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FACTORS CONTRIBUTING TO SPATIAL HETEROGENEITY IN THE ABUNDANCE OF THE COMMON PERIWINKLE *LITTORINA LITTOREA* (L.)

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ABSTRACT

Although *Littorina littorea* (L.) exhibits a relatively consistent pattern of vertical distribution throughout the North Atlantic, ranging from the mid-intertidal to the shallow subtidal zone, its horizontal distribution and abundance are highly variable. In this study, we first described the snail's horizontal distribution patterns on Appledore Island, ME, USA and then asked whether wave exposure, rugosity, predator density (e.g. *Carcinus maenas* and *Cancer borealis*), the percentage of the substrate covered by *Ascophyllum nodosum*, *Chondrus crispus*, *Polysiphonia* spp., and ephemeral green algae, or the percentage of uncovered substrate (bare rock) were correlated with *L. littorea* abundance in the intertidal zone (0.6 to 0.0 m relative to Mean Lower Low Water [MLLW]) and the shallow subtidal zone (-1.5 to -3.0 m MLLW) at nine study sites. Intertidal densities of *L. littorea* were highly variable across sites, ranging from 0 to >600 m⁻². In this zone, *L. littorea* density showed a significant positive correlation with rugosity and percentage of bare rock. Densities were very low in the subtidal zone (range: 0–19 m⁻²) and varied little among sites. Exploratory multiple regression analysis suggested that *L. littorea* density was positively correlated with the density of *C. maenas* in the shallow subtidal zone. Additionally, snails in the subtidal zone had thicker shells than snails of the same size in the intertidal zone. Our results suggest that structural elements of the habitat, such as rugosity and percentage of uncovered substrate, are among the most important predictors of *L. littorea* abundance on moderately protected, rocky intertidal shores.

INTRODUCTION

Plants and animals rarely exhibit uniform patterns of distribution across either large or small spatial scales (Levin, 1992; Menge, 2000). Variation in both abiotic and biotic factors has been shown to produce these between-site differences (Lubchenco & Menge, 1978; Menge, 1978a, b, 1983, 1991; Petraitis, 1987; Ritchie 2000; Robles & Desharnais 2002). In intertidal environments, physical factors such as wave exposure (Lewis, 1964; Menge, 2000), desiccation (Stephenson & Stephenson, 1972; Menge, 1978a, b) and substrate complexity (Johnson, 1994; Beck, 2000), in particular, affect the abundance of intertidal organisms. As in other environments, variation in biological factors, such as predation (Paine, 1966; Menge 1978a, b; Robles & Desharnais, 2002) and competition (Connell, 1961), may also play important roles in producing spatial heterogeneity in the abundance of intertidal species.

Many distributional studies in the intertidal zone have focused on carnivorous or sessile species (e.g. *Nucella lapillus* Linnaeus, 1758 and *Mytilus edulis* Linnaeus, 1758) (Menge, 1978a, b, 1983; Petraitis, 1987). Comparatively few studies have examined the effects of abiotic and biotic factors on the distribution and abundance of herbivorous species (but see Lubchenco & Menge, 1978). Because herbivores link upper and lower trophic levels, variation in their abundance and distribution may have important ramifications for both secondary consumers and primary producers. Understanding how various physical and biological factors affect the distribution of

herbivorous species may provide insight into the organization of the intertidal community as a whole (Levin, 1992; Benedetti-Cecchi, 2001).

In the North Atlantic, the herbivorous gastropod *Littorina littorea* (Linnaeus, 1758) is a common inhabitant of rocky shores. The snail ranges from the mid-intertidal to the shallow subtidal zones (see extensive references in Reid, 1996) and grazes preferentially on macroalgal germlings (Lubchenco, 1983), diatoms (Hunter & Russell-Hunter, 1983), and ephemeral green algae (e.g. *Ulva* spp., *Enteromorpha* spp., and *Cladophora* spp.) (Lubchenco, 1978; Bertness, 1984). Grazing by *L. littorea* can produce dramatic effects on both the algal assemblage (Lubchenco, 1978, 1983) and habitat structure (Bertness, 1984) of the intertidal zone. However, the magnitude of these effects may be controlled by the snails' response to cues from predatory crabs (Trussell, Ewanchuk & Bertness, 2002, 2003).

In addition to studies of ecological interactions over the past century, extensive investigations of the biology of *L. littorea* have focused on its abundance, habitat use, vertical distribution, spawning and recruitment patterns, growth rates, movement and intraspecific competition (e.g. Huntsman, 1918; Moore 1937, 1940; Stephenson & Stephenson, 1954; Lewis, 1964; Williams, 1964; Vermeij, 1972; Underwood, 1973; Petraitis, 1982, 2002; Behrens Yamada, 1987; Addy & Johnson, 2001). However, despite considerable evidence of spatial heterogeneity in abundance, no studies have examined the factors contributing to such variation.

On Appledore Island in the Gulf of Maine, *L. littorea* exhibits extreme variation in abundance across similar habitats, ranging from 0 to >600 m⁻² over a distance of about 100 m

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(Carlson, 2002). In this study, we first examined variation in *L. littorea* abundance across the range of intertidal and shallow subtidal habitats on Appledore Island and then investigated whether *L. littorea* density was correlated with a variety of physical (wave exposure, substrate rugosity) and biological factors (predator density, abundance of algae) across sites.

