

Mechanisms of species coexistence: a field test of theoretical models using intertidal snails

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Competitor coexistence is often facilitated by spatial segregation. Traditionally, spatial segregation is predicted to occur when species differ in the habitat in which they are either superior at competing for resources or less susceptible to predation. However, predictions from a behavioural model demonstrate that spatial segregation and coexistence can also occur in the absence of such interspecific trade-offs in competitive ability and vulnerability to predation. Unlike other models of competitor coexistence this model predicts that when species rank both habitat productivity and 'riskiness' similarly, but differ slightly in their habitat-specific vulnerabilities to predators, they will tend to segregate across habitats, with the species experiencing the higher ratio of mortality risk across the habitats occurring primarily in the safer habitat. Here, we investigate the hypothesis that intraspecific trade-offs between resource availability and mortality risk can lead to spatial segregation of competing species by (1) documenting the spatial (i.e. intertidal) distribution of two marine snails, *Littorina sitkana* and *L. subrotundata* and (2) performing field experiments to quantify growth and mortality rates of each species at 'low' and 'high' intertidal heights. Our results indicate that both species agree on the rankings of habitat riskiness and productivity, experiencing higher predation and higher growth in low- than in high-intertidal habitats. However, *L. sitkana* and *L. subrotundata* experienced differences in their habitat-specific mortality risks and growth rates. Despite both species being similarly at risk of predation in high-intertidal habitats (where mortality was lower), *L. subrotundata* was subject to significantly higher mortality than *L. sitkana* at the low-intertidal height. In contrast, growth rate differences between habitats were greater for *L. sitkana* than for *L. subrotundata*. Whereas both species grew at the same rate at the high-intertidal level (where growth was lower), *L. sitkana* individuals grew more rapidly than *L. subrotundata* snails at the low-intertidal level. As predicted by the behavioural model, the species that experienced the higher ratio of mortality across habitats (i.e. *L. subrotundata*) occurred exclusively in the safer, high-intertidal habitat. Taken together, these results provide support for the hypothesis that spatial segregation, and potentially competitor coexistence, can occur in the absence of interspecific trade-offs in resource acquisition ability or vulnerability to predation.

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When two species compete for access to common resources and are at risk of being consumed by shared predators, their continued coexistence is frequently facilitated by spatial segregation. Typically, spatial

segregation is predicted to occur when (1) species differ in the habitat in which they are superior at competing for resources (MacArthur and Levins 1967, Lawlor and Maynard Smith 1976, Vincent et al. 1996), (2) species

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differ in the habitat in which they are better at avoiding predators (Kotler 1984, Longland and Price 1991, Brown 1998), (3) species differ in their perceptions of safe and risky habitats and each species has a higher foraging efficiency in its riskier habitat (Brown 1998) and (4) one species is better at avoiding predators in all habitats while the other is the superior competitor in all habitats (Brown 1998). Most such models imply (or explicitly require) the presence of strong interspecific trade-offs in traits related to competitive ability and/or vulnerability to predation. Such trade-offs might be expected to evolve when the foraging and/or anti-predator strategies required for survival in one habitat differ from those required in other habitats, perhaps because habitats provide different types of resources or harbor different species of predators (e.g. benthic and limnetic stickleback fish, *Gasterosteus aculeatus* L.; Vamosi 2002).

Recently, Grand and Dill (1999) and Grand (2002) suggested that spatial segregation of competing species can also occur in the absence of such interspecific trade-offs, and in particular, when the same resources and predators are present in alternate habitats. This suggestion stems from their theoretical investigations into the effects of differences in competitive ability and habitat-specific vulnerability to predation on the outcome of intraspecific foraging–predation risk trade-offs during habitat selection. Unlike most other models of competitor coexistence (references above), their model predicts that segregation can occur even when species rank similarly both the productivity and ‘riskiness’ of different habitats; if species differ slightly in their habitat-specific vulnerabilities to predators, they will tend to segregate across habitats, with the species experiencing the higher ratio of mortality risk across the habitats occurring primarily in the safer habitat. Thus, the species found at the riskiest location need not be the one that experiences the lowest risk of mortality there. This pattern of spatial segregation occurs because the relative mortality cost of inhabiting the riskier habitat is offset by increased foraging gains for one species (the species with the lower ‘risk ratio’) but not the other, even in the face of resource competition.

Such spatial segregation has been observed in a two-species system of marine snails (*Littorina subrotundata* [Carpenter] and *L. sitkana* Philippi) that coexist along the rocky intertidal shores of the northeastern Pacific Ocean. Whereas *L. subrotundata* seems to thrive on wave-exposed headlands and in salt marshes, *L. sitkana* predominates on moderately-exposed to sheltered shores (Reid 1996). Segregation is not absolute, however, and the two species do co-exist on many shores. There is no published data on the vertical distribution of these two species where they coexist on the same shore, but in sheltered inlets near the Bamfield Marine Sciences Centre, Barkley Sound (West coast of Vancouver

Island), *L. subrotundata* seems to predominate in the high-intertidal and *L. sitkana* in the mid intertidal (R. Rochette, pers. obs.). On these shores, snails are subject to strong predation pressure by crabs (e.g. *Cancer productus* Randall), and, to a lesser extent, fish (e.g. perch; McCormack 1982, Robles et al. 1989, Behrens Yamada and Boulding 1996, Boulding et al. 1999).

On wave-sheltered shores, littorinid snails face greater predation risk in the lower, than upper, parts of the intertidal zone (Behrens Yamada and Boulding 1996, Rochette and Dill 2000), presumably due to differences in submergence time related to tidal fluctuations, but perhaps also because fish and crabs are themselves at risk of being preyed upon by birds (e.g. herons) and terrestrial mammals (e.g. otters, minks) if they venture too close to the surface. Importantly, the greater safety of higher-intertidal areas seems to come at a cost of reduced feeding opportunities. *Littorina subrotundata* and *L. sitkana* feed mainly on diatoms and unicellular algae that they scrape off algae and hard substrates (e.g. rocks, oyster shells) with their radula, and to a lesser extent on macroalgae and lichens. To avoid desiccation, they graze more actively when submerged than emerged, and reciprocal transplant experiments in Barkley Sound have shown that *L. sitkana* grows more rapidly in lower, than in upper, parts of their intertidal range (McCormack 1982, Rochette et al. 2003).

Here, we investigate the hypothesis that intraspecific trade-offs between resource availability and mortality risk can lead to spatial segregation of competing species by (1) documenting the intertidal distribution of *L. sitkana* and *L. subrotundata* at two study sites and (2) performing field experiments to quantify growth and mortality rates of each species at ‘low’ and ‘high’ intertidal heights. Growth and mortality rate data were used to differentiate between five potential mechanisms of spatial segregation (Table 1 for a summary of each hypothesis’ key assumptions and predictions).

