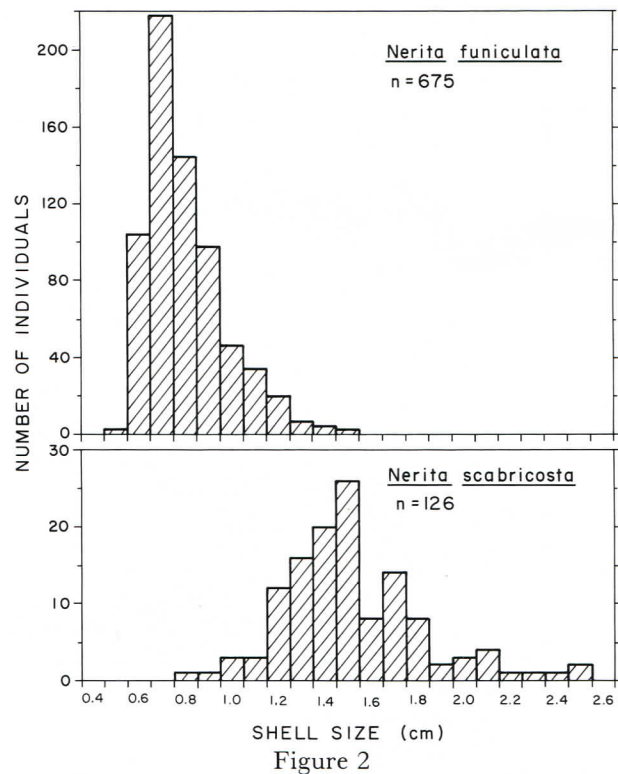


Figure 2

Shell-size distribution of *Nerita funiculata* and *N. scabricosta* at Punta Peñasco, Sonora, Mexico (September 1983).

slopes. With this same data set, I also generated a size-frequency distribution for both species.

To evaluate the hypothesis that rates of change in shell size with tidal height for *Nerita funiculata* were different in the zone of overlap with *N. scabricosta* (+3.1 to +4.6 m) than in the non-overlap zone (+1.2 to +2.8 m), I tested for equality of regression-line slopes in the two regions using an analysis of covariance.

Transplant experiments were initiated at Punta Peñasco during night low tides in November 1983. One hundred *Nerita funiculata* were collected from +1.2 m tidal height, marked with fluorescent paint, and randomly divided into equal control and experimental groups. The 50 controls were replaced at +1.2 m and the 50 experimentals were transplanted up to +4.3 m tidal height. A similar procedure was used with *N. scabricosta* except that the 100 individuals were collected from +4.3 m tidal height, controls were replaced at +4.3 m, and the experimentals were transplanted down to +1.2 m.

On the low tide of the following night, I returned to the study site and searched for the marked snails of both species. For all treatments, I recorded the distance and direction travelled by recaptured individuals of each species. For each snail, I converted migration vectors from polar to rectangular coordinates and, using Mann-Whitney tests, evaluated the following one-tailed hypotheses: (1) experimental *Nerita funiculata* moved significantly greater dis-

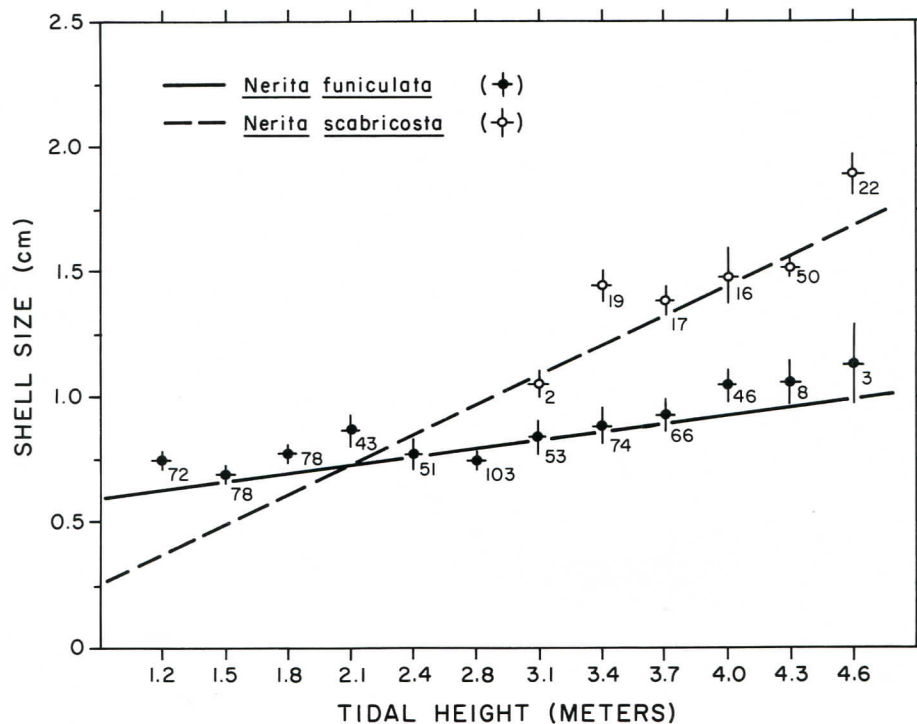


Figure 3

Linear regressions of mean shell size vs. tidal height for *Nerita funiculata* and *N. scabricosta* at Punta Peñasco, Sonora, Mexico (September 1983). Vertical bars represent  $\pm 1$  SE.