MATERIAL AND METHODS

Data collection

The study was carried out on Appledore Island, ME, USA, (42°58'N; 70°37'W), located approximately 10 km off the coast of New Hampshire. The eastern side of the island faces the open ocean and is exposed to heavy wave action, whereas the western side is protected from high waves in all but the most intense storms. We measured *L. littorea* density and several biological and physical features at nine sites on Appledore Island in order to study variation in patterns of *L. littorea* abundance. The sites were distributed relatively evenly around the perimeter of the island (Fig. 1) and represented two categories of rocky habitat: (1) coves: moderately sloped rocky beaches (Broad Cove, Sandpiper Beach, Siren's Cove and Smith's Cove); and (2) ledges: relatively smooth, algae-encrusted rock benches (Larus Ledge, Appledore Ledges, Norwegian Point, Transects 5 & 6 and Transect 24).

L. Littorina littorea density was sampled at four tidal heights [0.6 m, 0.0 m, -1.5 m and -3.0 m relative to Mean Lower Low Water (MLLW)] at all sites in mid- to late July, 2001, during diurnal low tides. These tidal heights encompass most of the vertical distribution of *L. littorea* on Appledore Island. A 0.25 m² quadrat was placed randomly at four (-3.0 m) or six (0.6 m, 0.0 m and -1.5 m) locations along a 10-m transect line and all snails present in the quadrat were counted. At cove sites, the transect line was placed as close to the centre of the beach as possible.

Twenty snails were randomly selected from four quadrats at each height and taken back to the laboratory for morphometric

analysis. If fewer than twenty snails were present in a given quadrat, all snails were included. Using digital callipers (± 0.01 mm), we measured shell height (maximum dimension parallel to the axis of coiling), aperture length (distance from the junction of the outer lip with the body whorl to the furthest point of the anterior lip) (Reid, 1996), and lip thickness (thickness of the shell at the middle of the aperture lip).

The number of predatory crab species *Cancer borealis* (Stimpson, 1859), *C. irroratus* (Say, 1817) and *Carcinus maenas* (Linnaeus, 1758) (Ojeda & Dearborn, 1991) were counted and each individual crab measured (maximum carapace width: ± 1 mm) along three 10 × 1-m belt transects at each tidal height at all sites. At Siren's and Broad Coves, only 1 and 2 transects respectively were censused because of the sizes of the sites. During censuses, we searched in crevices, between boulders, and on the surface of the substrate for crabs. Because we did not search under rocks or boulders, it is likely that we have underestimated natural crab densities. However, our censuses were performed in the same manner at all sites, thereby making among-site density comparisons valid.

To quantify wave exposure, we measured the height of the top of the barnacle zone relative to a permanent marker located at 4.1 m at each site. The height of the barnacle zone has been shown to be positively correlated with wave exposure (Stephenson & Stephenson, 1972). Four to six measurements of the height of the zone were taken at each site.

Preliminary observations indicated that substrate rugosity was similar at 0.6 m and 0.0 m and at -1.5 m and -3.0 m. As a result, we measured rugosity only at 0.0 m and -1.5 m at each site. Rugosity was measured by laying three metres of measuring tape horizontally taut across the substrate and marking the end points. The tape was then carefully re-laid to follow the contours of the surface along the same linear distance and the final length recorded. Three rugosity measurements were taken at each tidal height. To facilitate statistical analysis, an index of rugosity was calculated by computing the final tape length/initial tape length. Measurements at 0.0 m were taken at all nine sites and at -1.5 m at eight sites; intense wave action precluded data collection at -1.5 m at Norwegian Point. However, substrate rugosity was similar between 0.0 m and -1.5 m at this site and, therefore, we used our measure of rugosity at 0.0 m for rugosity at -1.5 m.

We quantified the substrate cover at each site using a 0.0625-m² (25 cm × 25 cm) quadrat divided into 16 equal squares placed randomly at 10 locations along each height contour. We counted the number of squares (to the nearest quarter of a square) occupied by algae, the blue mussel *Mytilus edulis* and sand. We also counted the number of squares containing uncovered substrate (bare rock). All algae, with the exception of specimens in the genera *Cladophora*, *Poly-siphonia* and *Rhizoclonium*, were identified to species level using Hillson (1977), Lee (1977) and Villalard-Bohnsack (1995).

Statistical analyses

We had two goals when undertaking statistical analysis of our data. First, we sought to describe patterns of variation in *L. littorea* abundance and shell shape both within and among sites on Appledore Island. Second, we sought to identify the physical and/or biological factors correlated with among-site variation in snail abundance.