Methods

We conducted our study between 6 April 2000 and 16 March 2001, on two gently-sloping gravel beaches in wave-sheltered Bamfield Inlet (48°50', 125°08'), Barkley Sound (Canada), northeastern Pacific (map in Boulding et al. 1999). These two shores are separated by approximately 800 m and were chosen because they harbor high densities of littorinids across a relatively wide range of intertidal heights (ca 1 to 3 m). The substrate of beaches up Bamfield Inlet tends to vary with intertidal height, gradually changing from fine sediments at the lower level to gravel and bedrock higher in the intertidal. Different species of vascular plants and macroalgae are normally present at different levels; the subtidal eelgrass *Zostera marina* L. extends up to about the 0-m mark, the

Table 1. A summary of five spatial segregation mechanisms and their key assumptions and predictions.

Mechanism	Habitat attributes	Species' perceptions of habitats		Predicted distribution
		Resource availability	Risk of mortality	
Differential competitive superiority (MacArthur and Levins 1967)	Habitats differ in resource availability only	Species rank habitats differently	Not considered	Each species in habitat in which it's competitively superior
Differential vulnerability (Kotler 1984, Brown 1998)	Habitats differ in risk of mortality only	Not considered (Kotler 1984) or species rank habitats identically (Brown 1998)	Species rank habitats differently	Each species in habitat in which it's least vulnerable
Differential foraging efficiency and vulnerability to predation (Brown 1998)	Habitats differ in risk of mortality only	Species rank habitats differently; each species has a higher foraging efficiency in a different habitat	Species rank habitats differently; each is more vulnerable to predation in the habitat in which its foraging efficiency is greatest	Both species found in both habitats; each uses one habitat for food and the other for safety
Interspecific trade-off in foraging efficiency and vulnerability (Brown 1998)	Habitats differ in risk of mortality only	Species rank habitats identically, however, one species is the more efficient forager in both habitats	Species rank habitats identically, however, one species is less vulnerable to predation in both habitats	One species is found exclusively in a single habitat, the other occurs in both habitats
Differential ratios of mortality risk across habitats (Grand and Dill 1999)	Habitats differ in resource availability and risk of mortality; high risk habitat most profitable	Species rank habitats identically; species may differ in competitive ability, but resource acquisition abilities similar in both habitats	Species rank habitats identically; small, habitat-specific differences in vulnerability to predators between species	Species with the lower ratio of mortality risk across habitats in the riskier habitat, regardless of which species is absolutely at greater risk there

filamentous green algae *Enteromorpha intestinalis* (L.) is common between 0 and 1 m, and the brown algae *Fucus distichus* L. is common to dominant on boulders and bedrock between the 2- and 3-m intertidal marks. The density of littorinids on these shores is partly related to the abundance of hard substrate, such as cobbles, boulders and bedrock; littorinids are uncommon on mud and sand bottoms.

There are four species of littorinids in Bamfield Inlet, two that undergo benthic larval development inside gelatinous egg masses (*L. sitkana* and *L. subrotundata*) and two that possess a pelagic larval stage (*L. scutulata* Gould and *L. plena* Gould). In this study, we decided to focus on the former two species, because we expected benthic larval development to be more conducive to consistent (both temporally and spatially) vertical distribution patterns and habitat segregation among species. Furthermore, selecting these two species meant not having to consider the role of larval dispersal and settlement in mediating snail distribution. *L. sitkana* and *L. subrotundata* are very similar morphologically, but they show some differentiation with respect to body pigmentation (i.e. head, foot, and tentacles), shell sculpturing, and the shape of female reproductive organs (Reid 1996). In this study, we used shell sculpturing for species identification, because it is non-destructive and more reliable than body pigmentation (R. Rochette, pers. obs.). The shell of *L. sitkana* has relatively high “ridges”, or bumps, and fine striations between the ridges, whereas that of *L. subrotundata* has relatively long and flat ridges with no microsculpturing between (Reid 1996). In order to confirm the accuracy of our identifications based on shell sculpturing, we dissected more than 40 adult females of each species and identified them based on the shape of the pallear oviduct (Reid 1996). Shell sculpturing proved to be highly reliable as a means of discriminating the two species at our study sites; the only two “mistakes” committed were for very large and eroded shells.

Snail spatial distribution

We determined the vertical distribution of *L. sitkana* and *L. subrotundata* at our two study sites in late April (site A) and early July (site B) 2000. Each site was 6 m long, and ranged from 1.2 to 2.8 m above 0 datum (Canadian Hydrographic Service); approximately 6 and 11 m separated the 1.2 and 2.8 m levels at sites A and B, respectively. For ease of comparison with earlier work done in the same area, intertidal heights were estimated using as a reference point the site described in Rochette and Dill (2000); there was a +0.12 m tidal anomaly the day the reference site was established, but we present non-corrected (e.g. 2.5 m instead of 2.62 m) tidal amplitudes throughout the paper for simplicity.

We used random quadrat (0.1 × 0.1 m) sampling to evaluate the density of snails at 0.4-m increments in intertidal height (i.e. 1.2, 1.6, 2.0, 2.4, and 2.8 m) at both study sites. At each level, we first laid down a measuring tape parallel to the shoreline, and then used a table of random numbers to determine quadrat positions. We determined the position of each quadrat by taking two random numbers (x and y coordinates), one between 0.0 and 5.9 (0.1 increments), which set the position of the quadrat along the measuring tape axis, and a second between 0 and 4, which set quadrat position perpendicular to the measuring tape (0 = two squares below the measuring tape; 1 = immediately below; 2 = immediately above; 3 = two squares above). There were thus a total of 240 possible locations where quadrats could be placed at each intertidal level. We thoroughly searched each quadrat, picking up and inspecting every cobble and oyster shell at the lower intertidal levels and cutting off *Fucus* parts at higher levels, and collected all snails greater than 2 mm in shell length. We sampled until we had a minimum of 50 snails at each intertidal level, and a minimum of 15 different quadrats had been taken. The maximum number of quadrats taken at any intertidal level was 40. All snails were brought back to the laboratory, identified under a dissecting microscope, and measured (maximum shell length) to the nearest 0.01 mm using digital calipers.

We used chi-square analyses of contingency tables to test two hypotheses: (1) *L. subrotundata* and *L. sitkana* are randomly, or uniformly, distributed among tidal levels and (2) *L. subrotundata* and *L. sitkana* have similar vertical distributions. We did separate analyses for the two species (hypothesis 1) and sites (hypotheses 1 and 2). We then determined whether snail size varied among intertidal heights. We first tested for homogeneity of variances among groups using Bartlett's test (we did not use Cochran's test because sample sizes were unequal), analyzing different species and sites separately. Data for *L. sitkana* at both sites, and for *L. subrotundata* at site B, passed the homoscedasticity test ($P > 0.05$), and were analyzed with ANOVA's followed by Tukey-type multiple comparisons. Data for *L. subrotundata* at site A did not pass the test ($P < 0.01$), and were analyzed with a Mann-Whitney U-test (*L. subrotundata* was only found at 2.4 and 2.8 m) using the normal approximation for statistical testing.

