



Why are intertidal snails rare in the subtidal? Predation, growth and the vertical distribution of *Littorina littorea* (L.) in the Gulf of Maine

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ABSTRACT

The North Atlantic gastropod *Littorina littorea* exhibits a characteristic “intertidal” distribution: the snail is abundant in the littoral zone but scarce in the shallow subtidal and the relatively few subtidal individuals are larger (in shell size) on average than those in the intertidal zone. For highly mobile species like *L. littorea*, this vertical distribution is primarily determined by directional movement. Biotic and abiotic factors vary across tidal heights, and natural selection for movement to shore levels where fitness is maximized provides the ultimate (evolutionary) explanation for vertical distribution patterns. In this study, we asked whether variation in growth rate and/or predation pressure among tidal heights provide an ultimate explanation for vertical gradients in *L. littorea* size and abundance. We used a cage experiment to compare juvenile growth rate among tidal heights and a series of field and laboratory experiments to examine variation in predation pressure among tidal heights and snail size classes. Juvenile growth rates were highest in the low intertidal zone, declining at both higher and lower levels. Predation risk for tethered *L. littorea* increased with both decreasing tidal height and decreasing body size (shell height). Almost all tethered prey were consumed by shell-breaking predators and a census revealed that the two most abundant such predators were the crabs *Carcinus maenas* and *Cancer borealis*. Laboratory feeding experiments were used to compare size-dependent prey vulnerability and prey-size preferences for these two key predators. We found that *L. littorea* vulnerability decreased with increasing snail size and increased with increasing size of both predator species. However, whereas *C. borealis* were capable of consuming even the largest *L. littorea*, most *Carcinus* were unable to feed on individuals larger than 10 mm in shell height. Additionally, *C. borealis* preferred larger sizes of *L. littorea* than did *Carcinus*. Thus, *Carcinus*, which co-occurs with *L. littorea* in the intertidal, is a much less effective predator than *C. borealis*, which is found primarily in the subtidal. We conclude that predation on *L. littorea* by *C. borealis* and other subtidal consumers has resulted in the scarcity of this ecologically important grazer in the subtidal. This effect has been produced both through direct predation and by imposing strong selection for movement of *L. littorea* to higher tidal zones.

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1. Introduction

Classic studies of life on ocean shores describe a set of organisms found almost exclusively in the intertidal zone (Lewis 1964, Stephenson & Stephenson, 1972). Given that almost all are derived from marine ancestors, it is reasonable to ask why these intertidal species are so uncommon in subtidal habitats. In other words, what factors limit these species to the intertidal? A well-developed paradigm based on studies of sessile organisms states that the lower

limit of a species' vertical distribution is set by biological interactions (Connell 1961, 1972; Paine 1966, 1974). In the general scenario, recruits settle widely across vertical zones; individuals at lower tidal heights are then consumed by predators or out-competed by faster growing or more aggressive species (see Menge & Branch 2001) to yield a truncated, exclusively intertidal distribution.

This paradigm, however, is not necessarily applicable to mobile species because they have the ability to alter their location, both immediately after settlement and throughout benthic life (Rochette & Dill 2000). Many mobile intertidal animals, including snails, crabs and fishes, will migrate upward if experimentally or naturally displaced to lower levels on the shore. In doing so, the animals avoid the direct interactions with potential predators and competitors that have such profound and often mortality inducing impacts on sessile individuals

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(Vermeij 1972, Underwood 1979, Fawcett 1984). In mobile species, directional movement provides a proximate explanation for the absence of the species from the subtidal, while the factors that favor directional movement provide the ultimate explanation. Natural selection may favor movement to higher levels due to enhanced growth and fecundity (e.g. greater food availability, facilitation by co-occurring species) and/or higher survivorship (e.g. escape from predators).

Predation risk gradients have been shown to control the vertical distribution of several intertidal snail species. Their relative scarcity in the low intertidal and subtidal is due to both the direct effects of predators as well as movement of the snails away from areas of high risk (Fawcett 1984, Behrens Yamada & Boulding 1996, Rochette & Dill 2000). Additionally, many intertidal gastropods show a vertical gradient in shell size (and/or thickness) that is often linked to size-dependent predation risk (Vermeij 1972, McCormack 1982).

In this study, we investigate ultimate factors responsible for limiting the vertical distribution of an intertidal snail, the common periwinkle *Littorina littorea* (Linnaeus). *L. littorea* is found throughout the North Atlantic on both rocky and sedimentary shores. In both types of habitats, the snail is extremely abundant in mid- and low intertidal zones but very rare in shallow subtidal habitats (Reid 1996, Carlson et al., 2006). At many geographic locales, shell size (and/or thickness) increases with decreasing tidal height (Vermeij 1972, Saier 2000, Stefaniak et al., 2005). An ecologically important grazer in rocky (Lubchenco 1978, 1980, Lubchenco & Menge 1978), cobble, and salt-marsh *Spartina* habitats (Bertness 1984), *L. littorea* affects physical characteristics of the substrate (by bulldozing sediment) and the composition and productivity of algal/plant assemblages. The well-documented effects of *L. littorea* suggest that its near absence from the subtidal may have important ecological consequences.

Despite the snail's known (and potential) ecological effects, the factors determining its distributional limits and vertical gradient in size have received little previous investigation (Reid 1996). In this study, we first document abundance and size-distribution patterns of *L. littorea* and then investigate how two important components of fitness – growth and survivorship – vary across tidal height on rocky shores. We measured variation in growth rate among tidal heights by caging juvenile snails in the mid intertidal, low intertidal, and shallow subtidal. We performed a number of field and laboratory studies to determine whether survivorship is greater at higher tidal levels due to interactions with predators. First, we determined the vertical gradient of predation risk for *L. littorea* and other common molluscs and then surveyed the intertidal and subtidal distributions of crab and seastar predators. We then performed a series of laboratory feeding experiments to compare size-dependent prey vulnerability, and prey-size preferences between the two most common crab predators.