We modelled variation in *L. littorea* density on Appledore Island using a mixed model which included site type, tidal height and their interaction as fixed effects, with site nested within site type [site (site type)] and its interaction with height as random effects. We used the GLM procedure of SAS (v. 8.2, SAS Institute, Inc.) with the RANDOM/TEST

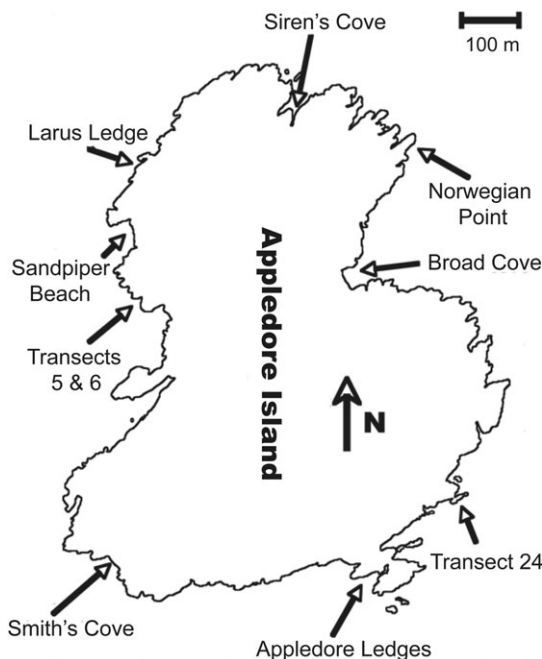


Figure 1. Map of Appledore Island, ME, USA, (42°58'N; 70°37'W), including locations of the nine study sites.

option to test the significance of each main and interaction effect. We used the LSMEANS/PDIFF ADJUST = TUKEY option to further examine any significant effects *a posteriori* using Tukey's HSD test. We also examined within-site variation in *L. littorea* density using single factor ANOVAs and Tukey's HSD post hoc tests. Variance in *L. littorea* density among heights and sites was heterogeneous. Therefore, data were log transformed ($\log(x + 1)$; Underwood, 1997) to increase homogeneity prior to analysis.

We modelled variation in the shell height, aperture length, and lip thickness of *L. littorea* shells using a mixed model which included site type, tidal height and their interaction as fixed effects and site(site type), tidal height \times site(site type) and quadrat nested within the tidal height \times site(site type) interaction as random effects. We used the MIXED procedure to test the significance of each effect and further examined significant fixed effects using least-squared means and Tukey's HSD test. When our analysis of shell aperture length or lip thickness revealed a significant tidal height effect, we used ANCOVAs (GLM procedure with shell height as a covariate) to examine the allometric relationship between that feature and shell height to determine whether snail growth proceeds at different rates according to tidal height.

We identified the five most common components of the substrate, ephemeral green algae (*Ulva* spp., *Cladophora* spp., *Enteromorpha* spp.), *Ascophyllum nodosum* (Linnaeus) Le Jolis, *Chondrus crispus* Stackhouse, 1797, *Polysiphonia* spp. and bare rock, and calculated the percentage of substrate covered by each component at each height and site. We arcsine-square-root transformed our percentage cover data (Underwood, 1997) to increase normality.

We used a series of correlation analyses to identify the factors that best explain variation in *L. littorea* density among sites on Appledore Island in the intertidal and shallow subtidal zones. We used correlation instead of regression analyses because all variables were measured with error. We constructed intertidal and shallow subtidal data sets for log-transformed *L. littorea* density, *C. borealis* density and *C. maenas* density, and arcsine-square-root transformed measures of percentage cover by *A. nodosum*, *C. crispus*, ephemeral green algae, *Polysiphonia* spp. and bare rock by calculating the mean value of each factor in the intertidal zone (both 0.6 m and 0.0 m) and shallow subtidal zone (both -1.5 m and -3.0 m) at each site. We did not examine the correlation between *L. littorea* and *C. irroratus* densities because the crab was absent from four sites and occurred only at low densities at the remaining five sites. We used our measure of substrate rugosity at 0.0 m and -1.5 m in the intertidal and shallow subtidal analyses respectively and our measure of wave exposure (the height of the barnacle zone) in both analyses. We performed Shapiro-Wilk's tests separately on the intertidal and subtidal data sets to test the assumptions of correlation analysis. The tests indicated that several factors were not normally distributed (factors: rugosity (intertidal, shallow subtidal), *C. borealis* density (shallow subtidal), *C. crispus* (intertidal), bare rock (intertidal, shallow subtidal), *Polysiphonia* spp. (shallow subtidal), all $P < 0.05$) and the normality of these factors did not improve significantly after transformation. Therefore, we used the CORR procedure with the SPEARMAN option to calculate Spearman's Rank correlation coefficients as well as the probability (P) that the correlation coefficient differed from zero.

Although our correlation analyses enabled us to measure the strength of the relationship between *L. littorea* density and each measured biological or physical factor, it is possible that a combination of factors, rather than a single factor, best explains variation in *L. littorea* density. Therefore, we used multiple regression techniques to explore this possibility. We used the REG procedure with the MAXR (maximum improvement in

R^2) option to investigate the ability of different combinations of factors to predict *L. littorea* density in the intertidal and shallow subtidal zones. The MAXR method seeks the best k -factor model for $k = 1 \rightarrow n$ where $n =$ the number of predictor variables. We selected the model yielding the smallest P -value (Myers, 1986).