Experiment 1: quantification of predation risk

We conducted tethering experiments at our two study sites, between 9 and 18 August 2000, to compare predation risk faced by *L. sitkana* and *L. subrotundata* at low (i.e. 1.2 m) and high (i.e. 2.5 m) intertidal levels. Based on results obtained recently by Rochette and Dill (2000), we selected these two intertidal heights for the

experiment because (1) they span nearly the entire vertical range of littorinids ($\approx 1\text{--}3$ m), (2) littorinid density typically peaks around these heights, and (3) predation risk faced by littorinids varies significantly between these levels.

For this experiment, snail sizes were chosen to reflect naturally occurring differences in adult body size between species and intertidal levels. Although larger snails experience a higher risk of predation than small snails (McCormack 1982, Rochette and Dill 2000) and *L. sitkana* typically reaches larger body sizes than *L. subrotundata* (R. Rochette, pers. obs.), we did not use similar-size *L. sitkana* and *L. subrotundata* because we wanted to mimic the actual mortality rates experienced by snails in nature. We therefore used random quadrat sampling (as described for the vertical distribution surveys) to collect snails appearing to be larger than 4 mm in shell length. Because *L. sitkana* showed a wide vertical distribution at both study sites (Results) and adults were larger at the 2.8- than at the 1.2-m level (Results), half of the *L. sitkana* snails used in the tethering experiments were collected from the 1.2-m level and the other half from the 2.8-m level. In contrast, we randomly collected all *L. subrotundata* snails from the 2.8-m level, because this species had a much narrower vertical distribution and did not show consistent size variation between intertidal levels (Results).

In the laboratory, we measured all snails collected to the nearest 0.01 mm with digital calipers, lined up individuals of a given species and origin (site and intertidal height), and used a random-number generator to determine which snails would be used in the tethering experiment and what position they would occupy on the transect (below). We then thoroughly air-dried each snail's shell, attached a 10 cm piece of 2.25 kg test monofilament (diameter = 130 μm) to the apex of each shell with epoxy (we made a small knot in the line to increase adhesion) and let the glue dry for approximately 30 min. Each snail was then placed in a separate, labeled eppendorf tube. We then half-filled each tube with fresh seawater and placed them in running seawater overnight. The following morning, we attached 10 snails of each species (5 *L. sitkana*'s from the 1.2-m level and 5 from the 2.8-m level; 10 *L. subrotundata*'s from the 2.8-m level) to each of four 6-m long transects (2 sites \times 2 intertidal heights) made of 25 kg test monofilament (diameter = 730 μm); we randomly determined the order of each snail on a given transect, and left 30 cm between snails to minimize interactions between individuals.

We recorded the fate of individual snails at 3-d intervals over a 9-d period (i.e. 3 temporal replicates), replacing dead or missing snails on each occasion with individuals of the same species (and origin, in the case of *L. sitkana*). For each position on the transect we recorded whether the snail was (1) alive (snail visible and responded to touch), (2) crushed (when only a

broken shell or shell fragments were found imbedded in the epoxy), (3) empty (when the shell was intact but without a snail), and (4) missing (when only a monofilament knot was recovered, or a piece of epoxy with no visible shell fragments). We estimated predation rates by calculating, for each temporal replicate and combination of factor levels (i.e. species, site and intertidal height), the number of snails that were recovered as crushed, missing or empty, and then dividing that quantity by the number of snails that had been released in that particular treatment (usually 10 snails, but occasionally 9 or 8 due to losses). In other words, we assumed that all snails not recovered alive had been killed by predators. We made this assumption because the recent study by Rochette and Dill (2000) indicated that tethered snails that are deployed in Bamfield inlet under predator-proof cages are virtually never recovered as "missing" or "empty".

We analyzed mortality rates with a 3-way factorial ANOVA, using site (A and B), intertidal height (1.2 and 2.5 m) and species (*L. sitkana* and *L. subrotundata*) as fixed-effect factors. We considered site to be a fixed-effect factor, as opposed to a random-effect factor, because we wanted to assess the consistency of effects across our two sites; we were not simply trying to control for site-dependent variability, but rather wanted to test statistically whether effects were the same at the two sites. The raw data was heteroscedastic (Cochran's $C_{8,2} = 0.684$; $P < 0.01$), because variances tended to increase with mean mortality rates. However, a square root transformation (i.e. $\sqrt{x} + \sqrt{x+1}$) satisfyingly stabilized the variances (Cochran's $C_{8,2} = 0.445$; $P > 0.05$). We used Tukey-type multiple comparisons (Zar 1984) and a "family-wise" error rate of 0.05 to interpret significant interaction terms. The critical value for all comparisons was $q_{0.05,16,2} = 2.998$ (16 corresponds to the number of degrees of freedom associated with the model error term, and 2 corresponds to the number of means involved in each family of comparisons).

We also performed a similar factorial ANOVA to determine if there were differences in mortality rates between high-origin and low-origin *L. sitkana* snails.

Experiment 2: quantification of growth rates

We quantified growth rates at our two study sites between February 22 and March 15, 2001. Using random quadrat sampling (as described for the vertical distribution surveys), we collected approximately 200 small (less than 4 mm shell length) *L. sitkana* from each intertidal height at each site. In contrast (due to their narrow vertical distribution), we randomly collected similar numbers of small *L. subrotundata* at each site, but only from the high-intertidal level. We also collected

substrate (small rocks and pieces of [chiseled] bedrock with and without *Fucus* attached) from each site/height combination.

Upon returning to the lab, we measured all snails to the nearest 0.01 mm, entered the data on a computer, and used a random-number generator (snails were aligned on paper towels) to create 16 groups of snails per site (i.e. eight *L. sitkana* groups and eight *L. subrotundata* groups per site). Each group consisted of ten individuals of the same species; in the case of *L. sitkana*, groups were composed of five high-origin and five low-origin individuals. Snails within each group were then individually color-marked. We used five different colors of enamel-based paint (white, yellow, red, blue and green) and two mark locations (body whorl only and body whorl+apex) to create 10 distinct marks. Snails were marked under the dissecting microscope using a single paintbrush hair, then left to dry for 30 min.

Each group of snails was placed in a small, plastic-framed cage (13 × 13 × 5 cm), with walls of 500 micron Nytex. Substrate from the appropriate site and intertidal height was added to each cage. Lids were hot-glued to each cage to prevent snails from escaping during the subsequent growth period. Cages were then tethered to bricks and placed in the field at the appropriate site and intertidal height. Thus, at each site, there were four replicate cages of snails of each species at each intertidal height. Cages were recovered on March 15, 2001, at which time we counted the number of snails still alive, and measured them to the nearest 0.01 mm.