2. Materials and Methods

2.1. Study Species

L. littorea is an abundant and wide ranging gastropod found on rocky shores throughout the North Atlantic (Reid 1996). The evolutionary origins of *L. littorea* in the Northwest Atlantic are controversial (Chapman et al., 2007, Cunningham 2007). However, it is well documented that *L. littorea* underwent a rapid range expansion south from Nova Scotia in the 19th century, and by 1890 had become the dominant intertidal snail on shores of the Gulf of Maine. *L. littorea* grazes on a variety of diatoms and algae and has a preference for and responds metabolically to ephemeral algal species (Lubchenco 1978, 1983; Shumway et al., 1993; McQuaid 1996). Though most common in the mid to low intertidal, *L. littorea* can also be found at low densities in the subtidal zone (Reid 1996).

Potential predators on *L. littorea* in New England include four species of predatory decapods inhabiting the intertidal and/or shallow subtidal: the American lobster *Homarus americanus* H. Milne-Edwards, the rock crab *Cancer irroratus* Say, the Jonah crab *Cancer borealis* Stimpson, and

the green crab *Carcinus maenas* (Linnaeus) (henceforth referred to as *Carcinus*). *Carcinus*, also introduced from Europe in the late 19th century, is an omnivore with slim, dimorphic chelae, whereas the native *C. borealis* is a specialized predator with thick, monomorphic chelae (Grosholz & Ruiz 1996, Behrens Yamada & Boulding 1998, pers. obs.). The monomorphic chelae of *C. irroratus* are intermediate in size between those of *Carcinus* and *C. borealis*. The carnivorous snail *Nucella lapillus* (Linnaeus) and two seastars *Asterias rubens* Linnaeus and *A. forbesi* (Desor) also commonly feed on mollusks on rocky shores in the Gulf of Maine (Bertness 2006). In addition, two species of fishes, *Pollachius virens* (Linnaeus) and *Tautoglabrus adspersus* (Walbaum), migrate into the intertidal during high tides and are capable of feeding on *L. littorea* (Edwards et al., 1982, Ojeda and Dearborn 1991). Although the Great Black-backed Gull *Larus marinus* Linnaeus and Herring Gull *L. argentatus* Pontopiddan have large seasonal breeding colonies in the study area, neither species consumes *L. littorea* (Rome and Ellis, 2004).

2.2. Study Site

This study was carried out between May and August of 2001, 2002, and 2004 in the vicinity of the Shoals Marine Laboratory, Appledore Island, Isles of Shoals, ME, USA (42° 59'N; 70° 37'W). Appledore Island, part of a nine-island archipelago, is located 10 km off the coast of New Hampshire. The eastern side of the island faces the open Atlantic Ocean and is exposed to heavy wave action, whereas the western side is relatively protected. At protected and moderately exposed sites on Appledore Island, the intertidal environment can be divided into three distinct vertical zones: a high intertidal zone dominated by blue-green algae, a mid- intertidal zone dominated by the brown algae *Ascophyllum nodosum* and *Fucus* spp., and a low intertidal zone dominated by the red alga *Chondrus crispus* (Stephenson & Stephenson 1972).

2.3. Vertical distribution patterns of *Littorina littorea*: Abundance and Size

The vertical abundance and size distribution of *L. littorea* at Appledore Island was studied at 8 sites during August, 2001. At each site, we censused and measured snails at 4 tidal heights: +0.6 m, 0.0 m, -1.5 m, -3.0 m (all relative to Mean Lower Low Water). Details of sampling methods, location of study sites, and the results of our studies of the relationship between *L. littorea* abundance and habitat variables are available in a companion paper: Carlson et al., 2006. In both studies, sites were chosen to encompass the breadth of natural variation in wave exposure, gradient, and substrate type across Appledore Island. We used the mean *L. littorea* density at each tidal height across the eight study sites (Fig. 2 in Carlson et al., 2006) as replicates in a one-way ANOVA to determine whether *L. littorea* density varies across tidal heights on Appledore Island.

We used shell height from the 676 intertidal and 188 subtidal measured individuals that were ≥ 10 mm in Carlson et al. (2006) to determine whether intertidal (+0.6 m and 0.0 m) *L. littorea* differ in size from subtidal (-1.5 m and -3.0 m) *L. littorea*. We considered only snails > 10 mm in height because our sampling methods likely did not adequately census new or recent recruits, which can be difficult to see and often hide in small crevices. Size-frequency distributions of intertidal and subtidal *L. littorea* in five size classes (10–16 mm, 17–21 mm, 22–24 mm; 25–26 mm, and ≥ 27 mm) were compared using a contingency table analysis. These size classes roughly correspond to age classes 1 yr, 2 yr, 3 yr, 4 yr, and ≥ 5 yr old respectively, assuming *L. littorea* on Appledore Is. exhibit growth rates similar to those of their European counterparts (Moore 1937, Williams 1964).

2.4. Variation in Growth Rates among Tidal Heights

We carried out a four-week field study to determine whether the growth rate of juvenile *L. littorea* varies among tidal heights. Sexually immature (4–6 mm shell height) *L. littorea* (Smith & Newell 1955,

Williams 1964) were labeled with a numbered bee tag (weight approximately 0.01 g) and measured (shell height; to nearest 0.01 mm) with digital calipers. Wet weight (± 0.01 g) was also measured after eliminating excess water by forcing the animal far into its shell and thoroughly drying it with a paper towel. Eight snails were then randomly placed in each of 40 open-bottom mesh cages (12.5 cm diameter; 7 cm height; 4 mm \times 4 mm mesh) in mid-July 2001. The density in each cage (65 snails m $^{-2}$) was within the range observed in the Appledore mid-low intertidal and shallow subtidal (see Fig. 1). Ten cages were placed approximately 1 m apart at 0.0 m, -1.5 m, and -3.0 m and five cages at 0.75 m and 0.5 m along the rock ledges on the northwest coast of Appledore Is. Cages were bolted into drill-holes in the rock and the bottom edges secured with marine epoxy.

After 32 days, three cages remained at 0.75 m, one at 0.5 m, seven at 0.0 m, nine at -1.5 m, and ten at -3.0 m. Due to cage losses at 0.75 m and 0.5 m, data at these heights were combined. We measured the final shell height and wet weight of each snail and calculated growth over the course of the experiment. Examination of residual plots indicated that the data were normally distributed with no outliers. To test for variation

in growth rate (both in wet weight and height) between tidal heights, we analyzed the data in a mixed model ANOVA (JMP v 5.01a) in which tidal height was treated as a fixed effect and cage nested within tidal height as a random effect. Post hoc comparisons of growth rate between tidal heights were made using Tukey's HSD.