RESULTS

Density of *Littorina littorea*

Littorina littorea was heterogeneously distributed both among sites and among tidal heights at a single site (site(site type) effect: $df = 7, 21, MS = 8.23, F = 4.41, P = 0.0037$; tidal height \times site(site type) effect: $df = 21, 162, MS = 1.91, F = 10.47, P < 0.0001$). However, it is possible to describe several general patterns of variation in the snail's abundance on Appledore Island. First, variation in *L. littorea* distribution among tidal heights was similar between cove and ledge sites (Fig. 2; tidal height \times site type effect: ANOVA, $df = 3, 21, MS = 3.37, F = 1.77, P = 0.18$), with higher snail densities in the intertidal zone (0.6 m and 0.0 m) than in the shallow subtidal zone (-1.5 m and -3.0 m) (tidal height effect: $df = 3, 21, MS = 17.05, F = 8.94, P = 0.0005$; Tukey's HSD, $P < 0.05$). At 0.0 m, where snail density was generally the highest, mean density ranged from 0 to 681 snails m^{-2} and was significantly higher at Broad Cove than at Norwegian Point, Siren's Cove, Transect 24, Larus Ledge or Transects 5 & 6 (Tukey's HSD, $P < 0.05$). At 0.6 m, *L. littorea* density varied from 0 to 432 m^{-2} . The three sites (Broad Cove, Transects 5 & 6 and Appledore Ledges) with the highest snail densities (88–432 m^{-2}) were significantly different from Siren's Cove, Larus Ledge and Norwegian Point, which had the lowest densities (0–39 m^{-2} ; Tukey's HSD, $P < 0.05$). At -1.5 m, mean snail density ranged from 0 to 103 snails m^{-2} , with significantly higher density at Appledore Ledges compared with all other sites (Tukey's HSD, $P < 0.05$). *Littorina littorea* was absent from -3.0 m at seven sites and occurred at low densities (1 and 19 m^{-2}) at the other two. There were no significant differences among sites at this height.

Second, sites generally exhibited one of three patterns of *L. littorea* distribution among tidal heights (Fig. 2): (1) significantly higher densities of *L. littorea* at one or both intertidal heights compared with both subtidal heights (Broad Cove, Sandpiper Beach, Transect 24, Smith's Cove and Transects 5 & 6; Tukey's HSD, all $P < 0.05$); (2) moderate snail densities (19–110 m^{-2}) at all tidal heights with no significant differences among them (Appledore Ledges; Tukey's HSD, $P > 0.05$); and (3) few to no *L. littorea* at any tidal height (Norwegian Point, Siren's Cove and Larus Ledge).

Morphometrics of *Littorina littorea*

Littorina littorea shells were similar in shape among sites on Appledore Island. Shells did not differ significantly in height, aperture length or lip thickness between site types (all $P > 0.05$). However, shells differed in lip thickness among tidal heights (tidal height effect: $df = 3, 6, F = 5.00, P = 0.046$). Because shallow subtidal snail densities were low at many sites, we combined data from all sites to examine the allometric relationship between shell height and lip thickness among tidal heights. Although there was a significant tidal height effect (ANCOVA, $df = 3, 859, MS = 1.40, F = 138.9, P < 0.0001$), pairwise analysis indicated that snails at 0.6 m and 0.0 m were morphometrically indistinguishable, as were snails at -1.5 m and -3.0 m (Tukey's HSD, both $P > 0.05$). We then performed an additional analysis to compare snails from the intertidal zone (0.6 m and 0.0 m combined) with those from the subtidal zone