We analyzed survivorship of snails during the growth experiment with a 3-way factorial ANOVA, using site (A and B), intertidal height (1.2 and 2.5 m) and species (*L. subrotundata* and *L. sitkana*) as fixed-effect factors. We then used hierarchical (i.e. nested) factorial ANOVAs to analyze the growth of snails remaining alive; sites, heights and species were again used as fixed effect factors, and cages were nested within these three factors. Significance testing for the main effects (and their interactions) was done using the nested variable (i.e. cage) as the error term (i.e. the MS for the nested factor was used as denominator of the F-ratios). We conducted three separate hierarchical ANOVAs, because high-origin and low-origin *L. sitkana* snails displayed different growth rates ($F_{1,12} = 7.99$, $P < 0.05$). In the first analysis, we “pooled” *L. sitkana* snails originating from high- or low-intertidal areas, and tested for overall growth differences between species. In the second set of analyses, we compared growth rates of *L. subrotundata* to high-origin or low-origin *L. sitkana* snails, separately. In the case of the comparison between *L. subrotundata* and low-origin *L. sitkana*, the raw data were heteroscedastic (Cochran’s $C_{8,3} = 0.450$; $P < 0.05$), but a square root transformation (i.e. $\sqrt{x} + \sqrt{x+1}$) satisfyingly stabilized the variances (Cochran’s $C_{8,3} = 0.346$; $P > 0.05$). In all of the above analyses, we used

Tukey-type multiple comparisons and a “family-wise” error rate of 0.05 to interpret significant interaction terms (Zar 1984). The critical value for these multiple comparisons was $q_{0.05,24,2} = 2.919$ (24 corresponds to the number of degrees of freedom associated with the nested [cage] factor, and 2 corresponds to the number of means involved in each family of comparisons).

We did not use initial length as a covariate in these analyses, because it was weakly and inconsistently related to snail growth; Pearson product-moment correlations indicated a significant ($P < 0.05$) positive relation between initial length and growth in only two of the 12 different treatment combinations. The absence of a consistent relationship between initial snail size and growth is not surprising considering the narrow size range of snails we used (i.e. 100% and 80% of individuals within a range of 1.0 mm and 0.6 mm, respectively). Furthermore, a hierarchical factorial ANOVA (above) indicated that snail shell length was uniform across treatments at the beginning of the experiment (all main effects $P > 0.6$).

Results

Snail spatial distribution

As expected, *L. sitkana* and *L. subrotundata* distributions were not random with respect to intertidal level, and each species predominated in a different part of the intertidal zone (Fig. 1). At both sites, the number of *L. sitkana* (site A: $\chi^2 = 78.8$, $DF = 4$, $P < 0.0001$; site B: $\chi^2 = 40.1$, $DF = 4$; $P < 0.0001$) and *L. subrotundata* (site A: $\chi^2 = 184$, $DF = 4$, $P < 0.0001$; site B: $\chi^2 = 79$, $DF = 4$, $P < 0.0001$) snails at different intertidal heights differed markedly from numbers expected based on the number of quadrats taken and assuming a random, or uniform, vertical distribution. But more relevant to our current

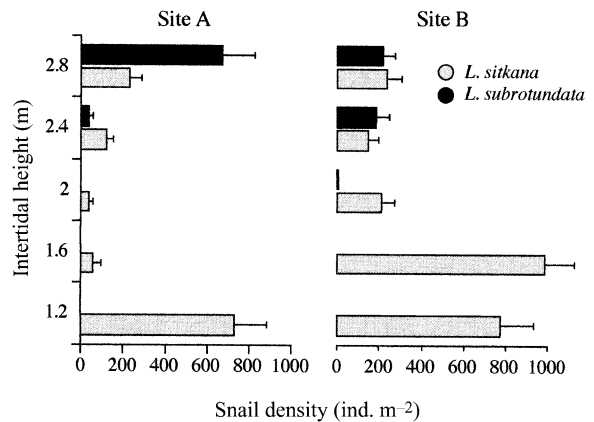


Fig. 1. Observed densities (snails per m²; $\bar{x} \pm 1$ SE) of *L. sitkana* and *L. subrotundata* at various intertidal heights at each of our two study sites.

hypothesis, *L. sitkana* and *L. subrotundata* showed nearly opposite distribution patterns at both of our study sites (site A: $\chi^2 = 216.1$, DF = 4, $P \ll 0.0001$; site B: $\chi^2 = 198.2$, DF = 4, $P \ll 0.0001$), with *L. sitkana* predominating in lower portions of the intertidal zone and *L. subrotundata* occurring only at the two highest levels sampled (Fig. 1).

Although not shown here, we also searched for snails below (i.e. 0.8 m) and above (i.e. 3.2 m) our study sites. However, very few were found and the identity of those that we did find was consistent with the distribution patterns presented above. Thus, at both sites small numbers of *L. sitkana* were found at the 0.8-m level, but no *L. subrotundata*. At site A, many snails were found underneath three rocks (each about 20 cm in diameter) sitting on bare bedrock at the 3.2-m level; all were *L. subrotundata*. No snails of either species were found at the 3.2-m level of site B, which was shaded and overgrown by the green algae *Enteromorpha intestinalis*.

In *L. sitkana*, snail size varied among intertidal heights at both study sites (Fig. 2; site A: $F_{4,194} = 26.34$, $P < 0.0001$, site B: $F_{4,197} = 62.59$; $P < 0.0001$). Multiple comparisons indicated that, at site A, *L. sitkana* were significantly larger at the highest intertidal level (i.e. 2.8 m) than at all other levels ($P < 0.05$), and that snail size was similar from 1.2 to 2.4 m ($P > 0.05$). At site B, snails at the three middle levels (1.4, 1.8 and 2.2 m) were of similar size ($P > 0.05$), but significantly larger than snails at the lowest level ($P < 0.05$), and smaller than snails at the highest level ($P < 0.05$). This vertical size gradient of *L. sitkana* snails (McCormack 1982) is likely due to larger individuals experiencing high mortality rates in low-intertidal areas (McCormack 1982, Behrens Yamada and Boulding 1996, Rochette and Dill 2000), and to differences in size at sexual maturity between high- and low-shore snails (Rochette et al. 2003). In *L. subrotundata*, snails collected at the 2.8 m

level of site A were significantly larger than those from the 2.4 m level ($Z = -3.231$, $P = 0.001$). This difference is of dubious ecological significance, however, because only 6 snails were found at the 2.4-m level; the density estimates indicate that less than 5% of the population occurred at that level. At site B, the size of *L. subrotundata* did not differ between intertidal levels ($F_{1,60} = 2.47$; $P > 0.121$).

Thus, in general, snail size tended to increase with increasing intertidal height. Furthermore, as expected from anecdotal observations (Table 1 in Behrens Yamada 1992), *L. sitkana* and *L. subrotundata* tend to be spatially segregated at our study sites, with *L. sitkana* occurring primarily at low intertidal heights and *L. subrotundata* exclusively at higher intertidal heights.