2.5. Relative Predation Risk by Tidal Height

We conducted a tethering experiment to determine the relative predation risk for *L. littorea* at different tidal heights and compare it to the risk experienced by its native congener *Littorina saxatilis* (Olivi) and the abundant mussel *Mytilus edulis* Linnaeus. The study site was located just north of Larus Ledge (Fig. 1 in Carlson et al., 2006). The mollusks were tethered at four tidal heights (+0.5 m, 0 m, -2 m, -4 m) for 7 days (July 21–27, 2004). Each of the 20 replicates included a single brick placed at each tidal height; all bricks were placed at least 1 m apart. Seven animals were tethered to each brick: 3 *L. littorea* [1 large (20–25 mm), 1 medium (15–19 mm), 1 small (8–13 mm)], 2 *L. saxatilis* [1 large (11–14 mm), 1 small (7–9 mm)], and 2 mussels [1 small (5–15 mm), 1 large (35–50 mm)]. Snails and mussels were glued (Loctite Superglue Gel) to the frayed end of a 35 cm nylon line attached to the brick. Three controls per tidal height each consisted of a brick with tethered prey placed within a plastic basket (9 \times 13 cm) lined with fine mesh. The condition of all tethered animals was recorded by SCUBA divers who checked the experiment just after dawn and before dusk each day.

Data were first examined using a Cox's Proportional Hazard model (JMP v. 5.0.1a) that included the three main effects (tidal height, prey species, prey size) and all possible interaction effects. We then excluded all non-significant effects ($P > 0.25$), combined the data for medium and large *L. littorea* because the two size classes did not differ significantly in mortality rate, and re-examined the data using a model that included tidal height, prey species, prey size, and prey species \times prey size.

2.6. Predator Vertical Distributions

We surveyed the density of common invertebrate predators in the rocky intertidal and subtidal at four tidal heights (0.5, 0.0, -2, and -4 m) in early August 2004 at a site just north of Larus Ledge (Fig. 1 in Carlson et al., 2006). At each tidal height, crabs (*C. borealis*, *C. irroratus*, and *Carcinus*) and seastars (*Asterias* spp.) were counted in five 1 m 2 quadrats randomly located along a 20 m transect line. Censuses were conducted by SCUBA divers during daytime high tides. Previous studies have shown that these crabs are active during daytime and move from the subtidal into the intertidal with the rising tide (Novak 2004, Ellis et al., 2007). Because all four predators were relatively rare, with at least one quadrat with 0 individuals at tidal heights at which they occur, we analyzed the log ($\times + 1$) abundance data using the SAS GENMOD procedure fitted to a Poisson distribution. We excluded tidal heights for which no individuals of a species had been found.

N. lapillus, a highly abundant but slow moving predator, was censused in five 0.25 m 2 quadrats at each tidal height. The -2 and -4 m quadrats were censused by SCUBA divers during high tide whereas the 0.0 and 0.5 m tidal heights were censused during low tides. We used a one-way ANOVA (JMP v5.01a) to test for significant variation in *N. lapillus* density among tidal heights. Tukey's HSD was used for post-hoc pairwise comparisons among heights.

2.7. Vulnerability of *Littorina littorea* to Predation by *Carcinus maenas* and *Cancer borealis*

Our survey of predator densities across tidal heights indicated that *Carcinus* is the most abundant decapod predator of *L. littorea* in the intertidal, whereas *C. borealis* is the most abundant predator in the subtidal. To better understand the potential effects of these predators on the density and size distribution of *L. littorea*, we performed a

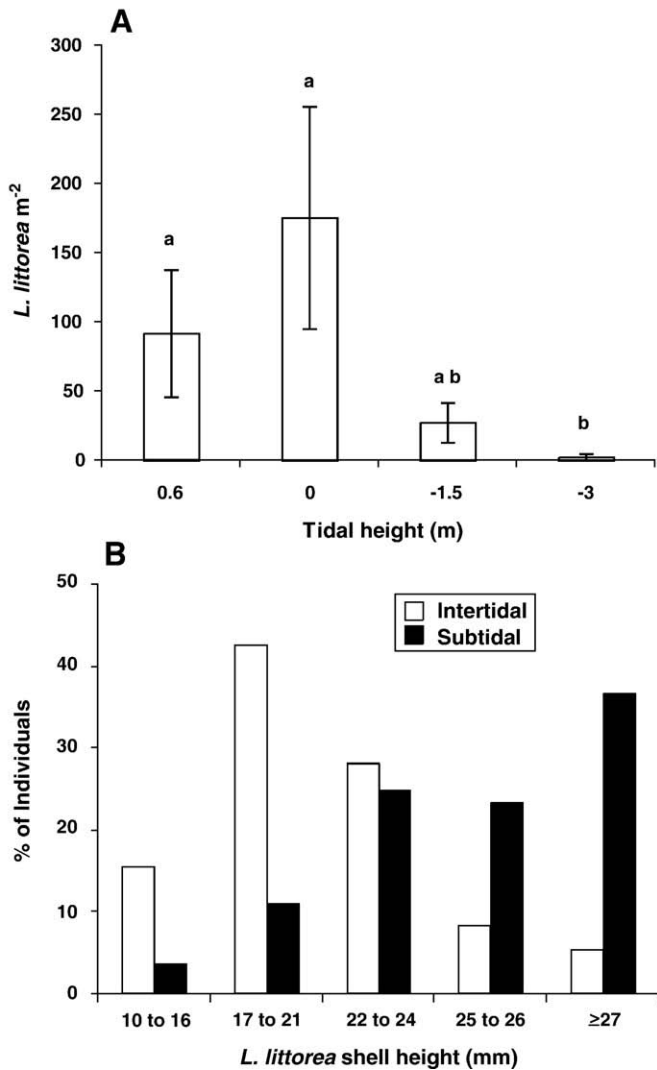


Fig. 1. Abundance and size distribution of *Littorina littorea* on Appledore Island, ME, U.S.A. (data from Carlson et al., 2006). A. Mean number of *L. littorea* m $^{-2}$ (± 1 SE) at four tidal heights. Tidal heights sharing the same letter are not significantly different from one another (Tukey's HSD, $P > 0.05$). B. Percent of *L. littorea* in five size (shell height) classes in the intertidal (0.6 m + 0.0 m) and shallow subtidal (-1.5 m + -3.0 m). Frequency distributions differ significantly between the intertidal and shallow subtidal (χ^2 test, $P < 0.0001$).

series of laboratory feeding experiments to determine the vulnerability of different size classes of *L. littorea* to predation by the two crab species.