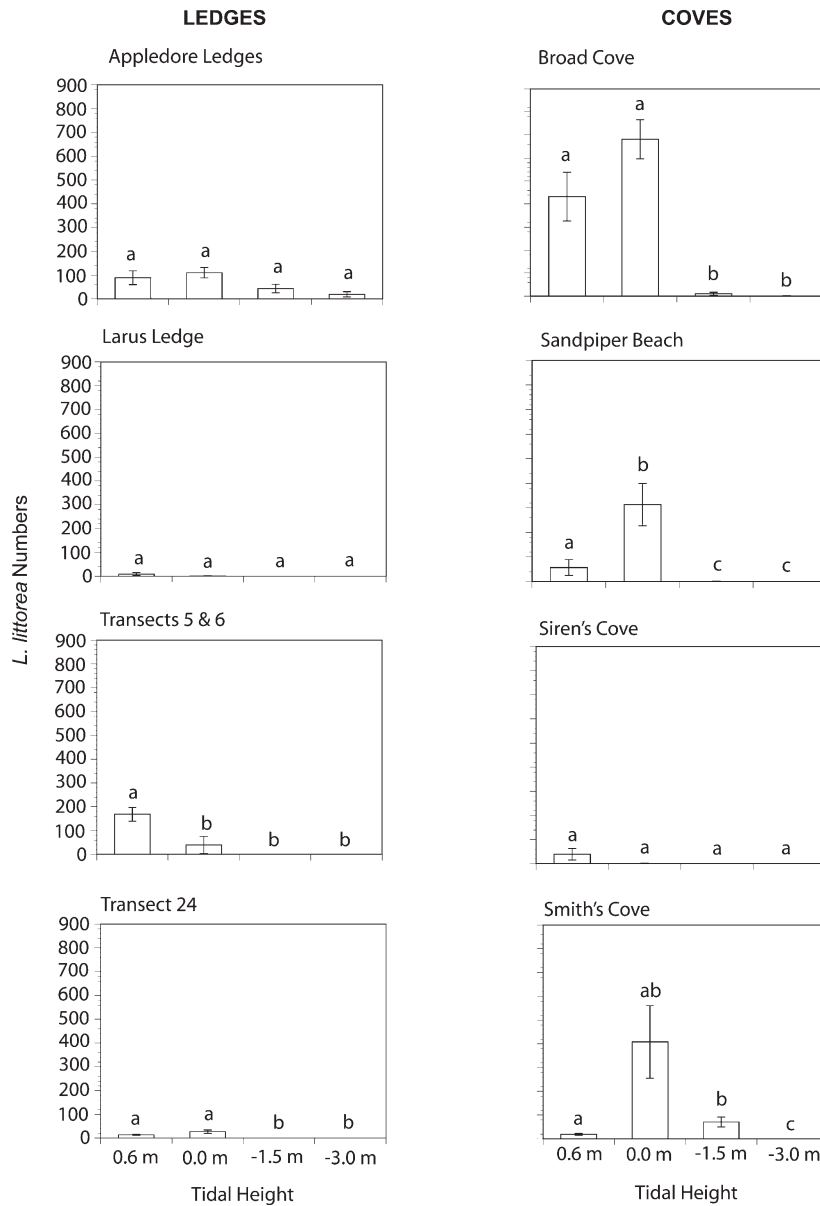


Figure 2. Mean number (\pm SE) of *L. littorea* per square metre at four tidal heights at eight sites on Appledore Island ($n = 6$ for 0.6 m, 0.0 m and -1.5 m, $n = 4$ for -3.0 m). Letters indicate heights that were not significantly different from one another (Tukey's HSD, $P > 0.05$). The fifth ledge site, Norwegian Point, is not included because snails were absent from all tidal heights.

(-1.5 m and -3.0 m). Our analysis revealed that shallow subtidal *L. littorea* have thicker shells than snails of the same size in the intertidal zone (Fig. 3; ANCOVA, $df = 1, 861$, $MS = 4.17$, $F = 415.9$, $P < 0.0001$). However, the curved rather than linear nature of the log shell height – log lip thickness regression based on snails found in the intertidal zone suggests that the rate of change in lip thickness may differ between height classes. We examined this possibility by dividing the sample of intertidal snails into two arbitrary size classes and fitting a regression line to each data set. We found that dividing snails into classes at 17.79 mm yielded the pair of lines that best explained the data. In fact, the pair of lines provided a better fit to the data (lower total error) than a single line suggesting that different height classes of snails in the intertidal zone thicken their shells at different rates. For both size classes, however, the rate of shell thickening by intertidal snails was slower than that of shallow subtidal snails of the same size (ANCOVA, < 17.79 mm:

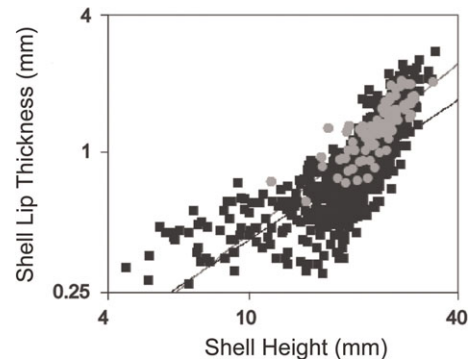


Figure 3. Relationship between lip thickness and height (mm) of *L. littorea* shells in the intertidal zone (0.6 m and 0.0 m; black squares) and shallow subtidal zone (-1.5 m and -3.0 m; grey circles) on a \log_{10}/\log_{10} scale.

df = 1, 145, MS = 0.23, $F = 21.69$, $P < 0.0001$; ANCOVA, ≥ 17.79 mm: df = 1, 713, MS = 1.88, $F = 245.59$, $P < 0.0001$).

Predator densities

Littorina littorea density was not correlated with either *C. borealis* or *C. maenas* density in the shallow subtidal or intertidal zones (*C. borealis*, shallow subtidal: $R_s = 0.14$, $P = 0.71$, intertidal: $R_s = -0.41$, $P = 0.27$, *C. maenas*, shallow subtidal: $R_s = 0.51$, $P = 0.16$, intertidal: $R_s = 0.52$, $P = 0.15$).

Wave exposure estimates

Sites on the eastern side of Appledore Island were generally more exposed (i.e. the barnacle zone was higher) than sites on the western side of the island. Norwegian Point had the highest barnacle zone (eastern side, $n = 5$, 2.9 ± 0.030 m), whereas Smith's Cove had the lowest (western side, $n = 4$, 2.3 ± 0.057 m). Although *L. littorea* densities tended to decrease with increasing wave exposure, the correlation was not significant in either the intertidal zone ($R_s = -0.27$, $P = 0.48$) or shallow subtidal zone ($R_s = -0.42$, $P = 0.26$).