Experiment 1: quantification of predation risk

We made a total of 232 observations on tethered snails, 51 of which (22%) were classified as predation events; 78% of the snails assumed to have been killed by predators were recovered as “crushed”, 16% as “missing” and 6% as “empty” (as described in Methods). The factorial ANOVA revealed two significant interactions between main effects (Table 2; Fig. 3). First, and most importantly, there was a significant interaction between snail species and intertidal height ($P = 0.001$), with variation in mortality rates between low- and high-intertidal areas seemingly greater for *L. subrotundata* than for *L. sitkana* (Fig. 3). The multiple comparisons indicated that at high-intertidal levels, both species had similar mortality rates ($q_{16,2} = 2.411$; $P > 0.05$), but at low-intertidal levels *L. subrotundata* was killed more frequently than *L. sitkana* ($q_{16,2} = 5.451$; $P < 0.05$). For both species, however, mortality rates were much greater in low- than in high-intertidal areas (*L. sitkana*: $q_{16,2} = 11.248$, $P \ll 0.05$; *L. subrotundata*: $q_{16,2} = 19.110$, $P \ll 0.05$). The second significant interaction was between site and intertidal height ($P = 0.023$). This weak interaction appeared due to mortality rates being slightly greater at site A (versus B) in the high-intertidal, and at site B (versus A) in the low intertidal, although the difference in mortality between sites was not significant

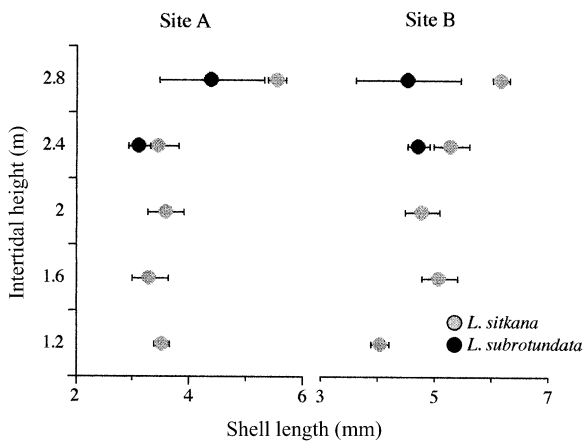


Fig. 2. Shell lengths (mm; $\bar{x} \pm 1$ SE) of *L. sitkana* and *L. subrotundata* at various intertidal heights at each of our two study sites.

Table 2. Tethering experiment. Factorial ANOVA comparing mortality rates among snail species, intertidal heights and study sites.

Source of variation	DF	SS ($\times 10^{-1}$)	F	P
Species (Sp)	1	0.353	2.311	0.148
Intertidal height (H)	1	35.212	230.396	$\ll 0.001$
Site (S)	1	0.002	0.013	0.912
Sp \times H	1	2.362	15.453	0.001
Sp \times S	1	0.360	2.356	0.144
H \times S	1	0.973	6.365	0.023
Sp \times H \times S	1	0.127	0.768	0.394
Error	16	2.445		

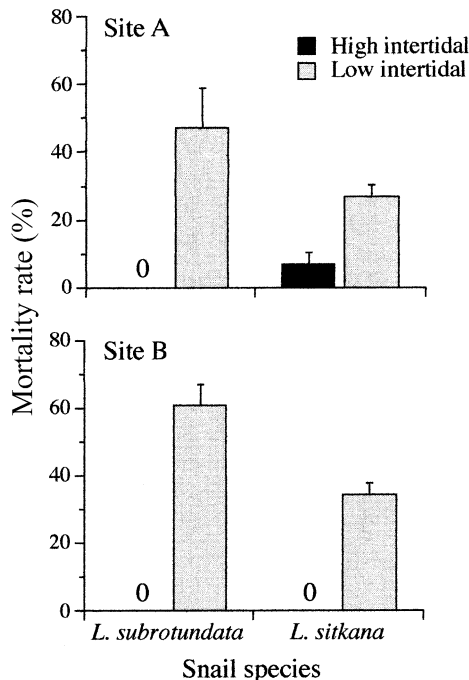


Fig. 3. Tethering experiment. Overall mortality rates (%; $\bar{x} + 1$ SE) of *L. sitkana* and *L. subrotundata* in the high- and low-intertidal zone at each of our two study sites.

at either height (high-intertidal: $q_{16,2} = 2.411$, $P > 0.05$; low intertidal: $q_{16,2} = 2.635$, $P > 0.05$).

Earlier studies have found that larger snails experience a higher risk of predation than small snails in Bamfield inlet (McCormack 1982, Rochette and Dill 2000). However, size did not appear to be a significant factor during this experiment, because we found no evidence of differences in mortality rate between *L. sitkana* snails originating from high-intertidal and low-intertidal areas ($P = 0.51$), despite the fact that the former were significantly larger than the latter (Fig. 2). *L. subrotundata* snails were larger than low-origin *L. sitkana* snails, but smaller than high-origin ones (Fig. 2).

Due to time constraints, snails that were recovered as "alive" were not replaced between temporal replicates; it would have been difficult to replace all snails during low tide at the end of a tidal sequence, in particular, when low-intertidal transects were only exposed for 1–2 h. Thus, the above analysis can be criticized on the grounds that data points are not truly independent. In order to address this criticism, we pooled the three temporal replicates and re-analyzed the data. In this case, percent mortality was analyzed by 2-way ANOVA, using snail species and intertidal height as factors and the two study sites as independent replicates. This analysis revealed a marginally significant interaction between snail species and intertidal height ($P = 0.09$), and multiple comparisons indicated that mortality rates differed between

species at the low- ($P < 0.05$) but not at the high- ($P > 0.05$) intertidal level.

Thus, regardless of which analysis is used, both species agree on the relative ranking of habitats with respect to mortality risk. However, *L. subrotundata* appeared to experience a higher ratio of mortality risk across habitats than *L. sitkana*.

Experiment 2: quantification of growth rates

Seventy three percent of the snails survived the field growth experiment, but patterns of survivorship differed between species (Table 3, Fig. 4). First, and most importantly, the factorial ANOVA revealed a significant interaction between snail species and intertidal height ($P = 0.002$). The multiple comparisons indicated that at high-intertidal levels, both species survived similarly well ($q_{24,2} = 0.289$; $P > 0.05$), but at low-intertidal levels survivorship was much greater for *L. sitkana* than for *L. subrotundata* ($q_{24,2} = 7.217$; $P \ll 0.05$). Further, and perhaps more importantly, survivorship of *L. sitkana* was independent of intertidal height ($q_{24,2} = 1.732$; $P > 0.05$), but that of *L. subrotundata* was significantly greater in high- than in low-intertidal areas ($q_{24,2} = 5.200$; $P \ll 0.05$). The second significant interaction was between site and species ($P = 0.008$). Survivorship of *L. sitkana* was greater at site B than A ($q_{24,2} = 4.619$; $P < 0.05$), whereas that of *L. subrotundata* was similar at both sites ($q_{24,2} = 1.155$; $P > 0.05$). Further, survivorship was similar for both species at site A ($q_{24,2} = 0.866$; $P > 0.05$), but significantly less for *L. subrotundata* than for *L. sitkana* at site B ($q_{24,2} = 6.640$; $P \ll 0.05$).