2.7.1. Prey Size Limits of *Carcinus maenas*

To determine the sizes of snails different size *Carcinus* can consume, we paired all possible combinations of three *Carcinus* size classes with four *L. littorea* size classes in a laboratory feeding experiment. Intertidal crabs with intact chelae collected from Appledore and nearby (to the east) Duck Island were divided into three size classes based on maximum carapace width: small (44 mm±2 mm), medium (54±2 mm), and large (64±3 mm). *L. littorea* gathered from Appledore were sorted into four size classes based on shell height: 10, 15, 20, and 25 mm (all±1 mm). Each of the resulting twelve treatments (3 crab sizes×4 snail sizes) was included in a single trial; each trial was repeated six times (N=6) for a total of 72 different crab-snail pairings.

Crabs were isolated and starved for approximately 50 hours before addition to shallow 7.6 L containers containing three snails of a given size class. Each tub was perforated with small (<10 mm in diameter) holes to facilitate water flow, covered with mesh, and placed in a flowing seawater table. A rock or brick was placed in each container to provide shelter for the crab. All trials began in mid- to late morning; after 20 hr the number of snails eaten was recorded. Any crab that failed to eat was offered a crushed snail to ensure the animal was willing to feed in the laboratory environment. Data were entered into an ordinal logistic regression analysis (JMP v5.01a) to determine whether *L. littorea* and *Carcinus* size categories had significant effects on the number of snails consumed.

Stefaniak et al. (2005) performed a parallel study on the ability of *C. borealis* to feed on *L. littorea*. Their research was conducted at the same location and with the same equipment; however, in each trial they paired a *C. borealis* with only a single *L. littorea*. To determine relative susceptibility to predation by *Carcinus* vs. *C. borealis*, we compared data for the two *L. littorea* size classes (20 mm and 24/25 mm) that were included in both studies. Stefaniak et al. (2005) used med-large size *C. borealis* (80–90 mm in carapace width). Thus, we compared their results to those for the medium and large *Carcinus* in our study. We used nominal logistic regression to determine whether the probability of one or more *L. littorea* being eaten in each trial was significantly affected by crab species or snail size class.

2.7.2. Prey Size Preferences of *Carcinus maenas* and *Cancer borealis*

A similar laboratory experiment was conducted to determine both the sizes of *L. littorea* preferred by different size classes of the crabs *Carcinus* and *C. borealis* as well as the relative predation rates of each crab species on different size classes of *L. littorea*. The experiment used the same size classes of *Carcinus* and *L. littorea* and the same experimental equipment employed in the previous experiment. *C. borealis* is a larger crab than *Carcinus*; thus the carapace widths for each size class of *C. borealis* were: 60 (±5) mm for small, 75 (±4) mm for medium, and >80 mm for large. In this experiment, we paired a single starved crab with four *L. littorea*, one from each size class. Because the preferred size is likely to be consumed first, the experiments were checked every ten minutes for the first two hours, every half-hour for the following three hours, and again fifteen hours later. A total of 28 replicates were performed with large, 32 with medium, and 17 with small *Carcinus* and 10 replicates with small, 9 with medium, and 16 with large *C. borealis*. We excluded from analysis 2 trials in which the crab did not feed on either a whole or crushed snail.

The experimental results were analyzed in several ways in order to address a series of questions. (1) For each crab species, we used a contingency table analysis to determine whether there were differences among crab size classes in the proportion of trials in which no snails were consumed. For those crab size classes with sufficient numbers of trials in which snails were eaten, we used goodness-of-fit tests to determine whether there were preferences for particular prey size classes. (2) In

order to compare prey-size preferences among crab species/size-classes, we used a contingency table analysis. (3) To compare potential predatory impact on *L. littorea* populations, we used a two-way ANOVA to determine whether crab species and/or crab size classes had a significant effect on total number of snails consumed in each trial.

3. Results

3.1. Vertical Distribution of *Littorina littorea*: Abundance and Size Patterns

Densities of *L. littorea* (Fig. 1A) were significantly higher in the intertidal (+0.6 and 0.0 m) than in the subtidal (-1.5 and -3.0 m) zone (ANOVA: $F_{3, 30}=4.1$, $P=0.015$; Tukey's HSD, $P<0.05$). Additionally, size distributions (Fig. 1B) were strikingly different between the intertidal and subtidal ($\chi^2=205$, $df=4$, $P<0.0001$) with fewer than 15% of subtidal *L. littorea* smaller than 22 mm and fewer than 15% of intertidal individuals larger than 24 mm.

3.2. Variation in Growth Rates among Tidal Heights

The growth rates (both shell height and wet weight) of the snails varied significantly with tidal height (both $P<0.0001$; Fig. 2). *L. littorea* at 0.0 m added an average of 2.0 mm in shell height, significantly more than at the other 3 tidal heights, while snails at -3.0 m grew only 0.93 mm, significantly less than individuals higher on the shore (Tukey's HSD: all $P<0.05$). The analysis of the growth in wet weight yielded a nearly identical pattern (Fig. 2).

3.3. Relative Predation Risk by Tidal Height

Predation rates on tethered, uncaged prey were high with a median survival time of 36 hr; only 13% of the prey remained alive by the end of the 6 days. Of the 487 prey consumed, significantly more were eaten during dusk/nighttime (60%) than during daytime (40%) [binomial test: $P=0.00001$]. The probability of being eaten during daytime vs. dusk/nighttime was not affected by tidal height, prey species, or prey size (logistic regression: all $p>0.3$). The vast majority (89%) of prey eaten had crushed or peeled shells, with shell fragments remaining attached to the tether or visible nearby. *Asterias* were responsible for 8% of the predation and a single large *L. littorea* was preyed upon by *N. lapillus*.