Rugosity

The index of rugosity was higher in the shallow subtidal zone (-1.5 m) than in the intertidal zone (0.0 m) at most sites. The index ranged from a low of 1.03 ± 0.015 m ($n = 3$) at Larus Ledge at 0.0 m to a high of 1.32 ± 0.088 m ($n = 3$) at Smith's Cove at -1.5 m. Intertidal *L. littorea* density showed a strong positive correlation with rugosity (Fig. 4A; $R_s = 0.77$, $P = 0.015$). However, the two factors were not significantly correlated in the shallow subtidal ($R_s = 0.42$, $P = 0.27$).

Substrate cover

More of the substrate was bare rock at the cove sites than at the ledge sites, with more bare rock at 0.6 m and 0.0 m than at -1.5 m and -3.0 m. Snail density increased with the percentage of bare substrate in both the intertidal and shallow subtidal zones with a significant correlation in the intertidal zone (Fig. 4B; $R_s = 0.71$, $P = 0.031$), but not in the shallow subtidal zone ($R_s = 0.26$, $P = 0.50$).

Ephemeral green algae were found at all four intertidal heights, covering 1–20% of the substrate, but were more abundant in the shallow subtidal zone than in the intertidal zone. The percentage of the substrate covered by ephemeral green algae generally decreased with increasing *L. littorea*

density, but cover by the algae was not significantly correlated with snail density in either the intertidal zone ($R_s = -0.55$, $P = 0.12$) or shallow subtidal zone ($R_s = -0.38$, $P = 0.31$).

Ascophyllum nodosum occurred only at Appledore Ledges, Sandpiper Beach and Transect 24 at the tidal heights surveyed. At these sites, the alga was most abundant at 0.6 m and completely absent from -1.5 m and -3.0 m. *Littorina littorea* density was not significantly correlated with cover by *A. nodosum* ($R_s = 0.24$, $P = 0.53$). We did not examine the correlation between cover by *A. nodosum* and *L. littorea* density in the shallow subtidal zone because the alga was not present at those tidal heights.

Chondrus crispus was most abundant around 0.0 m and decreased in abundance with decreasing tidal height. In contrast, *Polysiphonia* spp. were more common in the shallow subtidal zone than in the intertidal zone. The negative correlation between *L. littorea* density and cover by *Polysiphonia* spp. in the intertidal zone was nearly significant ($R_s = -0.64$, $P = 0.066$) whereas the remaining three correlations between cover by *Polysiphonia* spp. or *C. crispus* were not significant (*Polysiphonia*, shallow subtidal: $R_s = -0.18$, $P = 0.64$, *C. crispus*, intertidal: $R_s = -0.36$, $P = 0.34$, shallow subtidal: $R_s = -0.11$, $P = 0.77$).

Multi-factor analysis

In multiple regression analyses, colinearity among predictor variables can lead to inaccurate partial regression coefficients (Myers, 1986; Petraitis, Dunham & Niewiarowski, 1996). To account for the potential for inaccurate calculations of these coefficients, we carried out multiple regression analyses for exploratory purposes only, with the goal of identifying possible combinations of predictor variables that warrant further investigation in future studies of among-site variation in *L. littorea* abundance.

In the intertidal zone, variation in *L. littorea* density around Appledore Island was best explained by a combination of rugosity and cover by ephemeral green algae and *C. crispus* (Table 1); *Littorina littorea* density was positively correlated with substrate complexity and cover by the algae. In the shallow subtidal zone, *C. maenas* density was the best predictor of *L. littorea* density and was positively correlated with snail density.

Correction for multiple comparisons

Our statistical analysis included 17 correlation and two multiple regression analyses for a total of 19 tests. To determine whether the analysis identified more significant tests than expected by chance, we calculated a false discovery rate (FDR; Manly, Nettleton & Hwang, 2004). At $\alpha = 0.05$, approximately one out of

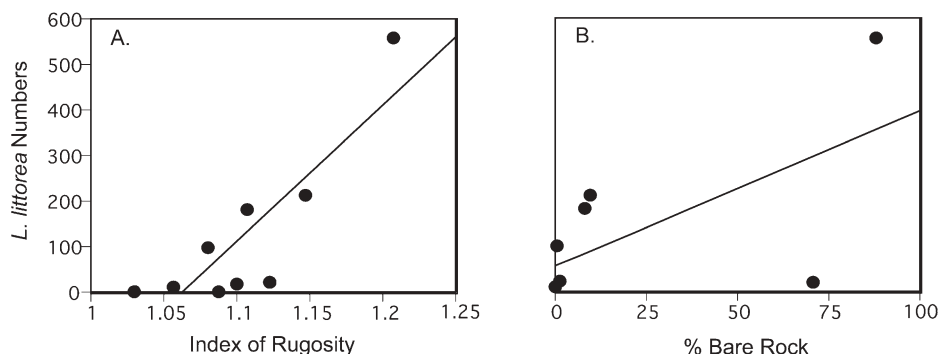


Figure 4. **A.** Correlation between mean *L. littorea* density at nine sites in the intertidal zone and the index of rugosity (a measure of substrate complexity) measured at 0.0 m ($R_s = 0.77$, $P = 0.015$). **B.** Correlation between mean *L. littorea* density at nine sites in the intertidal zone and the percentage of bare rock ($R_s = 0.71$, $P = 0.031$) on Appledore Island. A higher index of rugosity indicates a more complex substrate.