The hierarchical factorial ANOVAs indicated similarities, as well as differences, between growth patterns of *L. subrotundata* and *L. sitkana* snails (Table 4–6, Fig. 5). The first analysis revealed a significant interaction ($P = 0.002$) between snail species and intertidal height (Table 4, Fig. 5A), which indicated that the effect of intertidal height on growth was not the same for the two species. Multiple comparison tests indicated that both species grew more in the low intertidal than in the high-intertidal (*L. sitkana*: $q_{24,2} = 11.860$, $P \ll 0.05$; *L. subrotundata*: $q_{24,2} = 3.843$, $P < 0.05$), but the magnitude of

Table 3. Growth experiment. Factorial ANOVA comparing snail survivorship among species, intertidal heights and study sites.

Source of variation	DF	SS	F	P
Species (Sp)	1	0.211	14.083	0.001
Intertidal height (H)	1	0.045	3.000	0.096
Site (S)	1	0.045	3.000	0.096
Sp \times H	1	0.180	12.000	0.002
Sp \times S	1	0.125	8.333	0.008
H \times S	1	0.001	0.083	0.775
Sp \times H \times S	1	0.001	0.083	0.775
Error	24	0.360		

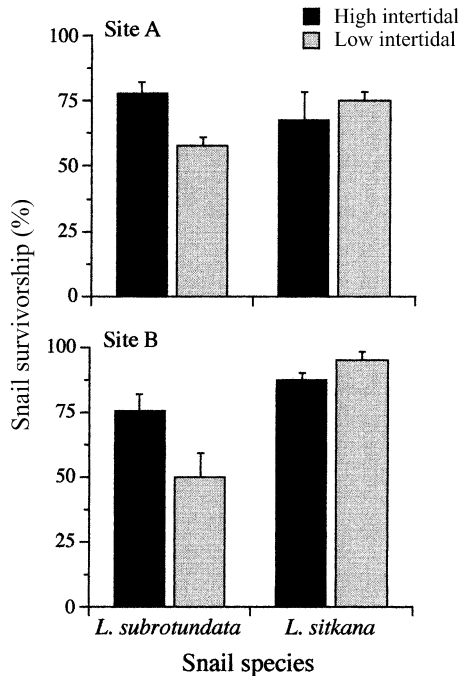


Fig. 4. Growth experiment. Survivorship (%; $\bar{x} + 1$ SE) of *L. sitkana* and *L. subrotundata* snails caged in the high- and low-intertidal zone at each of our two study sites.

Table 4. Growth experiment. Hierarchical factorial ANOVA comparing growth of *L. subrotundata* and *L. sitkana* in the high and low-intertidal zone. Significance testing for the main effects (and their interactions) was done using the cage factor as the error term (i.e. the MS for the nested factor was used as denominator of the F ratios).

Source	DF	SS	F	P
Intertidal height (IH)	1	2.229	56.858	<< 0.001
Species (Sp)	1	0.028	0.701	0.411
Site (Si)	1	0.001	0.031	0.862
IH \times Sp	1	0.495	12.635	0.002
IH \times Si	1	0.019	0.484	0.493
Sp \times Si	1	0.042	1.071	0.311
IH \times Sp \times Si	1	0.021	0.531	0.473
Cage [Sp, Si, IH]	24	0.941	1.164	0.279
Error	203	6.837		

Table 5. Growth experiment. Hierarchical factorial ANOVA comparing growth of *L. subrotundata* and high-origin *L. sitkana* in the high and low-intertidal zone. Significance testing for the main effects (and their interactions) was done using the cage factor as the error term (i.e. the MS for the nested factor was used as denominator of the F ratios).

Source	DF	SS	F	P
Intertidal height (IH)	1	1.859	86.223	<< 0.001
Species (Sp)	1	0.196	9.082	0.006
Site (Si)	1	0.008	0.367	0.550
IH \times Sp	1	0.514	23.830	<< 0.001
IH \times Si	1	0.031	1.418	0.245
Sp \times Si	1	0.003	0.118	0.734
IH \times Sp \times Si	1	0.003	0.147	0.705
Cage [Sp, Si, IH]	24	0.517	0.686	0.858
Error	136	4.273		

Table 6. Growth experiment. Hierarchical factorial ANOVA comparing growth of *L. subrotundata* and low-origin *L. sitkana* in the high and low-intertidal zone. To satisfy the homoscedasticity assumption, this analysis was performed on square-root transformed data. Significance testing for the main effects (and their interactions) was done using the cage factor as the error term (i.e. the MS for the nested factor was used as denominator of the F ratios).

Source	DF	SS	F	P
Intertidal height (IH)	1	1.302	26.622	<< 0.001
Species (Sp)	1	0.114	2.337	0.139
Site (Si)	1	0.040	0.812	0.377
IH \times Sp	1	0.184	3.771	0.064
IH \times Si	1	0.009	0.176	0.679
Sp \times Si	1	0.105	2.136	0.157
IH \times Sp \times Si	1	0.022	0.388	0.539
Cage [Sp, Si, IH]	24	1.174	1.122	0.328
Error	139	6.056		

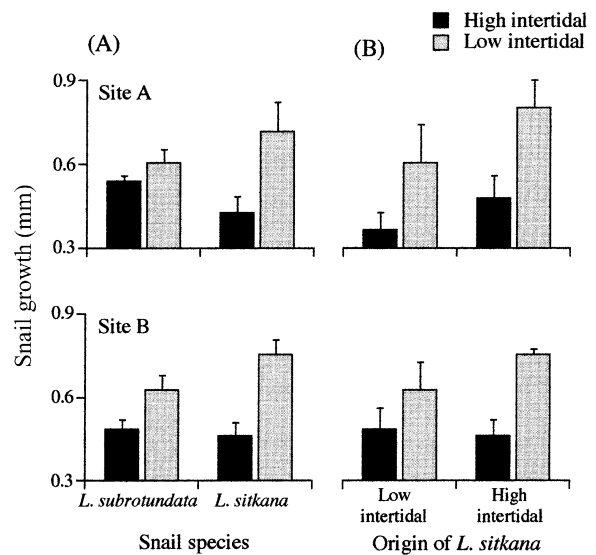


Fig. 5. Growth experiment. Growth (mm; $\bar{x} + 1$ SE) of *L. subrotundata* and *L. sitkana* in the high- and low-intertidal zone at each of our two study sites; (A) high- and low-origin *L. sitkana* pooled, (B) high- and low-origin *L. sitkana* plotted separately. Note that non-transformed values are shown throughout, even though the comparison between *L. subrotundata* and low-origin *L. sitkana* was done on square root transformed data.

this growth difference between intertidal heights appeared greater for *L. sitkana* than for *L. subrotundata* (Fig. 5A). This latter interpretation is supported by the fact that *L. sitkana* grew significantly more than *L. subrotundata* in the low intertidal ($q_{24,2} = 4.328$, $P < 0.05$), but not in the high-intertidal ($q_{24,2} = 2.901$, $P > 0.05$). In fact, the exact opposite pattern appeared true in the high-intertidal (*L. subrotundata* growing more than *L. sitkana*), but this species effect was not statistically significant (recall that $q_{0.05,24,2} = 2.919$). There was no significant difference in growth rates

among cages belonging to the same treatment ($P = 0.279$).