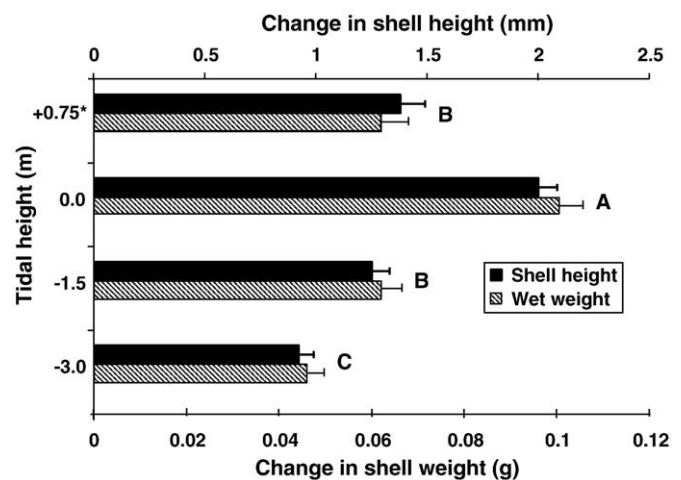


Fig. 2. Mean change (±1 SE) in shell height and wet weight of juvenile *Littorina littorea* over 4 weeks at different tidal heights. Data from growth at 0.5 and 0.75 m were combined to account for cage loss. Tidal heights sharing the same letter are not significantly different from one another in snail growth rate (Tukey's HSD, $P>0.05$).

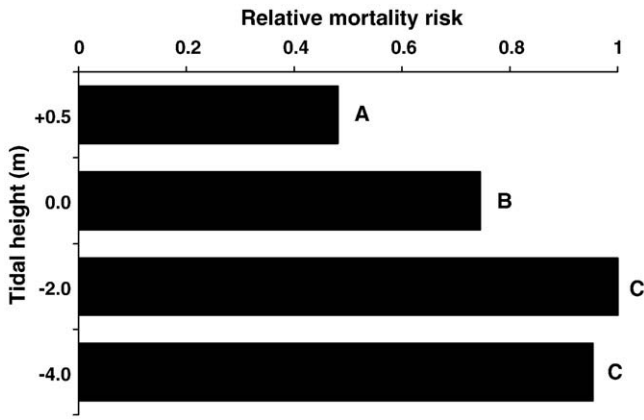


Fig. 3. Relative mortality risk at different tidal heights for tethered *Littorina littorea*. Mortality risk varied significantly with depth (Cox Proportional Hazard, likelihood ratio test: $P < 0.00005$). Letters indicate similarity in mortality risk among tidal heights (post-hoc likelihood ratio tests: $P < 0.05$).

Of the 81 animals in control cages, only 5 disappeared from the tethers. In 2 of these cases, *Carcinus* had entered the cage, and in the other 3 the prey had crawled out through the cage mesh. In all 5 cases there was strong evidence of predation: shell fragments were present on the bottom or still attached to the tether. In no cases did the prey pull themselves free from the tether.

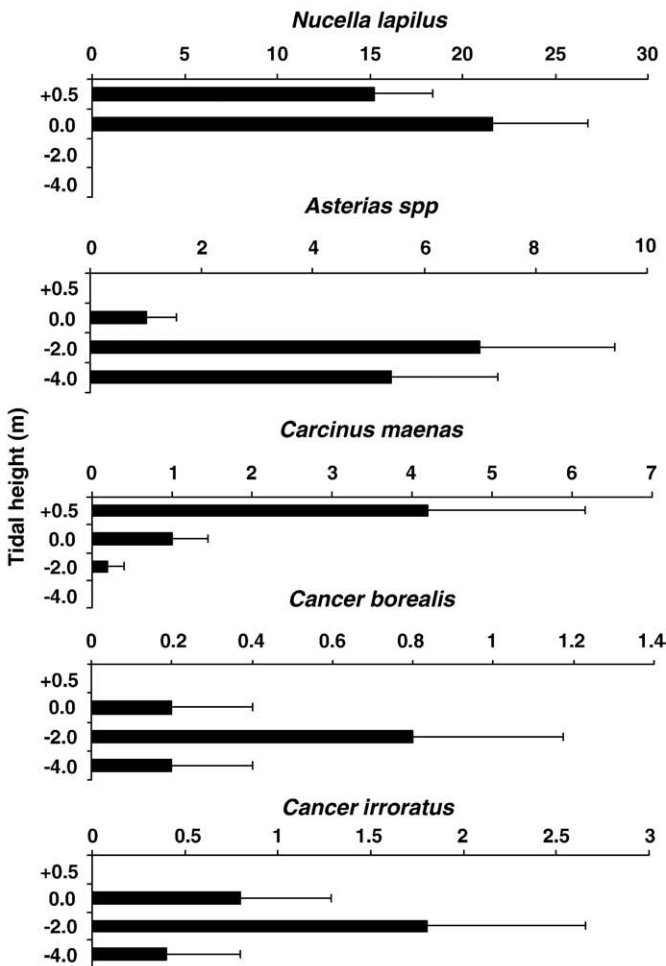


Fig. 4. Mean densities per m^2 (± 1 SE) of five different potential predators of *Littorina littorea* at four different tidal heights.

Survival rates of prey were significantly affected by depth (Cox Proportional Hazard, likelihood ratio test: $P < 0.00005$), prey size ($P = 0.0038$), and prey species ($P = .047$); no interaction effects were significant (all $P > 0.13$). Mortality risk increased from the mid-intertidal into the subtidal: survival was significantly higher at +0.5 m than at 0.0 m and both were significantly higher than survival in the subtidal (-2.0 m and -4.0 m) [likelihood ratio tests; all $P < 0.05$, Fig. 3]. The survival rate of *L. littorea* was significantly higher than those of *L. saxatilis* and *M. edulis* (likelihood ratio tests: both $P < 0.05$) with a mortality risk for *L. littorea* 83% of the mortality risk of the other two species. Large size-class prey had higher survivorship, incurring 87% of the mortality risk of the small size-class prey.