Table 1. Results of multiple regression analyses using the maximum increase in R^2 procedure.

	Factor	SS or MS	F	Slope	P
Intertidal zone	Rugosity	188814	59.84	+	0.0006
	Ephemeral green algae	38312	2.14	-	0.018
	<i>Chondrus crispus</i>	25027	7.93	-	0.037
	Model	82484	26.14		0.0018
Shallow subtidal zone	<i>Carcinus maenas</i>	3932	28.22	+	0.0011

We show the two models (one each for the intertidal and shallow subtidal zones) with the lowest overall P -value. The models include the combination of factors that best explains variation in *L. littorea* abundance among sites in the intertidal zone ($n = 9$) and shallow subtidal zone ($n = 9$) on Appledore Island. Sums of squares (SS) are presented for individual factors and mean squares (MS) for complete models.

our 19 tests is expected to be significant by chance alone. Four tests resulting from our analyses were significant at 0.05 yielding a FDR of 25%. This result suggests that three out of the four tests are expected to reflect true differences, although we cannot identify which test is significant simply as a result of chance.

DISCUSSION

The extremely heterogeneous distribution of *L. littorea* in the intertidal and shallow subtidal zones on Appledore Island can be explained by differences in several biological and physical factors among sites. In the intertidal zone, correlation analyses indicate that *L. littorea* density is positively correlated with two features of the substrate: rugosity and the percentage of bare rock. Thus, sites with more complex substrate and a greater percentage of bare rock support higher densities of *L. littorea*. Multiple regression analysis suggests that rugosity, in combination with the percentage of the substrate covered by *C. crispus* and ephemeral green algae (*Ulva* spp., *Cladophora* spp., *Enteromorpha* spp.), best predicts *L. littorea* density on Appledore Island. In the shallow subtidal zone, correlation analyses failed to uncover any factors that are significantly correlated with *L. littorea* density. However, multiple regression analysis suggests that *C. maenas* density best predicts *L. littorea* density, and that snail and green crab densities are positively correlated.

Intertidal distribution patterns

Although *L. littorea* reaches high densities in the intertidal zone, its abundance varies greatly among sites on Appledore Island. The results of our correlation analyses suggest that some of this variation can be explained by differences among sites in two characteristics of the substrate: rugosity and the percentage of bare rock.

Among-site variation in *L. littorea* density is highly correlated with rugosity at 0.6 m and 0.0 m. With only two exceptions (see below), sites with high substrate rugosity supported higher densities of snails than sites with low rugosity. *Littorina littorea* may achieve relatively higher densities at more rugose sites because these sites provide (1) more damp, shaded areas in which snails can escape thermal and desiccation stress (Reid, 1996), (2) more crevices that serve as refuges from predators, and/or (3) greater surface area or more attractive surfaces for recruitment. Williams (1964) considered recruit density to be a major determinant of adult *L. littorea* density. Substrate characteristics, particularly the availability of crevices, have also been shown to

be important for *L. littorea* on a wave-swept, ice-scoured shore in Quebec, Canada (Addy & Johnson, 2001).

The unusually low abundance of *L. littorea* at Siren's Cove (high rugosity) and unusually high abundance of snails at Appledore Ledges (low rugosity) are likely explained by each site's unique topography. Siren's Cove is a relatively narrow (approximately 5 m wide) cobble beach enclosed by steep rock walls. During storms and other periods of intense wave action, water accelerates as it funnels into the cove. The force of the incoming water causes the beach's cobbles and boulders to shift and move. If the percentage of the substrate covered by bare rock is indicative of cobble scour, then 0.6 m and 0.0 m at Siren's Cove are subject to more scour than the same heights at any of the other study sites. Thus, periodic storms may prevent the establishment of high densities of both algae and *L. littorea* at this site.

On the other hand, as a result of its low rugosity, Appledore Ledges should support few snails. However, the point's low, rocky ledges are located just seaward of a rocky beach. Juvenile *L. littorea* reach high densities on barnacle-encrusted and otherwise bare rocks in the mid- and low intertidal zone on this beach (personal observation). Smith & Newell (1955) indicated that juvenile *L. littorea* often move from their site of recruitment to other locations in the intertidal zone as they mature. At Appledore Ledges, snails may migrate from the boulders on the beach to the seaward ledge and persist there as adults.

Littorina littorea also reaches higher densities at sites with a higher percentage of bare substrate. Bare rock may provide an important substrate for settlement with more rock supporting more recruits. On Appledore Island, recently metamorphosed snails occurred in the highest densities on bare rocky substrate (R. Carlson, unpublished). Because *L. littorea* preferentially consume macroalgal germlings (Lubchenco, 1978), it is also possible that high snail densities actually increase the percentage of bare substrate at a site by grazing algal recruits and ephemeral algae before they can establish.