The analysis involving *L. subrotundata* and high-origin *L. sitkana* snails also revealed a highly significant ($P < 0.001$) interaction between species and intertidal height (Table 5, Fig. 5B). Multiple comparison tests indicated that both species grew more in the low intertidal than in the high-intertidal (*L. sitkana*: $q_{24,2} = 13.492$, $P < 0.05$; *L. subrotundata*: $q_{24,2} = 5.289$, $P < 0.05$), but the magnitude of this growth difference between intertidal heights appeared greater for *L. sitkana* than for *L. subrotundata* (Fig. 5B). This latter interpretation is supported by the fact that *L. sitkana* grew significantly more than *L. subrotundata* in the low-intertidal ($q_{24,2} = 8.293$, $P < 0.05$), where growth rates were greater, but not in the high-intertidal ($q_{24,2} = 1.981$, $P > 0.05$), where growth rates were lower. There was no significant difference in growth rates among cages belonging to the same treatment ($P = 0.858$).

The analysis involving *L. subrotundata* and low-origin *L. sitkana* snails also revealed a highly significant intertidal-height effect ($P < 0.001$); snails grew more in low- than high-intertidal areas (Table 6, Fig. 5B). Again, this effect seemed more pronounced for *L. sitkana* than for *L. subrotundata* (Fig. 5B), although the interaction between species and intertidal height only approached significance (Table 6, $P = 0.064$). There was no significant difference in growth rates among cages belonging to the same treatment ($P = 0.328$).

In summary, both species grew more rapidly in the lower than the upper parts of the intertidal zone, but the growth differential between high- and low-intertidal habitats is greater for *L. sitkana* than for *L. subrotundata*. These conclusions seem to hold whether we consider *L. sitkana* snails originating from the low- or the high-intertidal zone, although the latter grew faster than the former in all habitats ($F_{1,12} = 7.99$, $P < 0.05$).

Discussion

As suggested by earlier, anecdotal observations, *L. sitkana* and *L. subrotundata* tend to be segregated across intertidal heights at our study sites, with *L. sitkana* occurring predominantly in mid- to high-intertidal (~ 1 – 2.8 m) habitats and *L. subrotundata* exclusively in high- to extra-high (~ 2.4 – 3.2 m) intertidal habitats (Behrens Yamada 1992). More extensive surveys have revealed that this pattern is very consistent within Bamfield inlet (R. Rochette, unpubl.). According to the results of this study, both species experience higher predation and higher growth in low- than in high-intertidal habitats, and hence, agree on the rankings of habitat riskiness and productivity. Thus, both Grand and Dill's (1999) "differential risk ratios" hypothesis and Brown's (1998) "interspecific trade-offs" hypothesis

(Table 1) provide potential explanations for the observed spatial distribution of this pair of coexisting species.

Although both species agreed on ranking of habitats in terms of growth potential and mortality risk, *L. sitkana* and *L. subrotundata* experienced differences in their habitat-specific growth rates and mortality risks. Despite being similarly at risk of predation in high-intertidal habitats, they did not experience equal mortality in low-intertidal habitats. *L. subrotundata* was subject to significantly higher mortality than *L. sitkana* at the low-intertidal height. It is worth noting that this pattern was not only found with the tethering experiment, but also during the growth experiment, in which snails were protected from predators inside cages. This finding indicates that predators and some other factor(s) (e.g. grazing efficiency) more negatively impact the survivorship of *L. subrotundata* than *L. sitkana* in low-intertidal areas. Thus, *L. subrotundata* perceived a higher ratio of mortality (i.e. "risk ratio"; Grand and Dill 1999) across the two habitats than *L. sitkana* (regardless of the intertidal height of origin of the latter). In contrast, growth rate differences between habitats were greater for *L. sitkana* than for *L. subrotundata*. Whereas both species grew at the same rate at the high-intertidal level, *L. sitkana* individuals grew more rapidly than *L. subrotundata* snails at the low-intertidal level. This interspecific difference in habitat-dependent growth differential seemed to hold whether we considered high-origin or low-origin *L. sitkana* snails (Fig. 5), although the species by height interaction term was only marginally significant ($P = 0.06$) in the latter case.

According to Brown's 'interspecific trade-off' hypothesis, the observed pattern of habitat selection (and consequently, coexistence of the two species) is predicted to occur when *L. subrotundata* is more vulnerable to predation in both low- and high-intertidal habitats and *L. sitkana* better at acquiring resources in both habitats. Although *L. subrotundata* was more vulnerable to predators than *L. sitkana* in the higher risk, low-intertidal habitat, mortality rates did not differ between species in the high-intertidal habitat. Similarly, depending on the intertidal height of origin of *L. sitkana*, species growth rates appeared to differ at either high- (*L. subrotundata* > low-origin *L. sitkana*; Fig. 5B) or low-intertidal levels (high-origin *L. sitkana* > *L. subrotundata*), but not at both simultaneously. Thus, assuming that our experiment had sufficient power to detect such differences if present, the observed pattern of habitat selection cannot be solely attributed to interspecific trade-offs in competitive ability and vulnerability to predation. It should also be noted that this hypothesis (like Brown's 1998 two alternative hypotheses) assumes equal resource availability in the two habitats. It is unclear how the model's predictions might change if habitats differ in the quantity of resources they provide.

In contrast, Grand and Dill's (1999) "risk ratios" hypothesis does not require that each species be superior at a single task (i.e. competing for resources or avoiding predators) in both habitats for segregation across habitats, and consequently, coexistence (Grand 2002) to occur. Instead, the observed pattern of habitat segregation is predicted to occur when *L. subrotundata* experiences a higher ratio of mortality risk across the habitats than *L. sitkana*, regardless of which species is absolutely at greater risk of predation in the riskier, low-intertidal habitat. However, central to Grand and Dill's (1999) hypothesis is the assumption that the competitive abilities (i.e. the ability to capture and consume resources) of each species remain constant across habitats. Assuming that growth rate accurately reflects competitive ability, our growth experiment suggests that relative competitive abilities of the two species are not independent of habitat or for *L. sitkana*, habitat of origin. However, it is unclear whether violating this underlying assumption of Grand and Dill's (1999) model should lead to a pattern of habitat selection other than segregation of competing species across habitats. Indeed, one might expect segregation to be even more complete when each species is the better competitor in the habitat in which it predominates (MacArthur and Levins 1967, Lawlor and Maynard Smith 1976, Vincent et al. 1996), despite the additional complication of habitat differences in mortality risk. We are currently working on a model that addresses situations where interspecific differences in competitive abilities and vulnerability to predation both change across habitats.