3.4. Predator Vertical Distributions

N. lapillus exhibited a striking and significant change in density with tidal height (1-way ANOVA: $P = 0.001$; Fig. 4A). The dogwhelk was quite abundant ($56 m^{-2}$) in the intertidal (+0.5 and 0.0 m) and completely absent from the subtidal (-2 and -4 m). *Asterias* (Fig. 4B) showed a significant and nearly opposite pattern: highest abundance ($6.2 m^{-2}$) in the subtidal, a significantly lower density at 0.0 m (GENMOD pair-wise comparisons: both $P < 0.055$), and complete absence from +0.5 m.

Comparisons among the crab species revealed contrasting patterns between *Carcinus* and the two *Cancer* species (Fig. 4C, D, E). *Carcinus* abundances declined steadily with depth, from a high of $4.2 m^{-2}$ at +0.5 m to zero at -4 m. Density differences between the highest tidal height (+0.5 m) and 0.0 m and -2.0 m were marginally significant (GENMOD LSM Differences: $P = 0.053$, $P = 0.06$). In contrast, both *C. borealis* and *C. irroratus* were most abundant in the shallow subtidal at -2 m and entirely absent from the quadrats at +0.5 m. Due to low overall densities and high variation among quadrats, however, there was no significant effect of tidal height among the three levels at which the two *Cancer* crabs were present (GENMOD LSM Differences: $P = 0.20$ for *C. borealis*; $P = 0.16$ for *C. irroratus*).

3.5. Vulnerability of Littorina littorea to Predation by Carcinus maenas and Cancer borealis

3.5.1. Prey Size Limits of Carcinus maenas

Consumption rates of *L. littorea* by *Carcinus* varied with snail and crab sizes (Fig. 5A). Large crabs consumed snails in 38% of trials,

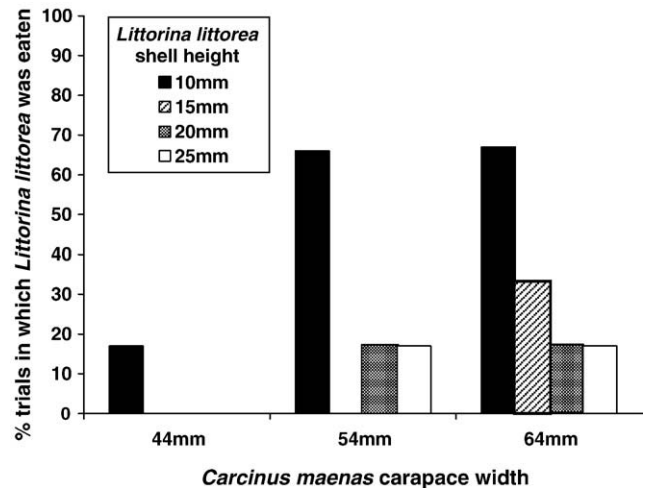


Fig. 5. Vulnerability of different size (shell height) *Littorina littorea* to predation by different size (carapace width) *Carcinus maenas*. Small *L. littorea* (10 mm) were significantly more likely to be eaten than snails in the three larger size classes. Small *Carcinus* (44 mm) were significantly less likely to eat a *L. littorea* than were the larger *Carcinus*.

medium crabs in 25%, and small crabs in 4%. Large crabs consumed all sizes of *L. littorea*, eating at least one from every size class. Although medium crabs consumed 10 mm *L. littorea* most often, they also occasionally ate larger snails. Small crabs generally did not consume any of the *L. littorea* sizes offered; only one 10 mm snail was eaten out of all the trials.

Analysis by ordinal logistic regression revealed that the numbers of snails eaten varied significantly with both snail size (likelihood ratio test: $\chi^2=15.1$, $df=3$, $P=0.003$) and crab size ($\chi^2=7.0$, $df=2$, $P=0.03$). The smallest snails (9–11 mm shell height) were significantly more likely to be eaten than any of the 3 larger size classes (all $P=0.0002$). *Carcinus* crabs in the smallest size class (43–45 mm carapace width) were significantly less likely to consume *L. littorea* than either of the two larger crab size classes (both $P<0.015$).

A comparison of predation rates by medium-large *Carcinus* and *C. borealis* (data for the latter species from Stefaniak et al., 2005) showed a large difference between the two crab species (logistic regression, likelihood ratio test, $\chi^2=14.3$, $df=1$, $P=0.0002$). *C. borealis* were 6.8 times more likely than *Carcinus* to consume *L. littorea* (20 and 24/25 mm sizes classes).

3.5.2. Prey Size Preferences of *Carcinus maenas* and *Cancer borealis*

Carcinus consumed snails in 45% of 75 trials, with large crabs feeding significantly more often than medium or small crabs ($\chi^2=36.3$, $df=2$, $P<0.0001$). Small and medium *Carcinus* ate too few snails for an analysis of prey size preferences. Large *Carcinus* had highly significant differences among the snail size classes in terms of which were eaten first ($\chi^2=26.36$, $df=3$, $P<0.0001$). The smallest (10 mm) *L. littorea* were consumed first in 64% of cases with the 15 mm consumed first in 32%. In contrast, the largest (25 mm) snails were never eaten.

C. borealis ate one or more *L. littorea* in 80% of 35 trials, with no significant differences in consumption frequency among the crab size classes ($\chi^2=1.6$, $df=2$, $P=0.46$). However, the crab size classes differed significantly in size of prey eaten first ($\chi^2=6.3$, $df=2$, $P=0.04$); the smallest *C. borealis* ate the smallest (10 mm) snails more frequently than did the medium and large crabs (Fig. 6). Snail size-class preference was very similar between small *C. borealis* and large *Carcinus* but differed between large *Carcinus* and medium-large *C. borealis* (Fig. 6). Medium-large *C. borealis* ate significantly more of the larger size classes of snails ($\chi^2=10.9$, $df=1$, Fisher's Exact $P=0.002$).