tances downshore than controls, (2) experimental *N. scabricosta* moved significantly greater distances upshore than controls, and (3) experimental *N. scabricosta* moved significantly greater distances upshore than experimental *N. funiculata* moved downshore.

## RESULTS

At Punta Peñasco, *Nerita scabricosta* inhabited a zone from +3.1 to +4.6 m above mean low water while *N. funiculata* occupied a zone from below +1.2 to +4.6 m (Figure 1; because of the tidal state, I sampled only as low as +1.2 m, but observed *N. funiculata* lower). Thus, the intertidal range of *N. scabricosta* was entirely contained within that of *N. funiculata*. *Nerita funiculata* was found in substantially higher overall densities than *N. scabricosta* (Figure 1) and was also noticeably smaller in size (Figure 2).

Both species exhibited a statistically significant increase in shell size with increasing tidal height (Figure 3; *Nerita scabricosta*,  $n = 126$ ,  $y = 0.279 + 0.312x$ ,  $r = 0.428$ ,  $P < 0.0001$ ; *N. funiculata*,  $n = 675$ ,  $y = 0.584 + 0.0928x$ ,  $r = 0.502$ ,  $P < 0.0001$ ). In addition, (1) the shell size of *N. scabricosta* increased at a significantly greater rate than that of *N. funiculata* (test for equality of slopes;  $F = 35.03$ ,  $P < 0.001$ ), and (2) the shell size of *N. funiculata* increased at a greater rate when in the zone of overlap with *N. scabricosta* than when in the non-overlap zone (test for equality of slopes;  $F = 45.38$ ,  $P < 0.001$ ).

For both species, experimental individuals moved significantly greater distances vertically (upshore or downshore) than the controls (Figure 4). Specifically, experimental *Nerita funiculata* moved downshore significantly more than controls ( $P < 0.001$ ) whereas experimental *N. scabricosta* moved upshore significantly more than controls ( $P < 0.001$ ). In addition, experimental *N. scabricosta* moved significantly greater distances upshore than experimental *N. funiculata* moved downshore ( $P < 0.01$ ).

## DISCUSSION

*Nerita funiculata* and *N. scabricosta* exhibit an overlapping pattern of vertical zonation on the intertidal basaltic boulder fields at Punta Peñasco. *Nerita scabricosta* inhabited the extreme upper intertidal and its range was contained entirely within that of *N. funiculata*. Throughout the intertidal zone, *N. funiculata* was substantially smaller than *N. scabricosta* and far more abundant. Both nerites also exhibited a significant increase in shell size with tidal height, thus supporting a prediction by VERMEIJ (1972) for upper-intertidal species. And lastly, when displaced up or down the tidal gradient, both species actively migrated in the direction of the habitat from which they were taken, thus suggesting that such behavior is in part responsible for the maintenance of interspecific zonation patterns.

Size-dependent zonation of intertidal gastropods has been described for many herbivorous and carnivorous species

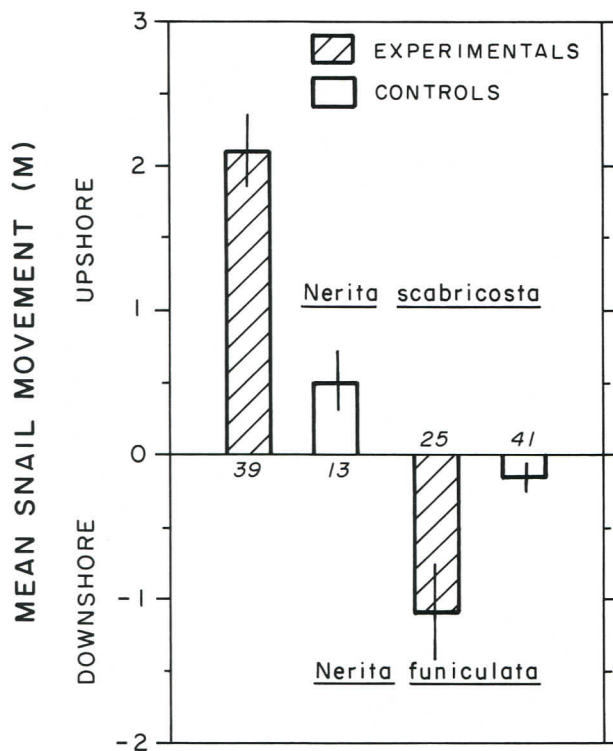


Figure 4

Mean upshore and downshore movements of marked *Nerita funiculata* and *N. scabricosta* (November 1983). The number of recaptured individuals (out of a possible 50) is listed for each mean. Vertical bars represent  $\pm 1$  SE.