In addition to rugosity, our multiple regression analysis suggests that variation in the percentage of the substrate covered by *C. crispus* and ephemeral green algae is predictably associated with variation in *L. littorea* density among sites. Specifically, the analysis suggests that *L. littorea* abundance is inversely related to the percentage cover of *C. crispus*. Although the common periwinkle does not usually consume *C. crispus* (Lubchenco, 1978), the presence of the alga may substantially alter characteristics of the snail's habitat. The short dense thalli and smooth fronds of *C. crispus* may make it difficult for snails to remain attached to the substrate during periods of strong wave action, thereby precluding the establishment of high densities of snails. Our analysis also suggests that *L. littorea* abundance in the intertidal zone is inversely related to percentage cover of ephemeral green algae. In contrast to *C. crispus* which may cause low snail densities, low densities of green algae may be a consequence, not a cause, of high snail densities. Several investigators have described a similar inverse correlation between high densities of *L. littorea* and its preferred food (Lubchenco, 1978; Petraitis, 1983; Bertness, 1984).

Even though wave stress can limit the abundance of intertidal consumers in a variety of ways (e.g. detachment from the substrate or reduction in foraging efficiency and/or range) (Lubchenco & Menge, 1978; Menge, 1978a, b), we found only limited evidence of these effects for *L. littorea* in the intertidal zone on Appledore Island. *Littorina littorea* was abundant across most of the gradient of wave exposure included in this study; snails were completely absent only from Norwegian Point, the most exposed site.

Variation in predator densities across sites also fails to explain between-site variation in *L. littorea* density. In general, few *C. borealis*, *C. irroratus* or large *C. maenas* (>55 mm carapace

width) are found in the intertidal zone. Although small *C. maenas* are often found in the intertidal zone, crabs in these size classes do not appear to be capable of consuming most sizes of *L. littorea* (Carlson, 2002).

Shallow subtidal distribution patterns

Below 0.0 m, *L. littorea* density decreases rapidly to only a few snails per square metre and varies relatively little among sites. This lack of variation may explain the failure of our analyses to uncover any factors that are significantly correlated with *L. littorea* density.

Wave exposure has been shown to have a tremendous effect on organisms in the intertidal zone (Lubchenco & Menge, 1978; Menge, 1978a, b). However, its effects on subtidal organisms are often less intense (Hurd, 2000). On Appledore Island, snails occur in similarly low densities at protected, moderately exposed and exposed sites, suggesting that wave exposure in fact has little effect on the abundance of *L. littorea* in the shallow subtidal zone.

However, the difference between the intensities of the wave stress experienced by inhabitants of the intertidal and shallow subtidal zones (Hurd, 2000) may explain differences in *L. littorea* shell shape between the two zones. The mechanical factors associated with wave stress have been shown to limit the absolute size of intertidal organisms (e.g. Denny, Daniel & Koehl, 1985). The smaller, thinner shells of intertidal *L. littorea* may be a result of greater wave stress in the intertidal zone compared with the subtidal zone. Alternatively, *L. littorea* shells may be larger and thicker in the shallow subtidal zone due to the presence of higher densities of *C. borealis* and large *C. maenas*. Large snails with thick shells often experience reduced predation pressure (Boulding, Holst & Pilon, 1999) and *C. borealis* and *C. maenas* have been shown to consume large snails less frequently than small snails (Carlson, 2002). Shell thickening in gastropods is a defence that can be induced by the presence of cues from predatory crabs (Appleton & Palmer, 1988; Trussell & Nicklin, 2002; Trussell *et al.*, 2003). The high density of predators in the shallow subtidal zone may thus result in a higher rate of shell thickening for *L. littorea* inhabiting this zone.

Although the results of our multiple regression analysis must be treated with caution, they do suggest the intriguing possibility that *C. maenas* density predicts *L. littorea* density on Appledore Island. Specifically, the analysis suggests that higher densities of *L. littorea* occur at sites with higher densities of green crabs. This result contrasts with previous investigations of littorinid and crab distributions along the Pacific Coast which found a strong inverse correlation between densities of predatory *Cancer productus* and *C. oregonensis* and densities of *L. sitkana* and *L. scutulata* (Behrens Yamada & Boulding, 1996; Rochette & Dill, 2000). On Appledore Island, *C. maenas* and *L. littorea* densities may be positively correlated because both species are responding to an additional, unmeasured factor in the same manner. For example, they may be responding to a shared predator (e.g. the American lobster *Homarus americanus*; Ojeda & Dearborn, 1991). Alternatively, *C. maenas* may preferentially migrate to areas of high snail abundance in search of prey, have similar habitat preferences (i.e. crabs may prefer rugose substrates) or recruit to the same surfaces (e.g. bare rocks) as the snail.

In summary, our study suggests that large-scale distribution patterns of *L. littorea* on the moderately protected, rocky shores of Appledore Island are best predicted by two structural elements of the habitat, substrate complexity and the percentage of the substrate that is bare rock. However, whether rugosity and the amount of bare substrate affect periwinkle densities through effects on food availability, recruitment, dislodgment, desiccation or protection from predation remains to be determined through additional experimental investigations.

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