Both "crab species" and "crab size" had a significant effect on the number of snails eaten per trial (species: $F_{1, 101}=41.1$, $P<0.0001$; size-

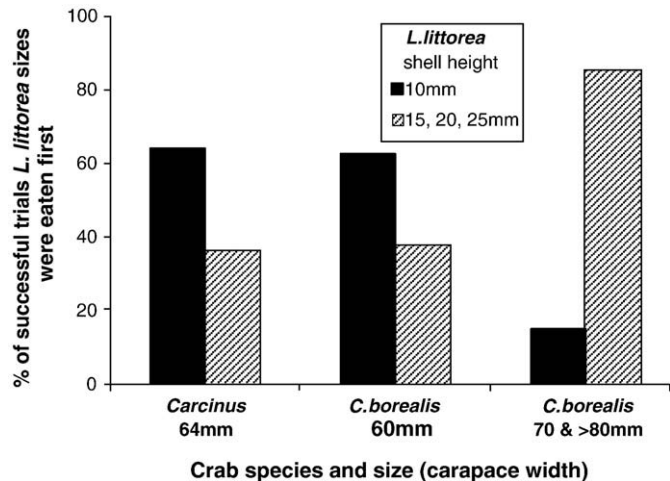


Fig. 6. Prey size preferences of *Carcinus maenas* and *Cancer borealis* when crabs were simultaneously offered four different sizes of *Littorina littorea*. Comparison of the largest *Carcinus* (65 mm) with the small *C. borealis* (60 mm) and medium plus large *C. borealis* (>70 mm) in the percent of trials in which the 10 mm size class or larger size classes were eaten first. Medium-large *C. borealis* consumed significantly more medium and large *L. littorea* (snails ≥ 15 mm) than were eaten by large *Carcinus* or small *C. borealis*.

class: $F_{2, 101}=20.6$, $P<0.0001$); the interaction effect was not significant ($P=0.66$). *C. borealis* ate an average 2.0 (+0.17) snails per trial while *Carcinus* ate only 0.74 (± 0.11). Large crabs (both species combined) ate significantly more *L. littorea* per trial ($\bar{x}=2.0\pm 0.16SE$) than either the medium (0.51 ± 0.17) or small (0.70 ± 0.18) crabs (Tukey's HSD: $P<0.05$).

4. Discussion

Like a number of marine gastropods, *L. littorea* is found almost exclusively in the intertidal. The species' virtual exclusion from the subtidal is not due to physiological limitations: many caged juveniles survived and grew at depths of -1.5 and -3 m (Fig. 2) and a small number of individuals—almost invariably having large and thick shells—are found in the subtidal (Fig. 1B, Carlson et al., 2006). Instead, our experiments suggest that relatively strong predation pressure in the subtidal is one of the proximate factors, as well as the primary ultimate factor, producing this vertical distribution pattern.

On Appledore Island, mortality risk for *L. littorea* in the subtidal (-2 and -4 m) is approximately 1.5 \times higher than in the low intertidal (0.0 m) and 2 \times higher than in the mid- intertidal (0.5 m). Observations on the fate of tethered prey indicated that nearly 90% of snails were consumed by shell-breaking predators, presumably crabs, lobsters, or larger fishes. In addition, tethered *L. littorea* suffered only a slightly lower mortality risk (83%) than the blue mussel, *M. edulis*. This comparison is important because *M. edulis* is the most common mollusk consumed by shallow-water decapods in the Gulf of Maine (Ojeda and Dearborn 1991, Witman et al., 2003).

The green crab, *Carcinus*, has previously been considered the most important predator of *L. littorea* on protected New England shores (Lubchenco 1978, Trussell et al., 2002, 2003, Bertness 2006). Though *Carcinus* is the most numerically abundant decapod predator in the intertidal, our results suggest that other predators are responsible for the near-absence of *L. littorea* in the subtidal. First, *Carcinus* is relatively rare in the subtidal. Second, our experiments and field data indicate that much of the *L. littorea* population has reached a size refuge from *Carcinus* predation; this is particularly true for *L. littorea* found in the subtidal. In our laboratory feeding experiments, *Carcinus* with a carapace width of 44 mm could not successfully prey on *L. littorea* greater than 10 mm in shell height. On the moderately-protected rocky shores of Appledore Island, 90% of *Carcinus* are smaller than 44 mm (P. League-Pike, unpubl. data). It is also likely that *L. littorea* spend a large portion of their lifespan at sizes that make them relatively invulnerable to predation by *Carcinus*. *L. littorea* are about 0.3 mm in shell height at metamorphosis (Thorson 1946), and, in Britain, have grown to 5 mm by 2 months and 10 mm by 10–14 months of age (Moore 1937, Williams 1964). Our short-term experiment showed similar growth rates for juvenile *L. littorea* in the low intertidal on Appledore Is. Assuming growth rates at all ages are similar to those in European *L. littorea*, Appledore Is. snails are vulnerable to *Carcinus* predation during the first 6–12 months of life. Our intertidal snail censuses revealed high densities of *L. littorea* older than 1 year (≥ 10 mm), with 42% of those individuals estimated to be 3 yrs or older (≥ 22 mm). The subtidal *L. littorea* population is even more heavily skewed to larger, older individuals (85% ≥ 22 mm), and therefore even less vulnerable to predation by *Carcinus*.

In contrast, large (20–25 mm) *L. littorea* are highly vulnerable to predation by the more powerful crab *C. borealis*. When the prey preferences of the two crab species were directly compared in feeding experiments, we found a nearly 7-fold increase in the likelihood of a large *L. littorea* being consumed by medium-large (80–90 mm) *C. borealis* compared to medium-large (54–64 mm) *Carcinus*. In experiments where the two species were offered multiple snail sizes, *C. borealis* consumed 2.7 times the number of snails eaten by *Carcinus*. The results of our laboratory feeding trials are mirrored by those from our field tethering experiment: *L. littorea* suffered the highest mortality

risk in the shallow subtidal (–2 m) where *C. borealis* are most abundant (this study; S. Lozyniak unpubl. data, P. League-Pike unpubl. data). Additionally, we directly observed *C. borealis* feeding on *L. littorea* as well as videotaped them feeding on tethered snails in the field.