Taken together, our results are most consistent with the mechanism of spatial segregation proposed by Grand and Dill (1999). *L. sitkana* and *L. subrotundata* tend to be segregated intertidally at our study sites not because each is superior at competing for resources or avoiding predators in different habitats, but because differences between species in habitat-specific predation risks result in *L. subrotundata* experiencing a higher ratio of mortality risk across habitats. The actual mechanism leading to this segregation pattern could be based on competitive exclusion or differences in behavioral preferences, or a combination of both processes.

One important assumption of our study is that the tethering experiment adequately reflects differences in relative mortality risk between species and intertidal heights. In other words, if snail mortality rates are affected by the tethering procedure, the magnitude of this bias (Zimmer-Faust et al. 1994) must be constant, or additive, among groups to be compared (Peterson and Black 1994). Rochette and Dill (2000) recently tested this assumption for *L. sitkana* and *L. scutulata* snails near our study sites using various experimental procedures (e.g. mark-release-recapture experiments, varying lengths of tethers, predator-proof cages) and they found no

evidence that tether biases were not constant across snail species, sizes or intertidal heights. We are therefore confident that our mortality estimates can be used to compare mortality risk of our different snail groups. In fact, not only are our tethering results reliable in relative terms, they probably even reflect absolute rates of snail mortality. Indeed, in their study Rochette and Dill (2000) reported similar rates of mortality for tethered and non-tethered snails. This lack of a tether bias should perhaps not come as a surprise, because snails can not outrun or outmaneuver their main predators (i.e. crabs and fishes) in these habitats (Barbeau and Scheibling 1994).

One may wonder how snail populations could be maintained under such high mortality rates (i.e. between ≈ 30 – 60% of snails killed in 3 d in the low intertidal), but it must be noted that predation rates are not always this high; they drop to ≈ 5 – 10% snails killed in 3 d during fall and winter months (Rochette and Dill, unpubl.). Furthermore, females are highly fecund, producing ≈ 25 – 175 eggs (depending on their size) per single spawning event, and laying several egg masses per year. Thus, although we do not possess the demographic data (e.g. annual fecundity is not known) to confirm that snail populations can sustain themselves under the mortality rates estimated using tethering, this appears quite probable.

Clearly, the high- and low-intertidal habitats described in this study pose different ecological challenges to the littorinid snails that inhabit them. Although littorinids are highly mobile animals, displaying oriented movement patterns in response to unfavorable conditions (Rochette and Dill 2000), the distribution patterns documented in this study are unlikely to result from immigration of snails from outside the study area, as they are not found above or below the intertidal range covered in our survey, nor are they likely to migrate from wave-exposed headlands many kilometers away. It also seems unlikely that snails would routinely move between upper and lower-intertidal areas to sample changes in environment conditions. In our study, individuals were physically prevented from moving between habitats in response to experimental manipulations, suggesting that the observed habitat-specific differences in competitive ability and vulnerability to predation reflect local adaptation over evolutionary time. Given the ongoing pressures faced by these two species, continued spatial segregation is likely to lead to further interspecific differences in traits related to competitive ability and vulnerability to predation. Indeed, an extension of Grand's (2002) model over evolutionary time scales suggests that coexisting pairs of species, such as *L. sitkana* and *L. subrotundata*, must continue to diverge in their abilities to compete for resources and/or escape predation for continued coexistence to occur (T. Grand, unpubl.). Interestingly, electrophoretic studies of enzyme

variations at the leucine-aminopeptidase locus suggest that natural selection may contribute to furthering niche segregation among sympatric and ecologically similar species of limpets (Murphy 1976).

The zonation pattern of intertidal organisms is undoubtedly affected by many biotic and abiotic factors operating in concert over both ecological and evolutionary time scales. Different studies have examined zonation of littorinid snails in light of interspecific differences in metabolic performance and physiological tolerance (Sacchi 1969, Sokolova et al. 2000, Sokolova and Pörtner 2001), feeding preferences and specialization (Sacchi 1969, Sacchi and Voltolina 1987), and susceptibility to predation (Elner and Raffaelli 1980). Over ecological time scales, these factors directly affect critical biological processes such as survival, growth, reproduction and (in the case of motile organisms) movement. Over evolutionary time scales, they select phenotypes that are better adapted to conditions prevailing in different parts of the intertidal zone. To the best of our knowledge, our study is the first to analyze niche partitioning among intertidal snails in relation to interspecific differences in trade-offs involving feeding potential and predation risk. We believe that the greater vulnerability of *L. subrotundata* in high-risk areas compared to *L. sitkana* is due to its shell being less resistant to crab predation. The mineralogy of both species' shell is similar (Reid 1996), but the shell of *L. subrotundata* is lighter (i.e. contains less calcified material) than that of a similar-sized *L. sitkana* (Boulding et al. 1999).

We hypothesize that vertical segregation between *L. subrotundata* and *L. sitkana* is further facilitated by their mode of development. In comparison to pelagic development, benthic larval development enhances the predictability of recruitment patterns (Underwood 1979). Furthermore, benthic development may reduce gene flow among individuals inhabiting different habitats, which should favor local adaptation and could therefore reduce niche overlap among species (above). This potential for localized adaptation is supported by the differences in growth rates we observed between high-origin and low-origin *L. sitkana*. These phenotypic differences appear to reflect life-history adaptation to spatial and size-dependent predation patterns in the intertidal zone (Rochette et al. 2003). More specifically, because mortality risk is greater in the lower intertidal and on larger snails, low-intertidal individuals grow slower but become sexually mature at a smaller size, whereas high-intertidal ones grow more quickly, but mature at a larger body size. Recent work suggests that these phenotypic differences have at least a partial genetic basis (Rochette and Dill, unpubl.). In Europe, another littorinid snail that lacks a long range dispersing larvae, *L. saxatilis* (Olivi), displays extensive phenotypic

variation between high- and low-intertidal areas, and much of this variation is under genetic control (Johannesson et al. 1993, 1995, 1997, Rolán-Alvarez et al. 1996).

Although much of the published competition-coexistence literature emphasizes the importance and prevalence of interspecific trade-offs in competitive ability and vulnerability to predation, such trade-offs may not be ubiquitous, in particular, when competitor species are morphologically similar, and habitats have similar types of resources and house the same species of predators. Under such circumstances, individual behavioural models are likely to provide explanations for coexistence that traditional, population models cannot. Furthermore, if behavioural diversification precedes morphological diversification (Wcislo 1989, McLaughlin et al. 1999), specialization of species on different resources or habitats may be an evolutionary consequence of differential habitat selection rather than a cause. Given the current interest in linking adaptive individual behavior to ecological patterns (Sutherland 1996, Brown 1998), illuminating the conditions under which morphologically similar species are likely to engage in different behaviors should be of general importance to both behavioural and evolutionary ecologists.

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