(BAKKAR, 1959; FRANK, 1965; EDWARDS, 1969; PAINE, 1969; SUTHERLAND, 1970; VERMEIJ, 1972; COOMBS, 1973; CHOW, 1975; BERTNESS, 1977; MARKOWITZ, 1980; MCQUAID, 1982). With the exception of BAKKAR (1959) and MCQUAID (1982), these studies have supported VERMEIJ's (1972) prediction that upper-intertidal mollusks increase in shell size with increasing tidal height whereas lower-intertidal species decrease in shell size with increasing tidal height.

Numerous factors may explain the patterns of intra- and interspecific shell-size variation observed in this study. First, owing to the effects of surface-to-volume ratios, desiccation tolerance usually increases with increasing size of individual gastropods. In most cases, this relationship applies to both within- and between-species comparisons (see review by UNDERWOOD, 1979). Thus, the results reported here are consistent with the hypothesis that surface-to-volume ratios explain the two intraspecific shell-size gradients. Second, VERMEIJ (1978) has noted that *Nerita scabricosta* can hold extravisceral water in its nonpartitioned shell while *N. funiculata* does not have this ability. Further, GARRITY (1984) showed that larger *N. scabricosta* hold proportionately more water than smaller individuals. These observations suggest that *N. scabricosta* may acquire a two-fold benefit from increases in shell size: (1) surface-to-

volume ratio effects and (2) extravisceral water effects. This double benefit may explain why the regression-line slope for *N. scabricosta* was significantly steeper than for *N. funiculata*; increases in body size are more valuable to *N. scabricosta* in combating environmental stress.

The significantly greater rate of increase in shell size for *Nerita funiculata* when co-occurring with *N. scabricosta* (+3.1 to +4.6 m; Figures 1, 3) may have resulted from interspecific competition. Perhaps larger *N. funiculata* are better able to compete with *N. scabricosta* than are smaller individuals. If this were the case, selection would favor the presence of larger *N. funiculata* in the overlap zone. Alternatively, water loss may be more pronounced in the upper intertidal such that only larger individuals can survive there. Thus, what appears to be a pattern suggesting interspecific interactions may actually result from variation in physiological tolerances to stress.

The transplant experiments indicate that both nerites must be able to (1) recognize their preferred habitat, (2) correctly assess the direction of this habitat when they have been displaced or when environmental conditions change, and (3) move in the direction of this region (Figure 4). Such behaviors can result from the ability of gastropods to respond to various environmental cues, such as gravity, light, water pressure, or inundation-exposure period (see review by UNDERWOOD, 1979).

In this study, downwardly displaced *Nerita scabricosta* showed stronger migratory tendencies than did upwardly displaced *N. funiculata*. The apparent difference in migration rates may have resulted from a stimulus difference; the transplanted *N. scabricosta* were moved completely outside their normal range and exposed to substantially longer periods of submersion, while the transplanted *N. funiculata* were moved only to the upper portion of their normal range (movement completely outside of their normal upper limits would have put them in an area outside of the splash zone). Thus, the environmental changes brought about by the transplants may have been greater for *N. scabricosta* than for *N. funiculata* and, as a consequence, the former tended to migrate greater distances. Alternatively, the observed difference in rates of movement could be due to the fact that transplanted *N. scabricosta* were significantly larger than transplanted *N. funiculata* and larger individuals can move greater distances. Supporting this contention is the work of LEVINGS & GARRITY (1983) and GARRITY & LEVINGS (1984) which document that the distance traveled by *N. scabricosta* increases with shell size.

In conclusion, this study has revealed numerous ways in which the ecology of *Nerita* in the northern Gulf of California differs from that reported for the two species in Panama (GARRITY & LEVINGS, 1981; LEVINGS & GARRITY, 1983). First, *N. funiculata* is far more abundant than *N. scabricosta* in the northern Gulf, whereas the reverse is true in Panama. Second, *N. scabricosta* does not forage over as wide a vertical range in the northern Gulf as it does in Panama. And third, *N. funiculata* commonly occurs in unprotected microhabitats while inactive in the

northern Gulf whereas it is restricted to crevices in Panama. This latter difference may be due to comparatively greater fish predation in the tropics (see BERTNESS *et al.*, 1981; GARRITY & LEVINGS, 1981).

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