While mortality risk declined with increasing tidal height, the growth rate of juvenile *L. littorea* peaked in the low intertidal (0.0 m). Because growth rates were measured on caged snails, the results are potentially subject to cage effects. Given that our interest is in quantifying relative growth rates across tidal heights, only cage effects that vary systematically across tidal height are of concern. These effects could include reductions in algal growth due to shading or decreases in water velocities. Although we are unable to exclude such potentially confounding effects, we observed no systematic pattern of community alteration with tidal height.

The slower growth of *L. littorea* at higher tidal levels is not surprising if grazing, and thus growth, is limited by immersion time. Slower growth in the subtidal, however, appears counterintuitive. One possible explanation is that food or appropriate grazing substrate is less available in the subtidal. At our study site on Appledore Island, the subtidal bedrock is covered by a layer of silt/detritus that supports a growth of microflora. These sediments may provide a poorer grazing substrate for *L. littorea* than the rock or tough algal surfaces available in the intertidal (Martinez 1985). Another potential explanation for lower growth rates in the subtidal is feeding inhibition due to cues that predators are present. A number of studies have shown that gastropod growth is inhibited by chemical cues from crabs (Appleton & Palmer 1988, Palmer 1990). In the subtidal, snails may be continually immersed in chemical cues from crabs (primarily *Cancer*), lobsters, and fishes. Previous studies have shown that chemical cues from *Carcinus* inhibit *L. littorea* grazing and growth rates (Trussell et al., 2002, 2003): it remains to be determined whether cues from other decapods or fishes produce a similar response.

In this study, we compared the growth rates of juvenile individuals at different tidal heights. However, directly studying characteristics of adults at different tidal heights could also provide information towards understanding the factors affecting *Littorina littorea*'s distinct size distribution. In particular, it would be valuable for future studies to measure other components of fitness, such as adult fecundity, at different tidal heights. A pattern of higher fecundity in the subtidal would explain the tendency of larger littorines to move towards lower tidal heights.

Another factor that could generate the observed size distribution is top down control by wave stress. Higher wave stress in the intertidal would cause increased drag forces on larger snails that would in turn negatively affect mobility and foraging efficiency. One possible consequence would be an increased abundance of larger snails in the subtidal relative to the intertidal. Trussell (2002) studied growth rate in a *Littorina* snail at sheltered and exposed sites and found that growth was higher in the protected areas. As the subtidal is more protected from wave action than the intertidal, it is possible that once *Littorina littorea* reach a predation refuge they prefer to forage in low wave stress areas.

Our field studies and laboratory experiments collectively established that *L. littorea*, an intertidal snail, experiences higher mortality risk and lower growth rates in the subtidal zone relative to the intertidal. We therefore infer that the proximate factors underlying the vertical distribution of *L. littorea* are directional movement and predation. Individuals displaced from the intertidal into the subtidal are either consumed by predators or migrate upwards (Underwood 1979, Petraitis 1982). Furthermore, McQuaid (1981) demonstrated that small snails, when dislocated from the intertidal into the subtidal clearly show movement back towards their origin. Smaller snails are also less likely than larger individuals to leave complex topographical habitat (Chapman and Underwood, 1992). We have previously shown that intertidal substrates are more complex than those in the shallow subtidal on Appledore Island

(Carlson et al., 2006). The ultimate factors underlying natural selection for upward migration appear to be a higher risk of predation and lower growth rates in the subtidal. The latter may be due, at least in part, to frequent exposure to predator cues. The small number of *L. littorea* found in the subtidal have larger and thicker shells, and thus are less vulnerable to shell-breaking predators than the smaller, thinner-shelled snails found in the intertidal (Carlson et al., 2006, Stefaniak et al., 2005).

It is important to note, however, that the interaction between *L. littorea* and predatory crabs in the Gulf of Maine is relatively recent and only occurred as a result of the snail's range expansion into the Northwestern Atlantic in the mid-nineteenth century (Chapman et al., 2007, Cunningham 2007). Given the relatively short history of this interaction, is it reasonable to expect *L. littorea* to show evolutionary responses to interactions with those predators? We believe so. Recent studies have demonstrated very rapid evolutionary responses to novel predators (e.g. Freeman and Byers 2006). Additionally, *L. littorea* has a long evolutionary history of interaction in the Northeastern Atlantic with *Carcinus* and a close relative of *C. borealis*, *C. pagurus* (Ingle 1996). As we found in the Gulf of Maine, *Carcinus* in the Northeastern Atlantic are primarily intertidal, while *C. pagurus* are almost exclusively subtidal (Crothers 1968, 1969). Thus, there may be very similar evolutionary pressures exerted by intertidal versus subtidal crabs on the western and eastern coasts of the North Atlantic.

At Appledore Island, mortality risk is elevated in the subtidal compared to the intertidal due to the much higher densities of shell-breaking predators, particularly *C. borealis*. In the 20th century, commercial fisheries drastically reduced populations of apex predators that fed on *C. borealis*, especially the Atlantic cod (*Gadus morhua*) and Atlantic wolffish (*Anarhichas lupus*) (Witman & Sebens 1992, Jackson et al., 2001, Collette & Klein-MacPhee 2002). Additionally, in the 1990's, an intense sea urchin fishery decimated populations of *Strongylocentrotus droebachiensis*, which in turn produced a phase shift towards an algal-dominated subtidal community that favored higher survival of *C. borealis* juveniles (Steneck & Carlton 2001, Leland 2002). Thus, *C. borealis* may currently be the dominant predator in Gulf of Maine subtidal communities (Leland 2002, Steneck et al., 2004).

While the lower vertical limit of *L. littorea* is strongly influenced by *C. borealis*, the upper limit and abundance of *C. borealis* in the intertidal zone is in turn limited by gulls foraging in the intertidal zone during low tide (Good 1992, Ellis et al., 2007). When gulls are experimentally excluded from the intertidal zone, *C. borealis* densities increase and the densities of gastropods (*L. littorea*, *N. lapillus*) and mussels (*M. edulis*) decrease. Thus, the interplay of vertical limitations on foraging of both gulls and *C. borealis* affect the distribution of *L. littorea*.

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